The small-scale pattern of *Cynodon dactylon* in Mediterranean pastures

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Abstract

The abundance of *Cynodon dactylon* was recorded in 50 plots presenting different geomorphological conditions and along a transect of 16 500 2 × 2 cm contiguous quadrats within a small basin 330 m in length, in the granite pediment of the Sierra de Guadarrama (Central Spain). Soil analyses were undertaken on samples from the 50 plots and the soil information matrix obtained was analysed using Principal Components Analysis and Discriminant Analysis. Results showed that in the Mediterranean pastures *Cynodon dactylon* was restricted to deep, well developed soils with relatively high values of cations, conductivity and organic matter, and could be used as an indicator of such soil conditions in these grasslands. The spatial pattern of the species was analysed using New Local Variances which revealed the existence of a small-scale pattern, ranging from 8 to 18 cm, present at all levels of the analysis. The size of small-scale patterns was positively correlated with species abundance and was interpreted as a relation between plant vigour and favourable soil conditions.

Introduction

The study of the microdistribution of plant species is a subject receiving increasing attention by vegetation researchers. As Greig-Smith (1979) stated, 'one of the few generalizations that we can make about vegetation is that it is spatially heterogeneous.' The development of ecosystem structure is constrained by the spatial pattern of the environment. The study of pattern is often the key to the understanding of how ecosystems work and what kind of processes condition vegetation organization.

The spatial distribution of vegetation presents patterns which are associated with different scales of perception and study. These distribution patterns are of interest to ecological studies determining which environmental factors condition species distribution, as each factor acts on vegetation at a certain scale. The analysis of pattern in vegetation helps to set a hierarchy of factors conditioning its structure.

There is general agreement amongst various workers that at certain scales of pattern (especially larger ones) species distribution may be explained by discontinuities or gradients in environmental factors. A long list of works have proved this point for very different species, habitats and environmental factors (Greig-Smith, 1961, 1964, 1979; Kershaw, 1958, 1963; Brereton, 1971; Anderson, 1961, 1965, 1967; Hall, 1967, 1971; Sterling *et al.*, 1984). It is, however, more difficult to give a precise account of how environmental factors act at very detailed scales. Highly accurate clump size measurement is needed, and few methods of vegetation pattern analysis provide such accuracy.

Anderson (1967) has pointed out that it is always

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necessary to consider species adaptability. The small-scale distribution of a species results from interaction between internal (physiological) and external (physico-chemical) factors, together with a random factor of seed dispersal. Nevertheless it is difficult to draw a clear-cut line between action on physico-chemical (environmental) and ecological (intra- or inter-species competition for space, nutrients, light, etc.) factors affecting the small-scale distribution of species.

In the present paper the small-scale pattern of *Cynodon dactylon* L. was studied in Mediterranean pastures in Central Spain. *Cynodon* is of great importance in such pastures, not only having a very high forage value but also being highly adapted to the Mediterranean climate. It normally appears on deep, well-formed soils where the impact of summer droughts can be counteracted by the development of a deeply penetrating root system reaching the water table. Being a C_4 plant, *Cynodon* grows mainly during the summer, when light conditions are maximal and temperatures are high. Growing at such an unfavourable time of the year (by Mediterranean standards), is an adaptation which avoids competition for light, water and nutrients with other species which lack *Cynodon*'s photosynthetic efficiency at high temperatures and radiation intensities. It is also clearly restricted to rangeland areas where grazing keeps the herb layer low and permits the penetration of light. *Cynodon* is an unusual species for Mediterranean grasslands, where practically all grasses have C_3 photosynthetic pathways. It is the only C_4 species that has colonized such pastures with success.

Study area

Geomorphological processes play a very important role in the distribution of species in most Mediterranean pastures, as they control key resources needed by plants such as water and nutrients. The slope-talweg system establishes a geomorphological gradient of material erosion, transport and accumulation which creates a variety of habitats for grassland species (González Bernáldez *et al.*, 1980). This geomorphological heterogeneity strongly conditions plant distribution in water stressed areas and cannot be overlooked in ecological studies. For this reason a study area consisting of a small basin 330 m in length was chosen for the present investigation on the granitic pediment of Sierra de Guadarrama (Sistema Central, Terán, 1952; Vadour, 1969). Its general geomorphological and floristic features are already known having been studied previously (Ruiz, 1980; Peco *et al.*, 1980). The basin could be described in general terms as being formed by a higher zone with a predominance of material exportation and a high proportion of coarse grain fractions in its substrate in which the main plant species are *Poa bulbosa* L., *Vulpia myuros* (L.) C. C. Gmelin, *Hypochoeris glabra* L., *Anthemis arvensis* L. and *Cerastium semidecandrum* L., and a lower zone characterized by moist conditions, predominance of fine materials and accumulation phenomena. The most common species in this zone are *Agrostis castellana* Boiss & Reuter, *Cerastium glomeratum* Thuill, *Trifolium dubium* Sibth, *Festuca ampla* Hackel, *Juncus bufonius* L., *Scirpus setaceus* L., *Cynodon dactylon* L., *Gaudinia fragilis* (L.) Beauv. and *Trifolium squarrosum* L.

Sampling

To estimate the general abundance of *Cynodon* the basin was divided for sampling purposes into 11 different geomorphological units with the aid of infrared false colour aerial photographs, scale 1:4.000. Each geomorphological sector was sampled in at least 4 8× 8 m plots, the total number of plots studied being 54. Within each sampling plot, 5 20 × 20 cm quadrats were randomly distributed and *Cynodon dactylon*'s presence/absence data recorded. In each plot four soil samples were taken and homogenized into one sample. Two geomorphological variables were measured in each plot: height (from a 0 level set in the lowest part of the basin) and distance to the bedrock measured with the aid of micro-seismographic techniques. Details of soil analysis methods used and a full description of the basin's geomorphological, soil and floristic structure can be found in Peco *et al.* (1980).

Data for the analysis of small-scale pattern were taken in a transect of 330 m placed from the upper to the lower part of the basin. *Cynodon dactylon* abundance was recorded in 2 × 2 cm sampling quadrats along the transect, using a 0 to 2 scale of cover (0: absent; 1: 0–50% cover; 2: > 50%). As *Cynodon dactylon* was practically absent from the first 100 m only the last 230 m (11 500 quadrats) were used in the analysis. Sampling was carried out in late spring, before the species flowered.

Methods of analysis

Among the numerical methods for pattern analysis nested-block analysis of variance, introduced by Greig-Smith (1952), especially in some of its most modern versions, is still a standard method used to analyse small-scale patterns (Greig-Smith, 1961, 1964; Kershaw, 1957, 1960; Usher, 1969; Hill, 1973; Galiano, 1982).

Some of the methods proposed for the study of pattern present disadvantages as far as the measurement of mean clumping area is concerned. Greig-Smith's analysis of variance, for instance, only offers relatively rough measures of pattern as block-analysis only provides values of departure from randomness at 1, 2, 4, 8... levels, omitting intermediate readings. Hill's (1973) Local Variances can be used with continuous intervals but clump sizes detected depend on interclump distances (see Galiano, 1982; Galiano *et al.*, 1984).

So far no satisfactory or complete study of analytical methods of vegetation pattern has been carried out, although Ludwig (1979) and Cormack (1979) discussed several methods and recommended respectively Hill's Local Variances and Mead's (1974) randomization test. Unfortunately local variances fail to detect small-scale patterns and only offer reasonably reliable results for greater block sizes.

To analyze *Cynodon dactylon* data New Local Variances (Galiano, 1982) were chosen, a modification of Hill's Local Variances which corrects the unwanted interclump distance dependence present in Local Variances and permits an accurate detection of small-scale patterns.

An exploratory analysis of the data, using all the information in the 230 m sampled, showed the presence of only one peak at block size 12 (24 cm) and suggested the convenience of dividing original information into several blocks with separate analyses of each.

The following blocks of information were analysed separately:

1 block of 230 m
4 blocks of 57.5 m each
23 blocks of 10 m each.

Soils were analysed with standard techniques for the following variables: pH, texture (coarse sand, fine sand, silt, clay), % saturation, Mg^{++}, Ca^{++}, K^{+}, Na^{+}, organic matter and conductivity. The environmental matrix – of 14 variables (12 from soil analyses and 2 from geomorphological records) × 54 observations – was subjected to stepwise discriminant analysis (BMDP, 1981). The discriminant function based on the environmental variables was calculated to distinguish between plots with and without *C. dactylon.*

The soil matrix (12 soil variables × 54 observations) was also analysed using Principal Component Analysis, PCA (Hotelling, 1933).

Results and discussion

General abundance of *Cynodon dactylon* in different geomorphological sectors was clearly shown by the data. In the upper geomorphological sectors, characterised by erosion or transport of materials this species was practically absent, being restricted to deep soils.

Results of the stepwise discriminant analysis of the environmental matrix showed that the presence of *Cynodon* was strongly correlated with soil and geomorphological information (canonical correlation of 0.872). *F* values were highly significant for most soil variables, especially – and in this order – for pH, height, saturation, organic matter, conductivity, Na^{+}, Ca^{+} and clay. *Cynodon* was positively associated to all these variables except height, with which association was negative. The coefficients for the canonical variables were 4.87 for pH, 0.05 for saturation and –0.16 for height, the constant being –27.32. Figure 1 shows the histogram of the canonical variable, revealing the high discriminant power of this set of variables for *Cynodon,* the species only being absent from one plot (out of 54) where its presence could be expected.

This analysis suggests that *Cynodon* has value as an indicator of areas of soil accumulation in Mediterranean acidic substrates in Central Spain. These areas are characterized by higher values of pH, organic matter and washable cations than surrounding territory and are located in topographical depressions.

PCA of the soil information confirmed this hypothesis. Figure 2 shows the frequency of *Cynodon* (number of times the species was found in the 5 elemental sampling plots) in the 54 plots, the coordinates of which were plotted in the plane formed by the first two PCA axes referring to the soil data. Positions of the soil variables were represented in the same plane. These first two axes explain respec-

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CYNODON DACTYLON
HISTOGRAM OF CANONICAL VARIABLE


                        A
                        A
                        A A A
                     A  A AAA AA A   A             P            P  P
      A    A AA  A   AA AAAAAAAAAAA AAA       AA   P  A  P  PPP PP P   P   P   PP          P
....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+....+
  -3.5      -2.5      -1.5      -.50       .50       1.5       2.5       3.5       4.5       5.5       6.5
       -3.0      -2.0      -1.0       0.0       1.0       2.0       3.0       4.0       5.0       6.0
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Fig. 1. Histogram of the canonical variable. The occurrence of *Cynodon* was taken as the discriminant variable. A: absence of *Cynodon;* P: presence of *Cynodon.*

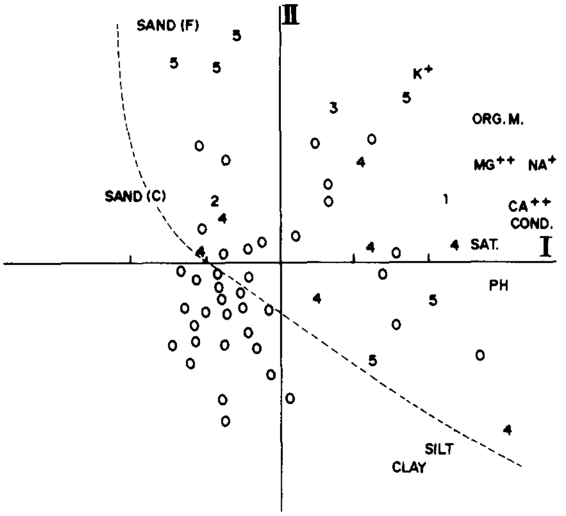

Fig. 2. Projection of plots *Cynodon dactylon*'s frequency and variables (see Table I for full names) on the plane defined by the two first axes of the PCA of the soil variables.

Table 1. Eigenvalues of soil characteristics in the first two axes of a Principal Components Analysis. Symbols used in the PCA diagram are added.

		I	II
pH	pH in water	0.74	-0.18
Sand (F)	sand (fine fraction)	-0.50	0.67
Sand (C)	sand (coarse fraction)	-0.62	0.34
Silt	silt	0.55	-0.50
Clay	clay	0.49	-0.61
Sat.	% saturation	0.70	0.01
Mg^{++}	Mg^{++}	0.72	0.26
Ca^{++}	Ca^{++}	0.87	0.16
K^{+}	K^{+}	0.47	0.64
Na^{+}	Na^{++}	0.85	0.26
Org. M.	organic matter	0.75	0.36
Cond.	conductivity	0.92	0.14

tively, 50% and 17% of the variation. Figure 2 shows that *Cynodon* was absent from the negative ends of both axes I and II. The positive end of axis I was strongly related to conductivity, Ca^{++}, Na^{+}, pH and organic matter and the positive end of axis II to fine sand and K^{+} (the eigenvectors of the variables are presented in Table 1). The negative end of axis I was related to predominance of sand and the negative end of axis II to silt and clay. The interpretation of the PCA results includes both axes at the same time. In Figure 2 a line was drawn separating the regions where *Cynodon* is absent and present respectively. Soil texture variables do not present positive high scores for both axes and the region where *Cynodon* was present is mainly related to chemical variables (K^{+}, Mg^{++}, Na^{+}, Ca^{+} organic matter, conductivity and saturation. The interpretation is that the presence of the species was dependent on the richness in ions and organic matter of the substrate and did not show any strong relation with soil texture, which agrees with previous information (Peco *et al.*, 1980).

Abundance records from the 230 m transect (which crossed areas of relatively deep soils) offered complementary information. The cover of *Cynodon dactylon* (grouped in 10 m plots) was measured in deep soils with 3 distinguishable texture categories in black and white aerial photographs (fine, coarse and irregular). The values of *Cynodon*'s cover obtained for the different geomorphological sectors were 0.265, 0.272 and 0.378 respectively (with *sd* of 0.101, 0.089 and 0.069) for the fine, irregular and coarse textures. There was a significant difference between the lowest part of the basin (characterized by a coarse texture) and the other geomorphological sectors, the lower sector showing higher species cover (up to an average of 50%). Differences in mean cover values of *Cynodon* between the coarse-texture area and the fine and irregular texture areas respectively were significant at the 95% confidence level (with values for the *t*-statistic of 2.87 and 2.26). This agrees with previous information concerning *Cynodon dactylon*'s ecological requirements in the Mediterranean climate. In relatively dry areas *Cynodon* tended to appear clearly associated with lower, well irrigated areas; its water requirements are relatively high by Mediterranean pasture standards.

Figure 3 shows the results of pattern analysis on the 230 m sampled (A) and in the four sectors into which the transect was divided for analysis (B to E). New 2-term local variances are plotted up to block size 32. In all cases a peak appeared at block sizes 4 to 8 (8 to 16 cm), which represented the main recognizable small-size clump of *Cynodon dactylon*. The elemental pattern shown in the figures may correspond to the size of a vegetative branch of *Cynodon*. Figure 4 presents a growing branch showing such a

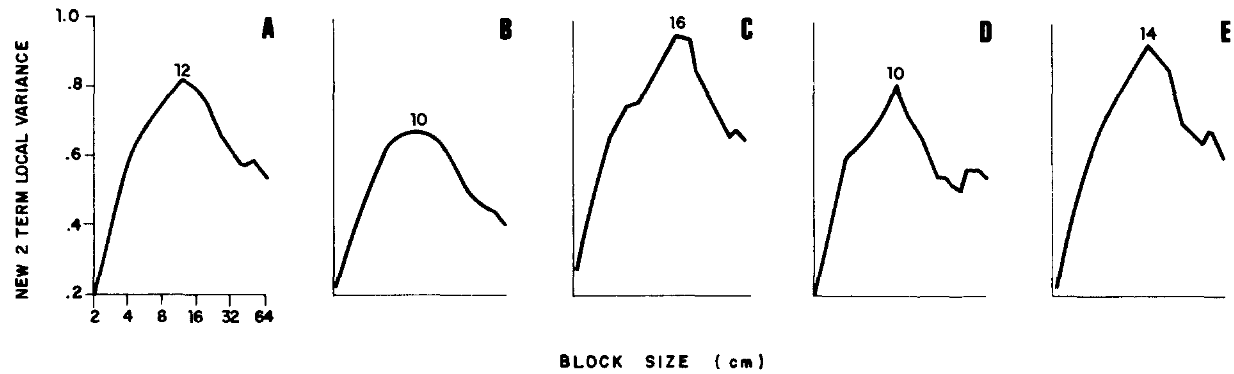

Fig. 3. Small-scale pattern of *Cynodon dactylon* in the whole transect (A) and its quarters (B to E).

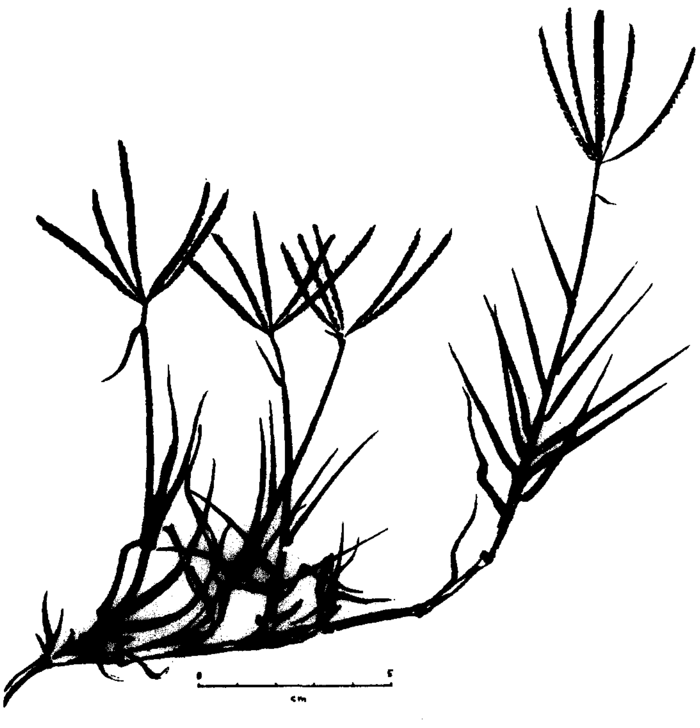

Fig. 4. Xerocopy of a branch of *Cynodon dactylon* showing the growing structure revealed by pattern detection.

structure. This species has a very clear growth pattern. From a rooted stem of *Cynodon* postrate runners tend to grow and branch in all directions. Old leaves die and disappear and the only green leaves maintained are those in the apical growing stems.

Analysis of small-size patterns in the 23 ten metre transects showed a great variety of possible elemental clumps of *Cynodon,* from 4 to 20 cm. When the first peaks in the 23 analyses were plotted against cover, (Fig. 5) they showed a relation between elemental clumping size and cover. The correlation obtained was 0.55, significant at the 95% confidence level. The regression line was $Y = 72.0X - 9.8$, Y being the expected size of *Cynodon* clumps and X the cover.

Where *Cynodon* is less abundant it may grow in less suitable conditions and therefore the vigour of growth – as shown by elemental clump size – is smaller. When the cover is less than 15% small clumps are found measuring from 8 to 10 cm. However, in plots where *Cynodon* appears with cover greater than 45% elemental clumps of 16 to 18 cm are found.

Pielou (1962) and others measured intraspecific competition in plants through the distance between any plant and its nearest neighbour. The main interest of such measures is in the evaluation of the effect of one individual on the growth of another. Overall numbers are only rarely considered. However, nearest neighbour distances can only be used when the individuals are well defined, which is not the case of most grassland species. The growing stems of many *Cynodon* individuals are intermingled in a complex mosaic and cannot be recognized individually. The data obtained could be interpreted in the sense that intraspecies competition is much reduced in *Cynodon.* Higher total cover resulted in larger clumps. The size of small-scale clumps is therefore mainly dependent on favourable soil conditions, which are in turn related to higher general species abundances. Most studies of intraspecific competition in pasture land have been carried out in pure stands of grass species seeded at different densities or in ungrazed natural grasslands. Grazing may be a mechanism reducing competition drastically by controlling total plant biomass. *Cynodon,* as most other C_4 plants, needs high light intensities during its period of growth, and in ungrazed pastures it may be strongly affected by shading by other plants.

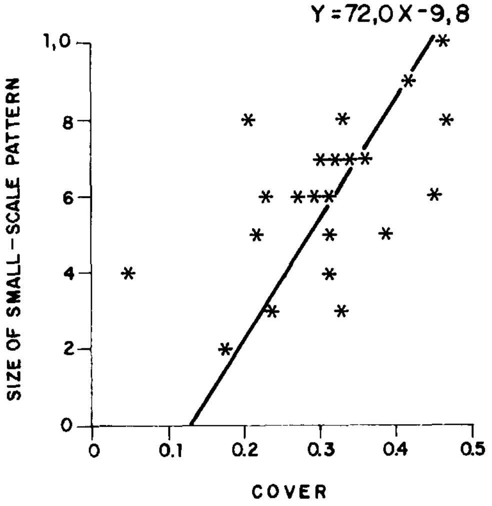

Fig. 5. Size of small-scale pattern of *Cynodon dactylon* in 23 10 m transects plotted against cover. The correlation (0.55) is significant for 95% confidence levels.

If other species are reduced through fire, which occurs occasionally in Central Spain, *Cynodon* may proliferate rapidly.

Conclusions

Cynodon has a very clear preference for deep, well-formed soils where it can resist summer droughts. This characteristic is shared with other perennial grasses in semi-arid climates. The study of the small-scale pattern of the species is a very useful tool to further investigate its growth efficiencies, provided the method of pattern analysis is sufficiently accurate and reliable.

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