SPATIAL PATTERNS AND DIVERSITY IN A POST-PLoughING
SUCCESSION IN HIGH PLATEAU GRASSLANDS (PAMPA DE SAN
LUIS, CORDOBA, ARGENTINA) *

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Abstract: Spatial arrangement and diversity along a post-ploughing succession are analyzed in a plateau at 1800 - 1900 m altitude in Central Argentina. Four successional stages were simultaneously studied: I (1 year of abandonment after ploughing), II (3-5 years), III (25 years) and IV (40 years). Detrended Correspondence Analysis and diversity analysis, comprising species diversity, spatial diversity and mean spatial niche width, were applied.

It is concluded that (i) Spatial organization of grassland changes with succession: during early stages vegetation distribution follows a topographical gradient from upper to lower positions on slopes, whereas mosaic patterns prevail in late successional stages. (ii) As succession advances, species diversity increases, making us reject the hypothesis that species diversity decreases with succession as a result of the dominance of the grass Deyeuxia hieronymi. This process is associated with a progressive reduction of mean spatial niche width.

Introduction

The aim of this investigation was to describe the variability in spatial distribution of grasslands along a post-ploughing succession in the mountains of Central Argentina. In the upper part of Córdoba mountains, ploughing can only be attained at high plateaus. Consequently, Pampa de San Luis is one of the few areas within the Grassland belt where post-ploughing successional changes can be studied.

Menghiet et al. (1988 a) and Cabido et al. (1987) agree that mosaic patterns prevail in mature grasslands from high plateaus at 1000 and 2100 m altitude in Córdoba mountains. This pattern is probably arising from a biological source: the presence of large perennial grasses determinates patches of tall grassland which alternate with lower grassland or turf units.

Acosta (1988) concludes that regardless of altitude, stabilized grasslands on the same substrate tend to exhibit similar organizational patterns. However, in the case of post-disturbance succession, several authors report that grassland structure suffers significant changes (De Pablo et al., 1982; Sterling et al., 1984; Facelli et al.,

* There is not a published flora from Central Argentina. When it has been possible, nomenclature follows Cabrera (1963, 1965 a, 1965 b, 1967, 1968 and 1970). Complete list of recorded species in the study area is available for request.
1987). According to them, changes on disturbed grassland communities can be expected not only at species composition level, but also at their spatial arrangement. In consequence, the study of succession in this paper was approached from two viewpoints: floristic composition and diversity parameters.

With respect to species diversity variations in different successional stages, two general models can be mentioned: (i) Authors like Odum (1960), Margalef (1969), Reiners et al. (1970), Mellingler and Mc Naughton (1975) predict an increase in species diversity as succession advances, as a result of the progressive reduction of effective niches by competition. (ii) Other authors (Peet, 1974; Glenn-Lewin, 1977; Grime, 1979; Houssard et al., 1980) argue against monotonic diversity increase as succession advances. They favour a decrease of diversity in advanced stages as a consequence of the dominance effect of certain populations within the community.

In herbaceous communities, this action is exerted by plants which accumulate large amounts of biomass (Nichols and Monk, 1974; Bazzaz, 1975; Facelli et al., 1987). These plants are "competitors" in the sense of Grime (1979) or "good competitors for light" according to Tilman (1982).

This report is based on the following hypothesis:
- According to Acosta (1988) we may expect a mosaic pattern for the mature stages similar to that exhibited by high plateau grasslands at lower altitudes.
- It is expected that, as a result of ploughing, the mosaic pattern will disappear during early successional stages. It is interesting to find out how long it would take to recover its original structure.
- Changes in spatial organization should be accompanied by variations in species composition, whether they are related to floristic or to relative abundance changes.
- Spatial segregation of species would increase as grassland recovers its original pattern of organization. If so, a decrease in spatial diversity may be predicted, as well as a consequent reduction in the mean spatial niche width.
- The tall tussock grass *Deyeuxia hieronymi* would become dominant during late successional stages. It is interesting to find out which diversity model grassland behaviour matches. Based on the monotonic diversity increase hypothesis, a rising species diversity $H(E)$ can be expected towards late successional stages. As an alternative hypothesis, $H(E)$ would fall due to the influence of dominant *D. hieronymi*, as succession advances.

**Study area**

Pampa de San Luis is a plateau located at 1800-1900 m altitude in the Central chain of Córdoba mountains, the Sierras Grandes (31° 20' S and 64° 45' W). Relief is slightly ondulated, with slopes around 5-7%. It has a thick layer of modern sediments, which makes horticulture and introduction of forage species possible through tilling. There are no climatic records for the area. However, Cabido et al. (1988) defined the climate, according to Köeppen (1948) as temperate rainy, with dry cold winter and short cool summer.

From a phytogeographical point of view, the area has been included by Luti et al.
(1979) in the Grassland belt, the upper vegetation zone of Córdoba mountains. Agriculture use has brought about a vegetation complex with several post-disturbance situations. Cabido et al. (1988) describe the vegetation of Pampa de San Luis and discuss successional status of surveyed communities. They suggest that the community dominated by the tall tussock grass *D. hieronymi* (a typical member of the Grassland belt) is the closest to potential vegetation within the area.

**Methods**

*Experimental design*

A statical approach (*sensu* Austin, 1977) was carried out: simultaneous sampling of neighbouring areas with different time of abandonment, which reduces the effect of climatic variations and enables to obtain satisfactory results in just one sampling period. Samples were taken in summer, during January, in order to prevent phenological differences among them.

Four different post-ploughing situations were found: stage I (1 year of abandonment after ploughing), stage II (3-5 years), stage III (25 years) and stage IV (40 years). The absence of intermediate stages between III and IV is due to the recently renewed interest in agricultural activities which was dropped in the 60' and reactivated only five years ago. All grasslands sampled were free of grazing and had not been burnt in the last ten years.

For general sampling design, criteria already applied in grassland surveys in Córdoba mountains were used (Menghi et al., 1988 a, 1988 b; Acosta, 1988). For each successional stage, sites including complete slopes of about 5% inclination were considered, in order to allow the expression of geomorphological dynamics. Stratified sampling based upon phytophysiognomic features was applied to the four stages. Within each stage, 3 x 5 m sampling plots were placed. Presence of plant species was recorded in all eight 20 x 20 cm sampling quadrats randomly distributed within each sample plot. The final expression of species abundance was a frequency value, ranging from 0 to 8. Details of sampling design are shown in Table 1.

*Data analysis*

Floristic composition and some aspects of spatial arrangement were analyzed by means of Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1981). Diversity parameters were studied following Pielou (1975, 1977) and Pineda et al. (1981) guidelines. According to these authors, total diversity may be subdivided into uncertainty about species richness and evenness $H (E)$, as well as uncertainty about spatial distribution of them within the community $H (P/E)$, defined as spatial or pattern diversity. The expression $A = H (P/E) / \log_2 N$, being $N$ the number of plots, is considered by De Pablo et al. (1982) as the mean width of spatial niche and is similar to niche width proposed by Pielou (1977).
Table I — Design of sampling carried out in Pampa de San Luis, in four successional stages, recorded in a single growing season: I = 1 year of abandonment after ploughing; II = 3-5 years; III = 25 years; IV = 40 years.

### Results and discussion

#### Floristic analysis

Figure 1 shows the projection of sample plots on the plane defined by the first two DCA axes. It may be noticed that axis I discriminates different successional stages: on the right extreme, stage I plots (1 year after abandonment) are concentrated; towards left, stage II plots (3-5 years) appear clearly separated from stages III and IV plots (25 and 40 years of abandonment, respectively). Stages III and IV plots are distinguished by axis II of DCA. Floristic heterogeneity within each stage (reflected on plots dispersion) diminishes as succession progresses.

Table 2 shows species associated to each successional stage defined by means of DCA. It may be noticed that stages I, II and IV are characterized by the occurrence of several "exclusive" species (i.e. species found in only one successional stage). For stage III only one "exclusive" species can be mentioned, and a few associated ones, even though there are several associated species shared with stages II and IV. The number of "exclusive" species is the same for stages I, II and IV. However, when comparing it with the total number of species found in each stage, it is found that
<table>
<thead>
<tr>
<th>STAGE I</th>
<th>STAGE II</th>
<th>STAGE III</th>
<th>STAGE IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>N° species: 42</td>
<td>N° species: 69</td>
<td>N° species: 54</td>
<td>N° species: 95</td>
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<tr>
<td>% &quot;exclusive&quot; species: 19</td>
<td>% &quot;exclusive&quot; species: 10</td>
<td>% &quot;exclusive&quot; species: 1.25</td>
<td>% &quot;exclusive&quot; species: 7.4</td>
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<tr>
<td>* Muhlenbergia ligularis</td>
<td>* Gallinsoga parviflora</td>
<td>* Paspalum dilatatum</td>
<td>* Gentianella achalensis</td>
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<td>* Zephyranthes longistyla</td>
<td>* Ambrosia tenuifolia</td>
<td>* Eleocharis dombeyana</td>
<td>* Sorghastrum pellitum</td>
</tr>
<tr>
<td>* Glandularia dissecta</td>
<td>* Verbena litoralis</td>
<td>* Cyperus reflexus</td>
<td>* Stipa filiculmis</td>
</tr>
<tr>
<td>* Nierenbergia hippomanica</td>
<td>* Medicago lupulina</td>
<td>* Carex macrorrhiza</td>
<td>* Bromus auleticus</td>
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<tr>
<td>* Polygonum aviculare</td>
<td>* Chenopodium chilense</td>
<td>* Poa resinulosa</td>
<td>* Carex boliviensis</td>
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<tr>
<td>* Lepidium bonariense</td>
<td>* Carduus nutans</td>
<td>* Carex boliviensis</td>
<td>* Grindelia globulariaefolia</td>
</tr>
<tr>
<td>* Solanum sp.</td>
<td>* Brassica rapa subsp. sylvestris</td>
<td>* Stipa-trichotoma</td>
<td>Bothriochloa saccharoides</td>
</tr>
<tr>
<td>* Euphorbia sp.</td>
<td>Acicarpha tribuloides</td>
<td>Pratia hederacea</td>
<td>Stipa-trichotoma</td>
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<tr>
<td></td>
<td>Cyperus phaeocephalus</td>
<td>Cuphea glutinosa</td>
<td>Pratia hederacea</td>
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<td></td>
<td>Cyperus manimae</td>
<td>Bidens triplinervia var. macrantha</td>
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</tr>
</tbody>
</table>

* "exclusive" species (species recorded exclusively in one successional stage)

Table 2 — Associated species to four successional stages in Pampa de San Luis: I = 1 year of abandonment after ploughing; II = 3-5 years; III = 25 years; IV = 40 years.
floristic change is more evident for stage I, decreasing throughout III and IV. For stage II, floristic change is very low, since only 1.25% of species is not found within other stages of succession.

During early stages (I and II), floristic changes occur, with species typical for each particular age of abandonment. Later on, these changes become gradual, with rearrangement of shared species (stage III) until a definite floristic composition is reached again in stage IV.

Spatial arrangement analysis

Figure 2 shows the projection of plots corresponding to the four successional stages individually considered on the plane defined by the first two axes of DCA. Figure 2A corresponds to stage I, where no spatial structure is clearly defined. Yet, there is a weak trend along the first axis to distinguish upper and lower topographical positions on slopes.

During stage II (Figure 2B) there is a clear discrimination along axis I of upper and lower positions, within a physiognomically homogeneous grassland.

Stage III (Figure 2C) evidences a similar segregation of upper and lower sectors on slopes along the first DCA axis. However, two different patches can be distinguished along axis II: plots from short grassland and those corresponding to...
Finally, in stage IV (Figure 2D), DCA first axis tends to draw apart short grassland patches from tall grassland ones, whereas axis II separates upper and lower topographical positions. This successional stage, which comprises the most stabilized situation found in the area, shows the typical pattern exhibited by high plateau grasslands reported for other altitudinal levels in the mountains of Córdoba (Cabido et al., 1987; Menghi et al., 1988a). These results agree with those of Acosta (1988), who pointed out that stabilized grasslands communities on the same geological substrate exhibit similar spatial patterns regardless of the altitude.

Changes in grassland spatial organization along time suggest that the main factors conditioning its arrangement are not the same in different successional
stages. Ploughing eliminates coarse-grained mosaic typical of late stages, replacing it by a different design, that follows topographical gradient and is related to water and nutrients flow from upper exportation areas toward lower accumulation ones. This process is favoured by ploughing carried out following topographical gradient, with furrows running down slope.

Spatial arrangement of vegetation is restablished with time, and during stage III the pattern closely resembles that of a stabilized grassland. However, mosaic pattern is not so definite as for stage IV, and several floristic differences still remain.

The trend of structural change detected in this study is in agreement with the general guidelines of Pineda et al. (1981), De Pablo et al. (1982), Sterling et al. (1984) and Peco and Pineda (1987), particularly in relation to the drastic disturbance in grassland spatial patterns caused by ploughing. It is worth noticing, however, that in the cases reported by these authors the final result is not a mosaic, but a structure related to the topographical gradient, since spatial organization of grasslands seems to be basically determined by the nature of the substrate.

Structural analysis of different successional stages is complemented with analysis of spatial diversity, shown on Figure 3. Pattern diversity diminishes as succession advances. This fact supports the prediction of a higher spatial heterogeneity, and consequently a higher segregation of species, towards late successional stages. Results agree with those reported by De Pablo et al. (1982), Sterling et al. (1984) and Peco and Pineda (1987). Mean spatial niche width decreases with succession, suggesting an increasing in the proportion of specialist species from a spatial viewpoint. Further analysis should elucidate whether there are generalist species in the first stages, which are replaced by specialist ones as succession advances, or else the same species behave as generalists or specialists at different stages, modifying their spatial niche width as resources distribution changes.

Species diversity analysis

Species diversity $H(E)$ shows a general trend towards increase from early to late successional stages (Figure 3 A), thus rejecting the idea of the dominance effect of $D. hieronymi$ and the consequent exclusion of other species.

An analysis of plots belonging to tall grassland patches leads to convergent results: specific diversity rises with succession, showing there is no progressive exclusion of species even within tall grassland patches (Figure 3 B). Large perennial grasses might bring about certain microhabitat conditions (such as water and nutrients uptake, protection, spatial support) that would favour an increase in species diversity. Similar results (specific diversity increase during advanced successional stages with the occurrence of tall tussock grasses) have also been reported by Menghi et al. (1988 b).

The progressive increase in diversity, together with the decrease in mean spatial niche width would support the ideas of several authors (Odum, 1960; Margalef, 1969; Reiners et al., 1970; Mellinger and Mc Naughton, 1975), about diversity
monotonic increase as succession advances. It may happen that stage IV has not yet overcome the inflexion point of diversity curve suggested by the second model, and predicted diversity decrease might occur in later successional stages. After several years, *D. hieronymi* might advance over the short grassland, changing the mosaic appearance into that of a continuous tall grassland. This finding would be supported by the presence of small *D. hieronymi* individuals out of tall grassland patches. Further studies on successional behaviour of these grasslands should test these assumptions and whether the changes, if any, are related to a fall in species diversity as result of dominance.

**Conclusions**

- Typical mosaic spatial arrangement found in plateaus at 1000 and 2100 m also occurs in stabilized grasslands at 1800-1900 m altitude. This finding supports the idea that the nature of the substrate is the main factor conditioning grassland spatial arrangement in Córdoba mountains.

- Spatial organization of stabilized grassland is eliminated by ploughing and does not restore during the first five years of abandonment. Later on, the arrangement tends to recover. However, after twenty five years of abandonment, floristic and diversity differences remain.

- Differences in species composition among successional stages are predominantly expressed as floristic changes, mainly during early stages. As succession progresses, spatial rearrangement of shared species becomes more significant, so increasing their habitat segregation and showing higher specialization from a spatial
viewpoint.

- Species diversity rises with succession. Therefore, no evidence of *D. hieronymi* is observed that might prevent coexistence with other species within grassland.

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