

CHANGES IN PASTURE COMMUNITIES SUBJECT TO BURNING IN THE CÓRDOBA MOUNTAINS, ARGENTINA

M. Menghi¹, M. Cabido¹, A. Acosta¹, B. Peco² and F. D. Pineda²

¹ Centro de Ecología y Recursos Naturales Renovables, Universidad Nacional de Córdoba, C. Correo 395, 5000 Córdoba, Argentina

² Departamento Interuniversitario de Ecología, Universidades Complutense y Autónoma de Madrid, 28040 Madrid, Espana.

Keywords: Central Argentina, Geomorphology, Mountain areas, Multivariate analysis, Pastures, Spatial niche, Succession

Nomenclature follows Cabrera (1963, 1965a, b, 1967, 1968, 1970), Burkart (1974, 1979) and Correa (1984a, b)

Abstract. The successional dynamics of pastures in a representative area of the Córdoba Mountains is studied. Traditionally, the pastures are periodically burned to eliminate the phytomass that accumulates in "pajonales", areas of tall grasses that are unpalatable for cattle. This is not an intense disturbance, and it permits development until the start of a new disturbance. In this study, succession is analyzed based upon multivariate ordination techniques and diversity analysis. It is shown that the floristic composition describes a relatively clear successional sequence, and the variability in the communities is not seriously affected in its relation with the geomorphological gradient on the slopes, although many species modify their spatial niche during succession.

Introduction

The structure of the pasture ecosystems in the Córdoba Mountains (Central Argentina) is affected by several sources of variation. Those related to local geographical aspects, such as altitude, lithology and geomorphology, including slopes gradients and edaphic development gradients, are regarded as important (Cabido *et al.* 1986, Cabido 1987, Menghi 1987, Acosta 1988). Some of these aspects, explained as "equipotentiality", "vectoriality" and "mosaicistic phenomena", according to Solntsev's terminology (1974), are described in a previous paper (Menghi *et al.* 1989).

The traditional burning of these pastures is another source of variation. It is carried out itinerantly, under relatively little control and it affects extensive areas. The purpose is to eliminate the large grasses, such as *Festuca hieronymi*, *Stipa filiculmis*, *S. tenuissima* and *Paspalum quadrifarium* which tend to form large patches of "pajonal" which is difficult for cattle or sheep to digest (Luti *et al.* 1979, Menghi 1981, 1987). Large areas of these pastures may be considered as semi-natural (Whittaker 1974).

Menghi *et al.* (1978a, b) found that grazing on these pastures reached the highest production values per unit of maintained phytomass. Alessandria and Casermeiro (1986) showed that with moderate grazing, controlled "pajonal" burning increased the productivity and the nutritive quality of these pastures. Galera (1986) observed successional changes in frequently burned areas under varying pressure from herbivores.

The study of changes occurring in the course of succession, aids the comprehension of the structure and function of the pastures and completes the perceptions offered previously (Poissenet *et al.* 1981, Mooney and Godron 1983, Prentice and van der Maarel 1987, Pomeroy and Aberts 1988).

Another type of traditional pasture management, acting as a disturbance disconnecting the successional sere, has been studied in Mediterranean environment (Pineda and Peco 1987, 1988). In this, disturbance involves ploughing the substratum itinerantly to avoid the invasion of sclerophyllous scrub. Under this, the pasture vegetation changes dramatically with time, both in its floristic composition and in the spatial organization (Pineda *et al.* 1981a, De Pablo *et al.* 1982, Sterling *et al.* 1983, Castro *et al.* 1986, Galiano *et al.* 1987).

In the Córdoba Mountains, disturbance seems less intense than the above. Phytomass accumulation until burning is not very large and the fire is unlikely to destroy the soil microflora or affect the seed bank in the mechanically unaltered soil. The object of the present study is to set out space-time changes caused by these fires in an area of the Córdoba Mountains largely covered by pastures. It was thought that burned pasture recovery would show changes in composition and spatial organization, as they occur in Mediterranean pastures, particularly in those referring to the dimensions and characteristics of community spatial niche (Pineda *et al.* 1981b). This idea is based on the use of the spatial changes described as a reference, ex-

Table 1. Names and abbreviations of the species found in sampling.

Tabla 1. Names and abbreviations of the species found in sampling.

ACC	<i>Acalypha communis</i>	CHI	<i>Chaptalia integerrima</i>
ACT	<i>Acicarpa tribuloides</i>	CHS	<i>Chevreulia sarmentosa</i>
ADB	<i>Adesmia bicolor</i>	CHH	<i>Chloris halofila</i>
ADC	<i>Adesmia corymbosa</i>	CHR	<i>Chloris retusa</i>
ADH	<i>Adesmia hispidula</i>	DAP	<i>Daucus pusillus</i>
ADI	<i>Adesmia incana</i>	DIH	<i>Dichondra sericea</i> v. <i>holosericea</i>
ALA	<i>Alternanthera albida</i>	DIM	<i>Dichondra microcalyx</i>
ALP	<i>Alternanthera pumila</i>	DIA	<i>Digitaria ascendens</i>
AMS	<i>Amaranthus</i> sp.	DIC	<i>Digitaria californica</i>
AMC	<i>Amblyopetalum coccineum</i>	DUI	<i>Duchesnea indica</i>
AMT	<i>Ambrosia tenuifolia</i>	ELT	<i>Eleusine tristachya</i>
ANT	<i>Andropogon ternatus</i>	ELM	<i>Elionurus muticus</i>
ANI	<i>Aneimia tomentosa</i>	ERB	<i>Eragrostis bahiensis</i>
ARS	<i>Apium leptophyllum</i>	ERL	<i>Eragrostis lugens</i>
ARA	<i>Aristida achalensis</i>	ERP	<i>Eragrostis polytricha</i>
ARP	<i>Aristida pallens</i>	ERR	<i>Eragrostis retinens</i>
ARS	<i>Aristida spegazzini</i>	ERC	<i>Erodium cicutarium</i>
ASQ	<i>Aster squamatus</i>	ERH	<i>Eryngium horridum</i>
ASC	<i>Astragalus carinatus</i>	ERN	<i>Eryngium nudicaule</i>
ASD	<i>Astragalus distinens</i>	EUP	<i>Euphorbia portulacoides</i>
BAA	<i>Baccharis articulata</i>	EUS	<i>Euphorbia serpens</i>
BAC	<i>Baccharis coridifolia</i>	AVA	<i>Evolvulus arizonicus</i>
BAR	<i>Baccharis rufescens</i>	EVS	<i>Evolvulus sericeus</i>
BOE	<i>Borreria verticillata</i>	FAR	<i>Facelis retusa</i>
BOB	<i>Bothriochloa barbinodis</i>	FEH	<i>Festuca hieronymi</i>
BOL	<i>Bothriochloa laguroides</i>	GAE	<i>Gaillardia megapotamica</i>
BOS	<i>Bothriochloa saccharoides</i>	GAG	<i>Galactia glaucophylla</i>
BOC	<i>Bouteloua curtipendula</i>	GAM	<i>Galactia marginalis</i>
BOM	<i>Bouteloua megapotamica</i>	GAA	<i>Gamochaeta americana</i>
BRP	<i>Briza paleapilifera</i>	GAF	<i>Gamochaeta filaginea</i>
BRS	<i>Briza subaristata</i>	GAS	<i>Gamochaeta spicata</i>
BRA	<i>Bromus auleticus</i>	GEA	<i>Geranium albicans</i>
BRU	<i>Bromus unioloides</i>	GLD	<i>Glandularia dissecta</i>
BUJ	<i>Bulbostylis juncoides</i>	GLP	<i>Glandularia peruviana</i>
CAB	<i>Capsella bursa-pastoris</i>	GNG	<i>Gnaphalium gaudichaudianum</i>
CAR	<i>Cardionema ramosissimum</i>	GOE	<i>Gomphrena perennis</i>
CAN	<i>Carduus nutans</i>	GOP	<i>Gomphrena pulchella</i>
CAS	<i>Carex</i> sp.	GRP	<i>Grindelia pulchella</i>
CEA	<i>Cerastium arvense</i>	GYS	<i>Gymnocalyun</i> sp.
CIV	<i>Cirsium vulgare</i>	GYG	<i>Gymnopogon grandiflorum</i>
COO	<i>Cologania ovalifolia</i>	HES	<i>Heimia salicifolia</i>
COV	<i>Commelina virginica</i>	HMV	<i>Heterospermum diversifolium</i>
COB	<i>Conyza bonariensis</i>	HEA	<i>Heterothalamus alienus</i>
CRA	<i>Croton argentinus</i>	HOS	<i>Hordeum stenostachys</i>
CRL	<i>Croton lorentzii</i>	HYP	<i>Hybanthus parviflorus</i>
CRP	<i>Croton parvifolius</i>	HYS	<i>Hybanthus serratus</i>
CUG	<i>Cuphea glutinosa</i>	HYA	<i>Hypochoeris argentina</i>
CYD	<i>Cynodon dactylon</i>	HYH	<i>Hypoxis humilis</i>
		HYM	<i>Hyptis mutabilis</i>

Table 1 (continued)

Tabla 1. Continued

CYH	<i>Cynodon hirsutus</i>	POS	<i>Portulaca</i> sp.
IRD	<i>Iresine diffusa</i>	RER	<i>Relbunium richardianum</i>
JUD	<i>Juncus dombeyanus</i>	RHM	<i>Rhynchosia minima</i>
JUU	<i>Juncus uruguensis</i>	RHS	<i>Rhynchosia senna</i>
LES	<i>Leontodon nudicaulis</i>	RIB	<i>Richardia brasiliensis</i>
LEF	<i>Lepechinia floribunda</i>	RUC	<i>Rumex crispus</i>
LEB	<i>Lepidium bonariense</i>	SCI	<i>Schizachyrium imberbe</i>
LEM	<i>Lesquerella mendocina</i>	SCM	<i>Schizachyrium microstachyum</i>
LUA	<i>Lucilia acutifolia</i>	SCS	<i>Schizachyrium spicatum</i>
MAN	<i>Malva neglecta</i>	SCP	<i>Schkuria pinnata</i>
MAC	<i>Malvastrum coromandelianum</i>	SES	<i>Selaginella peruviana</i>
MAP	<i>Margyricarpus pinnatus</i>	SEC	<i>Senecio ceratophylloides</i>
MEL	<i>Medicago lupulina</i>	SEP	<i>Senecio pampeanus</i>
MEN	<i>Melica macra</i>	SEC	<i>Setaria geniculata</i>
MES	<i>Melica stuckertii</i>	SEL	<i>Setaria leiantha</i>
MII	<i>Microchloa indica</i>	SIP	<i>Sida prostrata</i>
MIM	<i>Mitracarpus megapotamicus</i>	SIA	<i>Silene argentina</i>
NIA	<i>Nierembergia aristata</i>	SIC	<i>Sisyrinchium chilense</i>
NOC	<i>Nostoc commune</i>	SOI	<i>Solanum incisum</i>
NOI	<i>Nothoscordum inodorum</i>	SOR	<i>Sonchus oleraceus</i>
NOM	<i>Noticastrum marginatum</i>	SOP	<i>Sorghastrum pellitum</i>
OEI	<i>Oenothera indecora</i>	SPR	<i>Spergula ramosa</i>
OXC	<i>Oxalis cordobensis</i>	SPC	<i>Sphaeralcea cordobensis</i>
OXS	<i>Oxalis sexenata</i>	SPD	<i>Spilanthus decumbens</i>
OXA	<i>Oxypetalum arnottianum</i>	SPI	<i>Sporobolus indicus</i>
PAC	<i>Paronychia chilensis</i>	SPP	<i>Sporobolus pyramidatus</i>
PAB	<i>Paronychia setigera</i>	STR	<i>Stenandrium dulce</i>
PAH	<i>Parthenium hysterophorus</i>	STA	<i>Stenorrhynchos australis</i>
PAD	<i>Paspalum dilatatum</i>	STS	<i>Stevia satureiaefolia</i>
PAU	<i>Paspalum humboldtianum</i>	STA	<i>Stipa amethystina</i>
PAM	<i>Paspalum malacophyllum</i>	STF	<i>Stipa filiculmis</i>
PAN	<i>Paspalum notatum</i>	STX	<i>Stipa flexibarbata</i>
PAP	<i>Paspalum plicatulum</i>	STH	<i>Stipa hunzikeri</i>
PAQ	<i>Paspalum quadrifarium</i>	STN	<i>Stipa neesiana</i>
PAA	<i>Pavonia aurigloba</i>	STP	<i>Stipa papposa</i>
PFG	<i>Pfaffia gnaphaloides</i>	STU	<i>Stipa tenuissima</i>
PHV	<i>Physalis viscosa</i>	STT	<i>Stipa trichotoma</i>
PIB	<i>Piptochaetium bicolor</i>	STG	<i>Stylosanthes gracilis</i>
PID	<i>Piptochaetium medium</i>	TAF	<i>Tagetes filifolia</i>
PIM	<i>Piptochaetium montevidense</i>	TAM	<i>Tagetes minuta</i>
PIS	<i>Piptochaetium stipoides</i>	TAO	<i>Taraxacum officinale</i>
PLY	<i>Plantago myosurus</i>	TRG	<i>Tragia geraniifolia</i>
PLM	<i>Plantago australis</i>	TRR	<i>Trifolium repens</i>
POL	<i>Poa ligularis</i>	TUS	<i>Turnera sidoides</i>
POH	<i>Podocoma hieracifolia</i>	VEI	<i>Vernonia incana</i>
POM	<i>Polygala medocina</i>	VEM	<i>Vernonia mollissima</i>
POP	<i>Polygonum punctatum</i>	VIS	<i>Viola</i> sp.
POO	<i>Porophyllum obscurum</i>	WAL	<i>Wahlenbergia linarioides</i>
		ZEL	<i>Zephyranthes longistyla</i>

pecting fires to affect most seriously the patches of large grasses.

Material and methods

The Córdoba Mountains run for 430 km between 29° to 33° 30' S in a 110 km wide band. The highest point is Champaquí, at 2790 m. The lithology mainly consists of crystalline and plutonic rock, generally covered by acid soils except when quaternary loess sediments cover the rock on gentle slopes or flat surfaces (Vázquez *et al.* 1979). The vegetation is found in three characteristic altitudinal belts (Luti *et al.* 1979) and has been studied recently by Menghi and Luti (1982), Menghi (1987), Cabido (1985, 1987), Cabido and Acosta (1985), Cabido *et al.* (1986) and Acosta (1988) among others.

Sampling was centered on one lithological type in order to highlight the successional changes, ignoring those related to altitude or geology as sources of abiotic variations. The tertiary conglomerate zone of El Cuadrado was chosen. Its relief is gently undulating and the slopes are straight or almost concave. The correspondence between the spatial variation of the communities and slope morphology has been previously studied on well preserved or not recently disturbed slopes (Menghi *et al.* 1989). This area is representative of considerable areas of moderately grazed pasture.

Several neighbouring slopes were chosen with similar topographic and pedological characteristics oriented to the north, but which had been burned at different times. The sampling followed a transect from the upper to the lower part of each slope. Ten 2 x 6 m plots were placed regularly in each transect, with longer side perpendicular to the slope direction. The frequency of each species in each plot was determined using 10 elemental 20 x 20 cm sampling quadrats placed at random. The data were collected during the same growth season (summer of 1986), thus avoiding differences owing to meteorological and phenological variation. Eleven slopes were sampled. Two had been burned four months previously, while the rest consisted of three repetitions of slopes burned one, four and nine years before.

The data were analyzed using correspondence analysis (Benzecri 1973) in order to define space-time trends. A pattern diversity analysis was carried out to reveal the spatial niche behaviour of species and communities during succession (Pielou 1977, Pineda *et al.* 1988). The parameter $H(P/E_j)$ (De Pablo *et al.* 1982) was used as a representation of a measure of the equitability of species j abundance distribution along a group of regularly located sampling plots. This parameter is a non-standardized measure of the spatial niche width of the species. It was unnecessary to use the standardization parameter $A = H(P/E_j)/H(P)_{\max}$ (Pineda *et al.* 1981b) - where $H(P)_{\max}$ is the maximum alpha diversity value obtained from the distribution of

species abundance in all plots - because the number of basic sample units (10) was the same in every case.

Results and discussion

A total of 195 species were found in the 110 sample plots (Table 1). Only the 176 species whose presence exceeded 2% of the total sampling quadrats were considered for numerical analysis. The number present in each plot was highly variable, and the number on each slope was relatively similar. This number tends to be higher on the oldest slopes since burning, although a clear successional variation trend was not observed (Table 2).

The ordination analysis showed a relatively clear successional variation in the floristic composition from the negative part of axes 1-3 towards the positive end (Figure 1). The species with high loadings associated with each group defined in Figure 1 are shown in Table 3 while some of the most characteristic responses to successional change are shown in Figure 2. The initial stage of succession is characterized by the relative abundance of *Ambrosia tenuifolia*, *Stipa flexibarbata*, *S. filiculmis*, *Piptochaetium montevidense* and *Eragrostis lugens* among others. The abundance of some of these species hardly varies with time. Stabilized pasture is characterized by *Festuca hieronymi*, *Cologania ovalifolia*, *Dichondra microcalyx* and *Heterospermum diversifolium*, among others. These species are characteristic of stable "pajonales", where there is large accumulation of phytomass (5000 kg/ha; Menghi *et al.* 1978). The palatability for domestic herbivores is low and the grasses are regularly burned. This provokes a new successional cycle.

Table 2. Number of species found in 110 north oriented plots on 10 sites along each of the 11 Tertiary conglomerate slopes, burned at different times.

Time since burning	Slope	Number of species	Mean number
4 months	1	113	103.0
	2	93	
1 year	3	108	108.3
	4	109	
	5	108	
4 years	6	104	93.3
	7	83	
	8	93	
9 years	9	140	120.6
	10	114	
	11	107	

Table 3. Average frequency values (in brackets) of characteristic species of each group of plots shown in Figure 1. These values were obtained from groups of 20 plots (2 slopes with 10 plots each in initial stages, 4 months), and groups of 30 plots (3 slopes) in the remaining successional stages. Species are identified by the site which produced their highest value: E=upper eroded zones (first three plots along the transect); T=intermediate zones (next four plots); C=lower accumulation zones (last three plots).

4 months	1 year	4 years	9 years
<i>Ambrosia tenuifolia</i> (.040)T	<i>Schizachyrium imberbe</i> (.032)E	<i>Piptochaetium monteiv.</i> (.046)C	<i>Festuca hieronymi</i> (.060)T
<i>Piptochaetium monteiv.</i> (.045)C	<i>Stipa filiculmis</i> (.042)T	<i>Paspalum notatum</i> (.240)C	<i>Stipa filiculmis</i> (.050)T
<i>Eragrostis lugens</i> (.038)E	<i>Schkuria pinnata</i> (.038)T	<i>Dichondra microcalyx</i> (.050)C	<i>Cologania ovalifolia</i> (.060)T
<i>Aristida spagazzini</i> (.034)E	<i>Sida prostrata</i> (.030)T	<i>Eragrostis lugens</i> (.049)T	<i>Dichondra microcalyx</i> (.040)C
<i>Schizachyrium imberbe</i> (.033)E	<i>Chloris retusa</i> (.040)E	<i>Festuca hieronymi</i> (.035)T	<i>Heterospermun diversif.</i> (.040)T
<i>Schizachyrium spicatum</i> (.037)E	<i>Dichondra microcalyx</i> (.280)C	<i>Chloris retusa</i> (.045)E	<i>Sida prostrata</i> (.030)T
<i>Stipa filiculmis</i> (.036)T	<i>Borreria verticillata</i> (.030)E	<i>Chevreulia sarmentosa</i> (.030)T	<i>Chevreulia sarmentosa</i> (.030)T
<i>Schkuria pinnata</i> (.036)T	<i>Aristida spagazzini</i> (.044)E	<i>Stipa filiculmis</i> (.040)T	
<i>Sida prostrata</i> (.049)T	<i>Paronychia chilensis</i> (.028)E	<i>Stipa tenuissima</i> (.033)T	
<i>Tagetes filifolia</i> (.037)C	<i>Rhynchosia senna</i> (.038)E	<i>Ambrosia tenuifolia</i> (.041)T	
<i>Setaria geniculata</i> (.039)T	<i>Dichondra sericea</i> (.035)E	<i>Bromus unioloides</i> (.040)C	
<i>Paspalum notatum</i> (.037)C		<i>Sida prostrata</i> (.053)T	
<i>Oxalis sexenata</i> (.030)T		<i>Hypochoeris argentina</i> (.037)C	
<i>Dichondra microcalyx</i> (.039)C		<i>Gamochaeta spp.</i> (.035)E	
<i>Gamochaeta spp.</i> (.034)E			

Variation in the pasture composition along slope gradients has been described in numerous studies, including some carried out in this area (García-Novo *et al.* 1969, Pineda *et al.* 1981a, Sterling *et al.* 1983, Menghi 1987, Menghi *et al.* 1989). Nevertheless, in this group of slopes with different successional ages, the distribution of plots along continuous geomorphological gradients is discernable only in the case of the older successional pastures (ellipses in Figure 1) and unclear

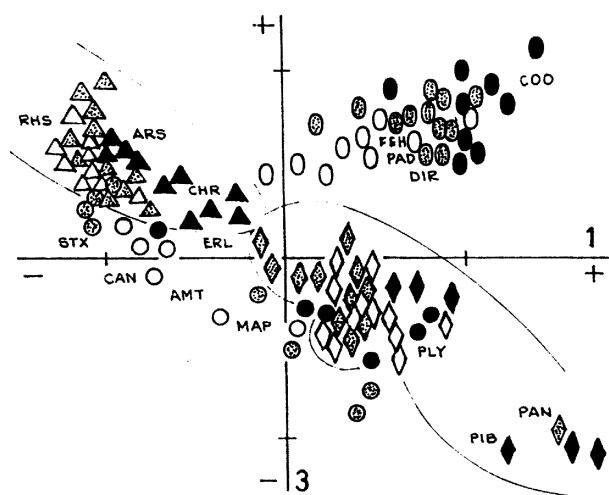


Figure 1. Correspondence analysis of all sample plots on 11 pasture slopes with different successional ages after burning. Circles= plots on slopes burned 4 months previously; triangles= 1 year; diamonds= 4 years; ellipses= 9 years. The shading of the symbols refers to the geomorphological position: open= upper zones on the slopes; dashes= intermediate; solid= lower. Some characteristic species are represented for each stage. See Table 1 for abbreviations.

on other slopes. The behaviour of characteristic species seems to indicate a certain regularity (Table 3): after 4 months and 1 year since disturbance, there are 5 and 7 characteristic species respectively associated to eroded sectors of the slopes (E). In more advanced stages, characteristic species belonging to these zones are not so abundant or are absent (2 and 0 after 4 and 9 years respectively). Fire appears to favour these species and they all disappear during the course of succession with the invasion of plants that promote edaphic stability in the advanced successional stages (Levassor *et al.* 1981, Sastre *et al.* 1982).

Separate correspondence analysis was performed for each slope (Figure 3). This reduced the noise that the simultaneous analysis of all the data could have produced in the first ordination analysis showed in Figure 1. The results indicate a clear floristic gradient along the slopes in the established "pajonales" and also in the preceding stages (Figure 3, 9 years and 4 years respectively). The community structures along the slopes do not appear to be much affected by fire disturbance, in contrast to the effect of severe disturbances elsewhere in similar ecosystems.

Table 4 shows the spatial niche width of the species along the slopes. The average value of the parameter $H(P/E_j)$ measured on each slope for each species at each successional stage is used. These values do not indicate a clear successional sequence in average niche width (0.72, 0.78, 0.77, 0.74). Nevertheless, the species with low width tend to be more abundant with succession (34, 34, 35, 48). Their relation with those of wide distribution along the slopes also seem to increase (0.93, 1.00, 1.20, 1.68). However, this is not very notable between the beginning and the end of succession, perhaps because after fire, the pastures still retain

a structure similar to the one prior to burning. This structure seems to be lost after the first year and recovers with time (Dell *et al.* 1986, Casado 1987).

The regularities pointed out in the individual behaviour of some species are also shown in Table 5. The progression in the recovery of the "pajonal" is clear: *Festuca hieronymi*, *Bromus unioloides*, *Paspalum plicatulum*, *Cologania ovalifolia* and *Dichondra microcalyx* change from a restricted spatial distribution

at the start of succession to a widespread distribution across the whole slope in the more mature stage. Other species, such as *Evolvulus sericeus*, *Stenandrium dulce* or *Chaptalia integerrima*, clearly behave like colonizers, being distributed across a whole recently burned slope and then later disappear. The majority of the species such as *Ambrosia tenuifolia*, *Stipa filiculmis*, *Relbunium richardianum*, *Schizachyrium imberbe*, stay in the pasture permanently. Others such as *Andropogon ternatus*,

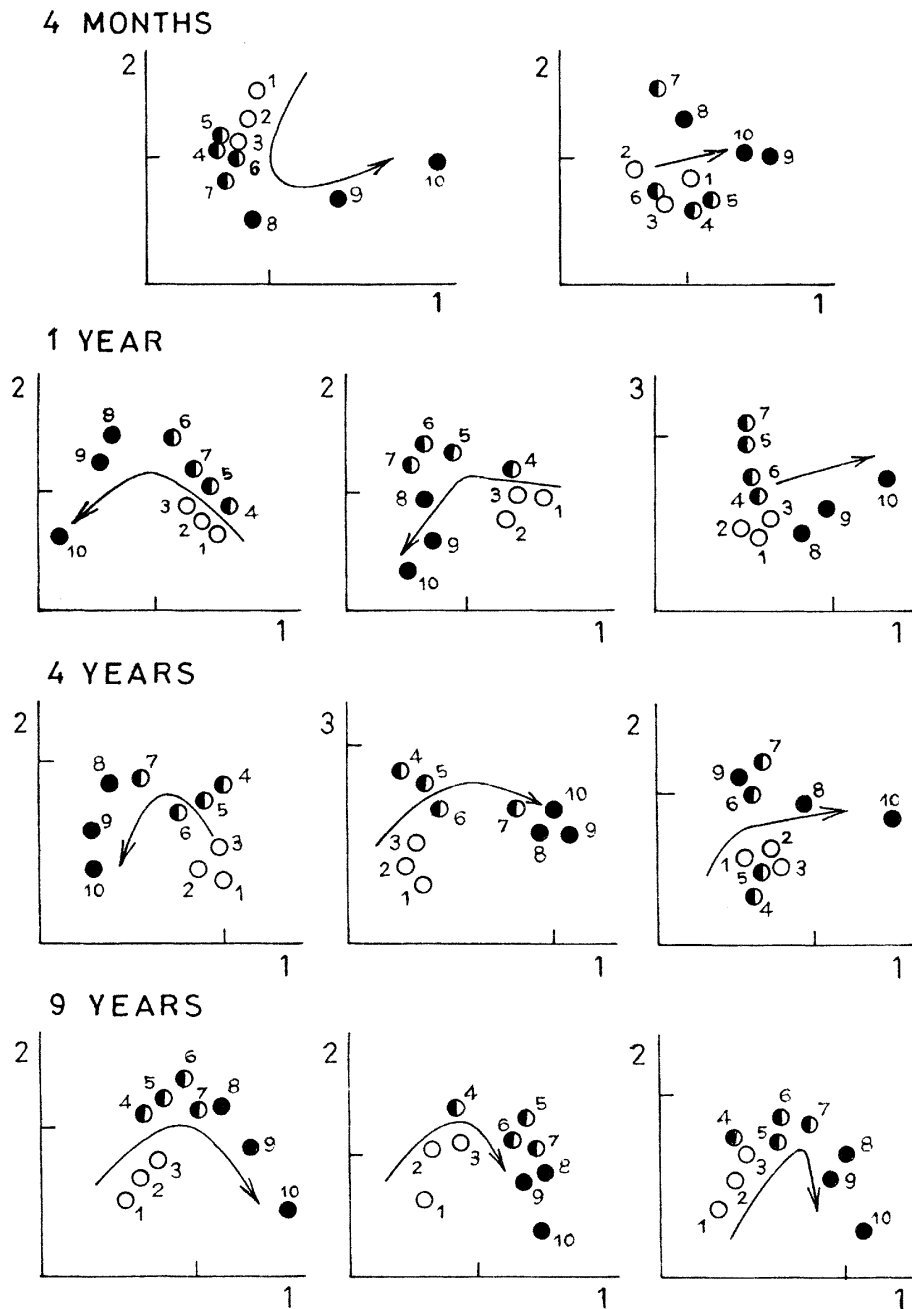


Figure 2. Variation in mean frequencies (ordinate) of some characteristic species of each successional stage (abscissae).

Poa ligularis and *Aster squamatum* colonize specific parts of the slopes and then immediately disappear.

The spatial distribution of many species, typically *Melica stuckertii*, *Stipa neesiana*, *Commelina virginica*, *Taraxacum officinale* and *Eleusine tristachya*, seem not to be affected by fire. These species remain on certain segments of the slopes and maintain this type of distribution throughout succession.

Fire seems to favour the spread of some species across the slopes. This is the case, for example, in *Alternanthera pumila*, *Aristida spegazzini*, *Borreria eryngioides*, *Stipa tenuissima* and *Glandularia peruviana*. During succession, however, these species tend to specialize, occupying restricted zones along the slopes and maintain this new spatial distribution during maturity.

Finally, Table 4 includes the number of species palatable to cattle in each successional stage. Palatability is estimated according to field observations that were contrasted with the knowledge of local graziers. Although the number of species is slightly higher in the mature stages, their successional evolution is not clearcut. Based on these considerations, traditional burning seems more justified by the initial

Table 4. Total number of species and average niche width at four successional stages. The average niche width was measured using the parameter $H(P/E)$ (Pielou 1977, Pineda et al. 1981b). For individual species niche width and spatial behavior, see Table 5.

	Time since pasture burning			
	4 months	1 year	4 years	9 years
Number of species, Nt	103	108	93	120
Average niche width, $H(P/E)$	.72	.78	.77	.74
	g l	g l	g l	g l
Number of species with high (g) and low (l) width	26 34	34 34	30 35	29 48
Relation l/g	.93	1.00	1.20	1.68
Relation l/Nt	.56	.50	.60	.62
Number of species consumed by cattle, c	32	30	27	35
Relation c/Nt	.31	.27	.29	.29

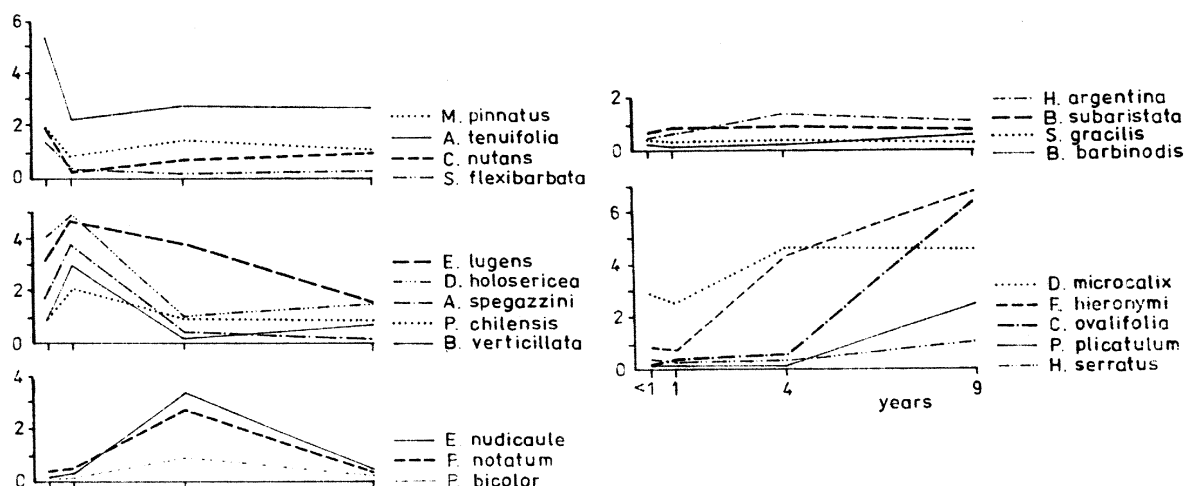


Figure 3. Separate correspondence analyses for data from each of the 11 slopes. The shading of the symbols refers to the geomorphological position of the plots from the upper (open symbols) to the lower (solid symbols) zones of the slopes. The half solid symbols indicate intermediate zones.

4 months			1 year			4 years			9 years						
g		l	g		l	g		l	g		l				
<u>AMT</u>	2.9	<u>ADC</u> * 0.0	<u>ACC</u> * 3.2	<u>ACT</u>	0.0	<u>ALP</u>	2.5	<u>ADC</u>	1.0	<u>ACC</u>	2.5	<u>ALP</u>	0.9		
<u>ALP</u> *	2.9	<u>ANT</u> * 1.0	<u>ADC</u> * 3.1	<u>ARP</u> *	0.0	<u>AMT</u>	2.5	<u>AMC</u>	0.0	<u>AMT</u>	2.9	<u>ANI</u>	0.0		
<u>ARS</u> *	2.6	<u>ASQ</u> * 0.0	<u>ALP</u>	2.6	<u>APS</u>	1.0	<u>ARS</u> *	2.5	<u>APS</u>	1.0	<u>BOC</u> *	2.5	<u>ADC</u> *	0.6	
<u>BOE</u> *	2.6	<u>BAR</u>	1.0	<u>AMT</u>	3.0	<u>BAA</u> * 0.0	<u>BOE</u>	2.6	<u>ARP</u> *	0.0	<u>BRS</u> *	2.6	<u>ASC</u>	0.0	
<u>BOV</u>	2.6	<u>BOL</u> * 1.0	<u>ARS</u> *	3.0	<u>BAR</u>	0.0	<u>BOL</u> *	2.6	<u>BAA</u>	0.0	<u>BRU</u> *	3.3	<u>ARS</u> *	0.9	
<u>BUJ</u> *	2.7	<u>BRU</u> * 0.0	<u>BOE</u>	3.2	<u>BOC</u> * 0.7	<u>BRS</u> *	2.7	<u>BAC</u>	0.0	<u>COQ</u>	2.6	<u>BAA</u> *	0.0		
<u>CHR</u> *	3.2	<u>CAR</u>	0.0	<u>BOV</u>	3.0	<u>BOM</u>	1.0	<u>CAS</u> *	3.0	<u>BRP</u> *	0.0	<u>CUG</u>	3.0	<u>BOE</u>	1.0
<u>CUG</u>	3.1	<u>COV</u>	0.0	<u>BRS</u> *	2.8	<u>COQ</u>	0.0	<u>COB</u> *	2.5	<u>BUJ</u> *	0.0	<u>CHS</u>	2.7	<u>BRP</u> *	0.0
<u>CYH</u> *	2.9	<u>CYD</u> * 0.0	<u>BUJ</u> *	2.9	<u>CUG</u>	0.9	<u>CUG</u>	2.6	<u>COV</u>	0.9	<u>CHR</u> *	3.3	<u>BUJ</u> *	0.9	
<u>ERL</u> *	2.8	<u>CRP</u>	0.0	<u>COV</u>	2.5	<u>CYD</u>	0.9	<u>CHS</u>	3.2	<u>CYH</u> * 0.2	<u>DIM</u>	3.3	<u>COV</u>	1.0	
<u>EUS</u>	3.0	<u>DAP</u>	0.0	<u>CHI</u>	2.5	<u>DIA</u> * 0.0	<u>CHR</u> *	3.1	<u>DIA</u> * 0.9	<u>DIH</u>	3.2	<u>CYH</u> *	0.0		
<u>EVS</u>	2.5	<u>DIM</u> * 0.0	<u>CHR</u> *	3.2	<u>EVA</u>	0.0	<u>DIM</u> *	3.2	<u>ELT</u> * 0.0	<u>ERP</u> *	2.8	<u>CAS</u> *	0.7		
<u>GLP</u>	3.2	<u>DIC</u> *	0.0	<u>DIM</u> *	2.6	<u>ERP</u> *	1.0	<u>ERL</u> *	3.0	<u>EUP</u>	0.0	<u>EUS</u>	3.0	<u>COB</u>	0.6
<u>GAM</u>	2.9	<u>ELT</u> * 0.0	<u>DIH</u>	3.2	<u>GAA</u> * 0.0	<u>ERN</u>	3.2	<u>GAE</u>	0.0	<u>FEH</u> *	2.7	<u>CHH</u> *	0.8		
<u>OXS</u> *	2.9	<u>ERH</u>	0.0	<u>ERL</u> *	3.2	<u>GDE</u>	0.0	<u>EUS</u>	3.1	<u>GAS</u>	0.0	<u>HYA</u> *	3.1	<u>DIA</u> *	0.9
<u>PIM</u> *	2.8	<u>ERN</u>	1.0	<u>ERN</u>	3.0	<u>GLD</u>	0.8	<u>EVA</u>	2.7	<u>GLD</u>	0.0	<u>OXS</u> *	2.9	<u>ERH</u>	0.0
<u>SEG</u>	3.1	<u>EUP</u>	0.9	<u>EUS</u>	3.2	<u>GNG</u>	1.0	<u>FEH</u> *	3.1	<u>GNG</u>	0.0	<u>PAL</u> *	2.7	<u>ERN</u>	0.0
<u>SIP</u>	2.7	<u>FAR</u>	0.0	<u>MAP</u>	2.5	<u>HYA</u> * 1.0	<u>GAM</u>	3.2	<u>GOP</u>	0.0	<u>PAP</u> *	2.6	<u>EVA</u>	1.0	
<u>STF</u> *	3.1	<u>FEH</u> * 0.9	<u>MIM</u>	2.6	<u>HYP</u> * 0.0	<u>GLP</u>	2.8	<u>LEB</u>	0.0	<u>PFG</u>	2.7	<u>GAA</u>	0.0		
<u>STX</u> *	2.7	<u>GAE</u>	0.0	<u>OEI</u>	2.8	<u>NIA</u>	0.0	<u>OEI</u>	3.3	<u>LUA</u>	1.0	<u>PIM</u> *	3.0	<u>GLP</u>	1.0
<u>STH</u> *	2.6	<u>HYS</u>	0.6	<u>OXS</u> *	3.1	<u>NOM</u>	0.0	<u>PAC</u>	2.8	<u>MES</u> * 0.0	<u>RHS</u> *	2.9	<u>HOS</u> *	0.8	
<u>STR</u>	2.9	<u>JUD</u> *	0.8	<u>PAC</u>	3.1	<u>PAU</u> * 0.0	<u>PAN</u> *	3.1	<u>NOM</u>	0.9	<u>RER</u>	3.1	<u>HYM</u>	0.7	
<u>STG</u>	2.5	<u>LEB</u>	0.0	<u>PIM</u> *	3.2	<u>PID</u> *	0.9	<u>PIM</u> *	3.0	<u>OXA</u>	0.0	<u>SCI</u> *	2.8	<u>LEM</u>	0.9
<u>SCI</u> *	3.0	<u>LUA</u>	0.9	<u>RER</u>	2.6	<u>PIB</u> * 0.0	<u>SCI</u> *	2.9	<u>PAH</u>	0.0	<u>SCS</u> *	3.2	<u>LUA</u>	0.8	
<u>SCS</u> *	2.7	<u>MES</u> * 0.0	<u>RHS</u>	2.6	<u>PIS</u> * 0.0	<u>SEC</u>	2.7	<u>PAU</u> * 0.0	<u>SEG</u> *	3.2	<u>MIM</u>	0.0			
<u>SCP</u>	2.5	<u>OEI</u>	0.9	<u>SEG</u> *	2.9	<u>RHM</u>	0.0	<u>SIC</u>	3.1	<u>PFG</u>	0.8	<u>SIP</u>	3.2	<u>NOM</u>	1.0
		<u>PAD</u> * 0.9	<u>SIP</u>	3.0	<u>SEC</u>	0.0	<u>SOI</u>	3.2	<u>PIB</u> * 0.9	<u>SIA</u>	2.3	<u>OXC</u>	0.0		
		<u>PAP</u> * 0.9	<u>SPI</u> *	2.6	<u>SPR</u>	0.0	<u>STF</u> *	2.9	<u>RHM</u>	0.9	<u>STF</u> *	2.9	<u>PAC</u>	0.8	
		<u>PIS</u> * 0.0	<u>STF</u> *	3.0	<u>SOP</u> * 1.0	<u>STU</u> *	3.0	<u>SIC</u> *	1.0	<u>TAF</u>	3.2	<u>PAH</u>	0.9		
		<u>POL</u> * 0.8	<u>STH</u> *	2.9	<u>STS</u>	1.0			<u>SPD</u> *	1.0			<u>PAN</u> *	0.0	
		<u>SOP</u> * 0.0	<u>SCP</u>	3.2	<u>STX</u> * 1.0				<u>SCP</u>	0.9			<u>PHV</u>	0.8	
		<u>STN</u> * 0.9	<u>SCS</u> *	3.2	<u>STP</u> * 0.0				<u>SPI</u>	0.0			<u>PIO</u> *	0.0	
		<u>TAO</u> * 0.0	<u>SPD</u>	3.2	<u>STA</u>	1.0			<u>STA</u> * 0.0				<u>POM</u>	0.0	
			<u>STR</u>	2.8	<u>ZEL</u>	0.0			<u>TAO</u> * 0.0				<u>SEP</u>	0.0	
									<u>WAL</u>	0.0			<u>SCP</u>	0.0	
													<u>SCM</u> *	0.0	
													<u>SIC</u> *	1.0	
													<u>SPD</u>	0.0	
													<u>SPP</u> *	0.0	
													<u>STA</u> *	0.8	
													<u>STU</u> *	0.9	
													<u>STG</u>	0.0	
													<u>TAM</u>	0.9	
													<u>TAO</u>	0.0	
													<u>TUS</u>	0.0	
													<u>VEM</u>	0.0	
													<u>VEI</u>	1.0	
													<u>VIS</u>	0.0	

productivity and palatability increase and by the elimination of tall grasses that impede grazing, than by an increase in the richness of consumed species. The analysis of pasture nutrient quality seems to justify this practice (Alessandria and Casermeiro 1986). Erosion and the disappearance of native species in natural pastures as a result of fire, on the other hand, signal the need for careful conservation management of this resource (Herrera *et al.* 1978, Luti *et al.* 1979).

Conclusion

Regular burning of pastures is a traditional activity which changes the floristic composition and spatial distribution of species. It also causes marked variability in the ecosystem. Dynamic criteria and other nonbiotic factors should thus be included in the typology of the pastures in mountainous regions (Menghi *et al.* 1989). The successional sequence after burning is relatively clear with respect to the variation of characteristic species abundance, many of which undergo changes in their spatial distribution along the slopes. Average spatial niche width does not show a clear trend with succession, but the number of species with low niche width tend to be more abundant in mature stages, particularly in those associated with the *Festuca hieronymi* "pajonales" which are specially affected by fire.

The general community structure of the Córdoba montane pastures is not severely disturbed by fire. During succession, there is always close correspondence between the biocenotic variability on the one hand, and erosion, material transit and material accumulation along the slope on the other. This contrasts with the results obtained for work with Mediterranean pastures which we already quoted. Nevertheless, the most abundant characteristic species in post-fire stages belong to the eroded upper zones on the slopes, excepting the mature pastures. Fires only superficially affect edaphic erosion processes.

Acknowledgements. The authors wish to thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the Consejo de Investigaciones de la Provincia de Córdoba (CONICOR) and the Instituto de Cooperación Iberoamericana and the Dirección General del Medio Ambiente in Spain for their assistance and support in this project. We are also very much indebted to Prof. D. Abal Solís who elaborated the illustrations.

REFERENCES

- Acosta, A. 1988. Estructura y variabilidad de pastizales de las Sierras de Córdoba en un gradiente altitudinal. Tesis Doctoral, Universidad Nacional de Córdoba. Córdoba, Argentina.
- Alessandria, E. and J. Casermeiro. 1986. Fenología de las especies de gramíneas de la estepa serrana. In: UNESCO/PNUMA/CERNAR (eds.). *Proyecto Regional Andino Pachón-Achala*, pp. 227-239. Montevideo, Uruguay.
- Benzecri, J. P. 1973. *L'analyse des données*, Vol. 2. Dunod, Paris.
- Burkart, A. 1974. *Flora Ilustrada de Entre Ríos, Vol. VI: Dicotiledóneas Metaclamídeas (Gamopétalas)*. Colección Científica del INTA, Buenos Aires, Argentina.
- Burkart, A. 1979. *Flora Ilustrada de Entre Ríos, Vol. V: Dicotiledóneas Metaclamídeas. Generalidades (Gamopétalas)*. Colección Científica del INTA, Buenos Aires, Argentina.
- Cabido, M. 1985. Las comunidades vegetales de la Pampa de Achala, Córdoba, Argentina. *Doc. Phytosociologiques* 9: 431-443.
- Cabido, M. 1987. Las comunidades vegetales del Subpiso Superior de Pastizales de las Sierras de Córdoba. Tesis Doctoral, Universidad Nacional de Córdoba. Córdoba, Argentina.
- Cabido, M. y A. Acosta. 1985. Estudios fitosociológicos en bosques de *Polylepis australis* BITT. en las Sierras de Córdoba, Argentina. *Doc. Phytosociologiques* 9: 385-400.
- Cabido, M., R. Breimer and G. Vega. 1986. Plant communities and associated soil types in a high plateau of the Córdoba Mountains, Central Argentina. *Mountain Research and Development* 6: 331-343.
- Cabrera, A. L. 1963. *Flora de la Provincia de Buenos Aires, Vol. VI: Compuestas*. Colección Científica del INTA, Buenos Aires, Argentina.
- Cabrera, A. L. 1965a. *Flora de la Provincia de Buenos Aires, Vol. IV: Oxalidáceas a Umbelíferas*. Colección Científica del INTA, Buenos Aires, Argentina.
- Cabrera, A. L. 1965b. *Flora de la Provincia de Buenos Aires, Vol. V: Ericáceas a Caliceráceas*. Colección Científica del INTA, Buenos Aires, Argentina.
- Cabrera, A. L. 1967. *Flora de la Provincia de Buenos Aires, Vol. III: Piperáceas a Leguminosas*. Colección Científica del INTA, Buenos Aires, Argentina.
- Cabrera, A. L. 1968. *Flora de la Provincia de Buenos Aires, Vol. I: Pteridófitas, Gimnospermas y Monocotiledóneas (excepto Gramíneas)*. Colección Científica del INTA, Buenos Aires, Argentina.
- Cabrera, A. L. 1970. *Flora de la Provincia de Buenos Aires, Vol. II: Gramíneas*. Colección Científica del INTA, Buenos Aires, Argentina.
- Casado, M. A. 1987. Organización espacial y temporal de pastos mediterráneos en respuesta a perturbaciones mecánicas e incendios. Tesis Doctoral, Universidad Autónoma de Madrid. Madrid, España.
- Castro, I., A. Sterling and E. F. Galiano. 1986. Multi-species pattern analysis of Mediterranean pastures in three stages of ecological succession. *Vegetatio* 68: 37-42.
- Correa, M. 1984a. *Flora Patagónica, Vol. IVa: Dicotiledóneas dialipétalas (Salicáceas a Crucíferas)*. Colección Científica del INTA, Buenos Aires, Argentina.
- Correa, M. 1984b. *Flora Patagónica, Vol. IVb: Dicotiledóneas dialipétalas (Croséráceas a Leguminosas)*. Colección Científica del INTA, Buenos Aires, Argentina.
- Dell, B., A. J. Hopkins and B. B. Lamont (eds.). 1986. *Resilience in mediterranean-type ecosystems*. Junk, Dordrecht.
- De Pablo, C. T., B. Peco, E. F. Galiano and F. D. Pineda. 1982. Space-time variability in mediterranean pastures analyzed with diversity parameters. *Vegetatio* 50: 113-125.
- Galera, F. M. 1986. Pastizales de altura, Subpiso Inferior: El Cuadrado. In: UNESCO/PNUMA/CERNAR (eds.). *Proyecto Regional Andino Pachón-Achala*, pp. 154-156. Montevideo, Uruguay.

- Galiano, E. F., I. Castro and A. Sterling. 1987. A test for spatial pattern in vegetation using Monte-Carlo simulation. *J. of Ecology* 75: 915-924.
- García Novo, F., F. G. Bernaldez and A. GIL. 1969. Essais d'analyse automatique de la végétation et des facteurs du milieu. V Symp. Flora Europaea, pp. 91-115. Sevilla, España.
- Herrera, M. A., A. Bertran, F. M. Galera, R. Luti y M. Menghi. 1978. Incendio y pastoreo en estepas de altura de las Sierras Chicas de Córdoba. *Ecología (Argentina)* 3: 95-100.
- Levassor, C., F. D. Pineda y F. G. Bernaldez. 1981. Tipología de pastizales en relación con el relieve: la Sierra del Castillo (Madrid). *Pastos* 11: 45-68.
- Luti, R., A. Solis, F. M. Galera, N. Ferreira, M. Nores, and J. C. Barrera. 1979. Vegetación. In: Vázquez, J.B., R.A. Miatello and M.E. Rouquéw (eds.). *Geografía Física de la provincia de Córdoba*, pp. 297-368. Boldt, Buenos Aires.
- Menghi, M. 1981. Productividad primaria neta de algunas comunidades de pastizal de altura de las Sierras de Córdoba, Argentina. *Bol. Soc. Venezolana Cs. Naturales* 35: 413-418.
- Menghi, M. 1987. Tipificación ecológica integrada de pastizales naturales del Subpiso Inferior de las Sierras de Córdoba, Argentina. Tesis Doctoral, Universidad Nacional de Córdoba. Córdoba, Argentina.
- Menghi, M., A. Bertran, F. M. Galera and R. Luti. 1978a. Productividad primaria y competencia de una comunidad de pastizales y arbustos de las Sierras Chicas, Córdoba. *Ecología (Argentina)* 3: 89-94.
- Menghi, M., A. Bertran, F. M. Galera, M. Herrera and R. Luti. 1978b. Productividad primaria de los pastizales de altura de las Sierras Chicas, Córdoba. *Ecología (Argentina)* 3: 101-110.
- Menghi, M., M. Cabido, B. Peco and F. D. Pineda. 1989. Grassland heterogeneity in relation to lithology and geomorphology in the Córdoba Mountains, Argentina. *Vegetatio* 84: 133-142.
- Menghi, M. and R. Luti. 1982. Mapa fisonómico de la vegetación de la cuenca de alimentación del embalse de Río Tercero. *Ecología (Argentina)* 7: 185-194.
- Mooney, H. A. and M. Godron (eds.). 1983. *Disturbance and Ecosystems. Components of Response*. Springer-Berlag, Berlin.
- Peco, B. and F. D. Pineda. 1987. Resposta de les pastures oligotrófiques a perturbacions i canvis meteorològics. In: Teradas, J. (ed.). *Ecosistemes Terrestres. La resposta als incendis i a d'altres perturbacions*, pp. 189-201. Quaderns d'ecologia aplicada, Diputació de Barcelona. Barcelona.
- Pielou, E. C. 1977. *Mathematical Ecology*. Wiley, New York.
- Pineda, F. D., C. T. De Pablo, M. A. Casado and J. M. De Miguel. 1988. Ecological structures recognized by means of entropy analysis: Assessment of differences between entropy values. *J. Theor. Biol.* 135: 283-293.
- Pineda, F. D., J. P. Nicolas, B. Peco and F. G. Bernaldez. 1981. Succession, diversité et amplitude de niche dans les paturages du centre de la péninsule ibérique. *Adv. Veg. Sci.* 4: 267-278.
- Pineda, F. D., J. P. Nicolas, A. Pou and E. F. Galiano. 1981. Ecological succession in oligotrophic pastures of central Spain. *Vegetatio* 44: 165-176.
- Pineda, F. D. and B. Peco. 1988. Pastizales adheridos del Area de El Pardo (Madrid). *Mundo Científico (La Recherche)* 79: 386-395.
- Poissonet, P., F. Romane, M. P. Austin, E. van der Maarel and W. Schmidt. (eds.). 1981. *Vegetation dynamics in grasslands, heathlands and mediterranean formations*. Junk, The Hague.
- Pomeroy, L. R. and J. J. Alberts (eds.). 1988. *Concepts of Ecosystem Ecology. A Comparative View*. Springer-Verlag, Berlin.
- Prentice, I. C. and E. van der Maarel (eds.). 1987. *Theory and models in vegetation science*. *Vegetatio* 69 (Special issue).
- Solntsev, V. N. 1974. O niekotorykh fundamentalnykh svoystvakh gheosistemnoi strukturi. In: Akademiya Nauk SSSR: *Metody kompleksnykh issledovaniy gheosistem*. Irkutsk.
- Sterling, A., B. Peco, M. A. Casado and F. D. Pineda. 1983. Influence of microtopography on floristic variation in the ecological succession in grassland. *Oikos* 42: 334-342.
- Vázquez, J. B., R. A. Miatello and M. E. Roque (eds.). 1979. *Geografía Física de la provincia de Córdoba*. Boldt, Buenos Aires.
- Whittaker, R. H. 1974. Climax concepts and recognition. In: Knapp, R. (ed.). *Vegetation Dynamics. Handbook of Vegetation Science*, Vol. 8, pp. 137-154. Junk, The Hague.

Manuscript received: April 1992