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VEGETATION-ENVIRONMENT RELATIONS IN ANTHROPOGENIC GRASSLANDS OF NORTHEASTERN SANTA CATARINA, BRAZIL

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Nomenclature: Smith et al. (1982), Reitz et al. (1983) and Valls (1973).

Abstract. Anthropogenic grassland stands, surveyed over 4,000 km^2 in northeastern Santa Catarina state, Brazil, are examined based on vegetation composition and site descriptors using multivariate techniques (classification, ordination, concentration analysis). Four grassland types are revealed, differentiated by soil organic matter content, grassland age, altitude and soil texture. Inferred species responses to these factors are described.

Introduction

The grasslands of northeastern Santa Catarina are mostly anthropogenic, as the original forest vegetation (Klein 1978) has been gradually replaced by crops since European colonization in the middle of the 19th century. These grasslands have usually originated after successive cultivation, resulting in decreased soil fertility. Grazing played a crucial role in preventing forest recovery. In 1980, grasslands covered about 26% of the region (FIBGE 1983). Apart from general observations in Klein (1979) and in Smith et al. (1982), we know of no quantitative description of the grassland vegetation.

In this paper we discuss results of a survey aimed at identifying grassland types and their environmental relations within the broader framework of a research project on grassland improvement. Specifically, we apply multivariate techniques to reveal homogeneous vegetation types from a set of relevés, to detect major site factors related to the types and to study likely species responses to these factors.

Study Area

The survey covered an area of approximately 4,000 km^2 in the northeastern region of Santa Catarina state in Brazil. The area occurs from the Atlantic coast to about 600 m a.s.l. in the Itajaí river basin (Figure 1). The regional climate is humid mesothermal, with hot summers and no dry season. (Cfa type according to Köppen's classification, Trewartha & Horn 1980). Mean annual precipitation ranges from 1400 to 1900 mm, while mean annual temperature ranges from 17 to 20°C (Ide et al. 1980). Land forms are in the morphoclimatic domain of the mountain regions of southeastern Brazil, mostly originated by planation and rounding processes on weathered crystalline rocks, forming deep valleys, meandering flood plains and round hills (Ab'Saber 1971). The survey was restricted to grasslands on hills where a podzolic-latosolic dystrophic soil type prevails (Santa Catarina 1973).

The dominant potential vegetation type is a dense evergreen ombrophilous forest (Klein 1978, Veloso et al. 1991). Early studies (Veloso & Klein 1957, Klein 1979, Reitz et al. 1983) describe mature forest fragments on well drained sites on lower altitudes as characterized by *Ocotea catharinensis, Sloanea guianensis, Guapira opposita, Cryptocarya moschata, Euterpe edulis, Garcinia gardneriana, Gomidesia spectabilis* and *Bathysa meridionalis*, which are typical elements of the southern parts of the Brazilian Atlantic rain forest.

At the present, land use is mostly small farming with dairy cattle, grasslands, forage (elephant-grass, sugar-cane) and annual crops (maize, cassava, sweet potato, tobacco and irrigated rice). Forest recovery on steep slopes formerly used for crops has been observed, possibly associated with a decrease in the population working in farms (Refosco et al. 1996). Additional information about the study area is found in Pillar & Tcacenco (1987).

Methods

Sampling

The siting of the stands was systematic on the regional scale and preferential on the local scale. Using maps (scale 1:50000), a random pivot was located and a grid was subse-

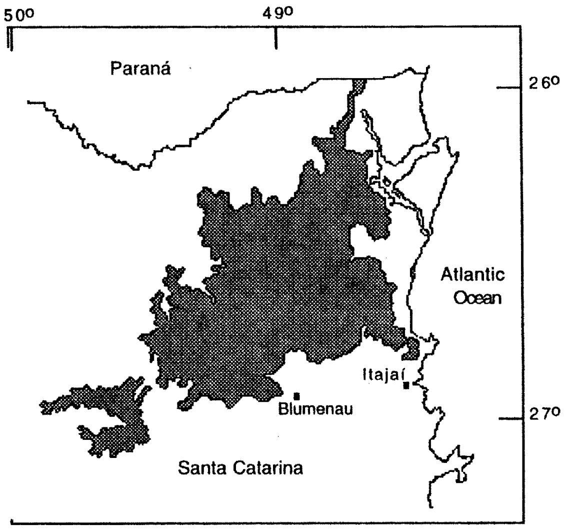

Figure 1. The study area (shaded) in northeastern Santa Catarina State, Brazil.

quently marked out with intersections at 1 minute geographic coordinates within the study area. In the field, three grassland stands on hills and with a known history of disturbances were selected closest to each intersection point. A single, relatively homogeneous 50 m x 30 m plot was established and described in each stand. In total 42 stands were surveyed in the period between October 1984 and January 1985.

The descriptions used cover of species or other higher level populations. Species cover was estimated by the point quadrat method (Mueller-Dombois & Ellenberg 1974). In each stand 150 points, at each 1m interval along three 50m transects, were recorded for species occurrence. This number of points is well above the minimum required of 90 points/stand determined in a pilot study in which a set of 300 points/stand was surveyed.

Information on environmental factors was also gathered in each grassland stand. These were altitude, precipitation, exposure, slope, grassland age, and 17 physical and chemical soil conditions. Soil analysis used the methods described in Tedesco et al. (1985). Information on the history of site disturbances and vegetation recovery was obtained by interviewing farmers.

Data analysis

Data analysis used the application programs described in Orlóci & Kenkel (1985) and Pillar & Orlóci (1993). Outliers were previously eliminated to avoid undesirable distortions (Wildi & Orlóci, 1983), resulting in a reduced data set with 37 of the 42 stands originally sampled. Grassland types were recognized, after agglomerative clustering of stands, based on compositional Euclidean distances, applying the sum of squares criterion (Orlóci 1967). Group homogeneity was tested by a randomization test as in Pillar (1996). Ordination of stands, based on covariance without standardization, used principal components analysis (Hotelling 1933). Randomization testing (Pillar & Orlóci 1996) evaluated the significance of differences in environmental conditions between grassland types.

The relationship between species performance and environment was examined by dispersion profiles generated in canonical contingency tables analysis, also known as concentration analysis (see Feoli & Orlóci 1985, Orlóci & Kenkel 1985, Pillar 1988). In this analysis stands were classified based on classes (we used 5 classes) of each environmental factor and the resulting contingency tables were subjected to analysis that decomposes the deviations from expectations in the contingency table into components. These component deviations provided the information for dispersion profiles.

Results and Discussion

Grassland origin

All grassland stands surveyed came into existence after deforestation and cropping. As far as previous land use was known by the farmers, the most common previous crops were maize and cassava cultivated in a period from one to 10 years before grassland formation. Usually after the last crop the land was abandoned and colonized by herbs and grasses, which under grazing formed a grassland vegetation. In some cases grass stocks were planted, mostly of *Axonopus obtusifolius,* a naturally occurring species in the region. Further disturbances were mainly from weed control. Grassland age varied from 4 to more than 100 years. Most grassland stands were on steep slopes having a high risk of soil erosion, in areas regarded as unsuitable for annual crops; in only four stands the slope was under 14%.

Grassland types

Table 1 and Figures 2 and 3 present the results of cluster analysis and ordination. A partition into four groups (grassland types) was chosen, inasmuch as a coarser partition would result in a sharp increase in the within group sum of squares and a finer one would be less useful in the context. Late testing for group homogeneity, using the technique in

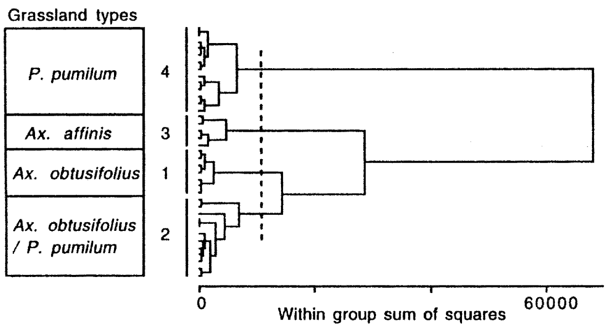

Figure 2. Cluster analysis of 37 grassland stands surveyed in northeastern Santa Catarina, Brazil. The four types referred in the text are indicated. The clustering criterion is sum of squares based on Euclidean distances (Orlóci 1967).

Table 1. Average percentage cover of species in types generated by cluster analysis on compositional data of grassland stands, northeastern Santa Catarina, Brazil. Group homogeneity test probabilities generated by randomization (Pillar 1996) are shown. The probability found is the proportion, in 1000 data sets produced under a null hypothesis of random composition, of within group maximum distances that are smaller than the one observed. The type is taken as homogeneous if the probability is not larger than the chosen threshold; if this is 0.06, only grassland type 3 is not homogeneous.

Species or species groups	Grassland types			
	1	2	3	4
Paspalum pumilum	5	22	13	50
Paspalum notatum	0	0	3	3
Paspalum conjugatum	1	1	7	0
Paspalum jesuiticum	5	5	1	2
Axonopus obtusifolius	47	35	13	12
Axonopus affinis	10	8	27	9
Axonopus spp	1	1	3	2
Panicum spp	1	1	7	1
Other grasses	1	3	1	1
Cyperaceae-Liliiflorae	23	17	15	12
Desmodium spp	2	2	6	3
Other families	4	5	5	5
Group homogeneity test ($P(d^o_{max}<d_{max})$)	0.014	0.058	0.131	0.037

Table 2. Average values of environmental variables in grassland types (see Table 1 for type description) and probabilities generated in randomization testing (Pillar & Orlóci 1996). The table shows only variables with more significant variation among types, i.e., with the lowest probabilities $P(Q_b^o \geq Q_b)$ of finding a sum of squares between types not smaller than the observed under a null hypothesis of random partition. In these, significant pair-wise contrasts between types at a probability level ≥0.1 (within parentheses) are also shown.

Variables	Grassland types				$P(Q_b^o \geq Q_b)$	Contrasts
	1	2	3	4		
Organic matter (%)	2.9	2.9	2.0	2.8	.033	2-3(.01), 1-3(.02), 3-4(.02)
Grassland age (years)	56	58	20	49	.084	2-3(.01), 1-3(.03), 3-4(.07)
Altitude (m.a.s.l.)	140	179	72	253	.085	3-4(.02), 1-4(.09)
Clay (%)	39	37	29	34	.122	1-3(.03), 2-3(.06)
Potassium (ppm)	56	50	32	54	.157	3-4(.03), 1-3(.04)
Silt (%)	19	21	20	25	.165	1-4(.06)
All 27 variables					.414	3-4(.07), 2-3(.08)

Pillar (1996), indicates that types 1, 2 and 4 are indeed homogeneous at a probability level < 0.06, while type 3 is not ($P(d^o_{max}<d_{max})$ = 0.13, Table 1). Grassland type 1 is dominated by *Axonopus obtusifolius* (average cover: 47%), and has high cover of *Cyperaceae-Liliiflorae* (23%). Grassland type 2 is a variant of Type 1, having high cover of *Axonopus obtusifolius* (35%) and *Cyperaceae-Liliiflorae* (17%) but with *Paspalum pumilum* (22%). Grassland type 3 has the highest cover of *Axonopus affinis* (27%). In addition, *Paspalum conjugatum, Panicum* spp. and *Desmodium* spp. cover are higher than in the other types. Type 4 is dominated by *Paspalum pumilum* (50%). The first two ordination components accounted for almost 80% of the total variation, reflecting along component I a sharp contrast between grasslands dominated by *Paspalum pumilum* vs. *Axonopus obtusifolius*, and along component II between grasslands dominated by *Axonopus affinis* and those dominated by *Axonopus obtusifolious* and *Paspalum pumilum*. Component III (8.9%, not shown) is mostly an expression of variation in the cover of *Cyperaceae-Liliiflorae*.

Vegetation-environment relationships are revealed by comparing the environmental conditions of grassland types.

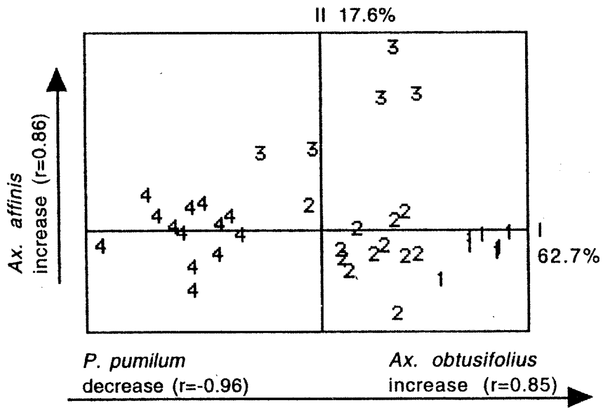

Figure 3. Ordination of grassland stands, northeastern Santa Catarina, Brazil. The ordination technique is principal components analysis based on the covariance matrix of species (Hotelling 1933). Components 1 and 2 are plotted. Types generated by previous cluster analysis are identified (1-4).

Table 2 and Figure 4 present the variables that differ significantly (based on randomization tests) among the four grassland types. The pair-wise contrasts and the ordination trends indicate that soil organic matter, grassland age, altitude, soil clay and potassium content explain vegetation variation on the second component, i.e., between grassland type 3 *(Axonopus affinis)* and the others. Due to confounding effects it is difficult to associate variation on the second axis to successional trends; grassland age is related to cropland use regime, which in turn is associated with altitude (tem-

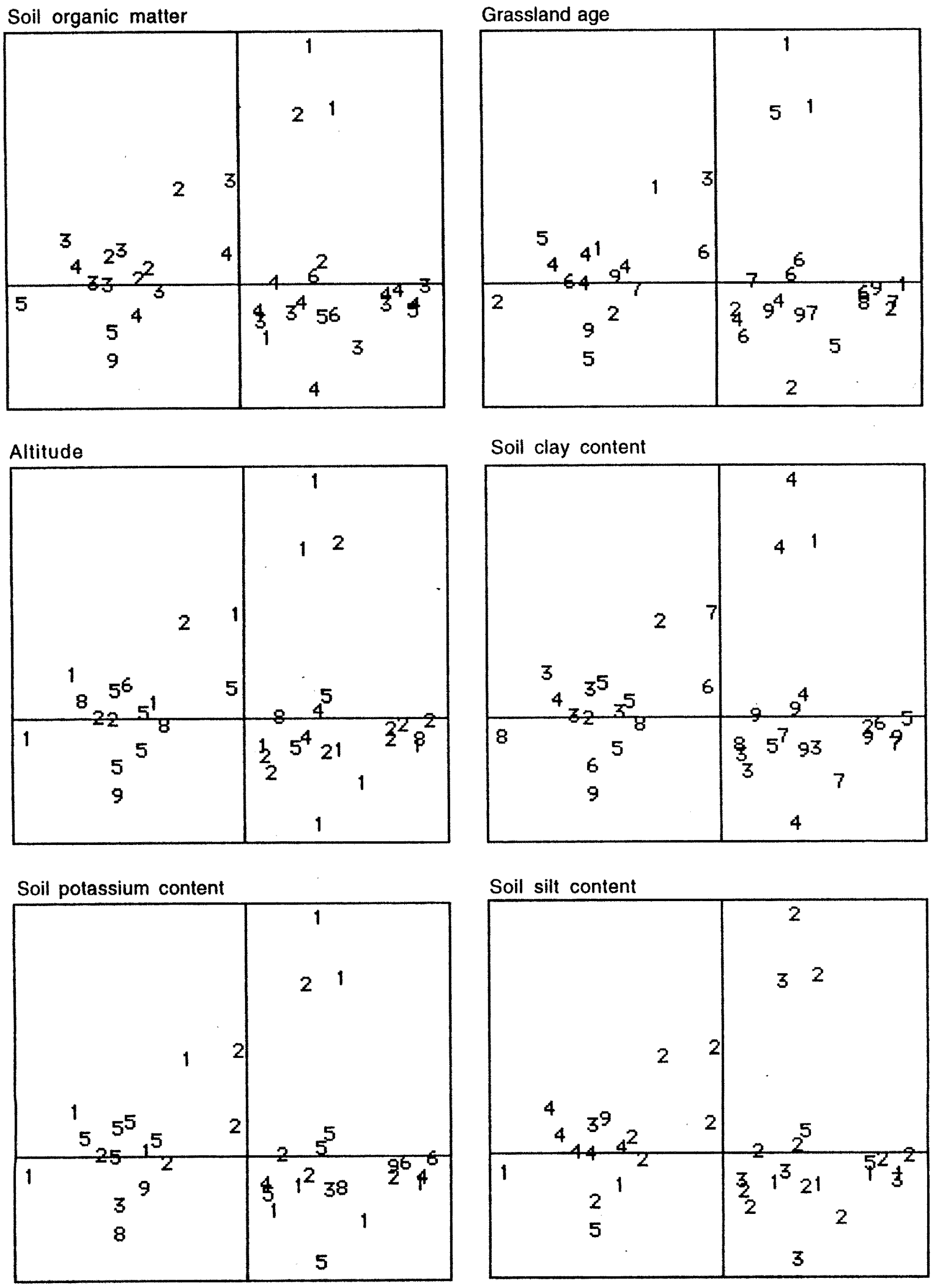

Figure 4. Vegetation-environment relationships in grassland stands, northeastern Santa Catarina, Brazil. The ordination diagram is the same as in Fig. 3, with numbers identifying the class (original values rescaled to 1-9) to which the grassland stand belongs for each variable.

perature) and soil texture; moreover, Fig. 4 (Grassland age) shows that a few younger grassland stands are also found in types other than type 1. Variation in altitude and soil silt content explains, to some extent, the vegetation differences along the first principal component of the ordination. Type 1 (*Axonopus obtusifolius*) occurs mostly at lower altitudes and on less loamy, more clayey soils, whereas type 4 (*Paspalum pumilum*) is most prevalent at higher altitudes and on more loamy soils.

Hypotheses on species responses to environmental factors

Dispersion profiles provide a useful summary of the behavior of species along environmental gradients. The technique is based on eigenanalysis. Therefore, the 'importance' of the trend expressed by a profile is proportional to the corresponding eigenvalue. Table 3 gives a summary of the first component profiles, for the 9 variables whose level of influence is greater than 45%. Some of the variables shown in Table 3 do not exhibit any definitive trend (e.g. silt and P). A convex trend is presented by *Paspalum pumilum* along the pH gradient, while *Axonopus obtusifolius, Axonopus affinis* and *Cyperaceae-Liliiflorae* present a concave trend along the same variable. A convex trend may indicate that the range of conditions detected in the survey is sufficiently wide to cover the range of conditions within which the species would occur. For some variables, linear trends may express part of this species range, either on the left side (ascending) or on the right side (descending). A concave trend may indicate competitive exclusion from the middle range of conditions.

A number of variables show interesting trends for at least some of the most important species, as summarized below:

Grassland age: the three most important species or group of species (*Paspalum pumilum, Axonopus obtusifolius* and *Cyperaceae-Liliiflorae*) increase in frequency with grassland age. Conversely, *Axonopus affinis, Desmodium* spp and *Paspalum conjugatum* decline in cover as grasslands age. It should be noted that grassland age comprises a complex of factors which interact with the vegetation through time; it roughly indicates a successional process. Species adaptations to grazing affect the successional process, since species that are more abundant in older grassland are more resistant to the high grazing pressures common to most of these stands. *Paspalum conjugatum* is a pioneer species that colonize cleared land; its exclusion from grassland after a few years may be attributable to grazing. However, *Axonopus affinis* shows a trend that is at variance with its supposed resistance to grazing as indicated in Valls (1973).

Soil organic matter content: in general species that tend to decrease with grassland age also decrease with increasing soil organic matter content; the one exception is *Paspalum pumilum.* A hypothesis is that organic matter content is a reflection of floristic composition, and not vice versa. If it is true, it can be said that old, more productive grassland (grassland types 1 and 2, dominated by *Axonopus obtusifolius* and *Cyperaceae-Liliiflorae*) have higher soil organic matter content due to litter accumulation and to animal faeces. Newer (younger) grasslands (*Axonopus affinis*) as well as those dominated by the less productive *Paspalum pumilum* have lower soil organic matter content.

Table 3. Summary of C1 profiles for species and environmental variables. See text for method explanation. Legend of profile shapes: A = ascending; As = sharply ascending; D = descending; Ds = sharply descending; Cc = concave; Cv = convex; Ss = seesaw; Fl = flat (no trend showed). The codes for environmental variables are: OM= soil organic matter percentage; AG= grassland age; Al= aluminium soil content; UM= soil moisture; SI= silt percentage; pH= soil pH; AT= altitude; P= soil phosphorus content; K= potassium soil content.

Species or species groups	Environmental variables								
	OM	AG	Al	UM	SI	pH	AT	P	K
Paspalum pumilum	D	As	As	A	Ss	Cv	As	Ss	Fl
P. notatum	D	Fl	Fl	Ds	Fl	Fl	Fl	Fl	Fl
P. conjugatum	Dd	Dd	Fl	Fl	Fl	Fl	Fl	Ss	Fl
P. jesuiticum	A	Fl	D	Fl	Fl	Fl	Fl	Fl	A
Axo. obtusifolius	As	A	Ds	As	Ss	Cc	D	Fl	A
Axonopus affinis	D	Ds	D	D	Fl	Cc	D	Ss	Fl
Axonopus spp	Fl	Fl	Fl	Fl	Fl	Fl	Fl	Fl	Fl
Panicum spp	Fl	Fl	Fl	D	Fl	Fl	D	Fl	Fl
Other grasses	Fl	Fl	D	D	Fl	Fl	Fl	Fl	A
Cyperac. -Liliifl.	A	A	A	As	Fl	Cc	D	Fl	Ds
Desmodium spp	D	D	D	D	Fl	Fl	Fl	Fl	Fl
Other families	Fl	Fl	Fl	D	Fl	Fl	Fl	Fl	D
% of the C1	81	80	71	68	60	59	54	49	49

Soil moisture: in general the same trends observed for grassland age for the most important species are observed for soil moisture, which suggests an association between these variables. This association may be a reflection of improved soil physical properties over time, resulting in increased soil field capacity and, consequently, better retention of water.

Altitude: grassland stands richer in *Paspalum pumilum* are generally found at higher altitudes (see grassland type 4 in Table 2). Although other factors associated to altitude could affect species performance, the dispersion profiles may be a reflection of adaptation of *Paspalum pumilum* to colder winter temperatures.

Aluminum: The major species present showed contrasting relationships to aluminum. *Paspalum pumilum* and *Cyperaceae-Liliiflorae* tend to increase in cover with increasing soil Al, whereas *Axonopus obtusifolius, Axonopus affinis* and *Desmodium* spp. show the opposite trend.

Potassium:. Axonopus obtusifolius cover increases with increasing soil potassium, while the opposite trend is seen in the *Cyperaceae-Liliiflorae.*

Some remarks

It is expected that the most important environmental factors in the dispersion profiles analysis should also explain the vegetational trends indicated by classification and ordination. This is partly the case for the variables grassland age, soil organic matter, and altitude, but not for the others. One reason for this is that in the former analyses site factors that could explain vegetation variation are sought; they are constrained by the data structure revealed by the principal components or by the number of groups chosen. By contrast, in dispersion profile analysis grassland stands are classified based on environmental gradients, and vegetational trends along these gradients are examined. This supports the idea of a multi-technique approach (Wildi & Orlóci 1990) for exploration of data. Another reason may be the large plot size used (1500 m^2). A smaller plot size may have increased the 'sharpness' of the vegetation and environmental data structures by reducing within-plot variation (Podani et al. 1993).

Finally, implications inherent to the analytical approach we used should be mentioned. First, the trends detected through dispersion profiles do not indicate the actual response of the species to the factor being considered, but rather the predictiveness of species performance. A controlled experiment would be required to test these predictions. Second, extrapolation beyond the actual conditions observed in the survey is not valid, since the survey may not represent the entire range of conditions within which the species could occur, nor all the combinations of conditions (see also Feoli & Orlóci 1985). Third, the analytical methods used assume linear relationships among biotic and abiotic variables, while nonlinear relationships are expected in the data (see Beals 1973, van Groenewoud 1976, Orlóci 1979). However, for all these implications, it seems reasonable to judge the utility of a technique by its ability of revealing structures in the process of data exploration.

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