

DISTRIBUTION OF HERBACEOUS COMMUNITIES OF THE RIVER PARANA VALLEY ALONG AN ELEVATION GRADIENT AFTER A CATASTROPHIC FLOOD

E.A. Franceschi and D.E. Prado, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, Santa Fe 2051, 2000 Rosario, Argentina

Keywords: River systems, River Paraná, Disturbance, Floods, Gradients, Hygrophilous vegetation, Communities, Distribution, PCA

Abstract. A 30-plot permanent transect along a topographic gradient was laid from the levee to the edge of the internal lake on an island in the River Paraná floodplain to study the distribution of new herbaceous vegetation replacing the previous one destroyed by a catastrophic flood. Principal component and cluster analyses were used to analyze the data. It was concluded that the communities' distribution follows environmental gradients related to topographic elevation, and that the main effect of the floods is to smooth down these gradients, thus producing homogeneization in the herbaceous vegetation.

Introduction

The River Paraná runs from north to south within its valley bounded on both sides by noticeable scarps. Although from Corrientes down to the outskirts to Buenos Aires, where it joins the River Uruguay to form the River Plate, it has a deltaic character, only the southernmost portion of the floodplain can be considered a true delta (Bonfils 1962). It has a yearly pulse by which the water reaches its highest level in autumn and its lowest in spring, and every few years there are great floods. Besides the annual floods and the periodic great floods, there are records of extraordinary floods from 1983, 1905, and, though anecdotal records of previous ones as well, during which the water reached very high levels and for a far longer periods. Catastrophic floods which occur once or twice in a century seem to be a normal event of the river regime.

The vegetation of the valley has been recorded by Morello (1949) and Burkart (1957), and more recently by Franceschi and Lewis (1979). Among the more stable plant communities are the insular forests, and another apparently stable one is the *Panicum prionitis* tall grassland, which previous to 1983 catastrophic flood was perhaps the more widespread plant community of the valley. This community was considered a seral stage, preceding the forest (Morello 1949 and Burkart 1957), though later on Lewis and Franceschi (1979) cast doubts about this being so.

Plant succession models of this vegetation space so far have been based on a static approach, so a quite different view of the problem may arise if a dynamic approach is followed. The last catastrophic flood destroyed completely the tall grasslands, and a very diverse community settled in their place; this is very different from what was supposed to be the pioneer community. As these catastrophic floods occur once or twice in a century the tall grasslands will never evolve further, so they are when mature a final community

of the valley (Lewis et al. 1987).

Before the 1983 flood we analysed and mapped the plant communities of the El Rico Provincial Reserve and neighbouring islands, located between 32°10' and 32°25' S latitudes and 60°40' and 60°45' W longitudes (Franceschi et al. 1985). Within the reserve, the island Campo Rico has a shallow lake in its centre connected only temporarily and during floods with the main river through very poorly defined water courses. From its centre to the higher peripheral levees where the forests thrive, there is a smooth elevation gradient, and several plant communities are arranged in concentric rings around the lake. Tall grasslands form the outer ring on high elevations, immediately before the forests. This distribution around the lake seems to reflect a primary successional sequence. However, not all zonation should be taken to signify such a sequence (Dansereau 1957).

The last catastrophic flood destroyed the vegetation of this area, which had been mainly *Panicum prionitis* grasslands. When we revisited the site in November 1985 the vegetation was just starting to reestablish, and its general coverage was about only 10 to 20% from the edge of the lake up to the levee. In the lowest part, with patches of *Panicum prionitis* crowns present, there were wilting patches of *Myriophyllum brasiliense* and *Nymphoides indica*, others of *Eichhornia azurea* and of *Thalia geniculata* alone or with *Echinochloa* sp., all on the sediments deposited during the flood. In a nearby location previously covered by *Panicum prionitis* grasslands, but without any apparent remains, there were *Ludwigia peploides* communities and patches of *Polygonum acuminatum*. Everywhere, hanging from or on the entangled plant stems, there were great quantities of dry, *Salvinia herzogii* fronds, some with the epiphytic *Scirpus cubensis* var *paraguayensis*.

We are addressing three different but related problems: 1) the distribution of the vegetation along the

Table 1. Data table. Plots and species ordered by SSA.

Species	Plots	A				B				C				D				E				F				G						
		2	5	7	6	8	1	22	3	4	12	16	19	27	21	11	13	15	20	14	17	18	9	10	24	25	26	23	28	29	30	
1. Mikania periplocifolia		2	4	3	3	2	3	2	+	+	1	2	2	2	4		1	3	1	2	+	2	+			1	(+)	+	+	+		
10. Baccharis pingraea		2	+	+	+	+	(+)			(+)		+	+		+			(+)		+	+	+		+								
6. Baccharis phyteumoides		2	1	1	3	1	1													+	+	+										
14. Panicum prionitis		2	4	4	4	2					+	2		+						+	+											
31. Cyperus vireus		+	+	+	+																	+										
29. Solanum amygdalifolium																																
32. Salix humboldtianum																																
33. Cissus palmata	Ia						(+)																									
34. Hemarthria altissima							(+)(+)																									
35. Ludwigia caparosa							1				+																					
36. Undetermined seedling							(+)																									
18. Setaria geniculata		+					+																									
37. Eleocharis nodulosa							2							+																		
39. Aspidia silphoides							(+)																									
40. Undetermined vegetative Gramineae							(+)																									
3. Borreria verticillata		+					(+)	+																								
8. Cyperus sp.(I)							+	+																								
11. Conyza bonariensis		+					+	+																								
4. Solanum sp.							+	+																								
9. Cayaponia podantha	Ib						+	+																								
12. Eleocharis viridans		+		(+)			(+)																									
19. Undetermined vegetative dicotyledoneous		+	+																													
16. Eryngium ebracteatum		1		(+)	+																											
17. Aeschynomene rudis		+																														
20. Gnaphalium gaudichaudianum		+																														
2. Ludwigia peploides		+	+	+			+	1	+	2	3	2	+	+	1	+				(+)		+	1	+	+	+	+	2	3	4	5	4
24. Bidens laevis			+				(+)				+	+																				
38. Enhydra anagallis										(+)	1				1	+	3	1	+	(+)												
47. Cleome sp.																																
23. Panicum elephanthipes	II	+		1	2	+	1	2			+	+	+	+	2	+																
44. Polygonum punctatum																																
54. Eichhornia azurea																																
55. Funastrum sp.																																
56. Sagittaria montevidensis																																
5. Alternanthera phloxeroides		+	+		+		+			(+)	+	1	+								+		+	+								
7. Leersia hexandra							1	1				+								1			+	+								
30. Echinochloa polystachya												1								3	5	5	3	2	+							
13. Polygonum hydropiperoides	III	+	+	+	+		+	+	2	+					1	+	+															
27. Oxalis sp.							+	+			+																					
21. Echinochloa crusgalli							(+)	+		+	1	+	(+)																			
22. Gimnocoronis spilanthoides							+	+			1	+								(+)	+	+										
15. Polygonum acuminatum		+	1	+	+	1		1	2	2	1	3	4	2	2	2	3	2	+	4	+	1	1	1	+		+					
41. Eleocharis elegans											2	2	4	2	+	+	2	1		+	+	4	+	(+)	+		+					
28. Echinoderus grandiflorus			+	+		(+)					+	+	+	+	+	+	+	+	(+)													
43. Mikania sp.(Franceschi 1954)											+		+		+	+	+	+		+												
26. Thalia geniculata											2																					
52. Tilia latifolia	IV														2	2	4	5		+												
25. Caperonia cordata																																
53. Anisela argentina																																
46. Caperonia hystrix																																
48. Eclipta prostrata																																
42. Rymenachne amplexicaule	V										3	+	+																			
57. Cyperus sp. (II)											+																					
45. Polygonum paraguayensis																																
49. Lathyrus nigrivalvis	VI																															
50. Spilanthes stolonifera																																
51. Scoparia montevidensis																																

elevation gradient; 2) the primary succession sequence around the lake; 3) the recovery of the vegetation, or secondary succession after a catastrophic flood. In order to analyse these we have established permanent plots in a transect from the edge of the lake to the high levee. In this paper we deal with the first problem presenting the data of the first year, and we make some considerations comparing the previous and present vegetation.

Material and Methods

On March 1986 a 600 m long transect was laid from the levee down to the edge of the central lake on the island Campo Rico. 2.5×2.5 m permanent plots were set along the transect at 20 m intervals. In each plot the dominant physiognomy, coverage of vegetation and stratification, coverage by layers and various environ-

mental characteristics were recorded. Floristic lists were made, and the abundance-cover of species was estimated by Braun-Blanquet's (1979) combined scale. Estimations of vitality and vigor were also made. A sample of each sediment layer down to 35-40 cm was collected in every plot. The analysis of these is not yet completed. Topographic elevation was determined with an optical level.

Vegetation samples were classified using sums of squares (SSA) and average linkage clustering (ALC) (Orl6ci 1967, 1978). Also, they were ordinated by principal components analysis (PCAR) using a covariance matrix. The analyses were performed on a Texas Instruments computer. The programs SSA, ALC and PCAR were taken from Orl6ci and Kenkel (1985). The botanical nomenclature follows Cabrera (1963, 1965 a & b, 1967, 1968, 1970) and Burkart (1969, 1974, 1979, 1987).

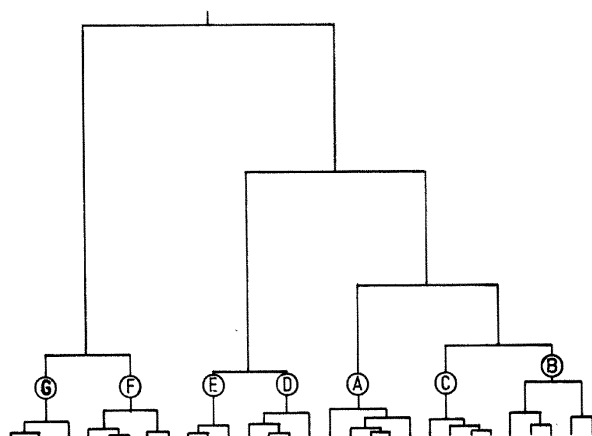


Fig. 1. Dendrogram for plots constructed by SSA. Sequence of plots left to right: 30, 29, 28, 23; 26, 25, 24, 10, 9; 18, 17, 14; 20, 15, 13, 11; 8, 6, 7, 5, 2; 21, 27, 19, 16; 12, 4, 3, 22, 1.

Results and Discussion

The transect intercepts the following communities from lake edge to levee: *Ludwigia peploides* "verdolagal"; *Polygonum acuminatum* "cataysal"; *Thalia geniculata* "achiral"; *Panicum elephantipes* and *Echinochloa polystachya* "canutillares" and a very immature *Panicum prionitis* tall grassland. Apart from the "achiral" which has very sharp limits, the communities are distinguished more by the relative abundance of the dominant species than by their floristic composition.

Cluster analysis

Seven clusters (A, B, C, D, E, F, and G) of ecological meaning were produced by SSA (Fig. 1, Table 1). Group A comprises samples of the tall grassland; C the entire

"cataysal"; D, "achiral"; E, *Echinochloa polystachya* "canutillar"; F, *Panicum elephantipes* "canutillar"; and G, "verdolagal". Group B consists of samples from transition zones (plots 1, 3, 4 and 12) or communities poorly represented over the transect (plot 22, *Hymenachne amplexicaule* "canutillar"). The between groups sum of squares is nearly 100%, showing the extreme compactness of the groups.

ALC also produced seven groups very similar to the SSA groups (Fig. 2, Table 2), but in this case group B consists of a single sample 22 from the *H. amplexicaule* "canutillar". Plots 3, 4 and 12 were grouped with those of the *Ludwigia peploides* "verdolagal" and plot 1 with the *Panicum prionitis* tall grasslands. Though both methods produced similar groups, SSA seems to be more strict than ALC on the delimitation of groups and the latter shows in a better way the relationships among the groups.

Species were also classified. The groups produced by the methods (Table 1 and 2) are not satisfactory. However, SSA (Fig. 3) produced a grouping which makes more ecological sense than those produced by ALC, but the between groups sum of squares is only 41.34%, indicating little internal coherence of the groups.

Species groups I_a and I_b are clearly different from the rest of the groups (Fig. 3) and all of their species are related to the tall grasslands (community A). Restriction of the species to this community becomes greater from top to bottom in Table 1; those of group I_b are the rarities of this community and when occur in community B, they are in a single sample (plot 1) which is very much like the tall grasslands, though lacking dominance. In both I_a and I_b the less hygrophilous species of the transect are present. On the other hand in group II, the most hygrophilous species occur which are typical of the *Panicum elephantipes* "canutillar", the

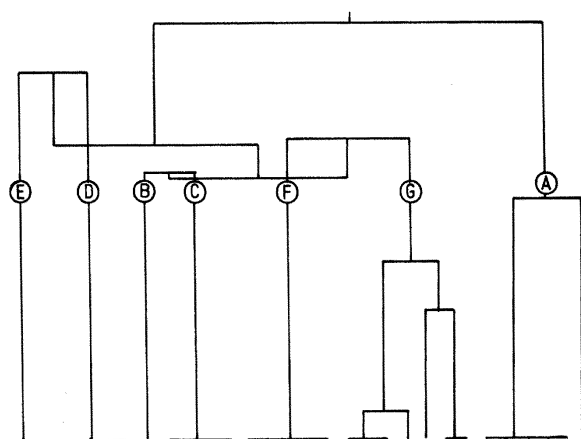


Fig. 2. Dendrogram for plots constructed by ALC. Sequence of plots, left to right: 17, 18, 14; 20, 15, 13, 11; 22; 27, 21, 19, 16; 25, 26, 24, 10, 9; 30, 29, 28, 23, 12, 4, 3; 8, 7, 6, 5, 2, 1.

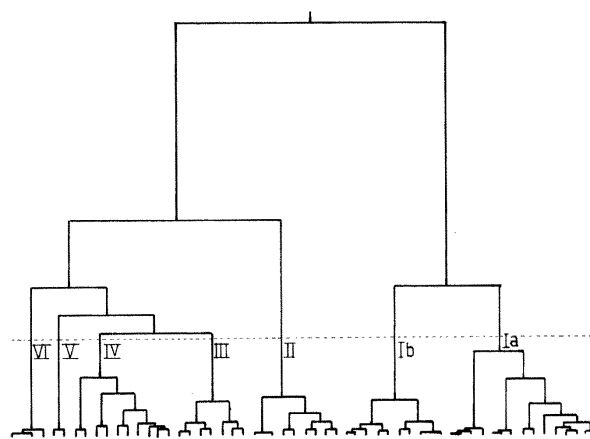


Fig. 3. Dendrogram for species constructed by SSA. Sequence of species, left to right: 51, 50, 49, 45; 57, 42, 48, 46, 53, 25, 52, 26, 43, 28, 41, 15; 22, 21, 27, 13, 30, 7, 5; 56, 55, 54, 44, 23, 47, 38, 24, 2; 20, 17, 16, 19, 12, 9, 4, 11, 8, 3; 40, 39, 37, 18, 36, 35, 34, 33, 32, 29, 31, 14, 6, 10, 1.

Table 2. Data table. Plots and species ordered by ALC.

[illegible]

Ludwigia peploides "verdolagal" (communities F and G), and to a lesser degree, the *Polygonum acuminatum* "cataysal" (community C) and transitional plots (community B). Group III and IV have less hygrophilous species than the previous one. In group III only *Echinochloa polystachya* has a high correlation with the community in which this species is the dominant (community E); all others are more closely related to communities A, B, D and F. Species in group IV are more related to communities C and D, which is not surprising as the patches of *Thalia geniculata* (community D) are within a matrix of *Polygonum acuminatum*, the physiognomic dominant of the "cataysal" (community C). The two remaining groups (V and VI) are of little importance;

the former has species related to the *Hymenachne amplexicaule* "canutillar", which occupied only one plot in the entire transect.

If these communities are compared with those described before the 1983 flood (Franceschi et al. 1985) two outstanding differences are seen: in the first place, previous communities had developed stronger dominance; after the 1983 flood, apart from the *Ludwigia peploides* "verdolagal", all communities are floristically richer and more diverse than their previous equivalents. This seems to be particularly so in the case of the tall grasslands, in which there were 24 species previous to the great flood, and 36 to 39 after the flood, based on the SSA and ALC grouping of the relevés. Prior to the

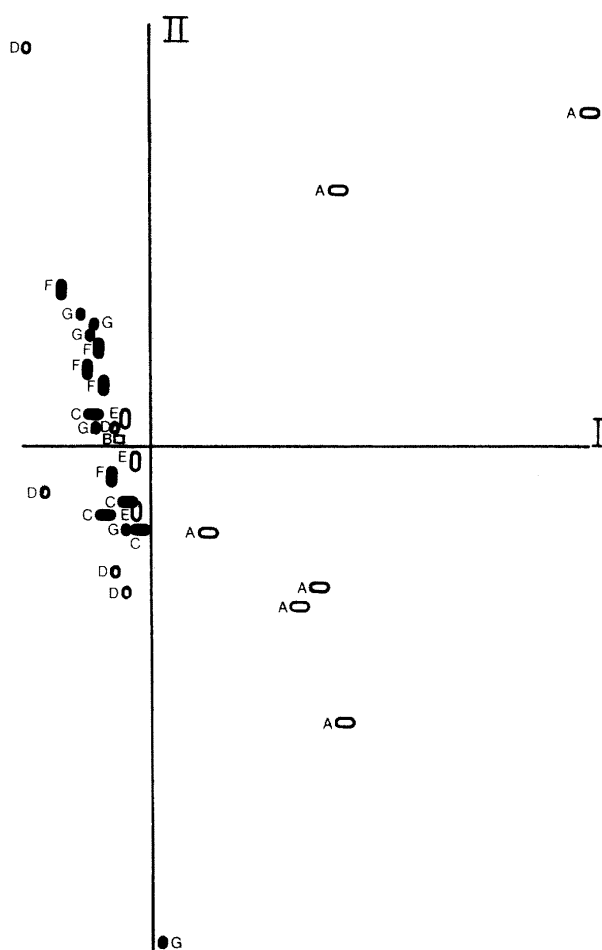


Fig. 4. Scatter diagram for relevés produced by PCA (Axes I and II). Sequence of relevés, left to right: 23, 11, 26, 28, 24, 29, 30, 27, 3, 25, 9, 19, 10, 13, 20, 22, 17, 15, 21, 4, 18, 14, 16, 12, 5, 8, 6, 1, 7, 2; top to bottom: 23, 2, 1, 26, 28, 30, 29, 25, 24, 9, 27, 17, 3, 20, 22, 18, 10, 11, 21, 19, 14, 4, 16, 5, 13, 6, 15, 8, 7, 12.

References:

Panicum prionitis community (A). *Polygonum acuminatum* community (C). *Echinochloa polystachya* community (E). *Panicum elephanthipes* community (F). *Hymenachne amplexicaule* community (B). *Ludwigia peploides* community (G). *Thalia geniculata* community (D).

flood, *Thalia geniculata* patches and *Echinochloa polystachya* "canutillar", quite important now, were negligible. There are other facts as well relevant to the discussion of secondary succession, outside within the scope of the present paper. As a whole the pre-1983 limits of the communities were better defined than what they are now.

Ordination

PCAR revealed successive gradients (axes) which absorbed very small amounts of the total variation (I:

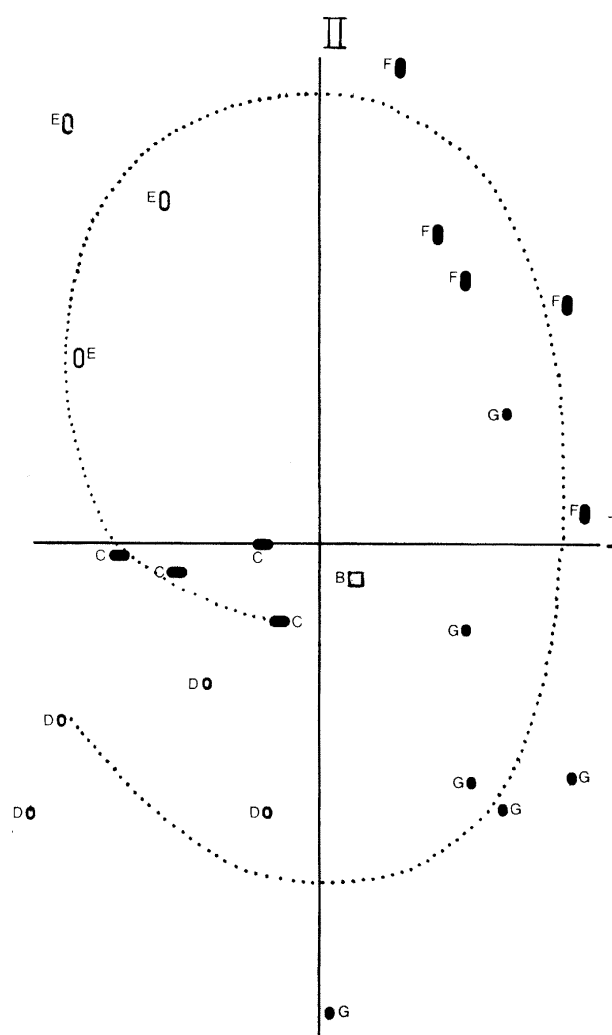


Fig. 5. Scatter diagram for relevés produced by PCA (Axes I and II). Outliers are excluded. Sequence of relevés, left to right: 15, 13, 18, 14, 19, 17, 16, 20, 21, 11, 27, 4, 22, 9, 10, 3, 24, 30, 28, 23, 25, 29, 26; top to bottom: 9, 18, 17, 10, 24, 25, 14, 23, 26, 21, 19, 16, 22, 27, 3, 20, 13, 29, 30, 28, 11, 15, 4.

References:

Polygonum acuminatum community (C). *Echinochloa polystachya* community (E). *Panicum elephanthipes* community (F). *Hymenachne amplexicaule* community (B). *Ludwigia peploides* community (G). *Thalia geniculata* community (D).

16.21%; II: 11.03%; III: 8.82%; IV: 8.16%), and only past axis XII did the accumulated variance absorbed exceed 80%. Nevertheless, axis I segregates the samples into two very distinct groups (Fig. 4). There are seven plots on the positive side with the less hygrophilous species of the higher part of the transect on slightly more developed soil. Plots containing the hygrophilous species of the lower part of the transect are placed on the negative side. The first group is related to *Panicum*

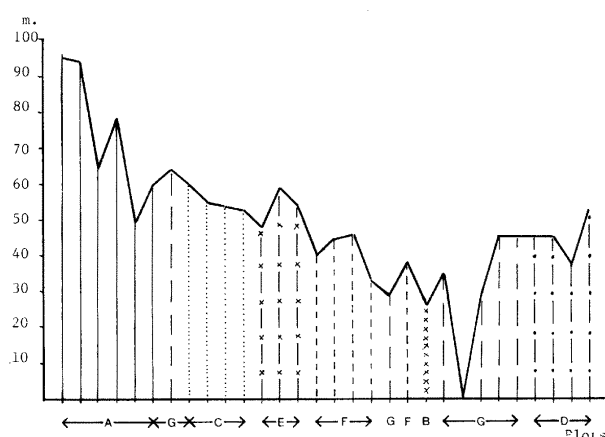


Fig. 6. Relative elevation of plots (m), ordered according to Fig. 5. (See the explanations in the text).

Sequence of relevés, left to right: 2, 1, 5, 6, 8, 7; 12; 27, 21, 16, 19; 14, 17, 18; 9, 10, 24, 25; 23; 26; 22; 3, 29, 30, 28, 4; 11, 15, 13, 20.

References:

Panicum prionitis community (A). *Polygonum acuminatum* community (C). *Echinochloa polystachya* community (E). *Panicum elephantipes* community (F). *Hymenachne amplexicaule* community (B). *Ludwigia peploides* community (G). *Thalia geniculata* community (D).

prionitis tall grasslands even though this species is absent from plot 1. Axis II (Fig. 4) segregates the extreme plots of the first group with the lowest scores of *Panicum prionitis*. Although the dispersion of the sample is suggesting a gradient, it is not clearly defined.

The plots with *Panicum prionitis* are very different from all the rest. These plots account for the high Beta-diversity within the sample. As such the extreme plots must be expected to produce a distortion of the analysis. In order to avoid this problem a further analysis was performed after eliminating the extreme plots from the set. Even in this case the first few axis did not absorb large amounts of variance (I: 21.22%; II: 16.56%; III: 13.36%; IV: 12.06%), and only after axis VI was 82.02% of the accumulated variance absorbed. The data projection on the plane of the first two axes (Fig. 5) has a spiral or helicoidal structure which shows the non linear responses of the species to environmental factors. This departure from linearity is the major intrinsic limitation of PCA (Orlói, 1978). The plots belonging to a definite community with a strong dominant species, are placed in the center of each quadrant of the dispersion diagram (Fig. 5); the samples of *Polygonum acuminatum* "cataysal" are close to axis I. All other samples are transitional between two or three communities and they appear in the diagram showing that relationship.

Assuming a spiral or helicoidal structure of the gradient, the order of the communities along this gradient is as follows: *Polygonum acuminatum* "cataysal" -

Echinochloa polystachya "canutillar" - *Panicum elephantipes* "canutillar" - *Hymenachne amplexicaule* "canutillar" - *Ludwigia peploides* "verdolagal" - *Thalia geniculata* "achiral". This picture could be completed with the *Panicum prionitis* tall grasslands at the beginning of the series as it is suggested by the diagram of Fig. 4 and field observations. The relationships of this sequence and topographic elevation is shown in Fig. 6. There is a general tendency to decreased elevation down to plot 29 and then it increases slightly. *Ludwigia peploides* "verdolagal" tend to be in the lowest part, even though plots 12 and 23 depart from this; however, plot 12 is far from being a typical case of this community and in fact it occupies the intertussock space within an only partially recovered *Panicum prionitis* tall grassland, and plot 23 is related to "canutillares", with which according to the season *Ludwigia peploides* may share or alternate the dominance with grasses as *Panicum elephantipes* and *Echinochloa polystachya* (Lewis and Franceschi, 1979). This relationship suggests the existence of environmental factors strongly associated with the elevation gradient, to which species and communities respond with their distributions in a complex nonlinear manner.

Conclusions

Catastrophic floods which are normal but rare events in the hydrological regime of the river destroy most of the vegetation, especially the more evolved communities, such as the *Panicum prionitis* grasslands (Lewis et al., 1987). On the reserve El Rico the 1983 flood produced that effect. It also laid a layer of fine texture sediments on which community recovery began.

Communities are distributed along environmental gradients on the floodplain related to topographic elevation around internal ponds. When the water recess vegetation starts to regenerate and communities equivalent to those found previous to the flood appear. However, the community limits are less well defined and most of the communities are floristically richer. An effect of catastrophic floods is therefore to smooth the gradients and enhance the appearance of a community continuum.

As the first few axes of PCA do not absorb a great amount of the total variance, there is not a single principal component that would explain an important portion of the general variability, yet, the scattergrams are suggestive of an orderly continuum of species and communities which make ecological sense.

Acknowledgements. The authors acknowledge CAFPTA financial support. We are indebted to Dr. J.P. Lewis for his critical reading of the manuscript. Professor L. Orlói very kindly provided us with computing programs. Eng. Domingo Bianchi of SAVYC and Mr Alfia López made this work possible.

REFERENCES

- BONFILS, C.G. 1962. Los suelos del delta del río Paraná. Factores generadores, clasificación y uso. *Revista de Investigaciones Agrícolas* 16: 257-370.
- BRAUN-BLANQUET, J. 1979. *Fitosociología*. H. Blume Ediciones, Madrid, 820 pp.
- BURKART, A. 1957. Ojeada sinóptica sobre la vegetación del delta del río Paraná. *Darwiniana* 11: 457-561.
- BURKART, A. 1969, 1974, 1979, 1987. *Flora Ilustrada de Entre Ríos*. Colección Científica del INTA, Buenos Aires.
- CABRERA, A.L. 1963, 1965a, b, 1967, 1968, 1970. *Flora de la Provincia de Buenos Aires*. Colección Científica del INTA, Buenos Aires.
- DANSEREAU, P. 1957. *Biogeography*. Ronald Press, New York. 394 pp.
- FRANCESCHI, E.A. and J.P. LEWIS. 1979. Notas sobre la vegetación del valle santafesino del río Paraná (República Argentina). *Ecosur* 6: 55-82.
- FRANCESCHI, E.A., D.E. PRADO and J.P. LEWIS. 1985. Comunidades vegetales y mapa de vegetación de la reserva "El Rico" e islas aledañas (Provincia de Santa Fe, Argentina). Servicio de Publicaciones de la Universidad Nacional de Rosario. Rosario. 40 pp.
- LEWIS, J.P. and E.A. FRANCESCHI. 1979. Notas sobre la dinámica de la vegetación del valle del río Paraná. *Ecosur* 6: 145-163.
- LEWIS, J.P., E.A. FRANCESCHI and D.E. PRADO. 1987. Effects of extraordinary floods on the dynamics of tall grasslands of the river Paraná valley. *Phytocoenologia* 15: 235-251.
- MORELLO, J. 1949. Las comunidades vegetales de las islas cercanas al puerto de Rosario. Tesis del Museo de la Plata n. 133.
- ORLÓCI, L. 1967. An agglomerative method for classification of plant communities. *J. Ecol.* 55: 193-206.
- ORLÓCI, 1978. *Multivariate Analysis in Vegetation Research*. 2nd ed. Junk, The Hague.
- ORLÓCI, L. and N. KENKEL. 1985. *Introduction to Data Analysis*. Statistical Ecology Monographs Vol. 1. International Cooperative Publishing House. Fairland, Maryland.

Manuscript received: February 1988

Notice

Professor G.P. Patil, a member of the COENOSSES Editorial Board and Director of the Center for Statistical Ecology and Environmental Statistics, Pennsylvania State University, was awarded an honorary degree in Biological Sciences from the University of Parma, Parma, Italy on December 17, 1988. His speech at the awards ceremony was entitled "Statistical Ecology, Encountered Data and Meta Analysis: a Few Perspectives in Statistical Ecology".

In his speech Prof. Patil emphasised the importance of the integrators and not just the specialists in different fields of science. He pointed out that prudent de-

cisions in environmental science must look as critically at the data as at the analysis: "while there are questionable statistical routines, there are no routine statistical questions".

Exploring the difference between comprehensive and comprehensible information, and the dilemmas faced in trying to define, understand, describe, predict, or manage a situation in the face of uncertainty, Dr. Patil emphasised the value of interdisciplinary effort. He proposed simultaneous three way interaction between resource managers, research scientists and statistical scientists as a suitable protocol for useful environmental decision making.
