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DISTRIBUTION OF PLANT COMMUNITIES IN THE BADLANDS OF THE UPPER LLOBREGAT BASIN (SOUTHEASTERN PYRENEES)

Roser GUARDIA & Josep M. NINOT

Keywords: Badlands, Erosion, Submediterranean vegetation, Vegetation dynamics.

Abstract: The plant communities of the badlands of a pre-Pyrenean area were studied by means of a geomorphological selection of the eroded areas and 71 phytocoenological relevés with topographic data. The relevés were subdivided into two groups, according to the two kinds of substratum (Eocene marls and Upper Cretaceous clays), and then submitted to Correspondence Analysis. According to these analyses and to abiotic parameters, nine vegetation types can be distinguished. Each community is characterized by ecological groups of species and by different life-forms spectra. The comparison among such communities, as well as with those of the non-eroded areas, allows to discuss their dynamic relationships in relation with erosion processes. As a general rule, erosive dynamics involves a regressive succesion from the previous community (normally a meso-xerophilous pasture) through the opening of gaps and the loss of mainly mesophilous species. Thus, the badland communities on each substratum are dynamically connected, most stands having medium- to very low coverages and diversity, the topographic position and the related erosive processes being the most influential factors on their distribution.

Introduction

In the Upper Llobregat basin badlands are widespread and, although they occupy only small areas, they are the main fluvial sediment source in the basin (Clotet & al. 1988). Geomorphological studies were carried out in the area mainly concerning erosion rates (Clotet & Gallart 1986), but no attempts were made to study plant communities of these badlands. Vegetation is a regulating factor of erosive processes as it protects the soil against the action of falling raindrops, reduces the speed of the surface runoff, increases the degree of infiltration (Cervera & al. 1991) and binds the soil mechanically (Zachar 1982).

The aim of the present study was to describe the plant communities in the badlands of the Upper Llobregat basin, in order to establish a model on the relationships between plant communities and abiotic parameters. The dynamic connection among plant communities, as well as between such communities and those of the non-eroded slopes, is directly related with the general dynamics of the badlands. This knowledge will be the basis for studying the quantitative dimension of the reduction of erosion by vegetation and, on the other hand, it provides useful information for the attempts of rehabilitation of the badlands or

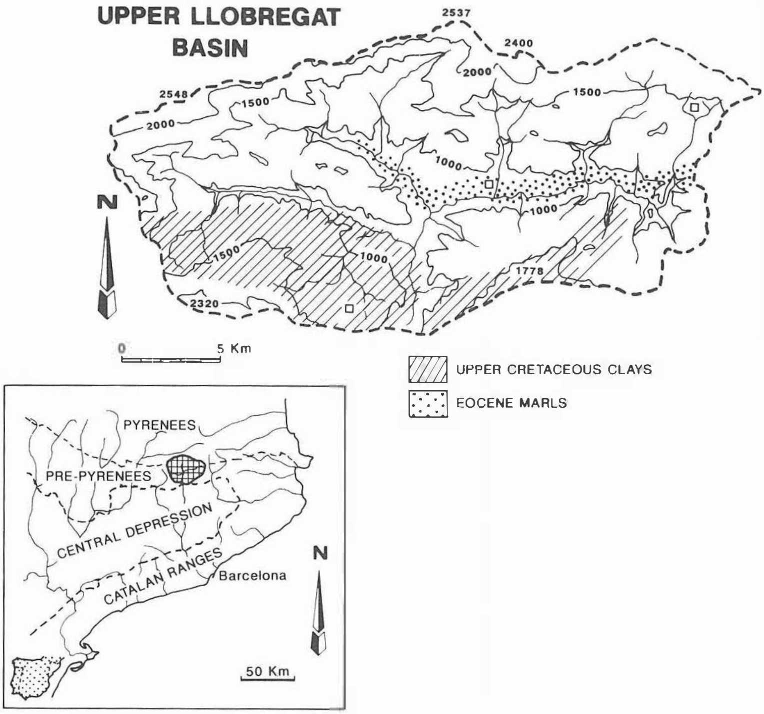


Fig. 1 - Location of the study area.

other bare areas.

Study Area

The study area is located in the Upper Llobregat basin, southeastern Pyrenees, Catalonia (Fig. 1). Most of the geological material is carbonated and is mainly part of the Pedraforca mantle Unit and the Cadí Unit. The elevation of the badlands ranges from 790 to 1320 m; they occur on all exposures, but are most common on north-facing slopes. The eroded patches develop mainly on two substrata: Eocene marls and upper Cretaceous clays.

The badland topography in the Eocene consists of marls interspersed with beds of more resistant rocks, mainly sandstones and calcarenites. Generally, the drainage network is less dense on marl than on clay, this fact being mainly related to lithologic characteristics. A main channel usually develops in the soft marls, the lateral outcrops of hardrock beds preventing branching of the drainage network. Thus, the slopes are long and steep with wide thalwegs holding deposits of debris, chiefly in their basal part (Fig. 2).

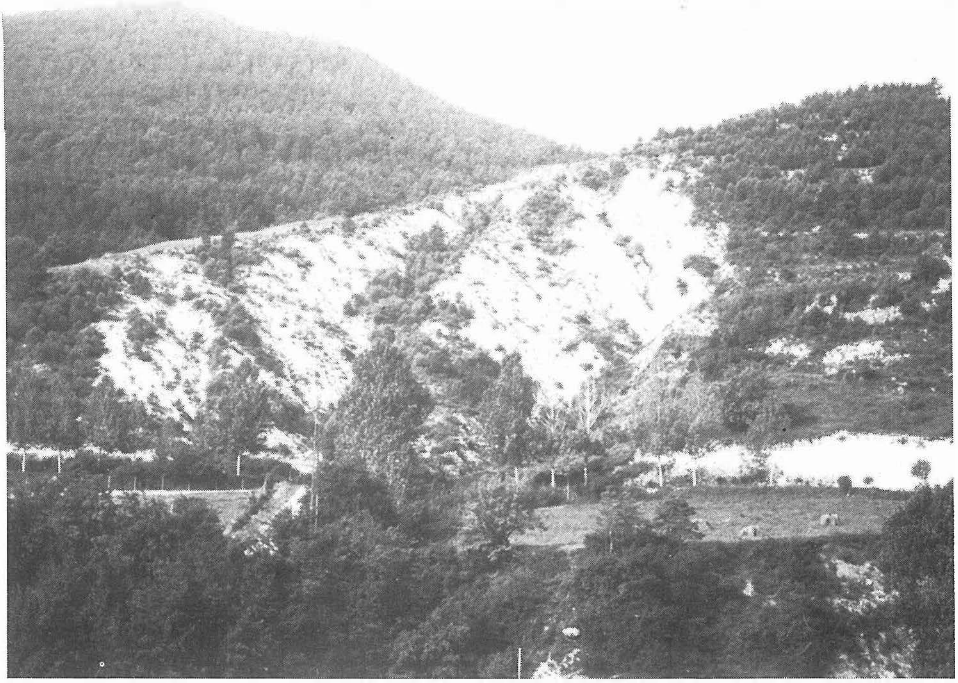


Fig. 2 - General view of badlands in Eocene marls.

The Cretaceous formation mainly consists of lacustrine clays. Badland topography is here more densely and deeply dissected than in Eocene marls. The slopes are short and steep and the thalwegs are quite narrow.

The climate is submediterranean-like with some continental features (Martín Vide & al. 1989). The annual average rainfall is 850 mm at lower altitudes and about 1100 mm at upper elevations, with two dry periods in January-February and July, the latter being very restrictive for plant activity. The average annual temperature is 11.4°C at 1000 m, with 17°C of amplitude among monthly averages.

The landscape of the area consists mainly of *Pinus sylvestris* forests and pastures, both of which ranging from xerophilous types at lower altitudes to meso-higrophilous in the moistest zones (Soriano 1984). Most of the *Pinus sylvestris* forests hold well-developed shrubby and herbaceous layers, with plenty of calcicolous and meso-xerophilous species (formerly *Buxus sempervirens*), and belong to the *Buxo-Quercetum pubescentis*. These submediterranean pine forests develop at almost all exposures and altitudes, with some secondary differences concerning composition, density of the different layers, etc. Only on the upper north-facing slopes there occur some moss-rich *Pinus sylvestris* forests (*Polygalo-Pinetum sylvestris*), adapted to colder and moister climates and related to the *Pinetalia sylvestris* alpine communities. The more extended pastures are those of the *Aphyllanthion*; these are calcicolous communities resistant to dry summers, especially those of the *Brachypodio-Aphyllanthetum*, inhabiting south-facing areas and chiefly formed by low shrubs and xerophylous grasses; the *Seslerio-Aphyllanthetum*, with meso-xerophilous to mesophilous plants, occurs on north-facing slopes. Mesophilous pastures (*Euphrasio-Plantaginetum mediae, Mesobromion erecti*) develop only on deep soils, normally on flat or gentle spots. Intermediate communities between pasture and forest are very frequent, consisting of an open layer of *Pinus sylvestris* and any of the mentioned pastures as herbaceous layer.

Methods

After the localization of the badlands with aerial photographs, some of them were selected to give a representative sample based on obvious environmental differences: substratum, exposure, altitude, size of the badland area and vegetation of the neighbouring slopes. Several plots were subjectively chosen in each badland zone according to their landform components: upper part of slope, backslope, footslope and main channel (thalweg; see figure 9).

The vegetation samples taken in each plot consist of phytocoenological inventories or relevés (Braun-Blanquet 1979). Nomenclature follows Flora Europaea (Tutin 1964-1980). Topographic data were also recorded, concerning elevation, exposure, slope angle and position in the slope. Moreover, some representative relevés of the neighbouring non-eroded areas were taken in order to allow a comparison between the communities of the normal sites and those of the badlands.

The 71 relevés were distributed into two tables according to the substratum (upper Cretaceous clays or Eocene marls), as this factor would have obscured the topographic factors. Each table was submitted to Correspondence Analysis (CA; Benzecri 1973), in order to obtain relevé groups. For each group formed by CA, frequency and average cover of each species were calculated. Some difficulties were encountered in associating the groups of relevés formed through CA with associations or higher phytocoenological syntaxa. However, each group of relevés can be characterized by some groups of species with a particular ecological significance, these species groups being related to phytocoenological alliances or to ecological groups with a broader meaning. The following species groups have been used in the typification of the relevés:
- plants of the submediterranean meso-xerophilous pastures (most of which are related to *Aphyllanthion*),
- plants of the centroeuropean mesophilous pastures (mainly related to *Mesobromion*),
- thermophilous plants (Mediterranean plants limited, in the study area, to

sunny and warm slopes),
- plants of humid and clayish soils.

Moreover, the biological spectra for each relevé group has been obtained, with the following life-forms: graminoid hemicryptophytes, non-graminoid hemicryptophytes, chamaephytes, phanerophytes, therophytes, geophytes.

Results

Eocene marls

Figure 3 shows the results of CA for the relevés of the marls arranged on the first two axes, which account for 23.95 % of the total variance. The points (relevés) tend to form four groups. Table 1 shows the frequency and the cover percentage of the species in each group. The inclination and exposure of each group of relevés are represented in Figure 4. Figure 5 displays the percentage cover of the species classified according to ecological significance and life-form. Specific percentage compositions are based on species cover as a percentage of the total vegetation cover for each community.

The relevé groups represent a sequence from the supposed vegetation preceding the erosive processes (a pasture belonging to the *Aphyllanthion* like those normally occurring above the badland, further up the slope) to the almost bare surfaces of the backslopes (Fig. 9). Thus, in the upper part of the badlands, where the erosive processes are relatively recent, a gradual transition between the pastures neighbouring the badland and the most eroded areas can be observed. These upper parts are the result of degradation of the initial pasture, through the loss of species and the opening of gaps among the remaining plants. Two different communities (groups I and II) can be distinguished in this upper slope position, the former mainly with south-facing exposures and the latter with north-facing aspects. Group III corresponds to backslopes, with a very degraded and poor vegetation. The remaining group (IV) includes the communities developing in the thalwegs.

Globularia vulgaris and *Aphyllanthes monspeliensis* community (I)

This community is closely related to the *Brachypodio-Aphyllanthetum*, with a rather diverse cover, although the average is somewhat high (48%). There chamaephytes clearly prevail (52.3% of the cover), most of them being thermophilous (*Thymus vulgaris*, *Lithodora fruticosa*, *Coris monspeliensis*, etc.). Among the herbaceous component, graminoid plants are the most abundant, mainly *Aphyllanthes monspeliensis* and *Avenula pratensis* subsp. *iberica*.

Satureja montana and *Sesleria coerulea* community (II)

This occurs on the same relative position of the slope as the preceding

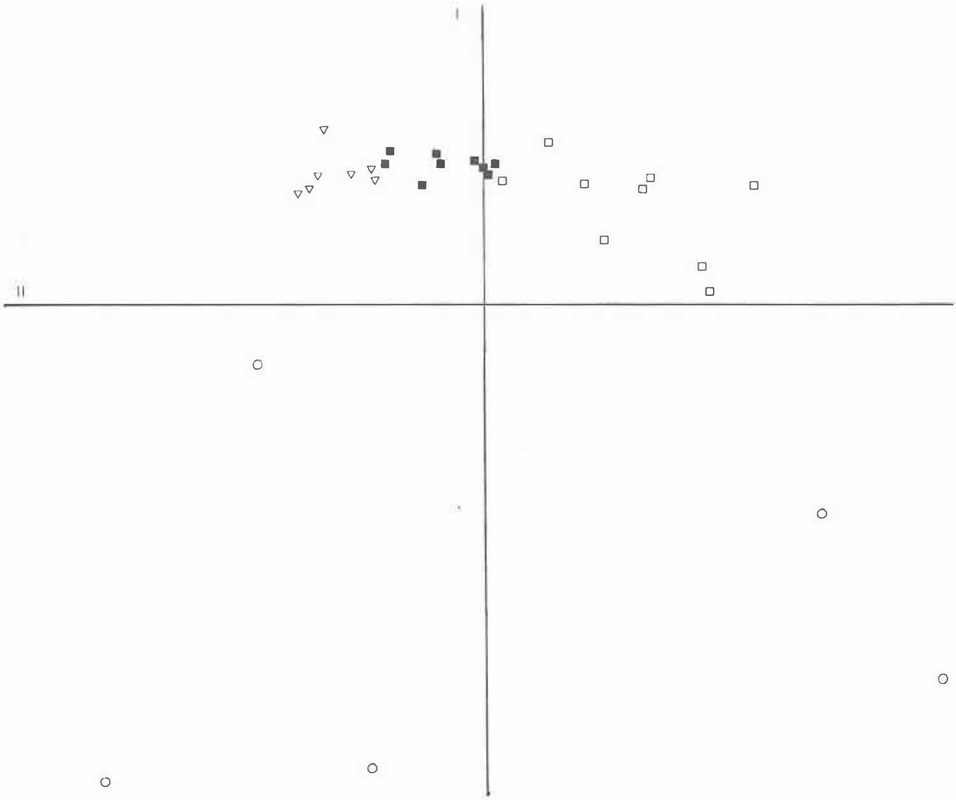


Fig. 3 - Arrangement of relevés from Eocene marls according to the two first axes of CA. Empty square: Group I; triangle: Group II; full square: Group III; circle: Group IV.

community, with similar cover, but the predominant north-facing exposures determine a different plant composition. Grasses are the most important group here, with *Sesleria coerulea* as the main component. There are some species of humid or clay soils (*Molinia coerulea, Plantago serpentina*, etc.) but with low covers. The community is a degraded form of the *Seslerio-Aphyllanthetum*, the most common pasture on the normal north-facing slopes in the area.

Laserpitium gallicum and *Erucastrum nasturtiifolium* community (III)

The most eroded areas in these badlands are the extensive backslopes, occurring mainly on north-facing exposures. The inclination is higher than for the other communities (35-40°). The poorest and most common community develops on such unfavourable place. Its cover is the lowest (26%), as it comes from a short list of plants with low abundances (+ or 1). The biological spectrum shows a similar cover for woody species (phanerophytes and chamaephytes,

Table 1 - Synthesis of the Eocene marls relevés, with the species arranged according to ecological groups. In each column the frequency (% of occurence) and the average cover in the community (CR, coverage rate, in %) for each species is shown.

GROUPS	I		II		III		IV	
Summarized relevés	9		7		9		5	
	%	CR	%	CR	%	CR	%	CR
Plants of the submediterranean pastures								
Anthyllis montana	33	0.03	71	3.25	12	0.01	14	0.01
Aphyllantes monspeliensis	88	4.74	14	0.01	12	0.01	14	0.01
Argyrolobium zanonii	55	0.6	14	0.01				
Asperula cynanchica	22	0.02	71	0.77	62	0.06	71	0.07
Astragalus monspessulanum	44	0.04	14	0.01				
Avenula iberica	77	6.42	42	0.04	62	0.67	42	3.92
Carduncelus monspeliacus	11	0.01	42	0.04			14	0.01
Carex humilis	44	1.13	28	0.02	12	0.01	14	0.01
Catananche caerulea							28	2.51
Coronilla minima	44	0.04	57	2.54			14	0.01
Euphorbia mariolensis	88	0.63	28	0.02	50	0.66	71	0.07
Globularia cordifolia	55	0.6	42	1.44	12	0.01	14	0.01
Globularia vulgaris	77	5.27	14	0.01	12	0.01		
Helianthemum italicum	44	1.13						
Koeleria vallesiana	77	5.03	57	0.75	25	0.63	28	0.02
Lavandula latifolia	100	4.75	28	0.72	37	2.82	42	3.22
Lavandula pyrenaica	11	0.01	71	1.47	25	0.02	14	0.01
Linum salsoloides	88	3.11	100	0.8	87	1.31	57	0.75
Santolina chamaecyparissus	77	1.71	28	0.02	62	0.06	57	0.75
Teucrium aureum	100	2.27	85	4.67	75	1.3	57	0.05
Thesium divaricatum	11	0.01			12	0.01		
Plants of the centroeuropean mesophilous pastures								
Bromus erectus	22	0.56					14	0.71
Euphrasia salisburgensis			28	0.02			14	0.01
Koeleria pyramidata	33	0.57	71	0.07	25	0.63	42	0.74
Onobrychis supina	33	0.57	85	1.48	12	0.01	57	1.45
Sesleria coerulea	33	2.51	85	21.0	50	3.45	42	7.87
Termophilous plants								
Coris monspeliensis	66	0.06						
Dorycnium pentaphylum	66	2.54	14	0.01			28	0.02
Fumana ericoides	33	1.12			12	0.01	14	0.71
Lithodora fruticosa	22	0.56						
Thymus vulgaris	88	4.2	42	0.04	25	0.63	28	1.42

Plants of humid and clayish soils

Carex flacca							57	0.75
Chlora perfoliata							28	0.72
Jasonia tuberosa	11	0.01	71	3.95			42	0.04
Molinia caerulea			71	0.07			42	20.3
Plantago serpentina	22	0.02	71	1.47	25	0.02	14	2.5
Tussilago farfara					25	0.02	14	0.01

Others

Achnatherum calamagrostis	22	0.02	71	5.04	37	5	57	3.94
Amelanchier ovalis	22	0.56	28	0.02	12	0.01	14	0.01
Anthericum liliago			28	0.02			14	0.01
Artemisia alba	55	1.14	14	0.01	12	0.01	42	0.04
Brachypodium phoenicodes	44	1.67					42	13.2
Brachypodium retusum	22	0.56						
Bupleurum rigidus	11	0.55					28	3.21
Buxus sempervirens	11	0.01	14	0.01	25	0.02	14	0.01
Campanula hispanica	22	0.02	71	0.07	12	0.01	42	0.04
Campanula speciosa	11	0.01	57	0.75	37	0.65	28	0.02
Cephalaria leucantha	44	0.58			12	0.62	42	2.52
Cirsium sp			14	0.01			14	0.01
Cirsium vulgare							14	0.01
Clematis vitalba					12	0.01	14	0.01
Convolvulus arvensis	11	0.01	14	0.01	12	0.01		
Crataegus monogyna	11	0.01					28	0.02
Cruciata glabra			42	1.44	50	0.05	42	0.04
Dactylis glomerata							42	3.92
Daucus carota	11	0.01					42	0.74
Echinops sphaerocephalon	11	0.01					14	0.01
Erucastrum nasturtifolium	22	0.02			100	1.32	42	0.04
Euphorbia nicaensis			42	0.04				
Euphorbia serrata	44	0.04			12	0.01	14	0.71
Festuca gautieri			42	0.04			14	0.71
Festuca sp	11	0.55			12	0.01	14	0.01
Fumana procumbens	22	0.02						
Galium lucidum	11	0.01			25	0.02	42	0.74
Galium pumilum	22	0.02			12	0.01	14	0.01
Genista scorpius	100	4.75	28	0.02	37	0.03	85	2.18
Hieracium cerinthoides			42	0.04	25	0.02	28	0.72
Hieracium sp			57	0.75	62	0.67	42	0.74
Knautia catalaunica	22	0.02	85	0.78	37	0.03	42	0.74
Laserpitium gallicum	44	1.13	71	2.55	87	6.88	57	2.85
Leontodon hispidus							28	0.02
Leucanthemum pallens	22	0.02					28	0.02
Linum catharticum							28	0.02

Linum viscosum	11	0.01			12	0.01	14	0.01
Lotus corniculatus							57	0.75
Odontites lutea	11	0.01	14	0.01				
Ononis fruticosa	33	4.73			37	2.21	28	0.72
Phyteuma orbiculare			42	0.04			14	0.01
Picris hieraciodes			14	0.01	12	0.01	14	0.01
Pinus nigra	11	1.94			12	2.18	14	0.01
Pinus sylvestris	55	0.6	71	3.25	75	5.65	57	0.75
Potentilla verna			14	0.01			28	0.02
Prunella grandiflora							28	0.72
Prunus mahaleb	11	0.01	28	0.02	12	0.01	14	0.01
Ptychotis saxifraga	11	0.01	28	0.72	25	0.63	14	0.01
Reseda phyteuma	22	0.02			37	0.03		
Reseda lutea					25	0.02	14	0.01
Rosa agrestis	11	0.01					14	0.01
Sanguisorba minor	33	0.03	71	0.77	100	1.32	100	1.5
Satureja montana	44	1.13	85	2.18	87	2.87	57	0.75
Scabiosa columbaria	22	0.02	14	0.01	12	0.01	14	0.01
Succisa pratensis			14	0.01			14	0.01
Teucrium chamaedrys	55	0.6	28	0.02	37	0.03	28	0.72
Valeriana montana			28	0.02				

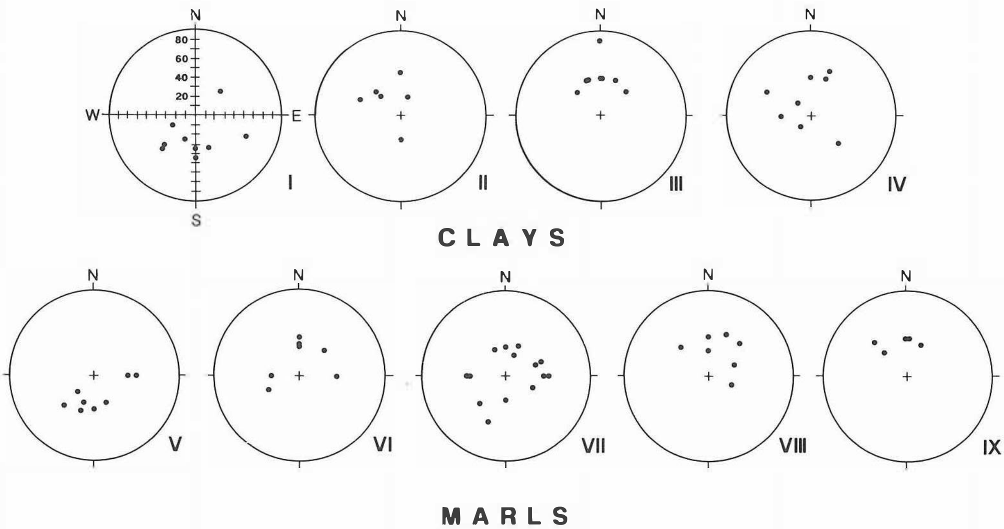


Fig. 4 - Schematic representation of the exposure and slope angle of each group of relevés. Dots represent the stands of the respective groups. The center of each circle represents a position of no slope and exposure, and the periphery of each circle is 100 % slope with exposure indicated.

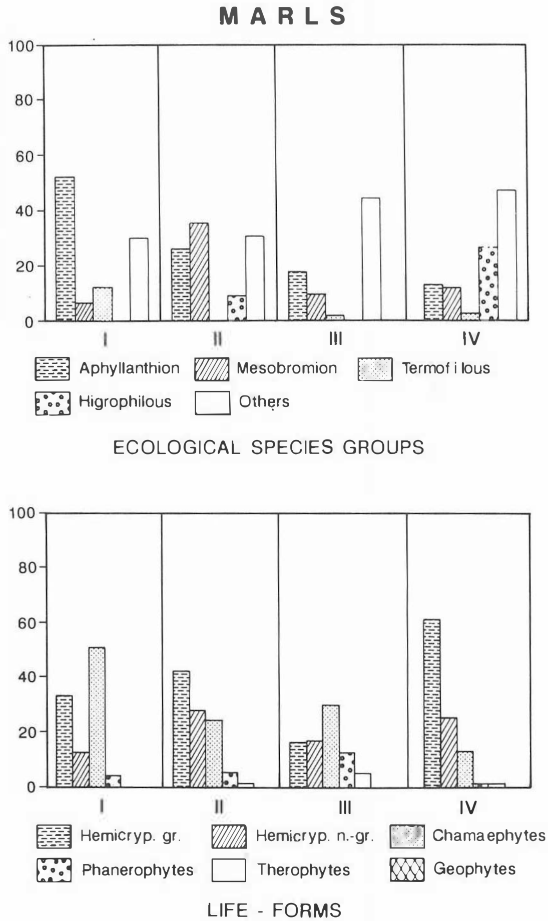


Fig. 5 - Percentage cover of species classified according to their ecological significance and to their life-form in the Eocene marls.

41.4%) and for herbaceous ones. Some of these species are also present in the *Aphyllanthion* pastures, where they, nevertheless, play a secondary role (*Linum salsoloides, Koeleria vallesiana, Santolina chamaecyparissus*, etc.). The weathering of the bedrock frequently produces a superficial layer of gravel that allows, on the other hand, the occurrence of some plants adapted to screes (*Achnatherum calamagrostis, Laserpitium gallicum*, etc.). Thus, this community turns out to be very different from the initial pasture

Thalweg vegetation (IV)

Although the relevés that make up this group do not seem closely related to one another in the CA (Fig. 3), as a whole they are rather distant from the others.

The thalwegs receive much of the runoff and sediment from the hillslopes, and this fact is reflected in the amount and type of herbage produced. This vegetation achieves the maximum cover in the badlands (74% average). The herbaceous layer is relatively dense, and mainly formed by grasses, as the higher water availability in the thalwegs allows the development of some mesic species (*Molinia caerulea, Sesleria coerulea, Carex flacca,* etc).

The inclination of thalwegs represented in Figure 4 corresponds to their axis, coincident with the maximum inclination of the general slope. However, each plot sampled is a strip including, on both sides of the axis, a range of different inclinations and exposures. Moreover, each sampled plot includes an upper and a lower part of a thalweg which are rather different in meaning of substratum depth, humidity, etc. Thus, the sampling method (based on the homogeneity of the plots) became rather unsuitable for thalweg study. Besides this heterogenity within each plot, thalwegs seem somewhat diverse as they are not very restrictive sites for species settling, as well as for remaining plants from the original communities.

Upper Cretaceous clays

The relevés from Cretaceous substrata are presented in Table 2, and the result of CA is shown in Figure 6, where the two axes account for 17.23% of the variance. Figure 7 displays the percentage cover of the species classified according to their ecological significance and to their life-form. A similar relevé distribution into groups as in Eocene marls can be observed, and also a similar vegetation dynamics relationship can be modeled, but some differences should be pointed out (fig. 9). The thalweg group (VIII) is not evidenced by CA because it is not a very well-defined community, but this set of relevés was taken as a whole to allow the comparison between the two substratum communities. On this substratum the transition between pasture and badland occurs suddenly, through a well-marked step. Below this step, a medium-covered zone represents a degradation of the original pastures as on the Eocene materials. Two similar communities can also be recognized here, south-facing (V) and north-facing (VI), the latter with lower cover. Backslopes are the harshest environements; they bear a community (VII) comparable to group III in Eocene marls but with lower plant cover. In addition, a new group (IX) restricted to Cretaceous materials, has appeared.

Brachypodium phoenicoides and *Aphyllanthes monspeliensis* community (V).

The relevé plots are mainly on south-facing exposure, and on medium inclinations. The prevalent life-form is the graminoid type (48.9% of the total cover), with *Aphyllanthes monspeliensis, Brachypodium retusum* and *B. phoenicoides* as dominant species. The community is close to the meso-xerophilous pastures,

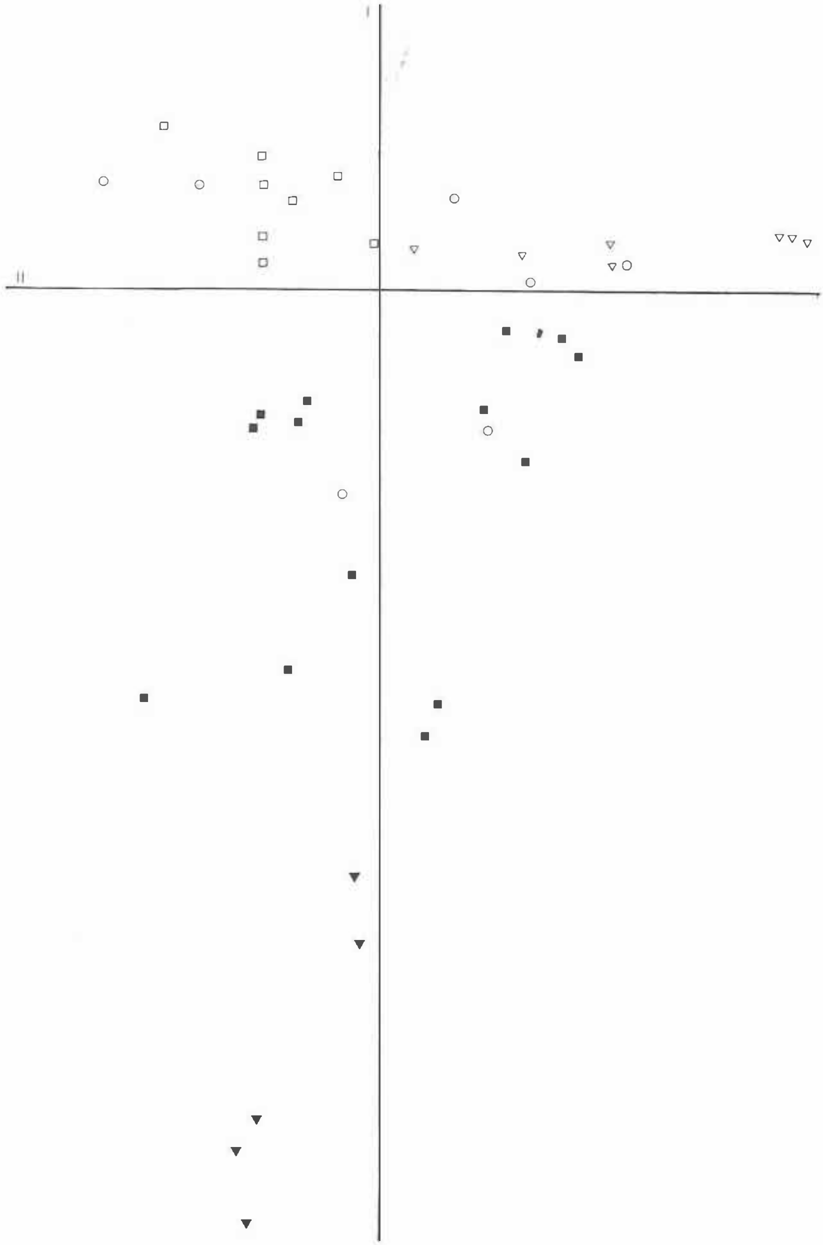


Fig. 6 - Arrangement of clay relevés according to the first two axes of CA. Open square: Group V; open triangle: Group VI; dark square: Group VII; open circle: Group VIII; dark triangle: Group IX.

Table 2 - Synthesis of the Upper Cretaceous relevés, with the species arranged according to ecological groups. In each column the frequency (% of occurence) and the average cover in the community (CR, coverage rate, in %) for each species is shown.

GROUPS	V		VI		VII		VIII		IX	
Summarized relevés	8		7		14		7		5	
	%	CR	%	CR	%	CR	% -	CR	%	CR
Plants of the submediterranean pastures										
Anthyllis montana	25	2.81	57	0.75	7.1	0.00	14	0.01		
Aphyllantes monspeliensis	87	12.2	57	1.45			42	11.4		
Argyrolobium zanonii	25	1.25					14	0.01		
Asperula cynanchica	25	0.63	14	0.01	35	0.03	42	0.04	20	0.02
Astragalus monspessulanum	62	1.9	28	3.21	14	0.01				
Avenula iberica	50	1.88	42	0.74	57	1.3	57	5.72	40	1.02
Carduncelus monspeliacus	75	2.25			21	0.02	14	0.01		
Carex humilis	37	6.56	57	0.75	7	0.00	57	1.45		
Coronilla minima	25	0.02	57	0.05	7	0.00	14	0.01		
Euphorbia mariolensis	50	0.05			14	0.01				
Globularia cordifolia	62	4.07	28	0.02	14	0.01				
Globularia vulgaris	25	0.02			14	0.36			20	0.02
Helianthemum italicum	62	0.67	71	2.17	14	0.01	28	0.72	20	0.02
Hippocrepis comosa			28	1.42	7	0.00				
Koeleria vallesiana	100	2.55	100	0.1	42	0.74	57	0.05	40	0.04
Lavandula pyrenaica	62	4.41	100	1.5	21	0.02	42	0.04	40	0.04
Linum salsoloides	100	1.93	42	0.04	50	0.05	42	0.04	20	0.02
Santolina chamaecyparissus	75	0.68	28	0.02	35	0.38	42	2.52		
Teucrium aureum	50	0.66	71	1.47	42	0.04	14	0.01		
Teucrium pyrenaicum	12	0.01			14	0.01	14	0.01		
Thesium divaricatum	12	0.01	14	0.01						
Plants of the centroeuropean mesophilous pastures										
Bromus erectus	25	0.63					14	0.01		
Carlina vulgaris	25	0.02								
Euphrasia salisburgensis					14	0.01			20	0.02
Koeleria pyramidata					7	0.00	14	0.01	20	0.02
Onobrychis supina	87	1.92	71	0.77	35	0.73	28	2.51		
Sesleria caerulea			100	16.4	28	0.72	28	5	40	0.04
Termophilous plants										
Coris monspeliensis	62	0.06								
Dorycnium hirsutum			28	0.72						
Dorycnium pentaphylum	75	1.91			14	0.01				

Fumana ericoides	62	0.06	14	0.01	14	0.01	14	0.01		
Lithodora fruticosa			14	0.71	14	0.71				
Sideritis hirsuta	12	0.01			21	0.02				
Thymus vulgaris	87	2.53	28	0.02	21	0.02				

Plants of humid and clayish soils

Carex flacca	12	0.01			14	0.01	57	6.8		
Chlora perfoliata	37	0.03					14	0.01		
Molinia caerulea			28	0.72			28	3.21	20	0.02
Jasonia tuberosa	12	0.01	42	0.04	14	0.01	71	2.55	20	0.02
Plantago serpentina	25	0.63	57	1.45	57	1.10	85	1.48	40	0.04
Tussilago farfara					35	1.08	42	0.74	100	15

Others

Achnatherum calamagrostis			42	3.92	7	0.00	57	3.94	20	0.02
Brachypodium phoenicoides	75	7.82	28	0.72	21	0.02	57	12.8		
Brachypodium retusum	62	14.0			7	0.00				
Buxus sempervirens			28	0.02			14	0.01		
Campanula hispanica	25	0.02							20	0.02
Campanula speciosa	37	0.03	42	0.74	50	1.1	14	0.71	40	1.02
Centaurea scabiosa	50	0.05	14	0.01	42	1.63	28	0.02		
Cirsium vulgare	62	0.06	14	0.71	7	0.00	28	0.02		
Convolvulus arvensis	37	0.65			50	3.58	14	0.01	60	0.06
Dactylis glomerata	37	1.26	28	0.02	14	0.01	42	2.52	20	0.02
Daucus carota							28	0.02		
Erucastrum nasturtifolium	12	0.01			21	0.37				
Eryngium campestre	37	0.03			7	0.00	14	0.01		
Festuca grovina	50	0.66			14	0.01			20	1
Festuca sp			14	0.71			14	0.01		
Galium pumilum	37	1.26			7	0.00	14	0.01		
Genista scorpius	100	15.3	71	4.65	78	0.42	85	0.08	40	0.04
Hieracium cerinthoides			28	0.72	7	0.00	28	0.02		
Hieracium piliferum	25	0.02							20	0.02
Hieracium pilosella	12	0.01	28	0.02	7	0.00	14	0.01		
Hieracium sp			28	2.51	14	0.01			20	0.02
Hypochoeris radicata	25	0.02	14	0.01	14	0.01	14	0.71		
Juniperus communis	25	0.02	14	0.01					20	0.02
Knautia catalaunica	25	0.02	28	0.02	35	0.73	57	0.75	20	0.02
Leontodon hispidus			14	0.01			14	0.01		
Leucanthemum vulgare					7	0.00	42	0.04		
Linum catharticum			14	0.01			14	0.01		
Lotus corniculatus	25	0.02	28	0.72	21	0.02	28	0.02		
Ononis natrix	12	0.01					14	0.01		
Orchis sp			28	0.72			14	0.01		
Pinus sylvestris	37	1.26	100	3.98	50	0.4	85	2.18	80	0.08
Plantago lanceolata					7	0.00	14	0.01		

Platanthera sp			14	0.01			14	0.01	20	0.02
Potentilla verna	12	0.01	28	0.02			14	0.01		
Prunella vulgaris	12	0.01			7	0.00	14	0.01		
Prunus mahaleb	12	0.01			7	0.00				
Ptychotis saxifraga	25	0.02	14	0.01	14	1.25	28	0.02	40	1.02
Quercus pubescens	12	0.01			7	0.00	14	2.5		
Reseda phyteuma					14	0.01				
Rosa sp	12	0.01					14	0.01	20	0.02
Sanguisorba minor	25	0.02	42	0.04	71	0.07	85	0.08	20	0.02
Taraxacum officinale	12	0.01			7	0.00	14	0.01	20	0.02
Tetragonolobus maritimus							28	0.02		
Teucrium chamaedrys	25	2.2			7	0.00				
Thymelaea nivalis			42	1.44			14	0.01		
Trifolium pratense					7	0.00	14	0.01		

as indicated by the high percentage of *Aphyllanthion* taxa (45.8% cover). This community is quite related to group I of Eocene marls, also holding thermophilous plants, but here grasses are more abundant than chamaephytes.

Helianthemum oelandicum and *Sesleria coerulea* community (VI)

The main differences from the preceding community lie in the fact that this community develops on moister soils, hosting species of the mesic pastures of *Aphyllanthion* (*Seslerio-Aphyllanthetum*). Grasses are dominant (45.1%), but here *Sesleria coerulea* clearly dominates, in the form of detached turfs among the bare parts of the slope (Fig. 8).

Plantago serpentina and *Campanula speciosa* community (VII)

Plant cover is lower here than elsewhere. Moreover, there are frequently plants with low vitality, over-developed root systems (often partially uncovered), abnormally reptant forms, some mechanical damages, etc. They belong to the so-called stress-tolerant group (Grime 1979). They are long-lived plants with a range of features which basically represent adaptations for endurance in conditions of limited productivity: slow rates of growth, evergreen habit, long-lived organs, less frequent flowering than normal, low fertility and the presence of mechanisms which allow the intake of resources during temporarily favourable conditions. In addition, there is an important variability: except for *Genista scorpius, Sanguisorba minor, Plantago serpentina, Campanula speciosa* and *Pinus sylvestris,* the remaining 64 species occur in fewer than the half of the relevés, and generally only in 1 or 2.

Thalweg vegetation (VIII)

The thalwegs on the Cretaceous clays are not so pronounced as those on marls, and rarely hold thick depositions of debris. Thus, although the

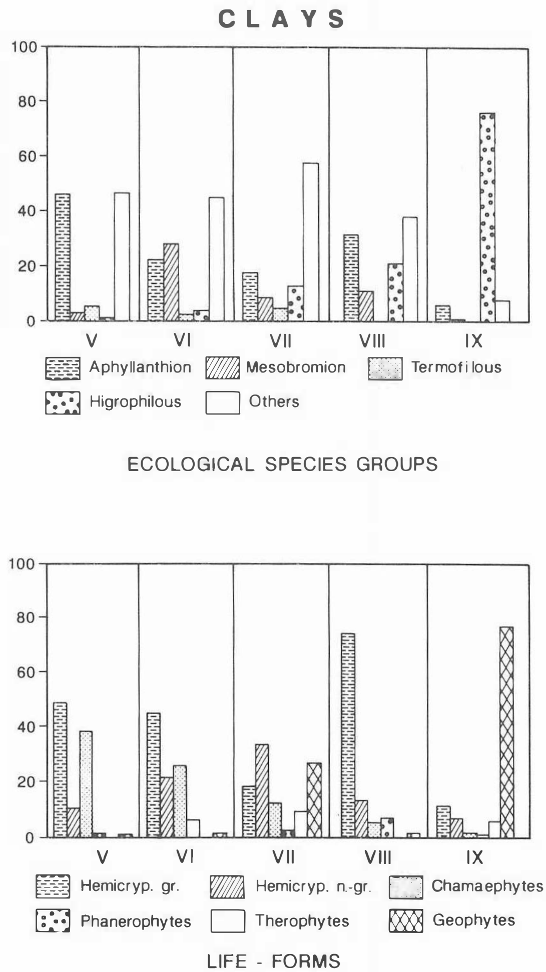


Fig. 7 - Percentage cover of species of Cretaceous clays classified according to ecological significance and to life-form .

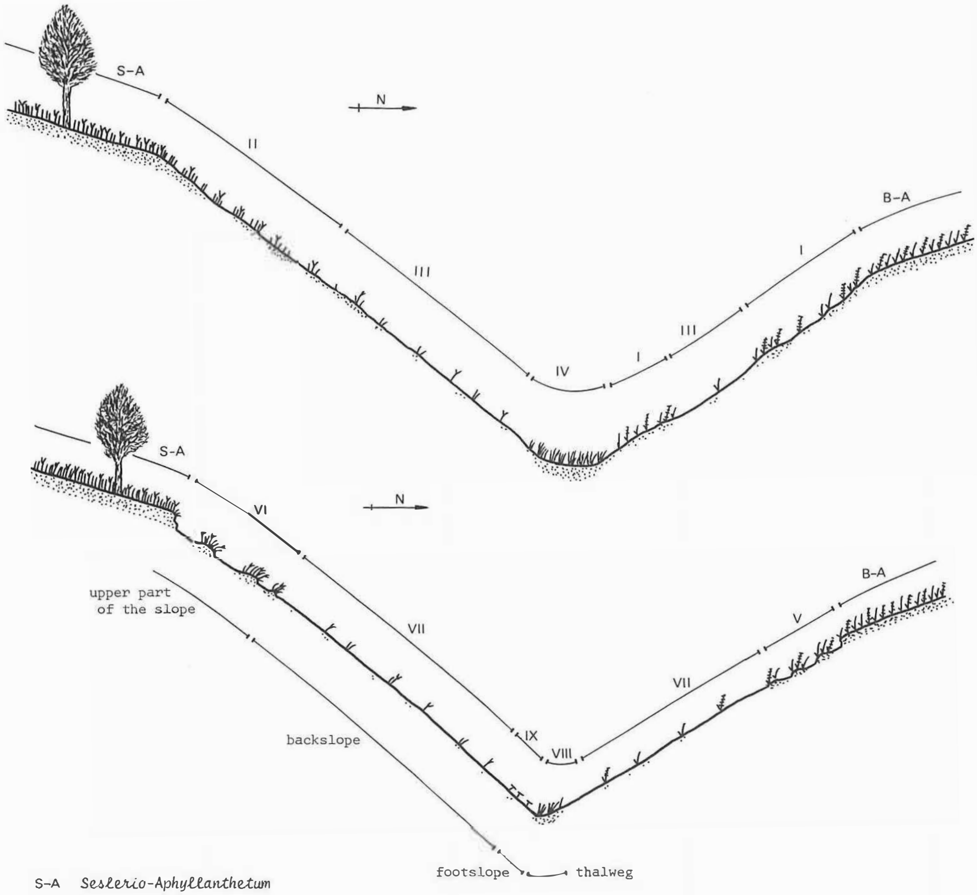
community of these thalwegs has higher coverage and diversity than those on the slopes, floristic differences are smaller than on Eocene marls. The graminoid type dominates (74.1%), and *Aphyllanthion* species are more abundant here (31.0% cover), this being one of the reasons for the weaker differentiation of the Cretaceous thalweg community.

Tussilago farfara community (IX)

Sometimes, when the footslope ends in a stream, a hygrophytic and clay-related community takes place. It is a very poor one, mainly with *Tussilago*

Fig. 8 - General view of a badland in Cretaceous clays. Detached sliding turfs in the upper part of slopes can be observed.

farfara, a rhizomatous herb capable of rapid vegetative spread, and well-adapted to the compact and anaerobic soils. The remaining species have very low covers, normally only one or two individuals being present in each plot, and do not have an homogeneous ecological significance.



S-A *Seslerio-Aphyllanthetum*
B-A *Brachypodio-Aphyllanthetum*
I *Globularia vulgaris* and *Aphyllanthes monspeliensis* community
II *Satureja montana* and *Sesleria coerulea* community
III *Laserpitium gallicum* and *Erucastrum nasturtiifolium* community
IV Thalweg vegetation (Eocene marls)
V *Brachypodium phoenicoides* and *Aphyllanthes monspeliensis* community
VI *Helianthemum oelandicum* and *Sesleria coerulea* community
VII *Plantago serpentina* and *Campanula speciosa* community
VIII Thalweg vegetation (Upper Cretaceous clays)
IX *Tussilago farfara* community

Fig. 9 - Idealized cross-section of a marl badland (top) and a clay one (bottom). Along the slopes a regressive transition going from initial pastures (*Seslerio-Aphyllanthetum* on north-facing exposures, *Brachypodio-Aphyllanthetum* on south-facing ones) takes place through several less dense communities. Note, in the clay badland, the sudden transition between pastures and badland communities, the more extensive backslope communities and the sharper thalweg.

Discussion

As a general feature, the vegetation inhabiting the badlands is always very scattered and heterogeneous. It is closely related to that of the non-eroded neighbouring zones. The erosive processes that lead to the formation of the badlands seem to involve a regressive succession going from pastures or light pine forests to less complex communities, ending in most cases in a complete lack of vegetation. Along this succession, most of the species gradually become rare and eventually disappear, because of the general loss of soil (decrease of water availability, etc.), the direct uncovering of roots or the falling downhill of turfs. Although in the study area disturbed lands are easily colonized by opportunist species, these plants are not very important in the badlands, probably because the substratum unstability renders impossible the permanence of the seed pool needed for their persistence.

The badland vegetation is normally herbaceous or low shrubby, those with a light tree layer of *Pinus sylvestris* (or *P. sylvestris* X *uncinata*) being very rare. However, as this pine has a strong settling power and is the commonest tree in the area, it is a very frequent species in the badlands in the form of seedling or sapling, with extremely low growing rates.

Badland development includes a wide range of erosive processes: rainplash, sheet wash, concentrate flow, etc. (Bryan & Yair 1982). The relative importance of these processes varies according to the topographic position in the badland. As these processes clearly determine the vegetation through the higher or the lower tolerance of each species, the topographic position is the most influential factor in the distribution of the communities in each badland. Brown (1971) related the distribution of seven plant communities in Montana Badlands to soils and physiographic characteristics. He concluded that distribution of plant communities in the badlands is determined by topographic and edaphic factors to the extent that they influence the availability of soil water. In North Dakota Badlands, Butler (1986) found that landscape position was correlated with vegetation composition, standing crop and soil characteristics, including soil moisture.

Some differences can be observed between the Eocene and the Cretaceous relevés. Generally, Cretaceous clays badlands present more extensive bare surfaces than Eocene marls. Besides that, in the colonized patches the plant cover is usually lower in the former, and abnormally growing plants are more frequent. The clayish nature of the Cretaceous materials allows the formation of a superficial crust, which makes stabilization and germination of seeds very difficult. Moreover, the badland morphology is not the same in the two substrata, allowing differences in the type and extension of several features (steepness, length of slopes, width of thalwegs, etc.). On the other hand, the Cretaceous badlands as a whole are located at slightly higher altitudes than the

Eocene ones, and this should be connected with the fact that the former bear communities which are slightly more mesophilous than the other.

Conclusions

The communities inhabiting the studied badlands are closely related to those of the neighbouring pastures. They represent a regressive succession from vegetation on neighbouring slopes. They are the result of the degradation of such original communities by loss or decrease of species, generally the mesophilous ones. Although in the study area disturbed lands are easily colonized by opportunist species, these plants are not very important in the badlands. Unstability and features of the rhegolit seem to be the main constraints for their settlement.

Topographic position and the related dynamics of the erosive processes are the most influential factors in the distribution of plant communities in each badland.

In the upper part of slope, vegetation is still fairly related to the initial pasture, through a gradual transition in the Eocene marls and a sharper one in clays.

Steeper backslopes are the harshest environments, especially on Cretaceous clays where bare surfaces are so extended. Vegetation cover is lower than elsewhere and abnormal-growing plants are frequent.

Downhill, thalwegs are the relatively most favourable places, mainly on Eocene marls where a dense herbaceous layer with several mesic species can be observed.

Marls and clays badlands hold some vegetation differences mainly connected to altitude and morphology of the badlands.

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Authors' address

Roser Guardia & Josep M. Ninot
Dep. Biologia Vegetal
Universitat de Barcelona
Av. Diagonal 645
E 08028 Barcelona - España