Journal of Biogeography, **28**, 977–983

Increase in the woody component of seasonal savannas under different fire regimes in Calabozo, Venezuela

Juan F. Silva*, Alexis Zambrano and Mario R. Fariñas *Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela*

Abstract

Aim We tested the hypothesis that exclusion from fire and cattle is responsible for the increase in tree cover in open savanna vegetation.

Location Four plots in open savanna vegetation from the Calabozo region in central Venezuela were studied. Plot A was located in a Biological Station (EBL) that was excluded from fire and cattle between 1961 and 1991, with only two burning events in 1964 and 1968. The other plots (B, C, D) were located within 2 km distance from A, in neighbouring farms with soils similar to those in A but under various regimes of land use and fire frequency.

Methods We measured the cover of isolated trees, small tree groups and groves of each plot in 1960 and 1977 using geographic information system (GIS) and digitalized aerial photographs. Additionally, the plots were located in the field and the open grassland was sampled in 1995 for species composition and density of stems above 20 cm height. Information on land use was obtained surveying people at the farms.

Results There was an increase in the woody component of all plots during the 17-year interval (1960–1977). Total woody cover in the four plots as a whole increased from 4.5% to 17.9%. All three components measured, groves, tree groups and isolated trees, increased despite differences in land use and fire frequency between plots. Contrary to our expectations, the field survey performed in 1995 showed that fire-sensitive species were abundant in the open savanna in plots B, C and D, which were not excluded. Plot B, with the most intense agricultural use showed the highest rate of woody increase, and plot C, under extensive cattle ranching, was second. The results also showed that woody cover increased by aggregation from single trees and small tree groups into groves. As a consequence of these changes, savanna physiognomy changed from open to dense savanna parkland with a woody cover reaching over 25% in one of the four plots.

Conclusions The results agree with other reported increases in woody cover in savannas under exclusion or with annual fires during the same time period in Africa (Dauget & Menaut, 1992). Our results support evidence from previous studies showing that fire and grazing are only part of a complex system of interacting factors affecting the structure of savanna communities.

Keywords
Tropical savanna, tree, fire, grazing, succession, tree cover, physiognomy.

*Correspondence: 22 Divinity Avenue, Cambridge, MA 02138, USA. E-mail: jfsilva@fas.harvard.edu

INTRODUCTION

The persistence of a tree layer is an essential feature of the savanna ecosystem. Fire is an important factor in both the persistence of substantial fraction of woody biomass and the carbon emissions budget. Burning of vegetation is increasingly important world-wide, and especially in the tropics where it affects mostly savanna woodlands (Dwyer *et al.*, 1998). Tropical savannas represent about 20% of all terrestrial vegetation and are considered an important sink in the global carbon flow (Tiessen *et al.*, 1998). Most of the savanna biomass lies belowground where it follows a slow process of decomposition and mineralization (Sarmiento, 1984; Castro & Kauffman, 1998). Consequently, savanna tree/grass ratio and the role of fire as a controlling factor is becoming a relevant issue in the scientific literature related to global change.

Although fire is considered one of the main determinants of savanna ecosystems (Frost *et al.*, 1983), there is little direct evidence of the role of fire as the driving force determining tree cover and tree density in tropical savannas. A few fire exclusion studies have shown a noticeable increase in tree density and tree cover in a period of a few years (Menaut, 1977; San José & Fariñas, 1983, 1991). Although these studies lacked a proper experimental 'control' to distinguish between the results of exclusion and of other intervening factors, they are commonly cited in the savanna literature as evidence for the direct effect of fire on savanna structure (Frost & Robertson, 1987; Solbrig *et al.*, 1996; Scholes & Archer, 1997).

Contemporaneous with the above studies, an experiment with four fire regimes (including complete fire protection but not grazing exclusion) was started in 1972 at Munmarlary in Kakadu National Park (Australia). Bowman *et al.* (1988) compared experimental plots after 13 years. The study showed the great importance of soil variation in floristic composition, and the role of this diversity in the response to fire regime both at the species and the community level. Floristic response to protection from fire was generally weak whereas structural responses were significant as a result of the development of dense understoreys. After 20 years, the experimental sites at Munmarlary continued this trend of structural changes (Bowman & Panton, 1995). Protection resulted in sixteen times more saplings, five times more poles, 2.5 times more trees and 7% less sprouts. Floristic responses continued to be weak and the authors concluded that rainforest species do not readily invade unburnt *Eucalyptus* savanna.

Started in 1990 also in Kakadu National Park, the Kapalga fire experiment was designed to overcome the limitations of previous savanna experiments (Andersen *et al.*, 1998). Four fire treatments were replicated three times using 15–20 km^2 experimental units and the study comprises six core projects including plant and animal aspects as well as soil nutrients and water. Some results indicate that survival of trees and stems depend significantly on fire regime, fire intensity, tree size and tree functional type. Despite the fact that tree survival declined linearly with increasing fire intensity, it remained relatively high because of the resprouting capacity of many species (Williams *et al.*, 1999).

There are accounts of increasing woody cover under prolonged fire exclusion in the Brazilian cerrados (Coutinho, 1982). Unfortunately, these lack experimental controls. A more recent study compared areas excluded from fire and grazing for more than 20 years to areas under fire every 2 years, with five different savanna physiognomies (Moreira, 2000). Results showed that exclusion increased woody plant abundance, and fostered fire-sensitive species. It also showed a complex interaction of fire and physiognomy.

These and other results are indications that fire alone is not determining the dynamics of woody cover in savanna communities. Grazing and browsing pressures, water availability, nutrient availability, land use, and other factors seem to be interacting in rather complex ways to influence woody cover (Higgins *et al.*, 1999; Eckhardt *et al.*, 2000). Grazing seems an important factor as it reduces competitive pressures from grasses but especially because it interacts with fire frequency and intensity (Roques *et al.*, 2001).

The Biological Station in the central Llanos region of Venezuela (Estación Biológica de Los Llanos, EBL) is well known as a fire and cattle exclusion site since 1960. Blydenstein (1961, 1963) started a long-term monitoring of the savanna community at EBL by sampling a 3-ha plot within the excluded area. Further sampling was conducted in 1969, 1977, 1983 and 1986 by San José & Fariñas (1971, 1983, 1991). However, no attempts were made to monitor surrounding savanna areas used for extensive cattle ranching or agricultural activities, under variable fire regimes.

Aerial photographs have been used to monitor changes in tree cover (Archer *et al.*, 1988; Mast *et al.*, 1997; Trollope *et al.*, 1998; Eckhardt *et al.*, 2000). In this study we took advantage of the existence of aerial photographs of EBL as a proxy control under the hypothesis that exclusion determine changes in tree cover in seasonal savannas. We compared changes in tree cover in the protected EBL with the surrounding but not excluded areas using available aerial photographs from 1960 and 1977. In order to get some insight in the mechanisms involved, we classified woody cover into three different components: isolated trees, small groups of trees and groves.

MATERIALS AND METHODS

The study area corresponds to the EBL and the surrounding farms. The EBL was created in 1960, and it is located 8 km south of the city of Calabozo (Guarico state, 8°52′ N; 67°37′ W) in central Venezuela. It is a seasonal savanna area of 265 ha, burnt annually until 1960 (Blydenstein, 1961). After the exclusion of fire and cattle in 1960, fire events took place again in 1964 (Eden, 1967) and in 1968 (M.R. Fariñas, personal observation). Thereafter it was not burnt until 1991. The surrounding areas are occupied by farms and ranches devoted to various agricultural activities and to extensive cattle ranching with the use of frequent burning.

We used aerial photograph No. 130 A (1 : 40,000) from Mission 172, Cartografia Nacional, 1960 and aerial photograph No. 365 (1 : 25,000) from Mission 0305109, Cartografia Nacional, 1977. In both photographs there is a good, clear view of the EBL and surroundings. Both photographs were enlarged to 1 : 10,000 and to 1 : 13,375, respectively, and then digitized. Using a geographic information system (GIS), the two areas in the photographs were properly geo-referenced and the precise location of the initial 3 ha plot set by Blydenstein in 1961 was determined.

Subsequently, surrounding areas with soils similar to those of the EBL (*Haplustox*) (COPLANARH, 1990) were demarcated in the 1960 digitized image and three additional plots were located in the seemingly less disturbed areas with savanna vegetation. Then, they were replicated in the 1977 photograph. The original plot within EBL was labelled 'A' and the other three as 'B', 'C' and 'D' (Fig. 1).

Using GIS, the four plots were analysed and tree cover mapped using the following criteria. A tree cover no larger than a pixel was identified with a node (1 pixel), and counted as an isolated tree; a tree cover occupying 2 or 3 pixels was delineated by a polygon, and identified as a 'tree group'; a tree cover larger than 3 pixels was considered a 'grove' and delimited by a polygon. The exact area (m^2) of each plot in each photograph was calculated, as well as the area occupied by each component. Cover of tree groups, groves and isolated trees in each plot were then expressed as percent of the plot area. Plots in 1960 and 1977 were then compared using a *G*-test for homogeneity of percentage (Sokal & Rohlf, 1998).

We estimated the relative increase rate (RIR) for the 16-year period for each component as well as total woody cover using RIR = (cover in 1977 − cover in 1960)/cover in 1960. The relative contribution in percent of each woody component to the changes in total woody cover was also calculated for each plot.

In 1995, the plots were located in the field with the use of a geographic positioning system (GPS) and a field survey of the four areas was conducted. All trees above 20 cm in height along transects in the open grassland were counted. This included groups of trees, but not the groves. Results were then expressed as trees ha^{-1}. To gather additional information, we recorded interviews with people at each of the farms where plots B, C and D were located.

Plot B was located in a farm named 'La Madera' on the eastern side of the EBL, the most intensely used of the four areas with either fertilized agriculture or extensive cattle raising and annual fires. Plot C was located in the ranch 'Los Aceiticos', which was also submitted to high fire frequency but was restricted only to extensive cattle raising. Plot D was located in the farm 'Mi Llanura' in an area that was mostly excluded from cattle with very little agricultural activity, and with less frequent fires.

RESULTS

It is important to consider the general physiognomy of the savanna communities in 1960, the starting point for the comparison. The four plots represented a physiognomy gradient D-B-A-C, from an open parkland savanna with higher total woody cover to a more open savanna with low woody cover (Table 1).

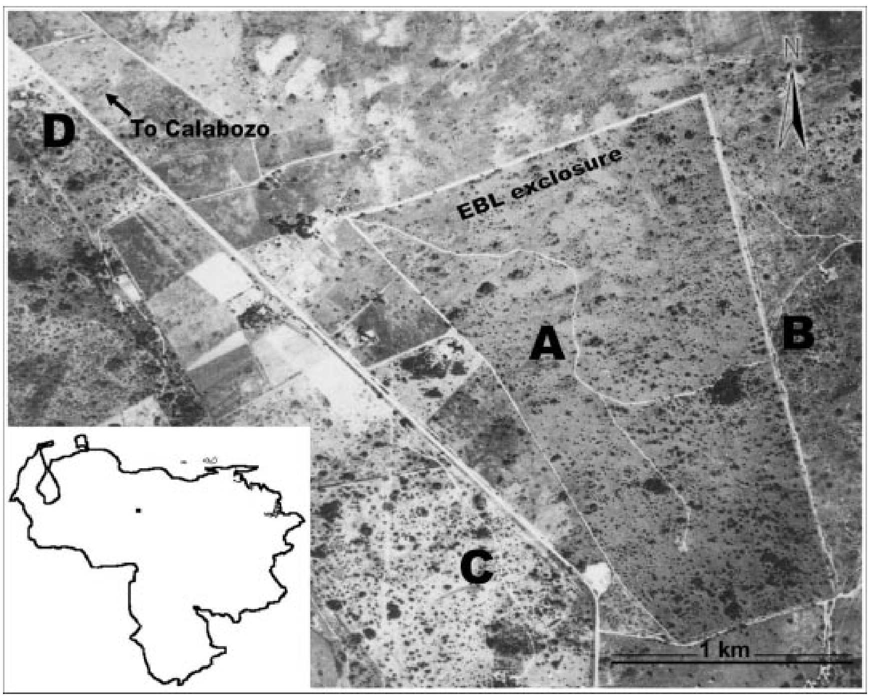

Figure 1 Location of the Biological Station (EBL) in Venezuela, and the position of the four plots and the EBL exclosure in the 1977 aerial photograph. Plot A, inside the EBL, protected from fire and grazing; plot B, in farm 'La Madera' fertilized agriculture, extensive cattle grazing, annual fires; plot C, in ranch 'Los Aceiticos', extensive cattle grazing, annual fires; plot D, in farm 'Mi Llanura', mostly excluded from cattle and agriculture, low fire frequency.

Table 1 Percentage cover of forest islands (groves), tree groups, and isolated trees in the four savanna plots in 1960 and 1977, as estimated from aerial photographs

	Percentage cover					
	Groves		Tree groups		Isolated trees	
Plots	1960	1977	1960	1977	1960	1977
A	1.9	6.71	1.7	4.8	0.00	0.58
B	3.95	20.68	0.05	4.7	0.29	0.58
C	0.25	10.83	3.2	5.5	0.05	0.32
D	5.78	14.36	1.1	2.5	0.00	0.76

Table 2 Relative increase rate (RIR) for each of the three woody layer components for the whole 16-year period between 1960 and 1977. (RIR = 1977 value – 1960 value/1960 value)

Plots	Groves	Tree groups	Isolated trees	Total
A	2.53	1.82	303.56	2.36
B	4.24	93.00	0.98	5.05
C	42.32	0.72	4.87	3.75
D	1.48	1.27	347.18	1.56

Changes detected in grove cover were important in all plots (Table 1). Grove cover was significantly different between plots both in 1960 ($G = 20.85$; $P < 0.001$) and in 1977 ($G = 25.35$; $P < 0.001$). Plot C had the lowest grove cover in 1960, and increased ten to twenty times more than the other plots (Table 2). Interestingly, plot A showed the lowest grove cover in 1977, with only 6.7%, and plot B had the highest grove cover with more than 20%.

Tree group cover also increased in the period (Table 1). Plots differed significantly in 1960 ($G = 11.96$; $P < 0.005$). Plot B, with the lowest tree group cover in 1960, showed a very high increase whereas the other three plots showed very similar lower rates of increase (Table 2). As a result, final tree group cover values in all plots were not significantly different in 1977 ($G = 3.57$; $P > 0.05$), ranging from 2.5% to 5.5% (Table 1).

Cover of isolated trees also increased markedly between 1960 and 1977 (Tables 1 and 2) but all final values are very small (< 1%). Plots were not significantly different either in 1960 ($G = 1.66$; $P > 0.05$) or in 1977 ($G = 0.57$; $P > 0.05$). Again, the magnitude of the increase was higher in those plots with fewer trees initially (A and D).

Total woody cover in the four plots as a whole increased from 4.5% to 17.9% (RIR = 2.99). Plots in 1960 were not significantly different ($G = 4.10$; $P > 0.05$), but they differed significantly in 1977 ($G = 17.89$; $P < 0.001$) (Fig. 2). Plot B showed the highest final total woody cover with more than 25%, and plot A the lowest with 12%.

It is remarkable that all four plots had a high relative increase rate in only one of the three woody components (Table 2). Plots A and D had a very high RIR of isolated trees and more modest RIR in cover of groves and tree groups. Plot B had a high RIR only in cover of tree groups and plot C only in cover of groves.

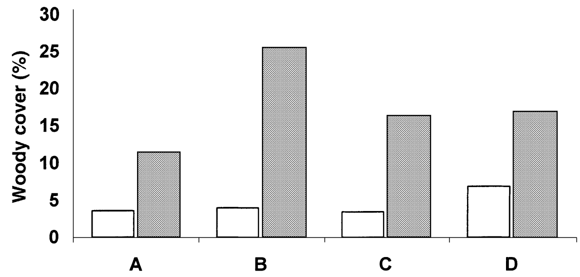

Figure 2 Changes in woody cover between 1960 (open column) and 1977 (filled column) in each plot. Plots in 1960 were not significantly different ($G = 4.10$; $P > 0.05$), but they differed significantly in 1977 ($G = 17.89$; $P < 0.001$).

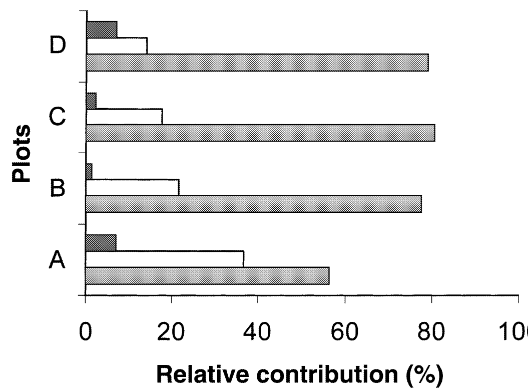

Figure 3 Relative contribution of groves (grey), groups of trees (empty) and isolated trees (dark) to the increase of woody cover, expressed as percent of the total in each plot.

Relative contribution to total woody cover increase (Fig. 3) followed the same pattern in all plots. Grove cover had the highest relative contribution and isolated trees had the lowest.

A total of ten woody species were registered in the 1995 field sampling of the open grassland (Table 3), compared with sixteen species recorded by San José & Fariñas (1991) in 1977. Four were deciduous species known as being fire sensitive. They are typically found in groves although two are also found in open savanna. One species is semi-deciduous and often found in large groves. The other five were evergreen, four from open savanna and one typical of large groves. Dominance was very strong, and the four most abundant species in each plot accounted for at least 90% of all trees.

DISCUSSION

Blydenstein (1963) based on the examination of aerial photographs from 1950 reported no changes in the woody cover of the EBL between 1950 and 1961, and pointed to

Table 3 Tree species density (trees ha^{-1}) in the four plots from field sampling in 1995. All stems above 20 cm in height in the open grassland were sampled

Species	Traits	A	B	C	D
Curatella americana L.	E/S	944	620	382	215
Byrsonima crassifolia H.B.K.	E/S	144	280	1624	577
Bowdichia virgiliodes H.B.K.	E/S	77	0	200	69
Cochlospermum vitifolium (Willd.) Spreng	D/G, S	658	280	76	2492
Godmania macrocarpa Hemsley	D/G, S	439	2680	70	131
Genipa caruto H.B.K.	D/G	30	120	53	31
Jacaranda obtusifolia H.B.K.	D/G	82	20	18	115
Copaifera oficinalis H.B.K.	E/G	2	0	0	38
Cassia moschata H.B.K.	SD/G	6	100	0	100
Psidium spp.	E/S	47	0	18	31
Total		2429	4100	2441	3799

Trait refers to leaf phenology and common habitat: E = evergreen, D = deciduous, SD = semi-deciduous, S = savanna, G = grove.

annual fires as responsible for the tree/grass cover equilibrium. San José & Fariñas (1983) showed that after the creation of the excluded area in 1960 the woody component of the savanna increased substantially in the EBL during the interval between 1960 and 1977. They also documented a further increase as the EBL remained totally excluded of fire and cattle between 1968 and 1991 (San José & Fariñas, 1991). They concluded that the exclusion was responsible for the invasion of the grassland by woody species at the EBL, provided soils were deep enough.

Our results clearly show that there was a general increase in the woody component in the study area during the 16-year interval (1960–1977) beyond the limits of the EBL and that this trend was still detectable in 1995. All three components measured groves, tree groups and isolated trees increased noticeably despite differences in land use and fire frequency between the plots. Consequently, the savanna community changed in physiognomy from an open savanna and open parkland savanna to a more dense parkland savanna, with a woody cover reaching over 25% in one of the plots. Despite differences between plots, the process of aggregation was more important than the invasion of open grassland by isolated trees, as shown by the relative contribution of groves and groups of trees to the increase of woody cover (Fig. 3). In all plots, the majority of groves and tree groups detected in 1977 did not exist in 1960. Farji-Brenner & Silva (1995) postulated that woody elements invade seasonal savanna grasslands through aggregation from single trees to groves and that this process is promoted as the result of synergic interactions with leaf-cutting ants.

It is intriguing that plot B, the most intensely disturbed and most frequently burnt area, showed an increase in woody cover from 4.29% in 1960 to 25.96% in 1977. Meanwhile, plot A (located in the EBL and totally excluded from cattle and agricultural use) ended with the lowest woody cover of 12% despite the fact that only two fires occurred in the 16-year interval. It is feasible that land use, fire regime and their interactions are related to the different trends between plots. For instance, the relative contribution of isolated trees was highest in the two plots with lower fire frequency and less intense land use (A and D). Plots B and C had about the same fire frequency, but B was under agriculture whereas C only had extensive cattle grazing. In the C plot, grove cover increased the most, whereas in B the highest growth was observed in tree groups. Because plots A and D had fewer fires and none or very little grazing, this combination may have favoured more intense and destructive fires compared with plots B and C. However, given the available information, these conclusions should be considered as mere hypotheses. The main finding of this study is that although there were differences between plots, all physiognomies converged toward a wooded parkland savanna, despite the different fire frequency and land use.

Annual RIR estimated from the data presented in Table 1 are well within the range of the estimations based on the data from San Jose and Fariñas (Silva, 1996). If these rates of increase were constant, all areas feasible to be invaded by trees would soon be forested. However, this is not the case. Annual rates of increase calculated from data on densities from the monitoring reported in San José & Fariñas (1991), changed drastically. In the interval between 1983 and 1986, the annual rate of increase of most species was 0.01 or lower (Silva, 1996).

An increase in woody cover was reported for an annually burnt savanna in Lamto (Ivory Coast) after 20 years (Dauget & Menaut, 1992). This was concurrent with a similar increase in woody cover detected in an experimental plot in the same area, in which fire and grazing had been excluded for 13 years (Menaut, 1977). The results of Dauget & Menaut (1992) can be taken as a control for the excluded plot changes reported by Menaut (1977), and showed that if fire exclusion had some effects on woody cover they were overridden by other factors. Different from our plots, the woody cover increase in the Lamto savanna was a result of the growth of existing groves. The authors interpreted the forestation of Lamto's savanna lands as a regional trend resulting from a humid spell that affected the whole region, despite differences in fire regime.

Tree species differ in their responses to changes in fire regime. In both cases, EBL and Lamto, field sampling allowed the monitoring of changes in species density or cover, thus the response of individual species could be followed. Contrary to Lamto, the initial increase in the EBL reported by San José & Fariñas (1991) was because of the evergreen, fire-resistant species growing in the open grassland. Later on, the deciduous fire-sensitive species invaded the open grassland. As our non-excluded plots were under more frequent fires, one could expect that the gain in woody cover detected in the present study was due to the sclerophyllous-evergreen and fire-resistant species. However, our field results showed that in 1995 (Table 2), both fire-resistant and fire-sensitive species were present in the open grassland in all plots. The evergreen fire-resistant species *Curatella americana* and *Byrsonima crassifolia* and the deciduous fire-sensitive *Cochlospermum vitifolium* are three of the four most abundant species in the four plots. *Godmania macrocarpa*, another deciduous fire-sensitive species is among the four most abundant species in three of the plots, and is fifth in plot C. Furthermore, *G. macrocarpa* is the most abundant species in plot B, with 65% of the total, and *Cochlospermum vitifolium* is the most abundant species in plot D with 66% of the total.

Studies have shown that besides fire and herbivory, other factors influence the tree/grass ratio in tropical savannas. They are related not only to water availability (Medina & Silva, 1990), kind of substrate (Trollope *et al.*, 1998) and soil depth (San José & Fariñas, 1983), but also to other less prominent factors, such as the episodic and chronic disturbances and small-scale heterogeneities (Van de Koppel & Prins-Herbert, 1998; Gomez-Sal *et al.*, 1999). It is very difficult to disentangle the effects of fire regime from these and other factors, as they are strongly interdependent and interact with each other (Silva, 1996). O'Connor (1985) reviewed seventy-two long-term experiments conducted in southern African savannas to conclude that it is not possible to draw a clear picture of the driving forces of savanna structure from those experiments because of the various defects in experimental design. One major obstacle is the detection of rainfall trends, as data is scanty or unreliable. Furthermore, the analysis cannot be limited to total annual rainfall but should include the distribution throughout the year and the behaviour of seasonality.

Although the methods used here underestimated tree cover, our results clearly reject our initial hypothesis that fire/cattle exclusion at the EBL was solely responsible for the increasing in tree cover. The changes reported here may differ from those reported from elsewhere (see Bowman *et al.*, 1988; Bowman & Panton, 1995; Williams *et al.*, 1999; Moreira, 2000), as they differ in time and space. However, they all point out to the conclusion that fire and grazing are only part of a complex system of interacting factors affecting savanna structure (Walker, 1987). In order to further investigate the possible causes of changes in savanna structure, we are now undertaking a thorough analysis of the available rainfall data and of the woody cover from aerial photographs in the Venezuela's Llanos region.

ACKNOWLEDGMENTS

This study was partially financed by CDCHT grant No. C-591-93 A, by CONICIT grant No. 98003404, and by IAI-CRN No. 040 (RICAS). We acknowledge the help of Rigoberto Andressen, Guillermo Sarmiento and Eulogio Chacon during various stages of the work. Thanks to Juan Lopez and Elvecio Pernia for help with the GIS, and to Rafael Duholste and Pablo Alvizu for technical help.

REFERENCES

Andersen, A.N., Braithwaite, R.W., Cook, G.D., Corbett, L.K., Williams, R.J., Douglas, M.M., Gill, A.M., Setterfield, S.A. & Muller, W.J. (1998) Fire research for conservation management in tropical savannas: introducing the Kapalga fire experiment. *Australian Journal of Ecology*, **23**, 95–110.

Archer, S., Scifres, C. & Bassham, C.R. (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs*, **58**, 111–127.

Blydenstein, J. (1961) La Sabana de Trachypogon del Alto Llano. *Boletín Sociedad Venezolana Ciencias Naturales*, **10**, 139–206.

Blydenstein, J. (1963) Cambios en la vegetación después de protección contra el fuego. Parte II. Análisis de una parcela de la Estación Biológica después del primer año sin quemar. *Boletín Sociedad Venezolana Ciencias Naturales*, **12**, 233–238.

Bowman, D.M.J.S. & Panton, W.J. (1995) Munmarlary revisited: response of a north Australian *Eucalyptus tetrodonta* savanna protected from fire for 30 years. *Australian Journal of Ecology*, **20**, 526–531.

Bowman, D.M.J.S., Wilson, B.A. & Hooper, R.J. (1988) Response of Eucalyptus forest and woodland to four fire regimes at Munmarlary, Northern Territory. *Australian Journal of Ecology*, **76**, 215–232.

Castro, E.A. & Kauffman, J.B. (1998) Ecosystem structure in the Brazilian cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *Journal of Tropical Ecology*, **14**, 263–283.

COPLANARH (1990) *Inventario Nacional de Tierras Guárico Central y Sur de Aragua*. Ministerio del Ambiente y los Recursos Naturales Renovables (MARNR), Caracas, Venezuela.

Coutinho, L.M. (1982) Ecological effects of fire in Brazilian cerrado. *Ecology of tropical savannas* (eds B.J. Huntley and B.H. Walker), pp. 273–291. Springer-Verlag, Berlin.

Dauget, J.M. & Menaut, J.C. (1992) Evolution sur 20 ans d'une parcelle de savana boisée non protégée du feu dans la réserve de Lamto (Côte-d'Ivoire). *Candollea*, **47**, 621–630.

Dwyer, E., Gregoire, J.M. & Malingreau, J.P. (1998) A global analysis of vegetation fires using satellite images: spatial and temporal dynamics. *Ambio*, **27**, 175–181.

Eckhardt, H.C., van Wilgen, W.B. & Biggs, H.C. (2000) Trends in woody vegetation cover in Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, **38**, 108–115.

Eden, M. (1967) The effect of changing fire conditions on the vegetation of the llanos, Calabozo. *Boletín Sociedad Venezolana Ciencias Naturales*, **111**, 104–113.

Farji-Brenner, A. & Silva, J.F. (1995) Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession? *Journal of Tropical Ecology*, **11**, 651–670.
Frost, P.G.H. & Robertson, F. (1987) The ecological effects of fire in savannas. *Determinants of tropical savannas* (ed. B.H. Walker), pp. 93–140. IUBS, Paris.
Frost, P.G.H., Menaut, J.C., Medina, E., Solbrig, O.T., Swift, M. & Walker, B.H. (1983) Responses of savannas to stress and disturbance. *Biology International*, Special Issue 10.
Gomez-Sal, A., Rey-Benayas, J.M., Lopez-Pintor, A. & Rebollo, S. (1999) Role of disturbance in maintaining a savanna-like pattern in Mediterranean *Retama sphaerocarpa* shrubland. *Journal of Vegetation Science*, **10**, 365–370.
Higgins, S.I., Shackleton, C.M. & Robinson, E.R. (1999) Changes in woody community structure and composition under contrasting land use systems in a semi-arid savanna, South Africa. *Journal of Biogeography*, **26**, 619–627.
Mast, J.N., Veblen, T.T. & Hodgson, M.E. (1997) Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *Forest Ecological Management*, **93**, 181–194.
Medina, E. & Silva, J.F. (1990) The savannas of northern South America: a steady state regulated by water–fire interactions on a background of low nutrient availability. *Journal of Biogeography*, **17**, 403–413.
Menaut, J.C. (1977) Evolution of plots protected from fire since 13 years in a Guinea savanna of Ivory Coast. *Actas del IV Simposio de Ecología Tropical*. Tomo II, pp. 541–558. Impresora de La Nación, INAC, Panamá.
Moreira, A.G. (2000) Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography*, **27**, 1021–1029.
O'Connor, T.G.O. (1985) *A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa*. South African National Scientific Programmes, Report no. 144. Foundation for Research Development, Council for Scientific and Industrial Research, Pretoria, South Africa.
Roques, K.G., O'Connor, T.G. & Watkinson, A.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, **38**, 268–280.
San José, J.J. & Fariñas, M.R. (1971) Estudio sobre los cambios de la vegetacion protegida de la quema y el pastoreo en la Estacion Biologica de Los Llanos. *Boletín Sociedad Venezolana Ciencias Naturales*, **119–120**, 136–146.
San José, J.J. & Fariñas, M.R. (1983) Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuela. *Ecology*, **64**, 447–453.
San. José, J.J. & Fariñas, M.R. (1991) Temporal changes in the structure of a *Trachypogon* savannas protected for 25 years. *Acta Oecologica*, **12**, 237–247.
Sarmiento, G. (1984) *The ecology of neotropical savannas*. Harvard University Press, Cambridge, MA, USA, 235 pp.
Scholes, R.J. & Archer, S.R. (1997) Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
Silva, J.F. (1996) Biodiversity and stability in tropical savannas. *Biodiversity and savanna ecosystem processes* (eds O.T. Solbrig, E. Medina and J.F. Silva), pp. 161–174. Springer-Verlag, Berlin.
Sokal, R.R. & Rohlf, F.J. (1998) *Biometry*, 3rd edn. W.H. Freeman, New York.
Solbrig, O.T., Medina, E. & Silva, J.F. (1996) Determinants of tropical savannas. *Biodiversity and savanna ecosystem processes* (eds O.T. Solbrig, E. Medina and J.F. Silva), pp. 31–41. Springer-Verlag, Berlin.
Tiessen, H., Feller, C., Sampaio, E.V.S.B. & Garin, P. (1998) Carbon sequestration and turnover in semi-arid savannas and dry forest. *Climatic Change*, **40**, 105–117.
Trollope, W.S.W., Trollope, L.A., Biggs. H.C., Pienaar, D. & Potgieter, A.L.F. (1998) Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe*, **41**, 103–112.
Van de Koppel, J. & Prins-Herbert, H.T. (1998) The importance of herbivore interactions for the dynamics of African savanna woodlands: a hypothesis. *Journal of Tropical Ecology*, **14**, 565–576.
Walker, B.H. (1987) A general model of savanna structure and function. *Determinants of tropical savannas* (ed. B.H. Walker), pp. 1–12. IUBS, Paris.
Williams, R.J., Cook, G.D., Gill, A.M. & Moore, P.H.R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology*, **24**, 50–59.

BIOSKETCHES

Juan F. Silva is Professor of Ecology at the Universidad de Los Andes in Merida, Venezuela. Most of his research is related to the ecology of neotropical savannas and the role of fire, and has published papers on the dynamics and population biology of savanna species, both grasses and trees. He leads a research network on the ecology of tropical communities and global change, sponsored by the InterAmerican Institute for Research on Global Change (IAI). Currently, he is at Harvard University, collaborating in the study of the ecological and economic implications of land use change in Brazil.

Alexis Zambrano graduated from the School of Science at the Universidad de Los Andes, Merida, in Biology (Ecology). He worked for several years as Superintendent of Canaima National Park (Ministry of Environment) and is currently working on ecotourism for Merida's State Tourism Office.

Mario R. Fariñas is Professor of Ecology at the Universidad de Los Andes, Merida, Venezuela. His research has focused on community structure and ecological determinants in tropical savannas and paramos using multivariate analysis. He is currently working on biodiversity responses of these two contrasting communities to variations along geomorphological and altitudinal gradients (mfarinas@ciens.ula.ve).