Competition and Coexistence in a North Carolina Grassland: I. Patterns in Undisturbed Vegetation

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COMPETITION AND COEXISTENCE IN A NORTH CAROLINA GRASSLAND

I. PATTERNS IN UNDISTURBED VEGETATION

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SUMMARY

(1) The phenological and spatial patterns of the plant species found in a mown field in the Piedmont region of North Carolina were described, as part of a study of the nature of the interactions among the plant species in this community.

(2) Most of the species present showed one of two distinct phenological patterns with little overlap in season of growth, and accordingly were classified as warm season or cool season species.

(3) It was concluded that seasonal separation of growth accounts for the continuing coexistence of these two groups of species. It is suggested that variations in abundance from year to year are also important to the coexistence of species.

(4) Two methods were used to investigate the spatial distribution of species in the study site, a neighbouring point analysis devised for this study and based upon pairs of points 2-8 cm apart, and an ordination analysis of quadrats. The results of these two analyses were in agreement. Each contributed information not available from the other.

(5) The species can be separated into two distinct associations. Quadrats fall on a continuum whose end points are these associations.

(6) The vegetational pattern is correlated with the depth of the soil above a clay layer, and perhaps with the frequency of local disturbances.

(7) The relationship of spatial pattern to the interactions among species is discussed.

INTRODUCTION

The observation that the distribution of species is not random but ordered, both with respect to the physical environment and, with respect to other species, is of course very old. The observation and explanation of such distributional patterns does not, however, account for the existence within one area of many species, growing and living in contact with each other. It is the object of this study to examine the relationships among species in a single plant community, with the ultimate object of understanding how the component species continue to persist.

Interference between plants occurs primarily between neighbouring individuals, although the action of predators or pathogens may extend the radius of the effect of an individual. Because of the localized nature of interactions, spatial pattern may have a large effect upon the dynamics of community structure: individuals which are far apart interfere less with each other than do neighbouring individuals. This may be one of the most important of the factors prolonging persistence and hence co-occurrence in an unstable system. Spatial pattern may also reflect a differentiation among species in micro-environment, which may result in the coexistence of these species. In this paper we therefore examine the spatial patterns of a grassland community. The phenology (temporal pattern) of the community is also examined.

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THE STUDY SITE

A community and study site were chosen to meet several criteria, the major ones being that the community should be a persistent one (i.e. non-successional) and that it should be practicable to manipulate it experimentally. The lower Piedmont region of North Carolina reverts rapidly to forest when left undisturbed—there is no natural grassland in this area—but large areas are now maintained as grassland by mowing or grazing. Therefore a 3 acre mown field in a relatively remote portion of the campus of Duke University, Durham County, North Carolina was chosen as a study site. This site was once used for gardens, but was allowed to revert to its present condition in the early 1940s. Since that time, it has been mown several times each summer but has received no other management or disturbance.

The soil is a sandy loam of the White Store series, and now consists of a sandy layer, 10–20 cm deep, overlying a clay layer. There are very few roots in the underlying clay. The upper layer of soil has a pH close to 5, 2–5% by weight of organic matter, and low fertility (e.g. phosphorus 1.5–6 μg g⁻¹). No separation of rooting zones among species was apparent in any of ten holes, perhaps as a result of the shallow depth of soil available for roots. Precipitation in this area averages 45 cm yr⁻¹, distributed evenly throughout the year. Temperature is more variable: mean maximum July temperature is 31 °C; mean minimum December temperature is 1 °C. There are on average 210 frost-free days per year. (Climatic data from Raleigh-Durham Airport weather station, 15 km away.) The 4% south-facing slope of the site and the rapid runoff due to the impermeability of the underlying clay layer make this site one of the driest in the area.

The study site supports an assemblage of primarily naturalized species, as do many of the other grasslands of North America. A list of the vascular plant species found at the site is given in Table 1. One large group of species has its origin in Europe, e.g. Plantago lanceolata, Poa pratensis, Rumex acetosella, Anthoxanthum odoratum, and many of the winter annuals. These commonly occur together in pasture and ruderal sites in Europe, where their association predates their naturalization in the New World. The various Paspalum species are most probably introduced from South America (Hitchcock & Chase 1971), and the species of Andropogon and Danthonia are native. This assemblage is therefore recent, but contains subsets of species whose association is much older. The vegetation varies in appearance from a lawn to a rough pasture, dependent upon the time since the last mowing. Mowing to 5 cm height was continued during the course of this investigation, approximately once a month from April to October. The individual plants of all species are small by comparison with those in more favourable sites. Total cover is low, never exceeding 70% during the course of the study, and often falling below 30%.

METHODS

Cover estimates

Optical point cover was used to describe the vegetation and assess changes in it (Greig-Smith 1964). Permanent quadrats were located by aluminium pipes sunk into the ground. Into these the legs of a plotter were fitted. The plotter had a moveable viewer, strung above and below with thread grids. By moving the viewer, the intersections of 14 rows and 36 columns, with 1 cm between each row and between each column, were defined by the thread grids. This therefore provided 504 points uniformly distributed over an area 13 × 35 cm. Vertical sighting of the vegetation directly below each intersection
TABLE 1. Vascular plant species present in the study site. Species constituting >1% of the total cover in the study area on at least one date are shown by *, those >5% by **. Voucher specimens of each species are deposited in the Duke University Herbarium.

**Gramineae**

*Aira caryophyllea* L.
*Andropogon ternarius* Michx.
*Andropogon virginicus* L.
*Anthoxanthum odoratum* L.
*Avenosus affinis* Chase
**Cynodon dactylon* (L.) Pers
*Danthonia sericea* Nutt.
*Digitaria ischaemum* (Schreb.) Muhl.
*Digitaria sanguinalis* (L.) Scop.
*Eragrostis spectabilis* (Pursh) Steud.
*Festuca elatior* L.
*Holcus lanatus* L.
*Panicum anceps* Michx.
*Penicillium cf. sphaerocarpon* Ell.
*Paspalum ciliatifolium* Michx.
**Paspalum dilatatum* Poir.
**Paspalum laeve* Michx.
**Poa pratensis* L.
*Setaria lutescens* (Weigel) F. T. Hubb
*Tridens flavus* (L.) Hitchcock

**Leguminosae**

*Trifolium arvense* L.
**Trifolium dubium* Sibthorp
*Trifolium repens* L.
*Vicia caroliniana* Walt.

**Compositae**

*Aster* sp.
*Gnaphalium purpureum* L.
*Hypochaeris radicata* L.
*Krigia virginica* (L.) Wild.
*Solidago* sp.

Other families

*Alchemilla microcarpa* Boissier & Reuter.
*Allium vineale* L.
*Cardamine hirsuta* L.
*Carex cephalophora* Muhl.
*Cerastium glomeratum* Trilullier
**Dickondra carolinensis* Michx.
*Geranium carolinianum* L.
*Houstonia pusilla* Schoepf.
*Lamium amplexicaule* L.
*Liquidambar styraciflua* L. (seedlings only)
*Luzula multiflora* (Retzius) Lej.
*Oxalis dillenii* Jacquin.
*Pinus taeda* L. (seedlings only)
**Plantago lanceolata* L.
*Poly-premium procumbens* L.
*Quercus phellos* L. (seedlings only)
*Ranunculus bulbosus* L.
**Rumex acetosella* L.
*Salvia lyrata* L.
*Veronica arvensis* L.
*Viola arvensis* Greene

was made by lining up the upper and lower grids. Only 252 of the 504 points were used routinely: in the odd numbered rows the odd numbered points were recorded and in the even numbered rows the even numbered points. Preliminary studies using the entire grid (504 points per quadrat) showed little or no increase in the variance of the estimates of cover as a result of recording only alternate points. Only one set of 252 points was recorded in each quadrat.

Only the topmost plant was recorded; thus total cover recorded never exceeded 100%. Because of the nature of the vegetation, however, overlaps were rare. Only green tissue was recorded by species. Dead vegetation, litter and bare ground were recorded as a single entity. In a few cases the vegetative parts could not be identified after close mowing. These cases were: (a) *Andropogon ternarius* and *A. virginicus* could not be distinguished except when flowering; (b) the species of *Paspalum* were not always distinguishable at the beginning of their growing period, in April and May; and (c) seedlings not assignable to species were recorded as dicotyledon or monocotyledon.

Since the coordinates of each point were known, the record of each quadrat could be regarded as a map of the vegetation and used to analyse spatial pattern, the approach that was used in the neighbouring point analysis of spatial pattern. The 252 points recorded in a single quadrat were also converted into estimates of the percent of the total cover.
contributed by each species in each quadrat. In all cases, percent of total cover, not percent of total vegetation, was calculated. This approach was used in the analysis of the phenological record and the principal components analysis of spatial pattern.

The repeatability of this method of measuring the composition of vegetation was estimated by reploting ten quadrats on the day following their initial plotting in August 1975. The average change in the estimate of percent cover of the sixteen most abundant species was only 0-3%. The changes in estimates of percent cover were not correlated with the magnitude of the estimates. Therefore the estimated cover of rare species is subject to proportionately more uncertainty than that of the common species. The identity of the species at any given point was much more variable: 42% of the 252 points plotted in the ten quadrats did not have the same species recorded on both days. The stability of the cover estimates was therefore due to the compensation of gains by losses of each species, not to the constancy of individual points. The variability of the record of individual points was the result of the movement of leaves and stems with wind, etc. and it was correlated with growth form. For example, long-bladed grasses were more variable than rosette species. It was not correlated with species abundance.

**Sampling designs**

We laid out 150 permanent quadrats, each 90 × 100 cm, in 10 rows of 15 contiguous quadrats each, separated by 20 cm paths. Each quadrat was sampled only in one 13 × 35 cm rectangle centred in the quadrat. The quadrat grid was deliberately located in as homogeneous an area of the site as was possible. A number of quadrats were excluded from the design, because they included minor topographic relief, or they had, in March 1975, vegetation different from the rest of the quadrats (Fig. 1). *Plantago* and *Salvia* were used in this determination of extreme quadrats since they could be easily counted. The

![Diagram](image_url)

**Fig. 1.** Map of the 13.5 × 12 m study site, showing the sampling design. Dotted areas are paths. Diagonal hatching indicates quadrats excluded from the design because they contained a small ridge (centre) or a small depression (right, left). Quadrats were also excluded from the design because they had, in March 1975, more than nine *Salvia lyrata* rosettes (horizontal hatching) or fewer than 10 or more than 200 *Plantago lanceolata* individuals (vertical hatching). Heavy lines indicate the boundaries of the 10 blocks. Letters indicate the plotting record of each quadrat: (a) plotted monthly; (b) plotted only between 1 April and 8 April 1975; (c) plotted only between 11 August and 23 August 1975; (d) plotted in April and August 1975, but not monthly.
experimental area was then divided into ten rectangular blocks. Quadrats were chosen randomly in each block for plotting, subject to the constraints of a removal experiment begun in the summer of 1975 on these quadrats (Fowler 1981). All the data discussed here were collected from quadrats that had no prior treatment. Between 1 April and 8 April 1975, five quadrats from each block were plotted. Between 11 August and 23 August 1975, seven quadrats from each block were plotted. The data from these two plantings were used in the analysis of spatial pattern. One quadrat from each block was plotted at approximately monthly intervals. The results of these monthly plantings were used to analyse community phenology.

Analysis of phenological patterns

The variation in phenological pattern among species was quantified by calculating, for each pair of the more abundant species, proportion similarity, PS. For species \( i \) and \( j \) this is given by

\[
PS_{ij} = 1 - 0.5 \left( \sum_{k=1}^{n} |P_{ik} - P_{jk}| \right)
\]

where \( k \) is a resource state (defined below) and \( P_{ik} \) is the proportion of the \( i \)th species that appears in the \( k \)th state (Whittaker 1975). Values of \( PS \) range from 1, identical phenological pattern, to 0, no overlap during the growing season. This measure was chosen because it is simple to calculate and makes no implicit assumptions about the intensity of competition, as alpha coefficients based on overlap measures do. Because the observations were not equally spaced in time, a correction for unequal spacing was necessary (Colwell & Futuyma 1971). Accordingly, for each species the number of days between each sequential pair of records was multiplied by the average percentage cover of that species during that period (that is, by the average of the preceding record and the following record). Each resulting product represents the appearance of the given species in the \( k \)th state. These products must be summed for the given species and then each product divided by that sum to yield the proportional appearance of the given species in the \( k \)th state, \( P_{ik} \) or \( P_{jk} \).

Neighbouring point analysis of spatial pattern

A ‘neighbouring point’ analysis based upon the original data points and their coordinates was used to analyse spatial pattern. At each recorded point of the grid, species \( x \) at the point and species \( y \) at each of the four nearest neighbouring points (each 2.83 cm distant) were recorded as four ordered pairs, \((x, y)\). Data from quadrats plotted during a single plotting period were combined and the sum \( m_{xy} \) of each different combination calculated. If there are \( N \) species then there is an \( N \times N \) symmetric matrix of values of \( m_{xy} \). The symmetry arises as a result of using each nearest pair twice. The goal of this analysis was the identification of those pairs of species whose joint occurrence, that is, the value of \( m_{xy} \), was significantly larger or smaller than a random arrangement of species would predict. A chi-square test on each cell was done to identify such pairs. The calculation of the expected values excluded all pairs in which the same species was recorded at both points (that is, the terms of the principal diagonal), and all pairs in which one member was non-green: dead vegetation, litter or bare ground. Many of the first kind of pair are simply two points over the same individual: the \( m_{xx} \) values are a function of the growth form and average individual size of the species as well as of spatial pattern. The pairs involving a non-green point were removed from the calculations because it was found
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that almost every species associated positively with the non-green points, and this effect was large enough to conceal all other positive associations.

The expected value corresponding to a given observed value, $m_{xy}$, of the $(x, y)$ pair of species, was calculated as follows:

The adjusted marginal sum of species $x$, $R_x$, equals the sum of all $(x, j)$ pairs minus the sum of $(x, x)$ pairs, or

$$R_x = \sum_{j=1}^{n} m_{xj} - m_{xx} = \sum_{i=1}^{n} m_{ix} - m_{xx}.$$  

The relative frequency of pairs in which $y$ is the second member, that is $(i, y)$ pairs, equals the proportion of $(i, y)$ pairs out of all pairs. The adjusted relative frequency of $(i, y)$ pairs, $P_{iy}$, differs from this by the removal of all $(i, i)$ pairs, and all pairs in which $x$ is the second member (since we wish to exclude $(x, x)$ pairs). Hence

$$P_{iy} = R_y (\sum_{j=1}^{n} R_j - R_x).$$

The expected number of $(x, y)$ pairs, $E_{xy}$, equals the adjusted marginal sum of species $x$ times the adjusted relative frequency of $(i, y)$ pairs or

$$E_{xy} = R_x P_{iy}.$$  

A chi-square statistic with one degree of freedom was calculated for each $(x, y)$ pair that had an expected value greater than 5. The observed number of $(x, y)$ pairs, $m_{xy}$, was compared with the expectation $E_{xy}$, and the number of other pairs in the row minus the diagonal element was compared with its expected value. The number of pairs in the row minus the diagonal element is the adjusted marginal sum, $R_x$. Of these pairs, we expect $E_{xy}$ to be $(x, y)$ pairs, and therefore $R_x - E_{xy}$ to be the number of pairs not of the form $(x, x)$ or $(x, y)$. This is therefore the expectation for the rest of the row. The observed number of such pairs is the sum of all $(x, j)$ pairs minus $m_{xy}$ and $m_{xx}$, or $R_x$ minus $m_{xy}$. Hence

$$\chi^2 = \frac{(E_{xy} - m_{xy})^2}{E_{xy}} + \frac{[(R_x - E_{xy}) - (R_x - m_{xy})]^2}{(R_x - E_{xy})}$$

$$= \frac{(E_{xy} - m_{xy})^2}{(E_{xy})(1 - E_{xy}/R_x)}.$$  

**Principal components analyses of spatial pattern**

Principal components analyses of spatial pattern were made on the arcsine square root transformed percentage cover results of the April and August 1975 plottings. Seven winter annual species were combined and treated as one variable, to permit their inclusion in the April analysis despite their relative individual rarity, and the two Andropogon species were combined because they could not always be distinguished. A total of twenty-seven species was included in one or both analyses; the others were too rare to include. Separate principal components analyses were made on the April 1975 data and the August 1975 data, so that the principal components analyses are not affected by seasonal changes in the vegetation. The variance-covariance matrix, rather than the more usual correlation matrix, was used, so that the relative importance of the various species in the determination of the axes was proportionate to their abundance in the community.
Soil depth

The depth of soil above the clay layer was measured in each quadrat. A spade was pushed through the soil until the clay layer stopped it, and the depth of the penetration into the ground measured. The clay layer can be dug up but it requires perceptibly more force to do so than to penetrate the looser soil above it.

RESULTS

Phenology

From the graphs in Fig. 2 it is evident that two phenological patterns are particularly common. These are exemplified by Cynodon dactylon (Fig. 2(a)) and Poa pratensis (Fig. 2(g)). The Cynodon pattern, shared by the various Paspalum species (Fig. 2(b–d)) and Carex cephalophora (Fig. 2(e)), includes dormancy broken in April, summer growth, and a resumption of dormancy in the autumn. The midsummer dips reflect the occurrence of

![Graphs showing changes in optical point cover throughout the year. Species (full names in Table 1) are grouped according to phenological pattern as explained in the text. Squares, 1975 records; circles, 1976; triangles, 1977.](image-url)
### Table 2. Proportion similarity between species (see text for definition) expressed as %, based upon values of percentage cover, on 26 dates over a period of 36 months. Possible range is 0–100. Species are grouped according to phenological pattern as described in the text. Self comparisons in parentheses.

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Temporal and spatial pattern in grassland
drought. Species that show this pattern will be referred to as warm season species. The Poa pattern, by contrast, has a major drop in the summer, reflecting summer die-back. The midwinter dip may be large or small, depending upon the severity of the winter. Species showing this pattern include Anthoxanthum odoratum, Rumex acetosella, and Allium vineale (Fig. 2(h–j)), the cool season species. The community, therefore, is divided into two temporal associations, a warm season association and a cool season association, whose growth alternates in time. This is corroborated by the values of proportion similarity between species (Table 2). The mean similarity between pairs of cool season species is 0.55 and that between pairs of warm season species 0.59, while the mean similarity of cool season/warm season pairs is only 0.26.

The summer annuals (Setaria lutescens and the Digitaria spp.) have the same phenological pattern and have been combined (Fig. 2(f)). Their phenology is analogous to that of the warm season perennial species: germination of the annuals occurs at the same time that the perennials are breaking dormancy, and the death of the annuals occurs at the same time as the die-back of the perennials.

All the winter annuals with the exception of Trifolium dubium show a common pattern and have been combined (Fig. 2(k)). Their period of growth is contained within that of the cool season species; the annuals die at approximately the same time, or somewhat earlier than, the perennials die back in the summer, but do not germinate until January or February, thus missing the autumn growing season. Trifolium dubium (Fig. 2(l)) continues growth for much longer into the summer than do the other winter annuals.

Several species have unique patterns. Plantago lanceolata (Fig. 2(m)), a very abundant species, is green throughout the year but grows most vigorously in the spring and autumn. It dies back in August after reproduction and again in the winter. Salvia lyrata (Fig. 2(n)) and Panicum sphaerocarpum (Fig. 2(o)) also grow throughout the year. The phenology of Dichondra carolinensis (Fig. 2(p)) is particularly interesting. It was very rare in 1974 and the spring of 1975. During the autumn of 1975 it became extremely abundant in one area, forming 60% of the total cover in some quadrats. Dichondra never recovered from the winter of 1975–76, a particularly harsh one, and the drought during the following summer. Only scattered leaves could still be found in the area where it had been abundant before July 1976. A possible explanation for this pattern is that the species was favoured by the particular weather pattern of 1975 and that it persists as a rare member of the community until unusual, favourable conditions occur.

Dichondra carolinensis provides the most dramatic example of a change in abundance from one year to the next, and this is reflected in its consistently low proportion similarities. Two species of Paspalum also showed year to year variation. Paspalum dilatatum was abundant in the summer of 1975 and the summer of 1976 (Fig. 2(b)). In the following spring it was scarcely recorded at all. However, individuals began to grow from rootstocks or from the stem bases late in the summer of 1977 and by the summer of 1978 the species had regained its former abundance. In contrast P. ciliatifolium (Fig. 2(d)), a rare member of the community in the preceeding years, was relatively abundant in 1977. It did not, however, replace P. dilatatum, as the two species were rarely abundant in the same quadrat.

Neighbouring point analyses

The results of the neighbouring point analyses separate the community, both in April and in August, into two groups of associated species, indicated as I and II in Tables 3 and 4. Within each association the associations between pairs of species are mostly positive,
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Table 3. Positive and negative associations among species from the neighbouring point analysis of spatial pattern, based upon results from fifty quadrats plotted in April 1975. '+' indicates a significant positive and '-' a significant negative association: 'NS' indicates a non-significant association. * , P < 0.05; **, P < 0.01; ***, P < 0.001. A blank indicates that no test was performed on the pair, either because the expected value was less than 5, or because it was a self-comparison (an x,x pair). Species (except Salvia lyrata and Panicum sphaerocarpon) are grouped into two associations, indicated as I and II. Within each association the order of species is: cool-season perennials; cool-season annuals; warm-season species. The species listed in the column on the left is the first member of each ordered pair (see text).
### Table 4. Positive and negative associations among species from the neighbouring point analysis of spatial pattern, based upon results from seventy quadrats plotted in August 1975. Organization and symbols as in Table 3.

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**Association II**

| **Plantago lanceolata** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Rumex acetosella** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Cynodon dactylon** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Digitaria ischaemum** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **D. sanguinalis** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Paspalum laeve** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **P. ciliatifolium** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Carex cephalophora** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Panicum sphaerocharpon** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| **Salvia lyrata** |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |

**N. Fowler and J. Antonovics**

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that is, more frequent than would be expected from the random assortment of species in space; between pairs of species in different associations the associations are negative. The analyses also reveal that the actual patterns are more complex than this. In particular, the winter annual species, all of which are in association II (April) are positively associated with Plantago, but negatively associated with one another.

The two analyses, on the April and August vegetation, have only a few species in common. Dichondra is found in the first association in both analyses and Plantago, Rumex and Carex in the second association in both analyses, suggesting that association I (April) is replaced by association I (August) and association II (April) by association II (August).

Principal components analyses and soil depth

The first axis of the principal components analysis accounts for 40% of the variance among quadrats in April and 54% in August. The first two axes together account for 60% and 65% of the variation among quadrats in April and August, respectively. In both analyses the first two axes produced a ‘shotgun’ scatter of points without any conspicuous clumps, ‘horseshoe’ effects, etc. (Fowler 1978). The first axis is in both cases positively correlated with the species of association I and negatively with those of association II (Table 5), thus corroborating the identification of the two associations by the neighbouring point analyses. The first axis is most highly related to the abundances of Plantago

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<td>Dichondra carolinensis</td>
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<td>Plantago lanceolata</td>
<td>-0.78</td>
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<td>Rumex acetosella</td>
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<td>Trifolium dubium</td>
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<td>Winter annuals</td>
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<td>Carex cephalophora</td>
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<td>Salvia lyrata</td>
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<td>Total cover</td>
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<tr>
<td>Soil depth</td>
<td>-0.56</td>
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<tr>
<td>Total cover</td>
<td>0.70</td>
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<tr>
<td>Soil depth</td>
<td>-0.65</td>
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r > 0.51 P < 0.0001
0.50 > r > 0.46 P < 0.001
0.45 > r > 0.34 P < 0.01
0.33 > r > 0.28 P < 0.05
n = 50 quadrats

r > 0.45 P < 0.0001
0.44 > r > 0.40 P < 0.001
0.39 > r > 0.31 P < 0.01
0.30 > r > 0.26 P < 0.05
n = 70 quadrats
lanceolata, Rumex acetosella, and Poa pratensis in April, and to the abundances of Carex cephalophora, Paspalum laeve, Dichondra carolinensis, and Paspalum dilatatum in August. The other correlations are smaller but also match the associations found earlier. The second April axis separates quadrats primarily upon the abundances of Plantago lanceolata (0.60 correlation) and Cynodon dactylon (0.76 correlation). Both of the second axes are also correlated with a variety of other species.

The first and second component scores of the quadrats calculated from the April data set are spaced relatively evenly along the first axis. Quadrats do not belong either to association I or II, but lie on a continuum between them, implying that the community changes gradually from quadrat to quadrat, i.e. that the changes from quadrat to quadrat

**Fig. 3.** Four examples of the relationship between the cover of a species within a quadrat and the first component score (position on the first ordination axis) of that quadrat in the principal components analysis, April 1975. (a) Poa pratensis and Anthoxanthum odoratum, both of association I, (b) Plantago lanceolata and Rumex acetosella, both of association II.

**Fig. 4.** Maps of the study area, showing the component scores (positions along the ordination axes) of quadrats. The dashed lines represent contours (see text). Shaded areas represent quadrats excluded from the design; blank areas represent quadrats not plotted on the given date. (a) First component scores (positions of quadrats on the first ordination axis), April 1975; (b) first component scores, August 1975.
are the results of a shift in the relative abundances of the two associations. This is shown explicitly by graphs of the abundances of four representative species against the first component score (Fig. 3). As the first component score increases the amount of *Anthoxanthum odoratum* and *Poa pratensis* in the quadrat increases and the amount of *Plantago lanceolata* and *Rumex acetosella* decreases. Thus the vegetational diversity among quadrats is due to a gradual, coordinated change in the abundances of the two groups of species. In August the continuum is less clear and the clustering of quadrats greater. In both analyses quadrats towards the left end of the x-axis contain a preponderance of association II species, and quadrats towards the right end, of association I species. The first component scores of both analyses have been plotted on a map of the area, and contours have been fitted, such that all the quadrats between any two contours have scores within an upper and lower limit (Fig. 4). It can be seen that both of the first component scores identify gradients across the study area or patches within it.

The soil depth is correlated with the first component score of quadrats, and it is also correlated with some of the other variation in species composition among quadrats (Table 5).

**DISCUSSION**

*Temporal patterns*

The temporal patterns are the most obvious factor structuring this community. A separation in the timing of growth is equivalent to a separation in resource use if the resource is one whose use is dependent upon frequent renewal, not storage. Examples of such resources are light, water (because the soil is shallow and runoff rapid), and perhaps nutrients, although nothing is known about seasonal fluctuations in nutrients at this site. The use of separate limiting resources by two competing species implies that all necessary resources are available to one species regardless of the presence or absence of the other, and hence that neither will exclude the other from the community. The continuing coexistence of the warm season species with the cool season species is therefore accounted for. The community is divided by the temporal separation of growth into two guilds, that is, groups of species among which competition is intense and niche overlap is great, but whose overlap with species that are not part of the guild is slight (Root 1967).

Within each seasonal guild there is further differentiation in phenological pattern among species as shown by the values of proportion similarity, and this differentiation may be great enough in some cases to permit the coexistence of pairs of species. Most of the species varied in abundance from year to year, especially * Dichondra carolinensis*, *Paspalum dilatatum* and *P. ciliatifolium*. This variation among years results in a separation in the timing of growth among species over a somewhat longer period than the seasonal pattern. It may account for the coexistence of some of the species, for example, *Dichondra*, which formed nearly pure patches when it was most abundant. This species may persist in the community because such periods compensate for long periods of suppression. Another form of temporal separation may be separation on a time scale of days or weeks. Casual observation showed that the timing of growth after summer rainfall differed among species. For example, *Plantago lanceolata* seemed particularly responsive to rainfall, putting out conspicuous new growth soon after rains, and being one of the first species to wilt during droughts. In contrast, *Cynodon dactylon* appeared to continue growth further into rainless periods than did most of the other species.
Seasonal separation of growth analogous to that observed among the species of this community has been described in other grassland communities (Al-Mufti et al. 1977; Grime 1978; Turkington & Harper 1979). The differentiation among species in this community is considerably more pronounced than that found in other grasslands; this is probably the result of the long (10–12 month) growing season, combined with a strongly seasonal climate, i.e. hot summers and relatively cold winters.

**Spatial patterns**

The neighbouring point analysis was devised for this study; it gave a ‘plants-eye view’ of the vegetation, like the plant-to-plant contact method of Turkington & Harper (1979), and the method of Stowe & Wade (1979), who used points at 2-cm intervals on a transect. Their results were similar to those found here, i.e. there were two primary associations of species plus a few independent species in each community. As was also true in the present study, the results of the small scale analyses were in agreement with the results obtained from larger scale sampling; the small scale methods were more sensitive, as for example, in the detection of negative associations among the winter annual species in association II in the present study. The principal components analyses were based upon quadrats much larger than the size of an individual plant. They were less sensitive to the relationships between pairs of species, but contributed information not available from the neighbouring point analyses, that is, the existence of a continuum of quadrant vegetation between associations I and II in each season.

The various factors that create and maintain patterns, such as the existing plants, soil heterogeneity, and chance, are of course not mutually exclusive, and it seems likely that several different ones were responsible for the spatial heterogeneity of plant distribution observed in this study. The distribution of Dichondra carolinensis was perhaps due to colonization spreading out from a single centre. It formed a single patch, has vigorous vegetative growth by means of stolons rooting at the nodes, and may have been a single clone. It is unlikely that this species controlled the distribution of any other species because it has a significant presence only in infrequent years, as discussed above. All of the other important species were found throughout the mapped area during the course of the study although many were quite rare in some sections. Therefore it is not likely that the observed pattern of any other abundant species was the result of accidents of colonization. The coordinated nature of the pattern displayed by the major species is also not compatible with the hypothesis that chance events of colonization and outwards spread were the mechanism creating and maintaining pattern.

The correlation of the vegetation of quadrats and the depth of the soil is further evidence that the spatial pattern was being actively maintained, rather than a result of chance events. Correlations provide no direct evidence of causality. In this case, however, the depth of the soil seemed to be positively correlated with the amount and frequency of disturbance of the soil, although no measurement of the frequency of disturbances was made. These disturbances included mole tunnels, spider holes, and ant colonies. Each disturbance was small (less than 10 cm in diameter), with only localized effects. It was not unusual, for example, to see an individual of Plantago lanceolata half covered by an ant mound but apparently thriving. As a result of disturbances, or of other unidentified factors, the total cover was often noticeably lower in the area of greatest soil depth (correlation =0.48, August 1975). The deeper soil may be more suitable for moles, etc., and hence have a greater frequency of disturbances, which in turn may shift the balance of interactions between species such that one or more members of association II
are favoured. The effects of molehills and ant mounds as factors contributing to the persistence of species in a community have been documented in other grassland communities (Jalloq 1975; King 1977a, b).

The interpretation of the association of species in space is difficult. Groups of associated species may or may not be guilds, depending upon the factors that lead to association. Species may be positively associated because they make similar demands upon the environment, that is, they are ecologically similar. Such species have major impacts upon one another and groups of such species may properly be considered guilds. On the other hand, species that make quite similar demands upon the environment may be separated in space, as the result of competitive exclusion. When this phenomenon is involved, groups of associated species do not represent guilds (except in the sense that physical proximity will necessarily increase the level of interspecific interactions among adult individuals of different species). The *Paspalum* species are probably an example: they are congeneric, have similar growth and morphology and may be similar ecologically. *Paspalum dilatatum* belongs to one association; *P. laeve* and *P. ciliatifolium* to the other. If competitive exclusion is an important factor in the creation of the associations found in this community, then the two spatial associations described above cannot be guilds. The interpretation of the temporal pattern is relatively free from this ambiguity because most of the phenological patterns are probably innate to the species (Beard 1973), and hence not ascribable to competitive exclusion.

The degree of spatial patterning in this community is probably typical and will surprise no one involved in other intensive studies of plant communities. Nevertheless spatial pattern is not generally included in quantitative models, although several authors have stressed its importance (e.g. Schaffer & Leigh 1976; Whittaker & Levin 1977). A community whose members are distributed in space as those of the community described here are does not function according to the assumptions of commonly used models, such as those based upon elaborations of the Lotka–Volterra equations. Some species may never contact certain other species as adults while other pairs of species may interact far more frequently than their population sizes would indicate. Population sizes cease to indicate the likely fates of individuals, especially of adults. Studies, especially demographic studies, made without reference to patterns may therefore overlook the role of different competitors, of small-scale variation, or of disturbance.

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**REFERENCES**


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