COENOSES 12(2-3):63-66, 1997
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DIRECTIONALITY OF SUCCESSION AFTER GRAZING EXCLUSION IN GRASSLAND IN THE SOUTH OF BRAZIL

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Keywords: Convergence, Divergence, Grassland, Stabilization, Succession.

Abstract. The research involved a grassland area at UFRGS Agronomic Experimental Station in Rio Grande do Sul, Brazil. The floristic survey in 1984, when the area was under grazing, was compared with the surveys of 1986, 1988 and 1992, when cattle was excluded. The vegetation analysis used 16 permanent plots (0.25 m^2) on which the cover of species was scored. The objective was to trace the dynamics of the vegetation. Ordination analysis allowed us to observe directional tendencies, and randomization tests verified divergence and the lack of stabilization of the community.

Introduction

The grassland communities of southern Brazil are usually grazed and this is determinant to maintain their characteristics. The exclusion of grazing animals in a natural field site, after a long history of grazing, is expected to lead to changes in the structure, richness, species coverage and dominance in the community. Changes of this kind were in fact observed by Boldrini & Eggers (1996), involving increase and decrease of dominant species cover as well as in the appearance and disappearance of species.

With grazing exclusion, Sala et al. (1986) observed much change in the vertical structure and variation in the distribution of basal area. Although the authors observed a small change in the total basal area, a predominance of a large number of small tussocks in the grazed sites and a smaller number of larger ones in the excluded areas were characteristics. A decrease in the coverage of grasses and an increase in the contribution of dicotyledons was observed by Facelli et al. (1988) in an area that had been grazed. After nine years of treatment, the grazed plot had 41% coverage of monocotyledons compared to 98% coverage of the ungrazed one.

Substantial changes in the structure and composition of the vegetation, in a non-grazing period of 6 years, were also seen in a New Zealand grassland, indicating that the presence of sheep and rabbits is the main factor maintaining the community (Allen et al., 1995).

Besides the direct comparison of grazed and non-grazed areas, it is possible to analyze a temporal sequence of data to evaluate the characteristics of the succession process. Succession is influenced by stochastic influences in the colonization phase in which the presence of diaspores and the germination capacity of the seeds play a preponderant role. However, after this initial period, well-organized and strongly directional stages follow (Anand & Orlóci 1997, Orlóci 1993, Orlóci et al. 1993). Clement's succession model considers the process directional and monoclimax, therefore convergent in a regional scale. However, Glenn-Lewin & van der Maarel (1992) have highlighted that successional histories make multiple trajectories, identifying community patterns such as convergence, divergence or cycles. These depend on the initial conditions and on the succession mechanisms, besides the diversity of species, the landscape complexity and the isolation of the community.

The results of temporal variation in the relative abundance of individuals of different species in the community that lead to changes in the community structure are easily observed, but not those changes in the species composition that are causing no modification in the structure. Yet the latter can be also very important (Whalley 1994).

A temporal data analysis was employed by Facelli & D'Angela (1990), who have followed the initial stages of a succession in the Argentinean Pampa. Alterations in the community were strongly directional, apparently not influenced by random tendencies such as variations in precipitation. Also, there were no differences between dissimilarities during the studied years so to indicate convergence or divergence among the sample units. The present paper focuses on the vegetation succession process in an exclusion area and presents results which go steps further in several respects. Its aims are (1) to verify whether the succession process is directional, that is to observe if changes in vegetation follow a determined direction throughout time; (2) to verify whether the process is convergent or divergent, that is to observe if sites become more similar or dissimilar as time passes; and (3) to verify whether the process is approaching stabilization, that is to observe if after initial fast changes the process decelerates and then reaches a state where the simple relationship of composition changes and time is lost in the sense as Orlóci (1993) describes it in the example of an Atlantic heathland.

Material and methods

The site

The study area is at the UFRGS Agronomic Experimental Station (30^0 05' 27" S and 51^0 40' 18" W), in Eldorado do Sul, Rio Grande do Sul, Brazil. The size of the experimental area is 1134 m^2. It is under a subtropical wet climate, with average annual precipitation of 1440 mm and monthly average temperatures of 9^0C to 25^0C (Bergamaschi & Guadagnin, 1990). The soil type is Dark Red Podzolic (Camargo et al., 1987); Rhodic Paleudult (Soil Survey Staff, 1990), characterized by being deep and well drained.

The data

The vegetation was evaluated through 16 permanent plots measuring 0.5 x 0.5 m^2, disposed over two transects. In October 1984, when the area was continuously grazed by cattle, the plots were settled and the first survey was made (Boldrini & Miotto 1987). In March 1985 the area was fenced, henceforth preventing animal grazing and trampling. Surveys were made in 1986, 1988 and 1992. Evaluations were made on cover of phanerogamous species, using the Daubenmire scale (1968).

The analysis

Succession of vegetation was analyzed with a view at changes in the species composition over 8 years. The data from the 1984, 1986, 1988 and 1992 surveys were arranged in a matrix with 64 sample units (16 plots x 4 years) and 134 species. The data matrix was submitted to ordination by principal coordinates analysis based on chord distances between sample units. The resulting diagrams were analyzed with special attention paid to tendencies of directionality or randomness.

The convergence and divergence test examined whether the differences of species composition between plots in 1984 differed from those between the same plots in 1992. The test involved a Euclidean distance matrix between sample units in each year and was of the randomization type (Pillar and Orlóci 1996). Each pair of permanent plots was considered as a block (16 x (16 -1) = 120 blocks) and the years were compared.

Randomization test was also employed to probe for stabilization. The test examines if the differences observed between 1984 and 1988 deviated significantly from the ones observed between 1988 and 1992. In the course of this, Euclidean distances between different periods of the same plot were compared, each plot being considered as a block. The software package MULTIV (Pillar 1996) performed the analyses. The randomization tests used 1000 iterations.

Results and discussion

The first two ordination axes accounted for 22% of the total variation in the data. In the diagram (Fig. 1), the first axis separates the sample units according to period. Most of the sample units of the 1984 and 1986 surveys are located on the right side. These represent the grazing period and the period soon after the exclusion of grazing. On the left side are the sample units of the 1988 and 1992 period. The graph shows that compositional changes in time followed a directional trajectory along the first axis. This axis has a high positive correlation with *Paspalum notatum* (0.86), *Eragrostis neesii* (0.60) and *Paspalum paucifolium* (0.54). Associated with these species are *Stylosanthes leiocarpa* (0.49), *Richardia humistrata* (0.47), *Richardia stellaris* (0.47), *Coelorhachis selloana* (0.46), *Danthonia cirrata* (0.45) and *Helianthemum brasiliense* (0.43) characterizing a grazed, shortgrass field. This species group is typical of 1984 and, less intensely of 1986. Negative correlation with the first axis was particularly noted for *Andropogon lateralis* (-0.80) and *Aspilia montevidense* (-0.40). These species are typical of the years 1988 and 1992. *Andropogon lateralis* forms erect tussocks and characterizes tallgrass fields with low or no grazing pressure.

Interesting to mention the close relationship of plant physiognomy and the first axis. Small and creeping species have larger cover in the sample units arranged on the right side of the first axis. *Paspalum notatum* dominates in these sampling units. The cespitous tall species have higher cover values in the sample units on the left side, although in this case there is no remarkable dominant species.

The second axis presents positive correlation with *Elyonurus candidus* (0.66), *Leptochoryphium lanatum* (0.53), *Clitoria nana* (0.44) and *Scleria hirtella* (0.42) and negative correlation with *Andropogon lateralis* (-0.47), *Dichondra sericea* (-0.44), *Galium uruguayense* (-0.44), *Chevreulia acuminata* (-0.38) and *Axonopus affinis* (-0.35). The hypothesis that the second axis is related to soil moisture is supported by the fact that the species with negative correlation are typical of moist sites while those that presented higher positive correlation values are typical of drier sites (personal observations by the authors, Pillar et al. 1992). Regarding this, it is important to note that soil moisture may have been influenced by the proximity of a large contiguous experimental land that used irrigation during a specific period. The plots that presented species typical of high moisture regimes were located nearer to this area.

In general, the vegetation in the plots presented directional changes throughout the years. This can be seen from the diagram in Fig. 1. However, four plots (1, 8, 12 and 13) differed in the magnitude of change. Plots 1 and 13 had the dominance of *Paspalum notatum* during all the years. Plot 1 was located near the fence and was still being grazed. For plot 13 there is no clear explanation for this apparent inertia in vegetation change. Plots 8 and 12 presented a high coverage of *Andropogon lateralis* right from the beginning of the experiment, since they were probably in patches already under a low level grazing. Zobel et al. (1996), using three experimental treatments during a period of four years, also observed directional changes in succession.

The randomization test indicated significant difference between the plots in 1992 (1.21) and in 1984 (0.96), showing that divergence occurred (Table 1). Facelli & D' Angela

Table 1. Randomization testing of the convergence/divergence hypothesis between 1984 and 1992. The probability is low and, therefore, divergence is significant. The average distance between plots was 0.96 in 1984 and 1.21 in 1992, indicating divergence.

Source of variation	Sum of squares (Q)	Probability P($Q^o \geq Q$)
Blocks	1.3283	
Between years	3.9527	0.001 ***
Within years	1.0434	
Total	6.32 45	

Table 2. Randomization testing for stabilization, comparing periods 1984-1988 and 1988-1992. The probability is high and, therefore, there was no stabilization. The average distance of the trajectories was 0.9144 in 1984-1988 and 0.9152 in 1988-1992.

Source of variation	Sum of squares (Q)	Probability P($Q^o \geq Q$)
Blocks	0.4918	
Between periods	4.9533e-06	0.983
Within periods	0.2467	
Total	0.7385	

(1990) in a similar study verified neither convergence nor divergence between the sample units, when the initial and the final periods of the survey were compared. The authors mentioned that the small number of plots might have influenced their results. Menges et al. (1993) found larger differences between types of vegetation affected by different histories of fire events than over a span of two decades. The authors reported that convergence was evident only within some areas and that shifts in similarity among vegetation types were small.

Other studies present different results indicating that succession can be convergent, divergent or neutral and factors such as temporal and spatial scales of observation, availability of resources and ecological amplitude of dominant species can determine this kind of behavior (Facelli & D'Angela, 1990). In the present paper, the appearance of divergence seems to have been influenced by the size of the sample unit. The 0.25 m^2 plots turned out to be small regarding the size that the plants reached. The plots that first displayed dozens of species lost richness, sometimes occupied by a large dominant tussock.

The idea of multiple trajectories has been incorporated into vegetation dynamics theory. Secondary succession can show multiple compositional trajectories in response to fire and grazing. Physiognomic convergence, diversity and other community properties are more questionable, depending on observation scale (Glenn-Lewin & van der Maarel, 1992).

Stabilization, or a slowing down in the process was not verified. There was no significant difference between the

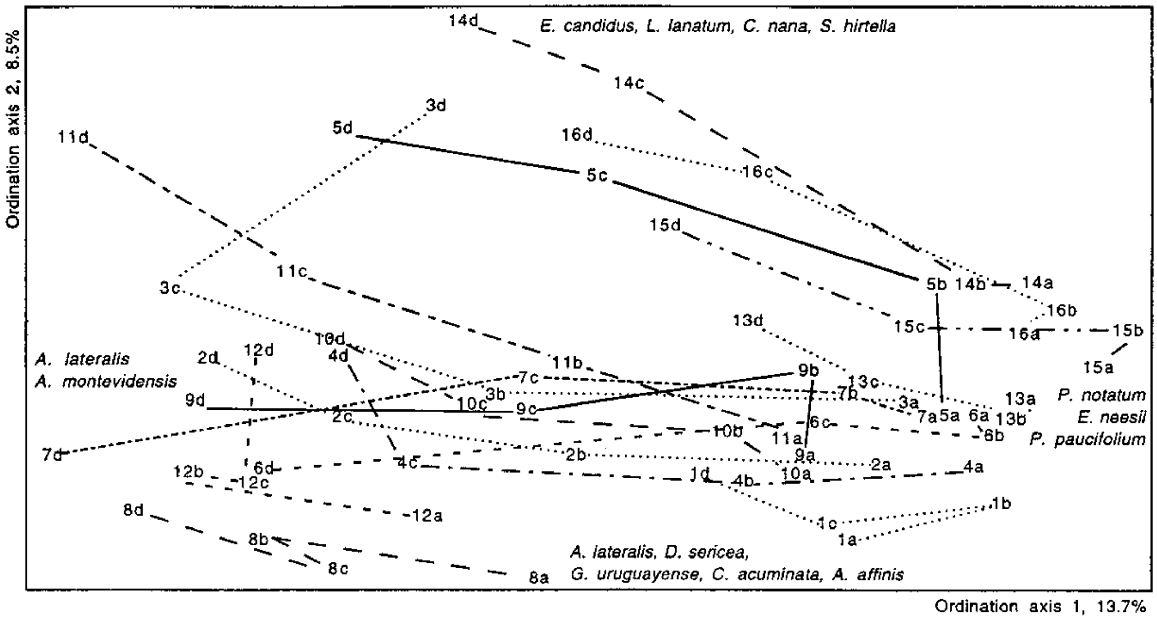

Figure 1. Ordination diagram of the plots. The method is Principal Coordinates Analysis. The data are from four years of survey (a=1984; b=1986; c=1988; d=1992). Lines connect the states of the same plot. The species most correlated to the ordination axes are indicated where they are expected with higher cover.

trajectories of the years 1984-1988 and 1988-1992 (Table 2). The same result was found by Facelli & D'Angela, in a succession study followed for five years, comparing distances each year. As these authors highlighted, these results sound contradictory with the theoretical expectation that successional rates should be high in the initial stages and decrease rapidly with time. Nevertheless, Allen et al. (1995), after a six-year exclusion, verified a slight tendency of vegetation stabilization. Also, Zobel et al. (1996) in a four-year experiment observed rapid changes in the initial stages. Some considerations can be made regarding the subject. In the case of Facelli & D'Angela's (1990) paper, the five-year survey may not have been sufficient to substantiate a stabilization. On the other hand, in the present paper, the comparison of long periods (four years each) can have lessened the differences of shorter periods. Annual surveys and comparisons on that basis would have been ideal. In fact, based on annual surveys Orlóci & Orlóci (1988) found the onset of a new stability after about 8 years in Atlantic heathland after fire and reduction of grazing. Anand & Orlóci (1997) discuss the chaos theoretical implications of this in detail. For a discussion of related topics, particularly a set of conjectures and scenarios we refer to Orlóci (1993).

Acknowledgments: We thank Valério De Patta Pillar for suggestions on the statistical analysis and comments on the manuscript.

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