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CORRELATION BETWEEN SPECIES COMPOSITION AND SOIL PROPERTIES IN THE PASTURES OF PLANA DE VIC (CATALONIA, SPAIN)

Carme CASAS[1] & Josep M. NINOT[2]

ABSTRACT

The correlation between the species composition of pasture communities and soil properties in Plana de Vic has been studied using two multivariate methods, Correspondence Analysis (CA) for the vegetation data and Principal Component Analysis (PCA) for the soil data. To analyse the pastures, we took 144 vegetation relevés (comprising 201 species) that have been classified into 10 phytocoenological communities elsewhere. Most of these communities are almost entirely built up by perennials, ranging from xerophilous, clearly Mediterranean, to mesophilous, related to medium-European pastures, but a few occurring in shallow soils are dominated by therophytes. As for the soil properties, we analysed texture, pH, depth, bulk density, organic matter, C/N ratio and the carbonates content of 25 samples, corresponding to representative relevés of the communities studied.

The species-based ordination (CA) and the property-based ordination (PCA) of soil samples were highly correlated. Thus, the gradients evidenced by the CA of the relevés may be interpreted as coincident with those shown by the PCA of the soil samples, taking into account the ecological requirements of the species.

CA is a powerful auxiliary tool in the phytocoenological classification of the relevés, as most of the resulting groups showed syntaxonomical basis. The most detached groups of relevés were those representing extreme situations within the study area (therophytic, xerophilous *Helianthemion* and *Thero-Brachypodion*, versus perennial, mesophilous *Bromion*), whereas most of the relevés evidenced the progressive transition from xeric to mesic aspects, described using the phytocoenological method (5 *Aphyllanthion* communities).

The soil variables first selected by PCA (depth, texture, and content of organic matter) were those governing water availability. Moreover, the occurrence of each pasture community also depends on other site conditions strongly related to soil water dynamics, chiefly the topographic situation.

Key words: Multivariate analyses, Vegetation ordination, *Bromion, Aphyllanthion, Thero-Brachypodietea*, Soil water, Topography, Soil-vegetation relationships

[1] Departament d'Indústries Agràries i Alimentàries, Escola Politècnica Superior, Universitat de Vic. C. de la Laura, 13. 08500 Vic. E-mail: carme.casas@uvic.es

[2] Departament de Biologia Vegetal, Universitat de Barcelona, Av. Diagonal, 645. 08028 Barcelona. E-mail: ninot@porthos.bio.ub.es

RESUM

Correlació entre la composició específica i les propietats edàfiques a les pastures de la Plana de Vic

Hem estudiat la correlació entre la composició específica de les comunitats de pastures de la Plana de Vic i les propietats dels sòls en què viuen, a través de dos mètodes d'anàlisi multivariant, l'anàlisi factorial de correspondències (AFC) per a les dades de vegetació i l'anàlisi de components principals (ACP) per a les dades edàfiques. L'estudi de les comunitats de pastura es basa en 144 inventaris de vegetació (en què intervenen 201 espècies), que prèviament havien estat classificats en 10 comunitats seguint la metodologia fitocenològica. Gran part d'aquestes comunitats són formades molt majoritàriament per espècies perennes, i mostren una transició des de les clarament xeròfiles, netament mediterrànies, fins a les mesòfiles, de caire medioeuropeu. Però algunes, que apareixen en sòls superficials i solen presentar poca extensió, són predominantment terofítiques. Pel que fa a les propietats edàfiques, vàrem obtenir 25 mostres de sòl corresponents a inventaris típics de les comunitats estudiades, i n'hem analitzat la textura, el pH, la densitat aparent, els continguts de matèria orgànica i de carbonats i la relació C/N, i n'hem avaluat la profunditat.

Les ordenacions multivariants obtingudes dels inventaris de vegetació (AFC) per una banda, i de les mostres de sòl (ACP) per l'altra, mostren una notable correlació. Així, si interpretem l'ordenació dels inventaris (AFC) a través de les tendències ecològiques de les espècies, en resulten uns gradients ecològics força coïncidents amb els que mostra l'ACP dels sòls.

L'AFC es manifesta com una important eina auxiliar en la classificació fitocenològica dels inventaris, atès que l'ordenació d'aquests i les agrupacions que en resulten tenen sentit sintaxonòmic. Els grups d'inventaris més evidents corresponen a situacions extremes dins de l'àrea d'estudi (comunitats terofítiques i xeròfiles d'*Helianthemion* i de *Thero-Brachypodion*, i pastures perennes i mesòfiles de *Bromion*), mentre que la majoria dels inventaris dibuixen una transició paulatina des dels sòls xèrics als mèsics, que en l'aspecte fitocenològic correspon a 5 comunitats d'*Aphyllanthion.*

Les variables edàfiques seleccionades en primer lloc per l'ACP (profunditat, textura i contingut de matèria orgànica) són les que tenen més influència en la disponibilitat hídrica per a les plantes. A més, la presència de cada comunitat de pastura en un lloc donat també depèn d'altres característiques molt relacionades amb la dinàmica de l'aigua, principalment de la situació topogràfica.

Mots clau: Anàlisis multivariants, Ordenació de la vegetació, *Bromion, Aphyllanthion, Thero-Brachypodietea*, Aigua edàfica, Topografia, Relacions sòl-vegetació

1. Introduction

The structure and species composition of plant communities are the result of the interactions among the species (mainly competition), and between plants and environmental factors (climate, soil features, topography, etc.; GREIG-SMITH 1979, EVANS 1989), altogether combined with biological history of populations and with random events. All species are found on a specific habitat and tend to be more abundant around their particular environmental optimum. Therefore, the composition of communities varies along environmental gradients, as species are successively replaced as a function of variation in the environment.

Ter Braak & Prentice (1988) reviewed the techniques of data analysis which may assist the interpretation of community composition as an expression of environmental gradients. Gradient analyses may be direct, i.e. the occurrence of the species is described as a function of the environmental variables recorded, or indirect, i.e. community samples are displayed along abstract axes through multivariate analyses, and these axes are interpreted in terms of environmental gradients (Whittaker 1967).

Multivariate analyses use two key techniques in the exploration of correlations between plant communities and the environment: first, the use of data on a large number of variables, and second, the treatment of variables, which may be inter-related or dependent (Gittings 1965). Among the main methods available, Principal Component Analysis (PCA) has been used to reveal associations between soil variables (properties) and the plant species distribution (Mercier *et al.* 1992). In several studies of pastures, soil variables have been analysed by PCA, whereas Correspondence Analyses (CA) have been used to rank communities according to their floristic composition (Guerrero *et al.* 1999, Rivas-Martínez *et al.* 1980, Sebastià 1991a, 1991b, Mengui *et al.* 1993, Behn-Shahar 1990, 1991, Madon & Médail 1997). According to Montaña & Greigh-Smith (1990), Correspondence Analysis is an appropriate method for finding broad correlations between groups of variables or categories and groups of species. Moreover, CA has been used by several authors as an auxiliary ordering tool in phytocoenological classifications (Lacoste & Roux 1971, Font 1993, Valls 1999). On the other hand, when the aim is to establish direct relationships between species composition of the communities and environmental variables, the main methods used are Canonical Correspondence Analyses (Ter Braak 1987, Wondzell *et al.* 1990, Rainer 1990, Escudero & Regato 1992, Didier & Poudevigne 2000) and Detrended Canonical Correspondence Analyses (Chang & Gauch 1986, Wondzell *et al.* 1990, Jha & Sing 1990).

In previous studies, we characterised the pasture communities of Plana de Vic by the phytocoenological method (Braun-Blanquet 1979), paying special attention to topographic and major ecological factors (Casas & Ninot 1995, 1996). Casas (2001) has also analysed the soil properties of some plots representing typical examples of each community and studied their soil water dynamics. The aim of the present study is to identify the main environmental factors that determine the species composition of the pastures studied, by multivariate analyses. We applied two numerical ordination techniques: CA on the vegetation data and PCA on the soil variables. Comparison between the two ordination methods allows us to evaluate the link between the floristic composition of the pastures, and their spatial distribution and soil properties.

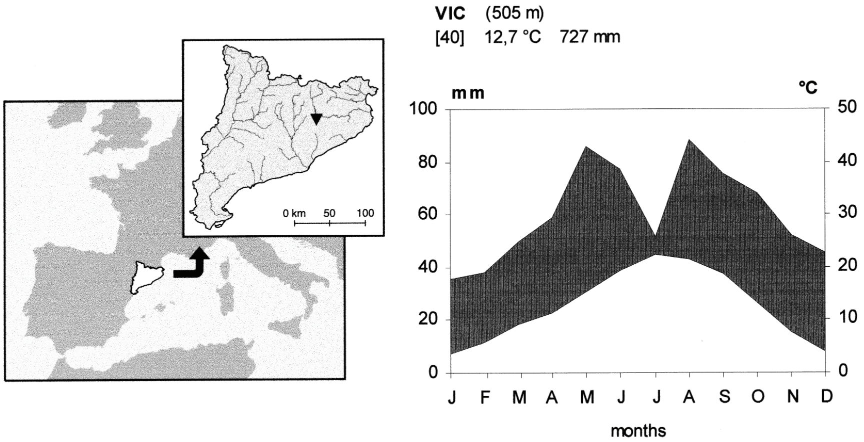

Figure 1. Location of the study area and climate diagram of the Vic observatory according to the Walter & Lieth system.

2. The study area

Plana de Vic is a small depression located in the northern half of Catalonia (Fig. 1), limited to the south and east by the Mediterranean, Catalanidic mountains, and to the north by the pre-Pyrenean ranges. It comprises flat, lime rich, Tertiary rocks, which are in the main Eocene marls. The vertical alternation of soft marl and harder outcrops (conglomerate, limestone) is particularly evident in a number of hills, where this study was centred. The macroclimate of the area is Submediterranean axeromeric, a transition climate between Mediterranean and Montane (Pyrenean). The mean annual temperature in Vic lies between 12 and 13 °C and the mean annual rainfall ranges from 650 to 750 mm (Fig. 1). Even though no arid season is apparent from the climatic diagram, the summer conditions result into noticeable stress situation where soil is poorly developed and generally in south-facing slopes. Thus, the vegetation is mainly mesoxerophilous, with xerophilous Mediterranean communities being restricted to drier habitats. The hills and the peripheral relieves of Plana de Vic stand out from the intensively farmed surrounding plains and are the main location of a varied semi-natural vegetation (Fig. 2). The climax vegetation is a deciduous, mesoxerophilous oak forest (*Buxo sempervirentis-Quercetum pubescentis*), which is present in a few gently sloped sites. Deforested slopes, with diverse exposure and with soils ranging from well preserved to highly eroded, harbour a wide variety of pasture communities.

3. Pasture communities

The previous phytocoenological study of the pastures reveals a noticeable diversity of communities in this area. Ten associations or sub-associations have been

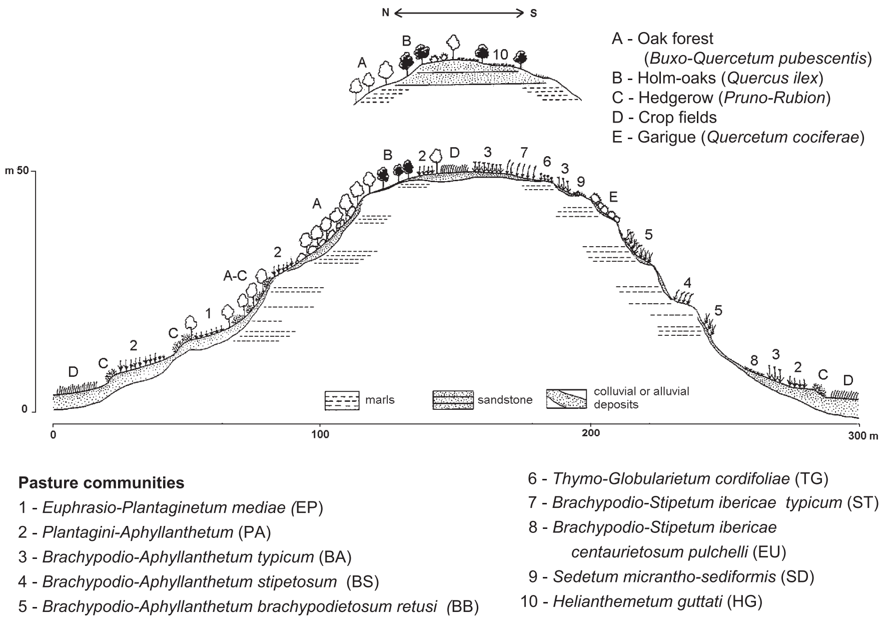

Figure 2. Transect of an idealised hill showing the situation of the communities studied.

characterised through their species composition, and their correlation to particular soil characteristics and topography conditions have also been discussed (Casas & Ninot 1995, 1996). The main properties of these pastures are summarised in Table 1, and their topographic location is shown in the idealised transect of Figure 2. The nomenclature of taxa and syntaxa in this paper follows the above referenced studies.

Most of the pasture surface corresponds to perennial communities, from xerophilous to mesophilous. *Euphrasio-Plantaginetum*, a *Bromion* association mainly formed by medium-European and Submediterranean taxa, develops on the least dry soils, which occur on gentle north-sloping surfaces. The other perennial communities are all included in *Aphyllanthion*, a well characterised alliance of Submediterranean to mild Mediterranean character. Within this alliance *Plantagini-Aphyllanthetum* is the most general association in the area, covering north-facing and intermediate slopes, and makes the transition from *Bromion* to the most typical *Aphyllanthion*, as it combines a bulk of species related to the latter with some *Bromion* differentials. *Brachypodio-Aphyllanthetum* is also a common association, dominated by xerophilous grasses, and differentiated into three subassociations: a) *typicum*, very common on south-facing aspects with deep soil; b) *stipetosum*, which settles on warm, rocky, dry slopes and is differentiated by the dominance of *Stipa iberica* (in some cases, *S. offneri* or *S. capillata*) and c) *brachypodietosum retusi*, dominated by the chamaephytic grass *Brachypodium retusum* and extended on steep, eroded, south-facing slopes.

Table 1. Main characteristics of the communities studied: Species with highest frequency/abundance (* subdominant, ** dominant); Li-Fm, life-forms (Hc, hemicryptophytes; Ch, chamaephytes; Th, therophytes; G, geophytes; M&L, mosses and lichens); Cv., mean of plant coverage; Ph-G, phytogeographic groups (in a broad sense: ME, Medium-European, including Submediterranean; Med, Mediterranean; Plr, Pluriregional); aspect and mean slope angle; Topographic position. Species percentages have been calculated from their mean coverage coefficients

Association (and Alliance)	**Main species**	**Li-Fm, %**	**Cv., (%)**	**Ph-G, (%)**	**Aspect, slope (°)**	**Position**
Euphrasio-Plantaginetum (*Bromion*)	*Brachypodium phoenicoides* * *Trifolium pratense* * *Lotus corniculatus* * *Avenula iberica* *Helianthemum nummularium*	Hc 86 Ch 10 Th 3	100	ME 40 Plr 34 Med 26	N (NE) 1	Shaded toeslopes
Plantagini-Aphyllanthetum (*Aphyllanthion*)	*Brachypodium phoenicoides* ** *Avenula iberica* *Aphyllanthes monspeliensis* *Carex caryophyllea*	Hc 78 Ch 20 Th 2	99	Med 53 ME 34 Plr 13	N (any) 4	Gentle slopes, toeslopes
Brachypodio-Aphyllanthetum typicum (*Aphyllanthion*)	*Festuca* gr. *ovina* * *Potentilla neumanniana* * *Aphyllanthes monspeliensis* * *Koeleria vallesiana* * *Teucrium polium*	Hc 61 Ch 35 Th 4	88	Med 66 ME 28 Plr 5	S (NE-NW) 9	Gentle toeslopes
Brachypodio-Aphyllanthetum stipetosum (*Aphyllanthion*)	*Koeleria vallesiana* * *Festuca* gr. *ovina* * *Stipa iberica* * *Thymus vulgaris* * *Aphyllanthes monspeliensis*	Hc 54 Ch 44 Th 2	78	Med 64 ME 33 Plr 3	S (SW-SE) 17	Diverse, steep slopes
Brachypodio-Aphyllanthetum brachypodietosum retusi (*Aphyllanthion*)	*Brachypodium retusum* ** *Koeleria vallesiana* *Teucrium polium* *Thymus vulgaris* *Aphyllanthes monspeliensis*	Hc 50 Ch 47 Th 3	89	Med 78 ME 16 Plr 6	S (SW-SE) 17	Diverse, steep slopes
Thymo-Globularietum (*Aphyllanthion*)	*Globularia cordifolia* *Koeleria vallesiana* *Fumana procumbens* *Aphyllanthes monspeliensis*	Ch 69 Hc 30 Th 1	91	CE 66 Med 32	Any 5	Rocky convex-ities
Brachypodio-Stipetum typicum (*Thero-Brachypodion*)	*Stipa iberica* ** *Koeleria vallesiana* *Festuca* gr. *ovina* *Leontodon taraxacoides* *Convolvulus cantabrica*	Hc 68 Ch 18 Th 14	87	Med 48 ME 43 Plr 11	S (any) 1	Flat summits, gentle slopes
Brachypodio-Stipetum centaurietosum pulchelli (*Thero-Brachypodion*)	*Dichanthium ischaemum* *Leontodon taraxacoides* *Brachypodium distachyon* *Euphrasia pectinata* *Plantago lanceolata* *Medicago minima*	Th 45 Hc 41 Ch 8 G 4 M&L 2	89	Med 41 Plr 39 ME 20	N (any) 3	Toeslopes with shallow soil
Sedetum micrantho-sediformis (*Thero-Brachypodion*)	*Sedum album* *Sedum acre* *Sedum sediforme* *Trifolium scabrum* *Bombycilaena erecta*	Ch 51 M&L 22 Th 15 Hc 11	75	Plr 69 Med 30	Any 0	Shallow soils, on flat, rock surfaces
Helianthemetum guttati (*Helianthemion guttati*)	*Sedum album* *Aira caryophyllea* *Logfia minima* *Leontodon taraxacoides* *Dipcadi serotina*	Th 40 Ch 24 M&L 19 Hc 12 G 5	74	Plr 75 Med 17 ME 8	Any 1	Shallow, sandy soils

Another community, *Thymo-Globularietum cordifoliae*, is a dwarf shrub formation, which settles on stony surfaces of the slopes or at the summit of the hills.

Therophytic communities are restricted to the driest places of the hills, normally settling on shallow soils and covering small surfaces. All of them, given the Submediterranean character of Plana de Vic, are rather extreme examples of the typically Mediterranean *Thero-Brachypodietea* class. *Brachypodio-Stipetum* includes dry pastures dominated by xerophilous grasses, though bearing a number of therophytes in the small gaps between the turfs; it includes two subassociations occurring in distinct topographic situations (*typicum* and *centaurietosum*), the first dominated by *Stipa iberica* (in places by *S. capillata* or *S. offneri*), and the second with diverse perennials and including particular therophytes. *Sedetum micrantho-sediformis* is a community dominated by *Sedum* spp., typical of shallow carbonated soils on flat surfaces, whereas *Helianthemetum guttati* is the only calcifuge pasture in the area, occurring in sandy soils and formed almost entirely by annuals.

4. Methods

4.1. Theoretical grounds for the multivariate analyses used

Correspondence Analysis (CA) and Principal Component Analysis (PCA) are two types of factor analyses appropriate for reducing a high number of variables into a few new variables (main components or factors), which explain most of the variance of the initial variables. These components are non-correlated, and may be taken as the orthogonal axes of a hyperspace. Thus, the samples may be represented in this space, and this may be used as an auxiliary tool in the ordination of the samples (Benzecri 1966, Guinochet 1973, Cuadras 1991).

The interest of PCA lies in the ability to extract ordination axes or components that maximise the dispersion of vegetation data and may be considered as latent environmental factors (Mercier *et al.* 1992), and thus related to the environmental data available (Ter Braak & Prentice 1988). In this analysis, the factors or main components are selected from the correlation matrix of variables. They are lineal combinations of the original variables, and explain most of the variance. A graph usually based on the most significant two or three factors (as axes) is a suitable tool to analyse differences between samples, when these are defined by quantitative data. The distance between two samples in these graphs may be assumed as an approximation to the mathematical distance between the samples, although the distortion caused by the reduction from multidimensional data onto a two- or three-dimension space.

CA is a particular ordination technique set by Benzecri (1966), which allows us to represent phytocoenological relevés (samples) as a function of their species composition (variables), or the species as a function of the relevés in which they occur; both species and relevés can also be represented in the same space. In phytocoenological studies, CA is a very interesting method, as it allows simultaneous comparisons of relevés and species, and thus gives evidence of the role of each species, or species group, in the affinities among relevés (GAUCH 1982, POUGET 1980). Several vegetation studies reveal the good concordance between the results obtained through CA and through the standard phytocoenological method (FONT 1993, LACOSTE & ROUX 1972, VALLS 1999, etc.).

From the ecological point of view, the main axes resulting from both CA and PCA may be interpreted as environmental gradients, according to the ordination of the samples along them. In the case of the relevés, this allows us to compare them in terms of environment conditions. On the other hand, although neither analysis provides any classification or clustering, which should be performed by discriminant or cluster analyses, they may both be used as assessing tools to classify samples (GUINOCHET 1973, MARGALEF 1980).

4.2. Analyses of phytocoenological relevés and soil data

CA was applied to the matrix vegetation data constructed with the 144 phytocoenological relevés of pastures obtained in the study area (representative of the 10 communities mentioned above) and 201 species. It was performed using the presence/absence data of species in the relevés, excluding those that were only present in 1 or 2 relevés. The matrix from the relevés was prepared by means of the XTRINAU package (FONT 1990), and CA using the ADCO program (CUADRAS 1991).

PCA was applied to the data matrix of soil variables, conducted with SPSS (v.9.0). We selected 25 plots from where we had previously obtained representative relevés of the communities studied. In each plot, one soil sample was taken from the level bearing the maximum root density (usually from the upper 10 cm) and the total soil depth was also measured. The main characteristics of the samples were then analysed (for detailed soil data see CASAS 2001) and the edaphic properties included in the PCA were: soil depth, percentages of sand, clay, gravel, carbonates and organic matter, C/N ratio, pH and bulk density. The analysis was performed using the original variables, except for the pH values and the gravel contents, which showed a non-normal distribution. Thus, we applied an antilogarithmic transformation (10^x) for the pH, and an arcsin$\sqrt{x}$/100 transformation for the gravel contents.

5. Results

5.1. Ordination of the relevés

The relevés were arranged along the two first axes of CA, which account for 10.4 % of the total variance (5.59 % for the first axis and 4.82 % for the second; Fig. 3). The first axis (horizontal) clearly separates perennial pastures from therophytic communities and may be related to the soil depth gradient. On the positive side of this axis, the relevés of the perennial communities (belonging to the alliances *Aphyllanthion* or *Bromion*) are grouped. They are almost entirely built up by perennials (hemicryptophytes, chamaephytes) and need deep soils, be they xeric or relatively

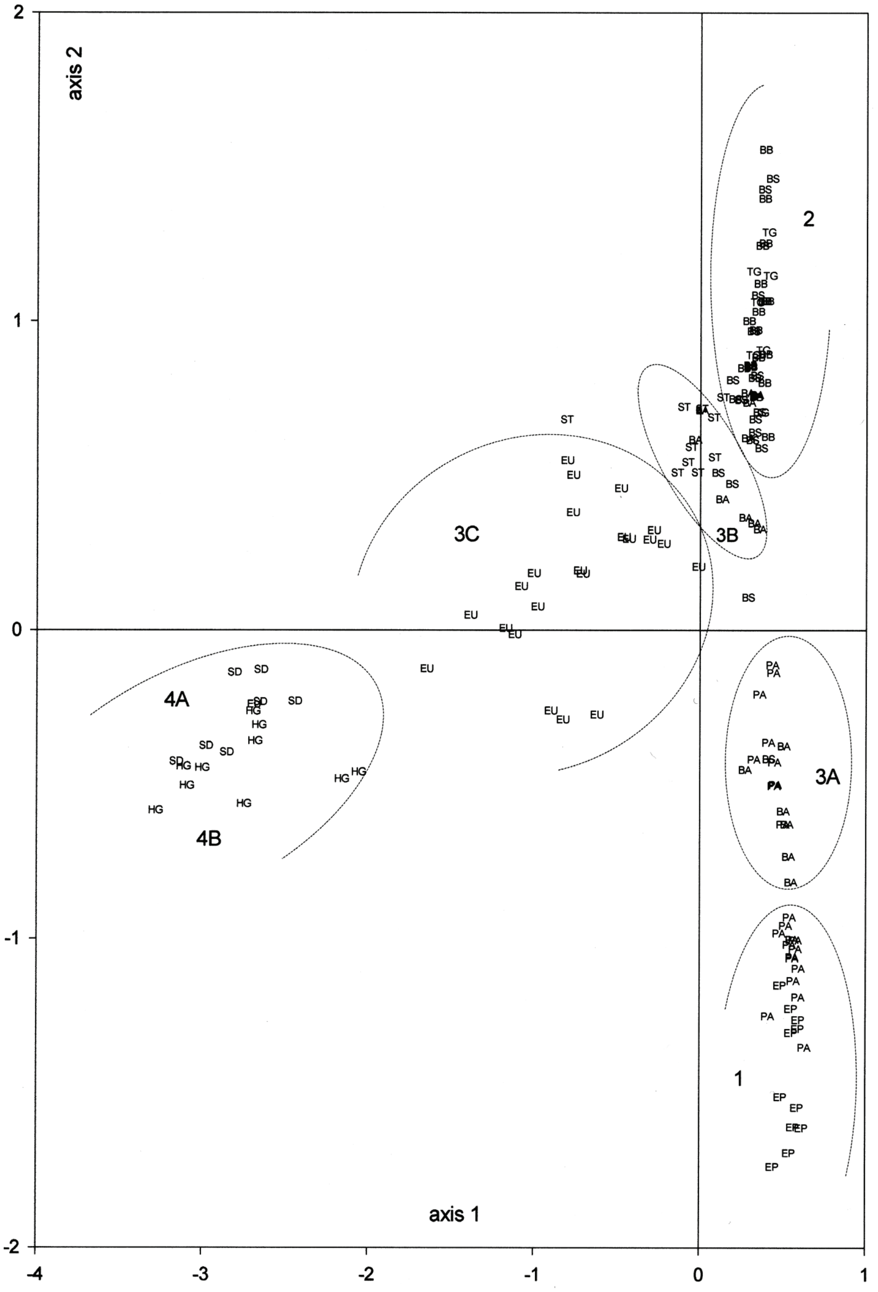

Figure 3. Ordination of the 144 relevés on the first two axes of CA, which express 10.4 % of the total variance. The groups limited by doted lines are explained in the text and in Table 3. The relevés are codified according to the community they belong to, according to Fig. 2.

moist. On the most negative part of the same axis, there is one group of relevés clearly detached, corresponding to *Helianthemetum guttati* and to *Sedetum micrantho-sediformis*. Both communities include high proportions of annuals, and occur on shallow soils which remain entirely dry for most of the period going from late spring to mid-summer. The transition between this group and the perennial pastures is shown by the relevés of the two *Brachypodio-Stipetum* communities, both of them including noticeable proportions of annuals in the gaps between the xerophilous perennials.

Along the second axis, the relevés of perennial communities are distributed according to their mesophilous-xerophilous character. The relevés situated on the top are included in the most xerophilous communities of *Aphyllanthion* (*Brachypodio-Aphyllanthetum brachypodietosum retusi* and *stipetosum*, and *Thymo-Globularietum*). In a lower position lays the intermediate *Brachypodio-Aphyllanthetum typicum*, then *Plantagini-Aphyllanthetum* and finally *Euphrasio-Plantaginetum*. This axis is related to the exposure of the communities, from steep south-facing (on the top) to gentle north-facing (on the bottom), although the intermediate communities may appear in a wide range of topographic situations.

The ordination of relevés, together with their phytocoenological classification (CASAS & NINOT 1995, 1996), allowed us to classify them into 6 groups. Three of them include the perennial communities (groups 1, 2, 3A, in Fig. 3), which were not well individualised by CA, whereas the other three correspond to more or less therophytic communities (3B, 3C, 4, in Fig. 3) and were displayed slightly more detached. The group on the bottom left (4) assembles two associations classified in separate phytocoenological orders (*Sedetum micrantho-Sediformis* in calcicolous *Thero-Brachypodietalia*, and *Helianthemetum guttati*, in calcifuge *Helianthemetalia*), because they share a number of indifferent annuals, as well as some chamaephytes and terricolous mosses and lichens. The two other therophytic groups (3C, 3B, in Fig. 3), which make the transition to the perennial communities, correspond to two subassociations of the same association, *Brachypodio-Stipetum*; although sharing most of their taxa, the particular annual species that differentiate the subassociation *centaurietosum pulchelli* place it in a singular position, also from a syntaxonomical point of view. The overlapping between the three perennial groups reflects their situation both in the environment and in the phytocoenological classification. They share a number of meso-xerophilous, broad niche plants, and from the most xerophilous to the mesophilous, Mediterranean xerophytes (sub-shrubs, grasses) are progressively replaced by medium-European mesophytes (e.g. broad-leaved hemicryptophytes).

5.2. Ordination of the species

The species ordination along the first two axes of CA (Fig. 4) is similar to the ordination of samples shown in Fig. 3. It may be related to the same gradients as the relevés, but in this case there is no evidence of any grouping. The first axis separates the therophytes (on the negative side) from the perennials (on the positive side). On the most negative part of axis 1 lays the calcifuge annuals characteristic of *Helianthemion*

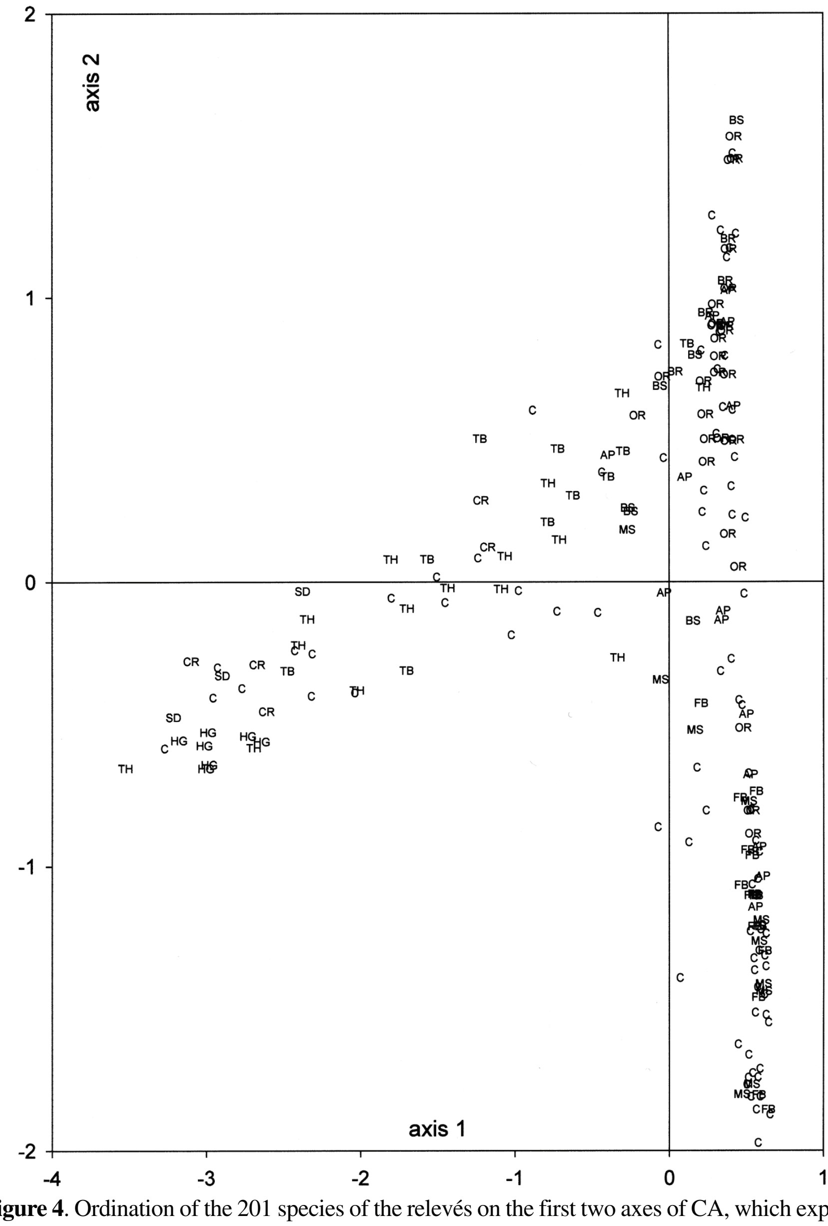

Figure 4. Ordination of the 201 species of the relevés on the first two axes of CA, which express 9% of the total variance. Each species is identified by a code indicating its syntaxonomic significance, as follows: MS, *Bromion*; FB, *Brometalia* or *Festuco-Brometea*; AP, *Aphyllanthion*; BR, *Brachypodio-Aphyllanthetum brachypodietosum retusi*; OR, *Ononido-Rosmarinetea*; TB, *Thero-Brachypodion* or *Thero-Brachypodietalia*; BS, *Brachypodio-Stipetum* (subass. div.); SD, *Sedetum micrantho-sediformis*; HG *Helianthemion guttati*; TH: *Thero-Brachypodietea*; CR, cryptogams (mosses and lichens); C, companions.

(*Logfia minima, Aira caryophyllea, Trifolium arvense, Scleranthus annuus*, etc.), the succulent *Sedum* species typical of *Sedetum micrantho-sediformis* (*S. album, S. acre, S. sediforme*), some annuals related to shallow soils (*Trigonella monspeliaca, Teucrium botrys, Poa bulbosa, Galium parisiense*) and a few terricolous cryptogams (*Grimmia pulvinata, Pleurochaete squarrosa, Cladonia foliacea*). On the middle of this axis appear the therophytes related to *Thero-Brachypodion* or to *Thero-Brachypodietea*, which characterise *Brachypodio-Stipetum* at the local scale (*Leontodon taraxacoides, Alyssum alyssoides, Desmazeria rigida, Euphorbia sulcata, Bombycilaena erecta*, etc.), and a few mesophilous taxa which differentiate the subassociation *centaurietosum pulchelli* (*Centaurium pulchellum, Orchis coriophora, Euphrasia pectinata*). The perennial species, which prevail in the floristic pool of the pastures, are on the positive part of the horizontal axis. As in the case of the relevés, this axis may be related to soil depth.

Along the vertical axis, perennial species are arranged according to a gradient ranging from mesic to xeric, and to their biogeographic character. On the bottom lay the mesophilous taxa, mainly medium-European hemicryptophytes. Some of them may be considered character-taxa of *Bromion* or *Festuco-Brometea* (*Prunella grandiflora, Thymus pulegioides, Ranunculus bulbosus, Salvia pratensis, Plantago media*, etc.), whereas others are just mesic companions (*Leontodon hispidus, Agrimonia eupatoria, Centaurea aspera*, etc.). On the top of this second axis occur the xerothermophilous, Mediterranean taxa related to *Ononido-Rosmarinetea* (*Brachypodium retusum, Helichrysum stoechas, Lavandula latifolia,* etc.), which are taken as differential-taxa of *Brachypodio-Aphyllanthetum brachypodietosum retusi* versus the other perennial pastures. The large group of taxa related to *Aphyllanthion* pastures stretches between these two extreme groups, drawing a long transition of more or less xerophilous hemicryptophytes (*Avenula pratensis* subsp. *iberica, Aphyllanthes monspeliensis, Carex humilis*, *Trinia glauca*, *Euphorbia nicaeensis*, etc).

5.3. PCA of the soil variables

The variance of the first three PCA axes accounted for 79.26 %: 42.83 % for the first axis, 23.72 % for the second and 12.71 % for the third. The contribution of the soil variables to each component extracted is summarised in Table 2. The relative importance of the soil variables for the first axis in decreasing weight order are: clay, sand, organic matter, depth and bulk density. For the second axis, the factors are: carbonates, pH and gravel, also decreasingly ordered. For the third axis, only the C/N ratio is significant.

These results and the ordination of the soil variables and the soil samples along the two first axes of PCA (Fig. 5) indicate that axis 1 represents the texture, fertility and depth of the soils. These are the main factors, those producing the maximum dispersion of the samples on the graphic ordination. And the second axis may be related to the carbonate percentage, the gravel content and the soil acidity.

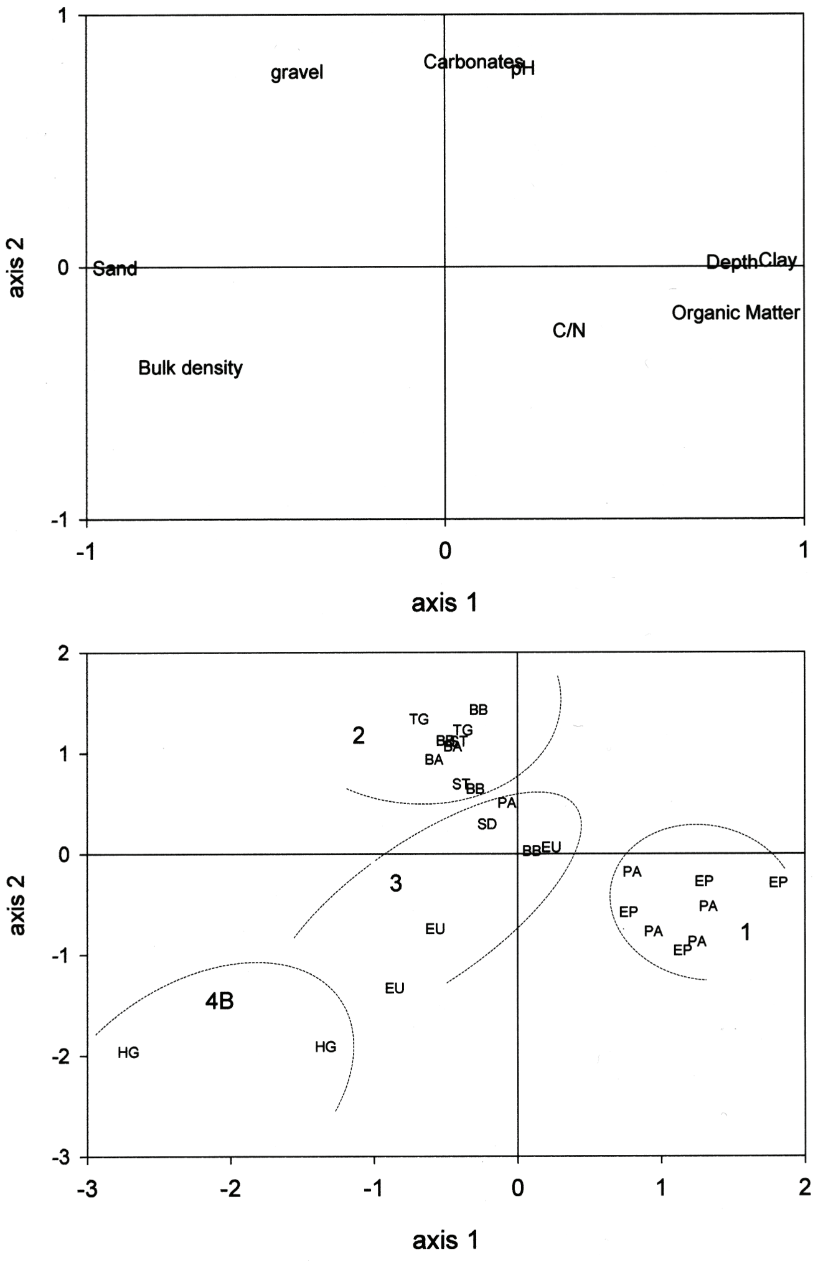

Figure 5. Ordination of the soil variables (upper) and soil samples (lower) on axes 1 and 2 of PCA, which express 79.3% of the total variance. Soil samples on the lower graph are identified by the corresponding community codes detailed in Fig. 2, and the groups limited by doted lines correspond to those of Fig. 3 and Table 3.

Table 2. Correlation between the soil variables and the first three components given by the PCA

Soil variables	Components		
	1	**2**	**3**
Clay	0.9278	0.0220	-0.2235
Sand	-0.9199	-0.0049	-0.1441
Organic matter	0.8114	-0.1859	-0.2730
Depth	0.8010	0.0134	0.0449
Bulk density	-0.7099	-0.3984	0.3255
Carbonates	0.0815	0.8117	0.2218
pH_{H_2O}	0.2195	0.7868	0.4053
Gravel	-0.4111	0.7728	-0.2829
C/N ratio	0.3469	-0.2559	0.7727

Thus, the group of spots on the right part of Fig. 5 (lower, group 1) includes the plots with deep, fine-textured soils, rich in clay and organic matter, and corresponds to the mesophilous pastures (*Euphrasio-Plantaginetum, Plantagini-Aphyllanthetum*). A second group (2) may be differentiated at the upper part of the vertical axis, formed by the perennial xerophilous communities (*Brachypodio-Aphyllanthetum, Brachypodio-Stipetum typicum, Thymo-Globularietum*), which develop on stony soils, rich in gravel and carbonates, but poor in organic matter. The sandy soils, devoid of carbonates and lightly acidic, are grouped on the bottom left side (group 4B, in Fig. 5). They correspond to the only calcifuge community (*Helianthemetum guttati*). The soil samples corresponding to the other communities are situated in intermediate positions.

The groups given by both ordination analysis (PCA and CA) may be classified into ecological groups and sub-groups, each including similar pasture communities, and can be defined by environmental variables and their whole species composition (Table 3).

6. Discussion

6.1. The species composition of the pastures

The ordination of the relevés obtained by means of CA fits well with the phytocoenological classification of the communities they belong to. This is evident in the gradual transition going from medium-European *Bromion* to xerophilous Mediterranean pastures, through the rich *Aphyllanthion* communities. The extreme situation of acidophilous (or neutrophilous) therophytic communities reflects that they contain a few specific taxa absent in all the other communities (calcifuge therophytes, *Sedum* spp.) and that they are devoid of a number of calcicolous, xerophytic to meso-xerophytic perennials that are the floristic nucleus of the other pastures of the area. And the intermediate situation of the *Thero-Brachypodion* pastures dominated by

Table 3. Main features of the groups evidenced by means of the factor analyses, referred to species composition, soil parameters and topography aspects

Group 1		Dense, hemicryptophytic pastures, including medium-European taxa (*Euphrasio-Plantaginetum*, *Plantagini-Aphyllanthetum*) Deep soils, clay-loam to clay-silt-loam, rich in organic matter and poor in gravel, carbonated though moderately basic. Flat or gentle sloped areas, mainly north-facing, resulting in good water availability in spring.
Group 2		Xerophilous pastures (*Brachypodio-Aphyllanthetum, Thymo-Globularietum*), mainly formed by Mediterranean species, some of them chamaephytes. Medium depth, clay-sandy-loam, more or less subject to erosion, rich in gravel, poor in organic matter, and basic. Mostly from upper to medium part of south-facing aspects, on sloped surfaces or on rocky shelves; lower water availability.
Group 3		Intermediate between 1 and 2, both in species composition and in soil features. Loam or clay-loam, shallow to medium deep, with lower organic matter content than Group 1; or clay-sandy-loam with lower gravel content than Group 2. Located on any exposition.
	3A	Some of the examples of *Brachypodio-Aphyllanthetum typicum* and *Plantagini-Aphyllanthetum*, transitional between 1 and 2
	3B	Therophytic communities, though dominated by *Stipa iberica* (*Brachypodio-Stipetum typicum*). On south-facing, upper part of slopes or summits.
	3C	Communities rich in short annuals, including meso-hygrophilous taxa, without *Stipa* (*Brachypodio-Stipetum centaurietosum*). On south-facing toeslopes, rooting in shallow, strongly seasonal soils.
Group 4		Therophytic communities, related to shallow, flat, initial soils
	4A	Calcicolous, on marl (*Sedetum micrantho-sediformis*)
	4B	Calciphugue, on sandstone, in sandy-loams with low pH and organic content (*Helianthemetum guttati*).

xerophilous grasses, between the most therophytic communities and the xerophilous *Aphyllanthion*, is also consistent with their syntaxonomic position.

These CA procedures furnish objective arrangements of the relevés, and are useful in corroborating their phytocoenological grouping, and in identifying transitional relevés, as evidenced in other studies (Lacoste & Roux 1971, Casanovas 1992, Font 1993). However, weighting the distance between groups and relevés involves the evaluation of the presence / absence of taxa in terms of their singularity (ecologic, biogeographic), thus following phytocoenological criteria. At the local scale, i.e. within a given local species pool, CA on floristic data evaluates the particular ecological conditions of each community (association, subassociation) versus those of the others, through their species composition, and supports the assumption that plant communities are correlated with particular environment conditions (Lacoste & Roux 1972).

The species ordination along the axes of CA reflects the correlation between the species according to their actual occurrence in the relevés. This allows us to test the cohesion of the group of character-taxa of each syntaxon, which appeared more or less clustered in each case. These species groups are more evident for lower rank syntaxa (alliances, associations), which represent extreme situations in the area (in our case study, *Bromion, Helianthemion*, xerophilous *Aphyllanthion*), whereas broad niche plants (characteristic plants of higher syntaxa, companions) do not show any particular arrangement, most of them appearing over the main nucleus of spots.

Another case is that of taxa related to extreme situations within the pasture vegetation, that occur also in non-pasture communities (fields, hedgerows). Their situation on the CA space may coincide with that of the group of character-taxa of one syntaxon, and only a broader phytocoenological knowledge gives evidence of their companion status. This is the case of some broad niche mesophytes (*Leontodon hispidus, Festuca rubra* s.l.*, Agrimonia eupatoria*, etc.), which may even be considered differential-taxa of *Bromion* at the local scale, but not character-taxa of this alliance.

The results of CA clearly evidence the two main types of communities which occur in the studied area: therophytic and perennial communities. The factors that seem to have more weight in the floristic composition and in the space distribution of these pasture communities are the soil depth and the gradient from mesic to xeric.

The knowledge of ecological preferences of the species (and communities), inferred from field work and reflected in floras and in vegetation literature (BOLÒS *et al.* 1993, Font 1993, Vigo 1979, etc.), allows us to evaluate the role of environmental features in the occurrence of plant communities, according to the CA results. For example, the occurrence of therophytic communities versus perennial pastures reflects shallow soils, which result in strong water shortage ending into a long dry period (DANIN & ORSHAN 1990, BAZZAZ & MORSE 1991). Under de Submediterranean general climate of the area, the therophytic strategy, or ephemerism, arises merely in the rock outcrops of the hilly landscape. Thus, annual-dominated communities appear secluded to highly reduced surfaces, where they represent, from a dynamical point of view, the initial stage of succession from rocky outcrops with immature, incipient soils (BOLÒS 1959, CASAS & NINOT 1996), generally shallower than 10 cm (CASAS 2001).

The gradient associated with the first axis of CA is clearly related to the primary succession of soil formation and vegetation settlement, from the rocky outcrops to medium depth soils, in which the perennial species compete successfully and mostly prevent the germination of therophytes. The determinant factor for the establishment of annual communities is the occurrence of shallow soils on shelves and summits, tied to ongoing erosive processes. They keep good water and resource availability only for a short period of time, coinciding with the rainy events that take place during the growing period, chiefly spring. Such seasonal conditions are a limiting factor for perennials, which can just produce light to very light coverages, and thus allow a noticeable occurrence of annuals.

Within the perennial pastures, the main gradient found, i.e. from mesophilous to xerophilous, parallels gradual shifts in the structure and functioning of the communities, and substrate features, as described for other pasture systems (Rivas-Martínez *et al.* 1980, Sebastià 1991a, Font 1989, 1993, Valls 1999). The spectra of life forms evidence environmental conditions and the resulting plant adaptations (Floret *et al.* 1987, Margalef 1980). In our case study, this corroborates that hemicryptophytes are dominant where soil water supply is higher, or at least where it follows a regular seasonal pattern, whereas chamaephytes (both woody and herbaceous) take over in irregular substrata, which showed steeper ups and downs in water availability and earlier shortage during spring (Casas 2001, Braun-Blanquet 1979, Shmida & Burgess 1988).

6.2. The soil factors as main controlling causes

Although PCA was performed only on 25 soil samples, while 144 vegetation relevés were analysed through CA, the ordination of samples was consistent with the phytocoenological classification of the communities they were related to, which reinforces the significance of the PCA. As in CA, the main gradient among samples is drawn from xerophilous to mesophilous communities, and is related to soil texture, depth, fertility (axis 1 in Fig. 5), carbonate content and stoniness (axis 2). These soil parameters condition the vegetation structure and function, and so the occurrence of each community, through water availability. Casas (2001) showed that these soil variables were clearly related to the seasonal dynamics of soil water content and soil water potential, and that the clue factor determining such a complex of features was the combination of soil depth and topographic situation.

Soil texture has been identified as the main driving force when determining the vegetation composition in diverse ecological situations, sometimes as an indirect factor, through soil permeability and the ability to keep water and nutrients supply (Lacoste & Roux 1972, Rainer 1990, etc.). In other cases, it has been correlated to geomorphic heterogeneity (Jha & Sing 1990).

Soil depth has no direct effect on the vegetation, but affects the amount of available water, which is clearly a vegetation conditioning constraint, as it determines the occurrence of certain species (Gittings 1965). Shallow soils drying out in summer prevent a good coverage of perennials with well developed root systems, thus favouring annuals, which become dominant in extreme cases. According to Puerto *et al.* (1983), the soils that sustain perennial pastures in Mediterranean conditions should be deeper than 40 cm. In the communities studied, Casas (2001) revealed that besides soil depth, the topographic situation also conditions water availability. In spring, during the main developing period, the best hydric situation took place in gently sloped areas, at the lower part of north-facing aspects, with finely textured soils. There, several factors controlling water dynamics reinforce eachanother (higher soil water reserve, low water losses via runoff and deep percolation, better microclimatic conditions). South aspects, frequently with shallower, coarser soils, and under more extreme climate conditions (CASAS & NINOT 1999), offer clearly harsher conditions to vegetation, as do summits and small shelves with very shallow soils, and subject the pastures inhabiting there to extreme temperatures and wind turbulence.

7. Conclusions

Our data point to the good concordance between the species-based ordination of the relevés found by means of CA and the ordination of soil samples based on their properties through PCA. The main substrate features analysed determine the species composition of the vegetation, and thus its structure and functioning.

The multivariate ordination of floristic relevés has proved to be a useful auxiliary tool in phytocoenological classification, although the biogeographic and ecological singularity of the species, together with syntaxonomic criteria, should be considered when interpreting the distance between relevés and between groups of relevés.

The main soil aspects conditioning the composition of the vegetation in the ecotone between Mediterranean and medium-European areas are those related to water availability: depth, texture and content of organic matter, together with the topographic situation, which produces diverse microclimates and hydrologic conditions.

The soil parameters controlling water availability are clearly associated with the species composition of the communities, as the gradients evidenced in the CA of the relevés may be interpreted as coincident to those shown by the PCA of the soils.

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References

BAZZAZ, F. A. & MORSE, S. R. 1991 - Annual plants: potential responses to multiple stresses. In: H.A. MOONEY, W.E. WINNER, & J. PELL (eds.), *Response of Plants to Multiple Stresses*: 283-305. Academic Press. London.

BEN-SHAHAR, R. 1990 - Soil nutrients distribution and moisture dynamics on upper catena in a semiarid nature reserve. *Vegetatio* 89: 69-77.

BEN-SHAHAR, R. 1991 - Abundance of trees and grasses in a woodland savanna in relation to environmental factors. *J. Veg. Sci*. 2: 345-350.

BENZECRI, J. P. 1966 - *Leçons sur l'analyse factorielle et la reconnaissance des formes*. Cours. Inst. Statist. Univ. Paris.

BOLÒS, O. DE. 1959 - El paisatge vegetal de dues comarques naturals: la Selva i la Plana de Vic. *IEC*, *Arx. Secc. Cièn.* 26: 1-175.

Bolòs, O. de, J. Vigo, R. M. Masalles & J. M. Ninot 1993 - *Flora Manual dels Països Catalans*. Pòrtic. Barcelona.

Braun-Blanquet, J. 1979 - *Fitosociología. Bases para el estudio de las comunidades vegetales.* Blume. Madrid.

Casanovas, L. 1992 - Contribució a l'estudi de les torberes dels Pirineus. *Actes Simp. Int. Bot. P. Font Quer, Lleida (1988)* 2: 241-250. Lleida.

Casas, C. 2001 - *Estudi topològic, ecològic i funcional de les pastures de la Plana de Vic*. Ph. D. Thesis (unpubl.). Univ. Barcelona.

Casas, C. & J. M. Ninot 1995 - Estudi fitocenològic de les pastures de la Plana de Vic. I: comunitats vivaces (Mesobromion i Aphyllanthion). *Butll. Inst. Cat. Hist. Nat.* 62: 25-52.

Casas, C. & J. M. Ninot 1996 - Estudi fitocenològic de les pastures de la Plana de Vic. II: comunitats terofítiques (Thero-Brachypodietea) i síntesi. *Butll. Inst. Cat. Hist. Nat.* 63: 27-50.

Casas, C. & J. M. Ninot 1999 - Relación entre microclima y vegetación pratense en «la Plana de Vic» (Cataluña). *Ecologia Mediterranea* 25(1): 41-56.

Chang, D. H. S. & H. G. Gauch 1986 - Multivariate analysis of plant communities and environmental factors in Ngari, Tibet. *Ecology* 67(6): 1568-1575.

Cuadras, C. M. 1991 - *Métodos de Análisis Multivariante*. PPU. Barcelona.

Danin, A. & Orshan, G. 1990 - The distribution of Raunkier life forms in Israel in relation to the environment. *J. Veg. Sci*. 1: 41-48.

Didier, A. & I. Poudevigne 2000 - Diversity patterns in grasslands along a landscape gradient in northwestern France. *J. Veg. Sci*. 11: 287-294.

Escudero, A. & P. Regato 1992 - Ordenación de la vegetación de las torcas de la Serranía de Cuenca y sus relaciones con algunos factores del medio. *Orsis* 7: 41-55.

Evans R. A. & , J. A. Young 1989 - Characterization and analysis of abiotic factors and their influences on vegetation. In: L.F. Huenneke & H. Mooney (Ed.), *Grassland Structure and Function: California Annual Grassland*: 13-28. Kluwer Academic Publishers. Netherlands.

Floret, C., N. J. Galan, E. Le Floc'h, G. Orshan & F. Romane 1987 - Local characterization of vegetation through growth forms: Mediterranean Quercus ilex coppice as an example. *Vegetatio* 71: 3-11.

Font, X. 1989 - Estructura, tipologia i ecologia de les pastures montanes de la Cerdanya. *Inst. Est. Cat. Arx. Sec. Cièn*c. 88: 1-200.

Font, X. 1990 - XTRINAU (ver. 1.0). Un programa para la gestión de los inventarios fitocenológicos. *Monografías del Instituto Pirenaico de Ecología*, 5: 531-539.

Font, X. 1993 - Estudis geobotànics sobre els prats xeròfils de l'estatge montà dels Pirineus. *IEC, Arx. Sec. Cièn*c. 105: 1-828.

Gauch, H. G. 1982 - *Multivariate analysis in community ecology. Cambridge studies in ecology.* Cambridge Univ. Press. Cambridge.

Gittings, R. 1965 - Multivariate approaches to limestone grassland community. I. A stand ordination. *J. Ecol*. 53: 385-425.

Greig-Smith, P. 1979 - Pattern in vegetation. *J. Ecol.* 67: 755-779.

Guerrero Campo, J., F. Alberto, J. Hodgson, J. M. García-Ruiz & G. Montserrat-Martí 1999 - Plant community patterns in a gypsum area of NE Spain. I: Interactions with topographic factors and soil erosion. *J. Arid Environments* 41: 401-410.

Guinochet, M. 1973 - *Phytosociologie*. Collection d'écologie, I. Masson et Cie. Paris.

Jha, C. S. & J. S. Sing 1990 - Composition and dynamics of dry tropical forest in relation to soil texture. *J. Veg. Sci*. 1: 609-614.

LACOSTE, A. & M. ROUX 1971 - L'analyse multidimensionelle en phytosociologie et en écologie. I. L'analyse des données floristiques. *Oecol. Plant.* 6(4): 353-369.

LACOSTE, A. & M. ROUX 1972 - L'analyse multidimensionelle en phytosociologie et en écologie. II. Analyse des données écologiques et l'analyse globale. *Oecol. Plant*. 7(2): 125-146.

MADON, O. & F. MÉDAIL 1997 - The ecological significance of annuals on a Mediterranean grassland (Mt. Ventoux, France). *Plant Ecology* 129: 189-199.

MARGALEF, R. 1980 - *Ecología*. Omega. Barcelona.

MENGUI, M., B. PECO & F. D. DÍAZ PINEDA 1993 - Spatial organization of gneissic grasslands related to relief and soil variability. *Ber. Geobot. Institut ETH, Stiftung Rübel, Zürich* 59: 106-123.

MERCIER, P. CHESSEL, D. & S. DOLÉDEC 1992 - Complete correspondence analysis of an ecological profile data table: a central ordination method. *Acta Oecologica* 13(1): 25-44.

MONTAÑA, C. & P. GREIG-SMITH 1990 - Correspondence Analysis of species by environmental variable matrices. *J. Veg. Sci.* 1: 453-460.

POUGET, M. 1980 - *Les relations sol-vegetation dans les steppes sud-Algeroises*. Travaux et documents de ORSTOM, 116. París

PUERTO, A., M. RICO, J. GARCÍA & R. RODRÍGUEZ 1983 - Estructura de la vegetación y profundidad del suelo en una microtranseción. *Studia Oecologica* IV: 153-166.

RAINER, H. 1990 - Community composition and soil propierties in northern Bolivian savanna vegetation. *J. Veg. Sci.* 1: 345-352.

RIVAS MARTÍNEZ, S., R. P. ABELLÓ, F. D. PINEDA, F. G. BERNÁLDEZ & C. LEVASSOR 1980 - Comunidades de pastizal del monte de el Pardo (Madrid). *Studia Oecologica* II: 59-80.

SEBASTIÀ, M. T. 1991a -*Els prats subalpins prepirinencs i els factors ambientals*. Ph. D. Thesis (unpubl.). Univ. Barcelona.

SEBASTIÀ, M. T. 1991b -Estructura horitzontal i vertical de les pastures de Sant Jaume de Frontanyà. *Ilerda «Ciències»*, 49: 103-111.

SHMIDA, A. & T. L. BURGESS 1988 - Plant growth-form strategies and vegetation types in arid environments. In: M.J.A. WERGER *et al*. (Ed.), *Plant form and vegetation structure*: 211-241. SPB Academic Publishing. The Hage.

TER BRAAK, C. J. F. & I. C. PRENTICE 1988 - A theory of gradient analysis. *Advances in Ecological Research* 18: 271-317.

TER BRAAK, C. J. F. 1987 - The analysis of vegetation-environment relationships by canonical correspondance analysis. *Vegetatio* 69: 69-77.

VALLS, A. 1999 - *Revisió sintaxonòmica dels prats oromediterranis mesoxeròfils de l'ordre Ononidetalia striatae*. Grad. Thesis (unpubl.). Univ. Barcelona.

VIGO, J. 1979 - Notes fitocenològiques, III. (Els prats calcícoles montans a la Vall de Ribes i zones properes). *Collect. Bot.* 11: 329-386.

WHITTAKER, O. 1967 - Gradient analysis of vegetation. *Biol. Rev*. 49: 207-264.

WHITTAKER, R. H. 1973 - *Handbook of vegetation science. V. Ordination and classification of communities*. Dr. W. Junk b.v. Publishers. The Hague.

WONDZELL, S. M., J. M. CORNELIUS & G. L. CUNNINGHAM 1990 - Vegetation patterns, macrotopography, and soils on a Chihuahuan desert playa. *J. Veg. Sci*. 1: 403-410.