COENOSES 6 (1): 47-52, 1991

EARLY STAGES IN THE PARANÁ RIVER TALL GRASSLAND RECOVERY AFTER AN EXTRAORDINARY FLOOD[1]

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Keywords: Argentina, Catastrophic events, Community regeneration, Disturbance, *Panicum prionitis*, Paraná River, Tall grasslands, Vegetation dynamics

Abstract. In 1983 an extraordinary flood destroyed the *Panicum prionitis* tall grasslands in the Paraná River Valley. In this paper phytosociological analyses of the communities, which in March 1988 were in the place of the tall grasslands along the transect from El Rabón to Puerto Piracuacito, are presented. These are compared with a previous analysis performed immediately following the flood. It is shown that pioneer communities evolve convergently into tall grasslands with slightly different variants. *Panicum prionitis* partially recovers, and its ground cover is inversely proportional to the *Cynodon dactylon* cover. Floristic richness and diversity decrease. As the floristic composition change, the proportions of therophytes decrease and the phanerophytes increase. It is concluded that exposed to an extraordinary flood, the *Panicum prionitis* grassland is very resilient.

Introduction

The Paraná River Valley is a complex flood plain covered by hygrophilous herbaceous communities, shrublands and different types of forests (Morello 1949, Burkart 1957, Franceschi and Lewis 1979, Franceschi *et al.* 1985). Among the most widespread is the *Panicum prionitis* community, particularly in the northern portion of the valley. This is a tall grassland that when mature has a dense upper layer of the dominant species with few individuals of the other herbaceous species.

Vegetation dynamic is strongly affected by the hydrological regime of the river. The water level has a yearly cycle reaching its highest in Autumn and its lowest in Spring. At irregular intervals of a few years the autumn flood is higher than usual and once or twice in a century there are catastrophic floods (Soldano 1947). The last catastrophic flood occurred in 1983.

Morello (1949) and Burkart (1957) suggested that the vegetation of the valley evolves to hygrophilous forest from other types of woody vegetation on sand bars, or from herbaceous communities through the *Panicum prionitis* grasslands in swampy areas. However, forests are restricted to peripheral levees of islands or to levees along the waterways of the valley, while the *Panicum prionitis* grasslands are much more widespread in the valley. Lewis and Franceschi (1979) suggested that the tall grasslands may be stable communities which would not evolve into forests, although a few trees, quite different from those which make up the forest, may pervade the grasslands.

Lewis *et al.* (1987) studied the effect of the last catastrophic flood (1983) in the northern part of the valley and found that the *Panicum prionitis* grassland was completely destroyed and replaced by different herbaceous communities composed largely of the rare species of the mature grassland. The substitute communities are fugacious ones, and presumably the *Panicum prionitis* grassland will regenerate and replace them in time, but it will not evolve further into an hygrophilous forest. This last step is prevented by the next destructive flood. However, if the period between the last and the next catastrophic flood is long enough the grassland may evolve into a *Panicum prionitis*-prickly *Mimosoideae* savanna, as the presence of few individuals of *Prosopis* sp and *Acacia* sp suggest (Lewis *et al.* 1987). In order to test these hypothesis the vegetation was analysed periodically. In this paper we describe the changes during the first five years of recovery.

Methods

The transect between El Rabón and Puerto Piracuacito (Province of Santa Fe, Argentina) was first analysed in November 1984 (Lewis et al 1987) and was analysed again in March 1988. Quadrats of 16 m^2 area were placed in the same stands. On each of the 24 quadrats, the records include general environmental characteristics, vegetation structure and species cover-abundance estimates on the Braun-Blanquet (1979) combined scale.

Quadrats were ordered in principal component analysis (PCA) using a covariance matrix and classified in a minimal variance clustering with chord distance (Wildi and Orlóci 1983). Floristic richness was measured as the number of species and diversity as Brillouin

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[1] The nomenclature follows Cabrera (1963, 1965a, b, 1967, 1968, 1970) and Burkart (1969, 1974, 1979).

entropy estimated by programme "Estimate H" (Orlóci and Kenkel 1985). The floristic lists and biological spectra of 1984 (Lewis *et al.* 1987) and 1988 were compared. On this basis definite recovery trends were detected.

Results

Axes I and II in the PCA of quadrats (Fig. 1) account for 34,30% and 11,88% respectively of the total variance. The first component (Axis I) segregates to the right a small group of quadrats with very alkaline soils and halophytes from all other quadrats which are pulled to the left. This component signifies response to factors epitomized by soil pH. All quadrats that pull to the left on the first component, scatter along the second component (Axis II) following a notorious pattern: quadrats with high cover of *Panicum prionitis* and low cover of *Cynodon dactylon* pull to the upper levels of the component while quadrats without or with low cover of *Panicum prionits* and high cover of *Cynodon dactylon* pull to the bottom. However, there is no clear evidence with what environmental factor this component is associated.

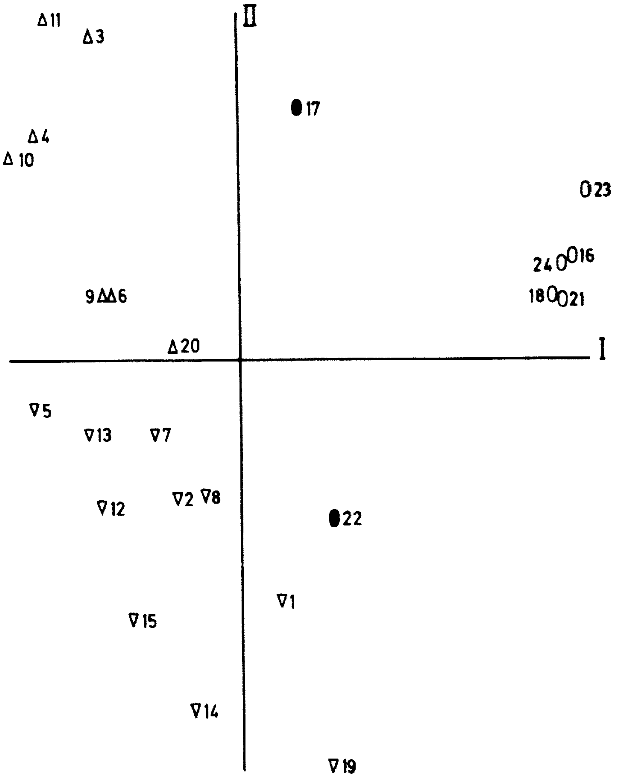

Fig. 1. Scatter diagram of quadrats on the plane of axes I and II. The method is PCA. Symbols for communities: empty oval E, black oval F, triangle G, inverted triangle H. See the description of communities in the main text.

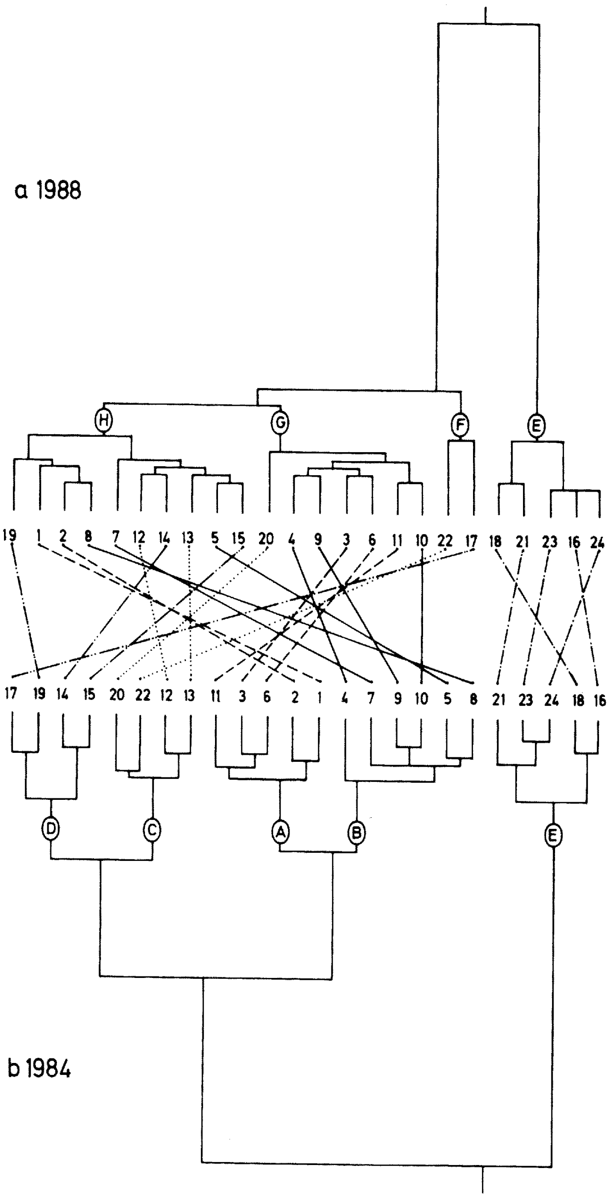

Fig. 2. Dendrograms of quadrats. The method is minimum variance clustering. Top (a) 1988 data; bottom (b) 1984 data.

Cluster analysis detects two groups of quadrats, (Fig. 2). The small group stands isolated (E) and the large group divides at a much lower level of dissimilarity into three subgroups (F, G and H). Table 1 gives a phytosociological description of the groups. Group E is a distinct community with hardly any species in common with the other groups; the species characterizing this group are all halophytes. The community has the very low cover (33%) and no *Panicum prionitis* whatscover. The other groups (F, G, H) are all variants of the same broady community characterized by high constancy and relative abundance of *Panicum prionitis* and *Cynodon dactylon*. The cover of these species are inversily related. Group F is an odd group, containing only two quadrat, with fewer species than G and H and hardly any characteristic species. Groups G and H are differentiated by the relatively

Table 1. Phytosociological table. Entries in the body are Braun-Blanquet cover/abundance estimates in the communities. See Appendix 1 for list of solitary species.

Communities			E			F					G									H					
Quadrat number	24	16	23	21	18	17	22	10	11	6	3	9	4	20	15	5	13	14	12	7	8	2	1	19	
Species																									
Sporobolus pyramidatus	3	3	3	1	+																				
Sesuvium portulacastrum	1	1	1	3	1																				
Portulaca cryptopetala	1	1	+	+	+																				I
Heliotropium curassavicum		+	(+)	+	+																				
Grindelia scorzonerifolia				1	3																				
Cynodon dactylon	+	+		1	+		2	3	2	3	2	3	4	4	5	5	4	5	4	3	5	5	5	5	
Panicum prionitis						5	+	4	5	4	5	4	3	3	+	3	2	1	3	3	2	3	+		
Panicum laxum							+	3	2	1	1	1	2	2	+	1	1		1	+		+			
Eupatorium candolleanum						(+)		+	+	+		+	+	+	+	+	+	+			(+)	+			
Setaria geniculata							1	1	+	+			+	+			1		+		+				
Eleocharis viridans						1		+	1				+		1	+	2	+						+	
Sesbania virgata						+		+		+	+	+	2								+				
Oxalis sp.						+					+		+			+	+		+						II
Scoparia montevidensis							+					+	+							+			+		
Aster squamatus						+	+							+	+		+	+	+	+				+	
Eriochloa punctata							5						(+)		+		1		+					+	
Eclipta prostrata						(+)								+	+						(+)				
Cyperus entrerrianus						+	+							1										+	
Ambrosia elatior							+		+										+						
Mimosa strigillosa					(+)			+												+					
Panicum milioides						2	1																	+	
Pluchea sagittalis						+	+							+											III
Sida rhombifolia							+											+							
Cyperus corymbosus								1		1	+	+			1	+	1	1	+		+	2	2	1	
Paspalum almum								+	+	+		1	+		2	2	+	2	3	4	1	+		+	
Solanum glaucophyllum								+	+	+	+	+	(+)			(+)	(+)		(+)	1	+	(+)			
Wedelia brachycarpa									+	+	1		1	+	+	1	1		+						
Polygonum spp.								(+)	1	(+)	+		+		+	+	+			+					
Ludwigia peploides								+	+	+	+		+		+	+			+						
Mimosa vellosiella								1	1		1	+	+	+	+	+	+		+				+		
Aniseia argentina								+			+	+	+		+	+	(+)								
Borreria eryngioides								1	1			+	1		+	1	+	+		+					
Spilanthes stolonifera										+	+		+			+				+	(+)	(+)	+		
Euphorbia adenoptera								+				+		+		+		1	+	+					IV
Holocheilus hieracioides								+		+		+			+	+		+	+						
Mimosa pigra								(+)	(+)		+	+	2								+	+			
Galactia striata								+		+	+					+	+								
Acacia caven								(+)			+									+	(+)	+			
Borreria verticillata										+	+						+		+				1		
Gerardia communis													+	1				+	+						
Baccharis albida								+	+								+			(+)					
Solanum amygdalifolium													(+)				(+)								
Spilanthes decumbens								+							+										
Alternanthera phyloxeroides									+						+										
Polygala linoides												+									+				
Phyla canescens														+										+	
Diplachne uninervia					+															+				+	
Echinodorus grandiflorus									(+)		(+)	+	+												
Mikania sp.								(+)	+		+														
Baccharis pingraea								+	+																
Cyperus reflexus								+	+																V
Eupatorium hecatanthum								+	+																
Hyptis lappacea									+					+											
Commelina sp.											+		+												
Eragrostis bahiensis															+	+									
Prosopis sp.																+		+							VI
Cyperus virens																	+						+		
Species in quadrat	4	5	4	6	8	10	12	27	23	16	20	17	24	15	20	21	22	13	18	15	13	10	8	10	
Average Nº species / quadrat			5.4			11					18.86								15						
Plant cover (%)	30	30	35	30	40	97	95	80	85	98	90	90	95	90	85	95	90	98	98	75	95	98	85	90	
Average cover			33			96					89.7							90.9							

Table 2. Diversity and floristic richness in different communities at the time of the surveys.

Year	Community	Diversity Mean H	 Maximum H	 Variance of H	 Mean H/ Maximum H	Floristic richness ssp/ quadrat
1988	H	3.12	3.95	0.0076	0.79	15.00
	G	3.46	3.95	0.0250	0.88	18.86
	F	3.12	3.30	–	0.95	11.00
	E	2.38	2.40	0.0840	0.99	5.40
	H+G+F	3.29	4.34	0.0062	0.76	16.53
1984	A+B+C+D	4.39	4.79	0.0089	0.92	29.63
	E	1.92	2.71	0.0005	0.71	7.20
	D	4.02	4.26	0.0002	0.94	28.75
	C	3.81	4.09	0.0055	0.93	28.75
	B	3.84	4.21	0.0051	0.91	33.50
	A	3.67	4.08	0.0173	0.90	26.40

higher cover of *Panicum prionitis* and *Panicum laxum* in G than in H, and the higher cover of *Cynodon dactylon, Paspalum almum* and *Cyperus corymbosus* in H than in G. Species restricted to these groups are those of V and VI of Table 1. Their constancy is low, and therefore their diagnostic value is also low.

If the present vegetation is compared with the vegetation that existed four years before (Lewis *et al.* 1987) there are profound differences. The five quadrats on alkaline soil (ph = 9,3) have the same community as in 1984. In this *Sporobolus pyramidatus, Sesuvium portulacastrum* and *Portulaca cryptopetala* remain the most prominent species, although there are changes in local cover, and the general cover is slightly higher. Other quadrats that formed four distinct communities in 1984 became part of a more homogeneous community with three slightly different variant. In general the quadrats' distribution among the 1984 communities (A, B, C, D) has very little relation to their distribution among the 1988 variants (F, G, H; Fig. 2). The species noted for their constancy and abundance throughout or in particular communities of 1984, such as *Setaria geniculata, Eupatorium candolleanum, Eragrostis hypnoides, Ambrosia elatior, Eupatorium hecatanthum, Eleocharis viridans* and *Gerardia communis*, are far less constant and abundant in 1988 and some disappeard altogether or at least are not present in recordable quantity. The only exception is *Cynodon dactylon* that spreads and is becomming important almost everywhere. *Panicum prionitis* recovered also and is becomming important throughout. Other species such as *Panicum laxum* and *Paspalum almum*, that were not present or were of very little importance in 1984 spread and appear far more important in 1988.

Floristic richness is lower in 1988 than in 1984 even in the community on alkaline soils, but it is more noticeable in the *Panicum prionitis* grassland.

Table 3. Biological spectra and total number of species recorded in the post-disturbed *Panicum prionitis* tall grassland at the time of the surveys.

Year		1984		1988	
Total number of species		119		78	
Amount of species of different life forms	Total %	only in 1984	In both years	only in 1988	Total %
Life forms					
Phanerophytes	0.8	1	–	4	5.1
Chamaephytes	11.8	6	8	–	10.3
Hemicryptophytes	41.2	28	21	10	39.7
Geophytes	16.8	10	10	3	16.7
Lianas	5.0	2	4	2	7.7
Therophytes	21.0	18	7	2	11.5
Undetermined	3.4	2	2	5	9.0
Total	100.0	67	52	26	100.0

Diversity (H) also decreases in all communities whether they are taken individually or combined (A+B+C+D in 1984 and F+G+H in 1988). Interestingly entropy increases during the same period in the case of the alkaline community (E) (Table 2).

The biological spectrum changes from 1984 to 1988 as well as the floristic composition; 67 species recorded in 1984 were not recorded again in 1988 while 26 species recorded in 1988 were not recorded in 1984. A most important aspect is that while therophytes decrease sharply, phanerophytes undergo significant increase (Table 3).

Discussion

An outstanding fact shown by the data is that *Panicum prionitis* recover very rapidly after destructive flood. This gives the tall grasslands high resilience (Westman 1978, Lepš *et al.* 1982, Westman and O'Leary 1986) in the face of this type of disturbance. When comparing to the pre-flood tall grasslands (Franceschi *et al.* 1985), complete recovery of the original composition has not occurred. The flood destroyes the tussocks and leaves only the crown fragments and other dead material. In these some living buds could start the rapid recovery. We have no other explanation, as it is very unlikely that new tussocks would develope from seed.

Soon after the flood ends, floristically rich communities (Lewis *et al.* 1987) came into existence with forbs most prominent. These are pioneer communities not unlike other types which develop after disturbance (Kaputska and Moleski 1976, Antos *et al.* 1983, Collins and Adams 1983, Callison *et al.* 1985). As we predicted these communities are fugacious and in a very short time they give way to the regenerating *Panicum prionitis* tall grassland.

During the last four years floristic richness and diversity decreases as expected (Lewis *et al.* 1987), correlated with the development of a dense canopy of *Panicum prionitis* or *Cynodon dactylon.* It is known that overwhelming dominance suppress floristic richness and diversity through specific interference mechanisms (Whittaker 1965, Del Moral 1972, Perino and Risser 1972, Bazzaz 1975, Houssard *et al.* 1980, Trabaud and Lepart 1980, During and Willems 1984).

In the last four years there is more than double species elimination than recruitment. Woody species (*Copernicia australis, Acacia caven* and *Prosopis* sp) of later stages establishe themselves at this stage, and probably have no further recruitment (Drury and Nisbet 1973, Glitzenstein *et al.* 1986). The evolution of the community into a savanna and later on into a forest, if true, would be very slow and unlikely to be completed before the next destructive flood.

The development of all the pioneer communities on the *Panicum prionitis* sites converged into a *Panicum prionitis* tall grassland. The alkaline soil community which is confined to pockets within the tall grassland in the higher parts of the valley did not evolve further. However, this community shows no relation to the *Panicum prionitis* grasslands in species composition. While the pioneer communities differed among themselves, the communities into which they evolved are homogeneous with only slightly distinct variants. The latter can be differentiated by the relative abundance of *Panicum prionitis* and *Cynodon dactylon.* It is possible that these variants developed as a consequence of different disturbance regimes, fire and overgrazing in one extreme and very low disturbance level at the other extreme.

So far the expectations (Lewis *et al.* 1987) were fulfilled. The effect of catastrophic floods on the vegetation of the southern portion of the valley being similar (Franceschi and Prado 1989), our conclusions can be generalized to the entire valley. The sporadic catastrophic floods have been reported for other river systems since ancient times, but their effect on vegetation has not been analysed elsewhere. We can only presume that along all the great rivers similar sporadic events may prevent the evolution of the vegetation into climax forests.

Acknowledgment. We greatfully acknowledge CAFPTA and CONCET financial support.

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Manuscript received: April 1990

Appendix 1

Species which appear only in one quadrat

Polygonum cf. *brasiliense, Alternanthera paronychioides, Cissus palmata, Cienfuegosia drummondii, denothera* sp., *Eryngium ebracteatum, Verbena* sp., *Lippia alba, Glandularia pulchella, Jaborosa integrifolia, Stemodia palustris, Gerardia genistifolia, Aspilia silphioides, Eleocharis elegans, Rhynchospora corymbosa, Cyperus* sp., *Scirpus californicus, Copernicia australis, Polypogon* cf. *semiverticillatus, Sporobolus indicus, Echinochloa* cf. *crusgalli, Paspalum vaginatum, Zephyranthes candida, Pontederia lanceolata*, and four unidentified species.