

Technical Report No. 306
STRUCTURAL CHARACTERISTICS OF SOME GRASSLAND
PLANT COMMUNITIES ASSOCIATED WITH THE
AVAILABILITY OF RESOURCES

Jorge Ares
Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523

GRASSLAND BIOME
U.S. International Biological Program
March 1977

TABLE OF CONTENTS

Title Page	i
Table of Contents	ii
Abstract	iii
Introduction	1
Materials and Methods	6
Example no. 1	6
Example no. 2	7
Example no. 3	7
Results	8
Plant community structure	10
Competitive interaction between species	15
Discussion	27
Conclusions	33
Acknowledgments	35
Literature Cited	36

Abstract

The assumption is made that the level of resources available to a grassland plant community determines certain characteristics of the distribution of biomass between the species that integrate the community. Two conceptual tools are used to investigate biomass partitioning among species:

(1) A measure of biomass apportionment between species, computed by means of two equitability indices.

(2) A measure of competitive two-order interaction between species computed by means of competition coefficients.

Three types of variations in the amount of resources which occur conspicuously in grassland plant communities are analyzed: Variations over space due to microtopography, variations over time due to changing conditions in the environment, and "man-induced" variations (irrigation and fertilization). Three examples in which these basic types are present are analyzed: A subtropical grassland in eastern Argentina, a tundra gradient in Canada, and a shortgrass prairie in the western United States.

A hypothesis on the nature of changes in species interactions along environmental gradients in grassland communities is developed, as well as some comments on the possible characteristics of stable ("nature-induced") variations in resource levels as compared to non-stable ("man-induced") variations.

This hypothesis and the relations observed in the data shown here could be profitably used as criteria when modeling species interactions in the plant community.

Introduction

Understanding the relationships between structure and function in grassland ecosystems is essential for better management of this type of resource. There is increasing evidence, both from ecological theory and from experimental results, that the way in which biomass is apportioned between the different components of the plant community is a dynamic characteristic, the analysis of which might indicate functional features of the community.

From the range manager's point of view, the way in which the total energy and available resources are channeled through the primary producers, so that some species may obtain more from what is available in the environment than others, is also of importance, since species differ in their nutritive value and palatability.

I shall refer here to biomass distribution by species, and for the purpose of the analysis here developed, it will imply the distribution of any measure of quantity of biomass, either weight, cover, abundance, etc., expressed on a species basis as a fraction of the total quantity of that same measure over all the species of the community.

Biomass distribution defined in these terms has been found to be the consequence and has been postulated as the reason for a wide range of ecological phenomena. It would be lengthy to quote the main bulk of the literature on this point. Some publications dealing explicitly with this subject are Preston (1962), Lloyd and Ghelardi (1964), Pulliam, Odum, and Barrett (1968), Whittaker (1965, 1972), and Ares (1972), while a similar list can be made of publications dealing implicitly with the

concept (MacArthur 1957, Odum 1969, Whittaker 1971, and Buzas 1972).

In another context, species distribution is related to the long debated problem of dominance in plant communities. Dominance has been alternately pointed out as a meaningful indicator of community productivity (Margalef 1963, Odum 1969), and even the cause of it (McNaughton and Wolf 1970), or contrariwise, a meaningless or negative indicator of productivity (Singh and Misra 1969, Risser and Rice 1971). Biomass distribution estimations are relatively easy to make in grassland plant communities, which is not the case with some other important characteristics of that system, as plant biomass or productivity by species.

Biomass distribution can be characterized in several ways. One of the simplest is to compute a relative value for each species (x_i), expressing the quantity in question (weight, cover, abundance) as a fraction of the sum of the same quantity for all the n species in the community. The vector of n fractions thus obtained can be used to characterize the distribution of biomass.

The quantity

$$H = -\sum_{i=1}^n x_i \log_2 x_i$$

which gives the information in bits per unit of x_i (Pielou 1965) depends on n , but also on the vector thus defined. The partial dependence of H on the vector of relative biomass can be expressed with comparable success by any of the equitability measures available (Whittaker 1972). One of them is the computation of Lloyd and Ghelardi's index (Lloyd and Ghelardi 1964) of e_1 in this paper; it has been interpreted as a measure

of overlap of the niches of species, and consequently as an indicator of competition between them (Pulliam et al. 1968). This is clearly a risky assumption since overlap does not imply competition unless an insufficient amount of resources is present in the region of the niche where overlap is manifest (Colwell and Futuyuma 1971). It is because of this that independent estimations of competition between species are desirable in order to investigate the use of resources by a plant community.

Equitability may also be conceived as a function (e_2) of the dispersion of species importance values, as

$$e_2 = \frac{\sum_1^n (x_i - \bar{x})^2 / n - 1}{n - 1}$$

The wider the dispersion of the relative biomass values, the greater the dominance is in the community.

The magnitude of competition between different components of a plant community can be estimated by computing the second-order interaction coefficient α_{ij} of the expressions:

$$dx_1/dt = rx_1 (k - x_1 - \alpha_{21}x_2)/k$$

$$dx_2/dt = rx_2 (k - x_2 - \alpha_{12}x_1)/k$$

used by Gause in applying Volterra equations for increase of species x_1 and x_2 in time. The α_{ij} represents the reduction in the rate of increase of both populations caused by one individual of the competing species as compared with one individual of the species under consideration (Levins 1968). Levins also proposes a way to estimate the α_{ij} coefficients for a community of n species, which is appropriate for the analysis of a wide range of ecological data. The inspection of the

matrix of coefficients obtained (community matrix) can be useful in understanding the competition process in the community, though great care should be applied when testing hypotheses since the distribution of coefficients has not been studied, and they are clearly partially interdependent. There is also a need of further research on the dependence of the terms of the alpha matrices on the size of the sample and spatial pattern of the species.

One of the habitat characteristics that may induce changes in competition and biomass distribution between species is the variation in the amount of resources available for the community. As a "resource" I refer here to any characteristic of the environment regulating or modifying species growth that may vary over space or time. The conceptual hyperspace defined by the upper and lower levels of the resources or environmental factors can be thought of as a characteristic of the habitat of the community; I will refer to *habitat width* estimators, following a suggestion of Whittaker (1972) to the estimators of the size of the space so identified.

If we define by certain criteria of homogeneity over space and time a certain set of species as composing a community (as may be done by phytosociological or classification techniques), we may find that the set of species, defined as a group or community, is found as such within certain limits of critical resources, like soil water, soil aeration, temperature, etc. These limits may be thought of as the boundaries of the n-dimensional space, identified above, which is the total fundamental niche (Slobodkin 1961) of the plant community so defined. It is also commonly observed, and the results shown in this paper stress this

point the more, that although the species list may remain *more or less* the same within the upper and lower limits of the factors considered, the relative biomass of species, i.e., the vector of relative biomasses, changes within the limits of the space so defined. According to classical community theory, this change in species abundance may be thought of as the combined expression of (i) the amplitude of tolerance (ecological amplitude) of each species with respect to certain critical habitat factors and (ii) the competitive interaction between species (Hanson and Churchill 1961).

This variation of levels of critical factors is evident over geographical space, as along any environmental gradient, and over time. In those environments where fluctuations of conditions for vegetative growth occur over time, there is an increase in the habitat width as the growing season proceeds and a decrease in it as conditions for growth begin to deteriorate. Finally, there is another kind of variation in total habitat width that is induced by man's activity: Irrigation and fertilization of grassland can be viewed as an artificial expansion (or perhaps reduction?) of total habitat space which may determine modifications in the relationships between species.

These considerations pose the question of measuring habitat width and somehow defining a scale for that measurement. The measures and scales of habitat width presented here were developed according to the structure of the data available. Consequently, they may be subjected to criticism on account of lack of linearity and arbitrary scaling (for example, see Colwell and Futuyuma 1971). No correction of these sources of error has been introduced, so no attempt will be made to ascertain

anything but generally increasing or decreasing trends in the data. Also, no comparisons between the examples shown will be made on the basis of the particular shape of the functions obtained.

Materials and Methods

Example no. 1

This set of data refers to the changes in biomass distribution observed in a subtropical grassland community in Corrientes Province, Argentina, 1 year after different levels of phosphorous fertilizer were applied. This type of pasture is described in some detail by Van der Sluij (1971), and it has a marked response to phosphorous fertilizers. Six different levels of fertilizers were applied in July 1971, equivalent to 0, 25, 50, 75, 100, and 125 kg of P_2O_5 per ha, respectively, over contiguous 25 x 800 m rectangular plots in a field subjected to grazing by cattle. On two occasions after fertilization (December 1971 and March 1972), plant cover-abundance by species was estimated and quantified by values of a six-point scale used previously for similar observations (Ares and Leon 1972). The e_1 and e_2 indices were computed with these values. The data can be analyzed in a gradient structure by dividing the set of six treatments into three groups of two plots each and using levels of fertilizer as units of habitat width scale, since phosphorus appears to be a limiting factor for this type of vegetation. A FORTRAN IV subroutine was developed to compute α_{ij} coefficients for each possible pair of i and j species taken in groups of two for each pair of treatments. Table 1 shows the raw data used. The subroutine was also used for the analysis of the other examples and is available upon request from the author.

Example no. 2

Observations on vegetation cover, microtopography, and depths of active layer were made along a transection of approximately 120 m in a southeast facing slope in subarctic alpine tundra in the Yukon territory of Canada by Price (1971). The original data are reported in the paper. Sites were ordered irrespective of the actual spatial location and according to the depth of the active layer. The virtual gradient thus obtained was subdivided into 10 intervals of equal length which were used to construct habitat width scale; e_1 and e_2 indices and community matrices were computed as in the previous example.

Example no. 3

The set of data selected for this example is concerned with habitat width variation over space and also over time, as intensive sampling of plant weight by species over time was made during the growing season of grasses.

The grassland community studied is a shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) in the western division of the Pawnee National Grassland in northern Colorado (USA). The native vegetation of the area has been described by Klipple and Costello (1960).

A homogenous area of approximately 10 ha was excluded from grazing in 1970, and different levels of water availability, soil nitrogen, and a combination of both were utilized at periodic intervals of time. The treatments applied to the area are nitrogen fertilization (150 kg/ha), irrigation (enough to maintain a constant level of water availability near field capacity during the growing season), and a combination of

both fertilization and irrigation. Data on habitat factors and plant community were recorded for each treatment during 1971 at 20-day intervals. Plant biomass was sampled at 30-day intervals by means of six square plots of 0.5 m^2 each. The live green standing material was selected from the material harvested and classified by species.

For the sake of e_1 index computation, all species represented by more than 5% of total biomass were considered, and a set of 32 equitability indices per treatment was generated by alternately taking the lower and upper 5% confidence level of each of the five dominant species biomass determinations. This procedure artificially generates a whole distribution of e_1 indices which was found to statistically fit a normal distribution in 90% of the sets analyzed within a 5% confidence level; on account of this, 5% confidence levels for equitability indices were computed by means of a t-test.

For the computation of competition coefficients, a set of 12 species with high representation in all treatments in all dates was selected. Since species values are taken by pairs to compute competition coefficients, the omission of some species from the list reduces the information available for the whole community, but does not modify the values computed for the selected species (Table 1).

Results

A similar set of data is presented for each of the examples treated: (i) a characterization of the plant community structure in terms of equitability indices and (ii) an analysis of the overall competition process by inspection of the community matrix. This last includes a

TABLE 1. Species selected for the computation of competition coefficients of example no. 3.

Aristida longiseta Steud.
Artemisia frigida Willd.
Bouteloua gracilis (H.B.K.) Lag.
Bouteloua hirsuta Lag.
Buchloe dactyloides (Nutt.) Engelm.
Carex heliophila Mackenzie
Chrysothamnus nauseosus (Pall.) Britt.
Festuca octoflora Walt.
Gutierrezia sarothrae (Pursh) Britt. and Rusby
Lepidium densiflorum Schrader
Penstemon angustifolius Nutt.
Sphaeralcea coccinea (Pursh) Rydb.

table of values of competition coefficients for different groupings of the species composing the plant community and graphs showing the variations in competitive interactions related to changes in habitat width.

Plant community structure

The values of Table 2 were used to compute e_1 and e_2 values for each of the levels of fertilizer added and each of the sampling dates in example no. 1. The curves obtained for both e_1 and e_2 indices are shown in Fig. 1a and 1b. Sampling of species cover in the middle of the growing season (December) indicates a decrease in dominance with increasing levels of resources; if the sampling is done at the end of the growing season (March) the contrary trend is observed. Though I will want to discuss this point further in the last section of this contribution, it seems worth pointing out here that whatever meaning one might want to assign to the concentration of dominance in the plant community it must be consistent with intraseasonal variation of that structural characteristic since it is evident that the variation of equitability induced by modifications of the amount of available resources may affect different trends during time.

Fig. 2a and 2b show the relationship between the indices e_1 and e_2 and the habitat width for the data of example no. 2. It is noticeable that while e_1 shows a unimodal increase as habitat width increases, e_2 shows a bimodal response. This is probably due to the fact that e_1 depends partially on the total number of species which increases markedly in the example shown as the depth of active layer increases while e_2 is independent of species number.

TABLE 2. Cover abundance estimated values for 23 species of a plant community under six different levels of fertilization with phosphorus. Fertilization: July 1971. Observations: December 1971, March 1972. Symbols in the table refer to cover-abundance values.^{a/}

Species	December 1971						March 1972					
	0	25	50	75	100	125	0	25	50	75	100	125
<i>Andropogon lateralis</i> Nees	3	3	3	3	3	3	3	3	3	3	3	3
<i>Aristida venustula</i> Arech.	1	1	1	1	1	1	+	1	+	+	+	-
<i>Axonopus argentinus</i> Parodi	+	1	1	1	1	2	2	2	1	1	1	1
<i>Axonopus compressus</i> (Swartz) Beauv.	1	+	1	1	1	1	1	+	-	+	-	-
<i>Baccharis</i> sp. L.	1	1	2	2	2	2	2	2	2	1	2	1
<i>Bothriochloa lagurioides</i> Herter	+	+	-	+	+	+	1	-	1	-	+	+
<i>Chloris retusa</i> Lag.	+	-	+	-	-	1	+	+	+	+	+	+
<i>Cyperus</i> sp. L.	+	+	+	+	+	1	1	1	-	1	+	-
<i>Desmanthus virgatus</i> (L.) Willd	+	+	+	+	+	1	-	+	1	+	+	+
<i>Desmodium canuum</i>	2	2	2	2	2	3	3	3	3	2	3	3
<i>Eragrostis lugens</i> Nees	+	+	-	+	-	+	1	1	1	1	-	1
<i>Eragrostis neesii</i> Trin.	-	+	+	+	+	1	1	+	1	+	+	1
<i>Evolvulus sericeus</i> Swartz.	+	+	+	+	+	1	1	1	1	+	+	+
<i>Indigofera asperifolia</i>	1	1	1	1	1	1	2	1	2	-	1	1
<i>Paspalum notatum</i> Fluegge	2	2	2	2	1	2	2	2	3	2	2	2
<i>Piptochaetium montevidensis</i> (Spreng.) Parodi	1	1	1	1	1	2	1	+	2	1	+	1
<i>Rottboellia selleana</i> Hack	1	+	1	+	1	1	1	1	2	1	1	1
<i>Schizachyrium paniculatum</i> (Kunth) Herter	-	1	1	1	1	1	1	1	1	+	-	+
<i>Setaria</i> sp. Beauv.	+	+	-	+	+	+	1	1	1	1	+	1
<i>Sporobolus poiretii</i> (Roem. & Schult.) Hitchc.	1	1	1	1	1	1	1	1	1	1	1	-
<i>Stylosanthes montevidensis</i>	+	+	-	+	1	1	1	1	+	+	+	+
<i>Verbena laciniata</i>	+	+	+	-	+	+	-	+	+	+	+	-

^{a/} + = <5% cover, occasional individuals, and 1% corresponding cover value.

1 = <5% cover, abundant or common individuals, and 5% corresponding cover value.

2 = 5 to 25% cover, very abundant or common individuals, and 15% corresponding cover value.

3 = 25 to 50% cover, any number of individuals, and 47% corresponding cover value.

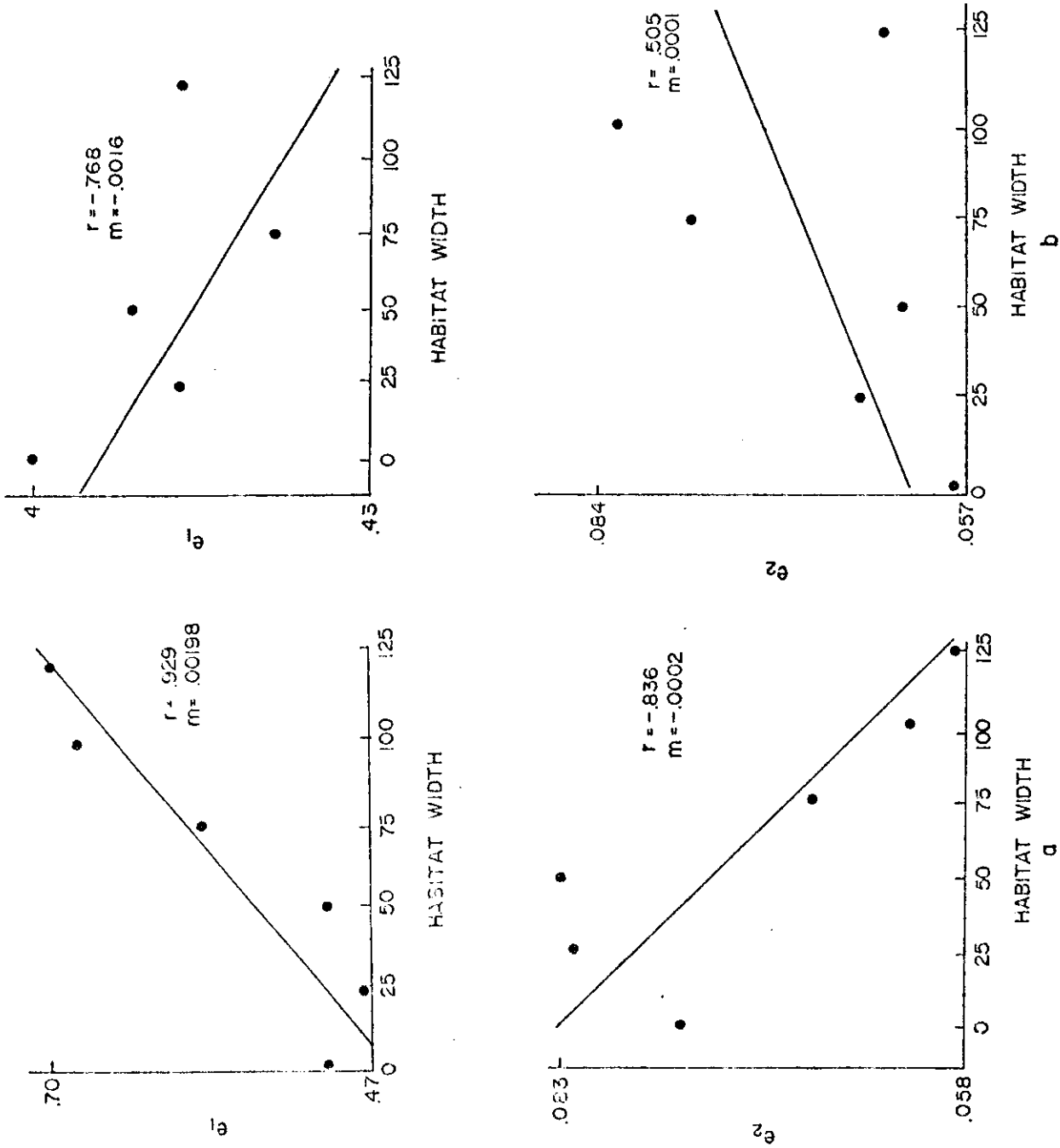


Fig. 1. Structural modifications of plant community as characterized by equitability indices e_1 and e_2 (see text) observed when modifying the amount of resources available through fertilization. Data plotted correspond to observations carried out 6 and 10 months after fertilization (a: December 1971, b: March 1972). Growing season in the location of the experiment extends from approximately August to March. Example no. 1.

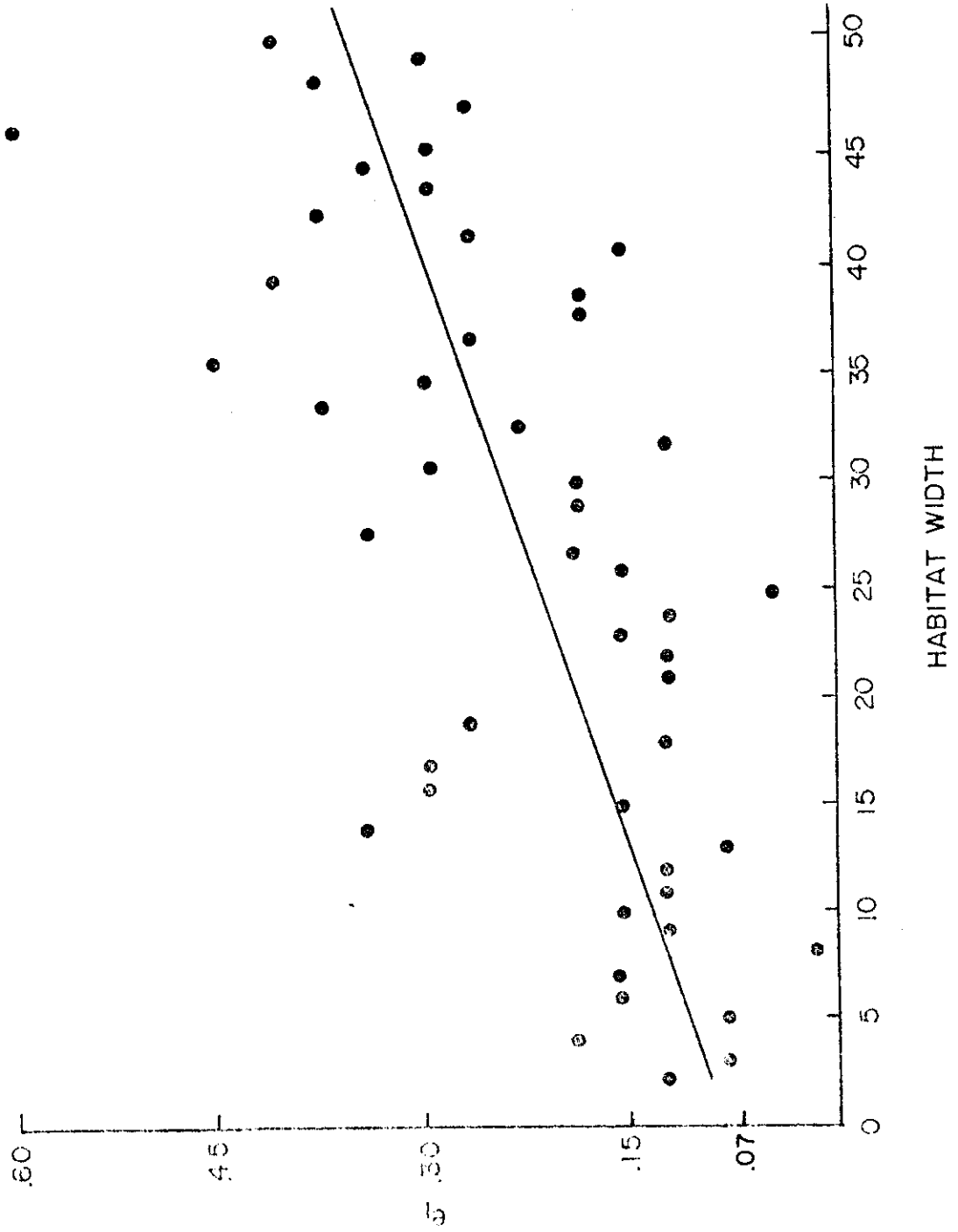


Fig. 2a. Changes in plant community structure as shown by equitability index e_1 . Example no. 2.

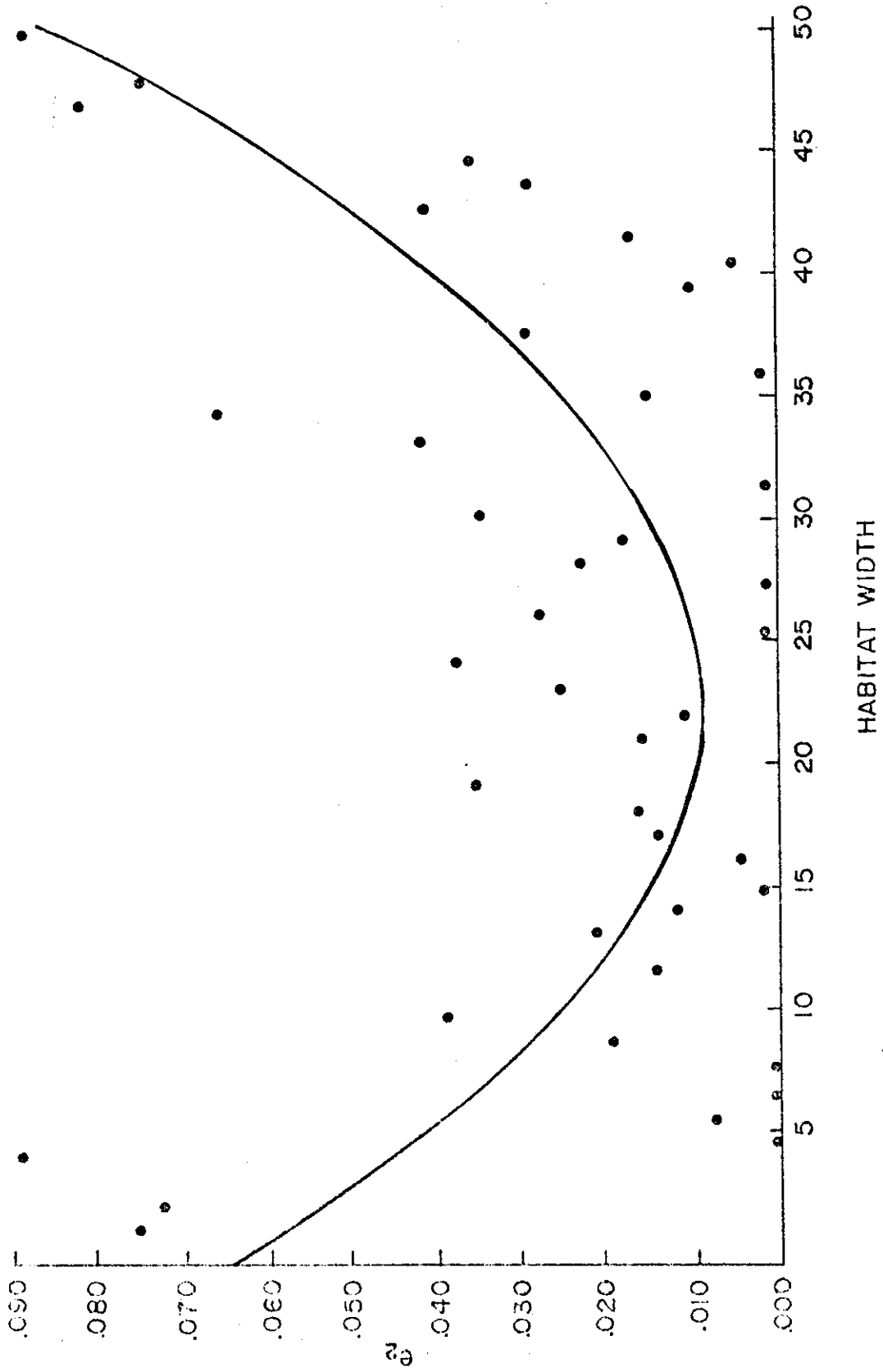


Fig. 2b. Changes in plant community structure as shown by equilibrium index e_2 . Example no. 2.

Fig. 3a and 3b show the changes in e_1 and e_2 observed during the growing season in the shortgrass prairie referred to in example no. 3. The variations observed are consistent with some ideas concerning seasonal succession already developed (Ares 1972). The addition of resources for which competition may arise increases dominance, and this is reflected in the decrease of e_1 (or increase of e_2) during the growing season. The inspection of e_1 variations show that while the addition of nitrogen increases dominance during the beginning of the growing season, in which most of the vegetative growth occurs, the addition of water increases dominance during the second (dry) part of the season. Changes in e_2 do not show this last fact, though the decrease in dominance in all treatments as the middle part of the growing season is reached is more evident than when examining variations in e_1 . It is evident that the changes in both e_1 and e_2 depend on the time of the growing season in which the observations are made (see, for instance, the differences in Fig. 1a and 1b between samples taken in December, and also the changes observed in the control treatment in Fig. 3a and 3b).

Competitive interaction between species

The elements of the community matrix are all the second-order competition coefficients between species. The subroutine used to compute community matrices arranges the computer printout in such a way that the rows represent all the competitive effects of one species upon all the rest of the species, and also that the order of rows in the matrix corresponds to the order of importance of the species, on a biomass basis, over the whole gradient analyzed. This makes it simple to group the matrix rows into a small number of importance or rank categories, or to inspect the behavior of individual species.

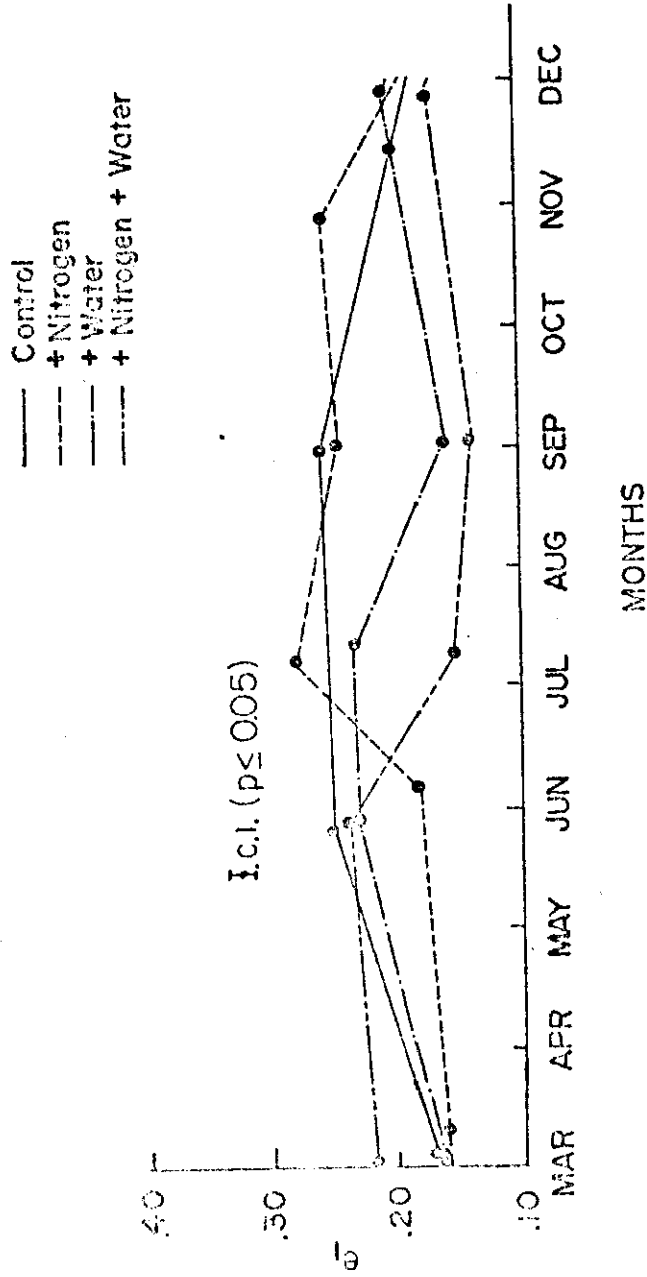


Fig. 3a. Changes in plant community structure over time induced by artificially increasing the availability of water and nitrogen, as measured by index e. Vertical segments indicate average confidence intervals at the 5% level for each point in the figure. Example no. 3.

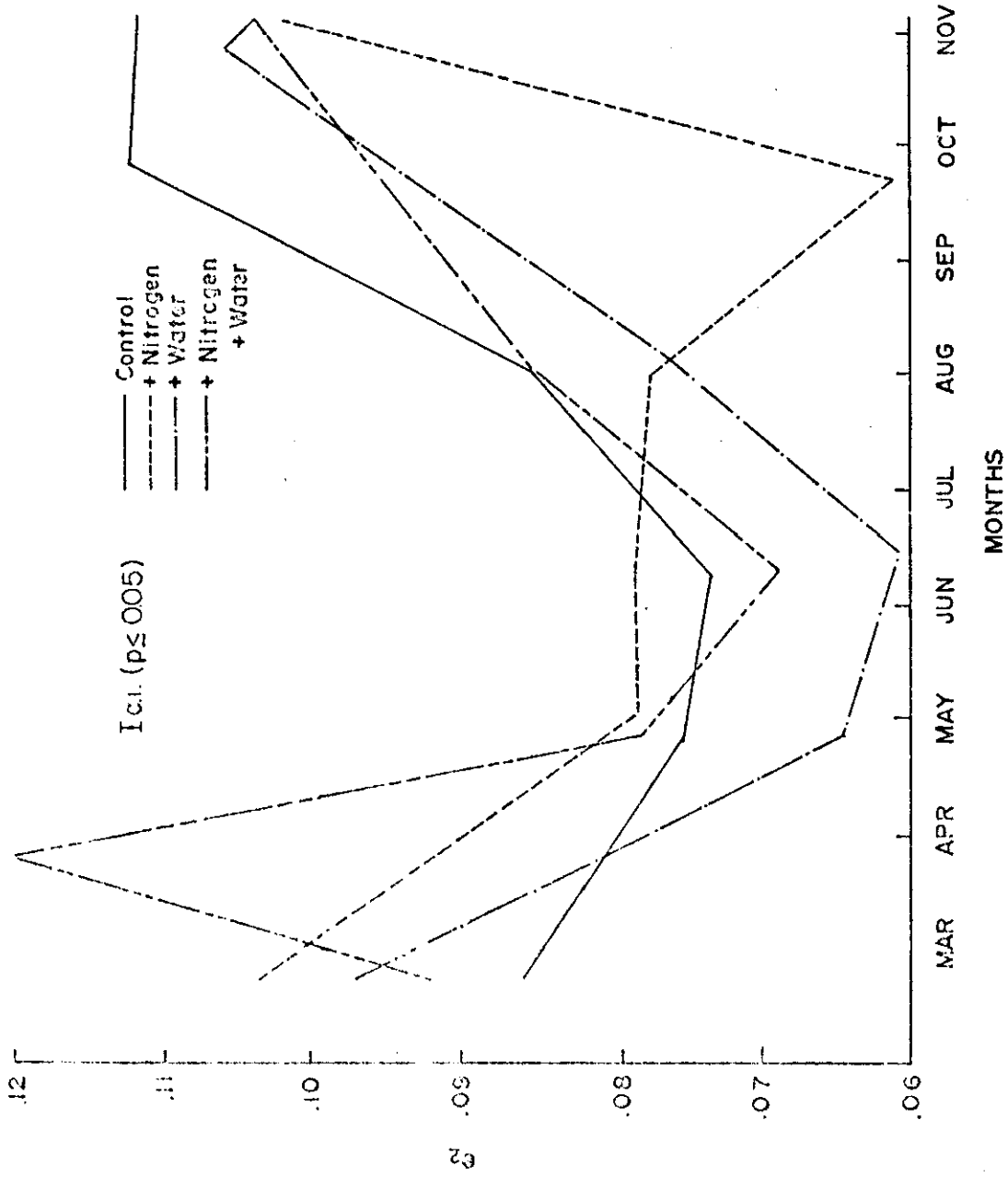


Fig. 3b. Changes in plant community structure over time induced by artificially increasing the availability of water and nitrogen, as measured by index e_2 . Vertical segments indicate average confidence intervals at the 5% level for each point in the figure. Example no. 3.

The following refers to the average intensity of competition as estimated by the mean of off-diagonal elements of the community matrix.

Fig. 4 shows these averages computed for samples of example no. 1 taken in December and March. Fig. 1a and 1b show the corresponding changes in dominance in both cases. Changes in structure induced by level of resources shown by e_1 and e_2 indices are not reflected in changes in level of competitive interaction. Though dominance is decreased in the middle of the growing season by the addition of resources and increased at the end of the season, competitive activity is enhanced in either moment.

Fig. 5 shows the means of competition coefficients computed for example no. 2, which is described in terms of species distribution in Fig. 2a and 2b. In this case, dominance seems to be associated with an increase in the overall level of competition.

Fig. 6 shows the changes over time in average competitive interaction between a selected set of species (Table 1) in the control treatment and in the irrigated and fertilized treatment. Fig. 3a and 3b describe structural changes in species distribution. In this case, increasing competition is observed when dominance increases; also, competition coefficients seem to be very sensitive to seasonal variation of plant environment.

The detailed analysis of the competitive behavior of species occupying different positions in the rank or importance order of all species in the community can be made, as suggested above, by examining row averages of community matrices. For the purpose of synthesis,

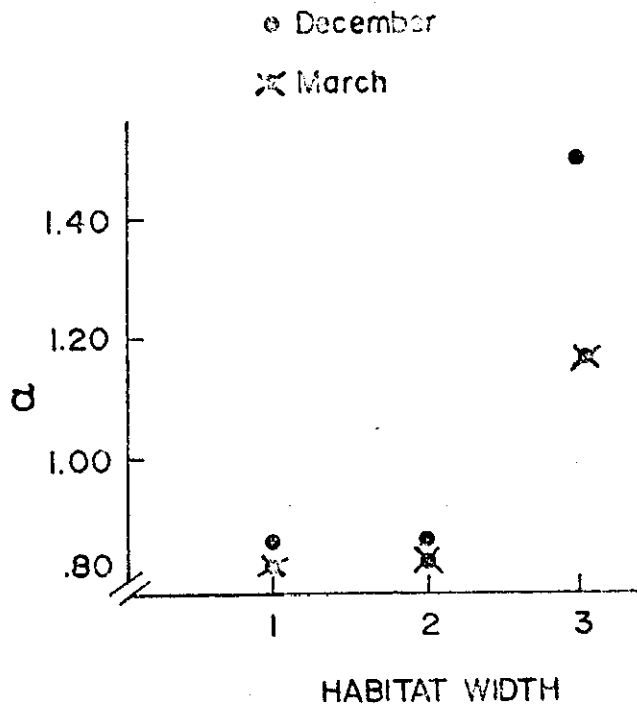


Fig. 4. Average of all competition coefficients between 23 species in plots in which six different levels of phosphorous fertilizer were applied. Increasing habitat width corresponds to increasing fertilizer level. Example no. 1.

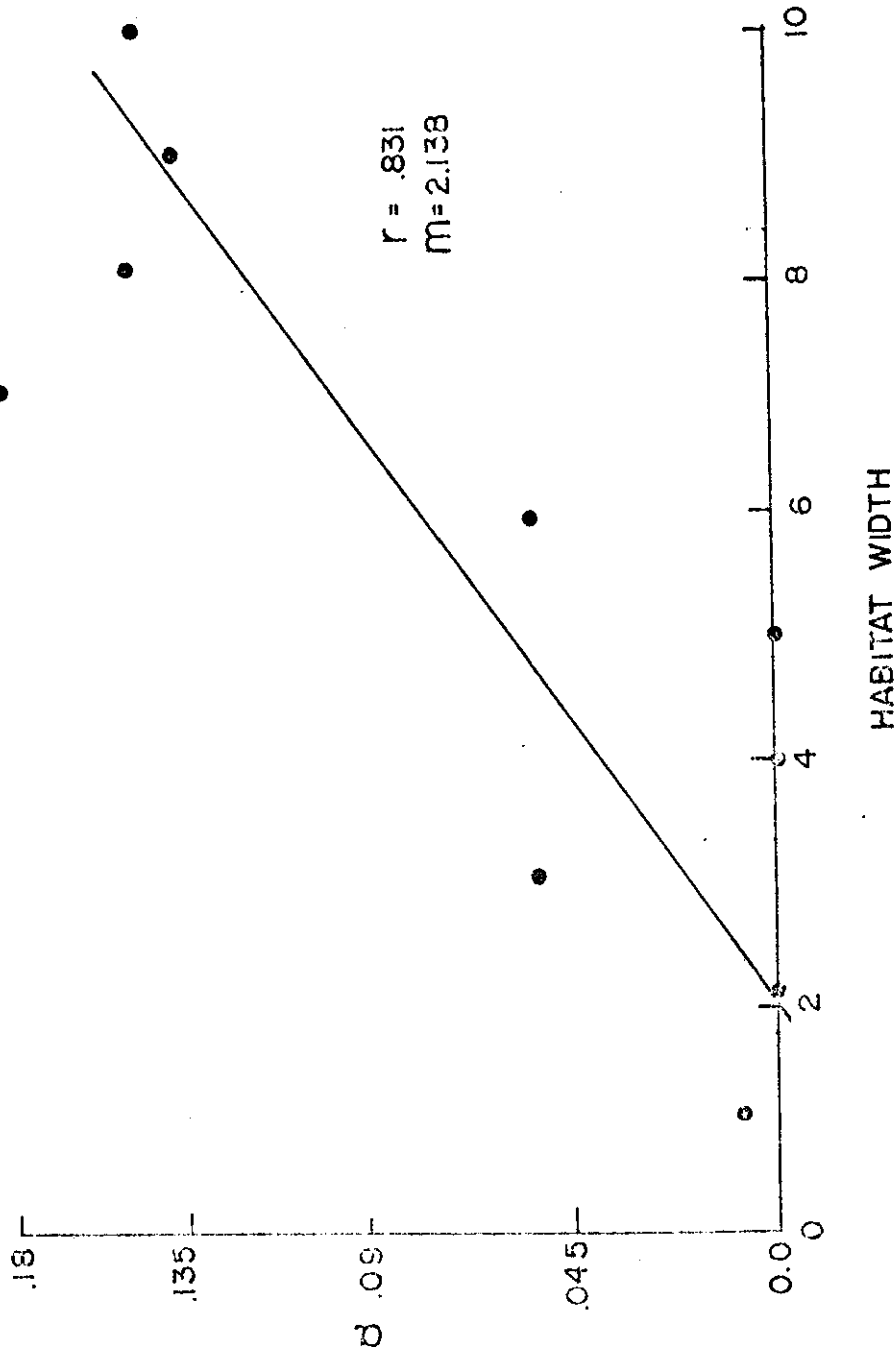


Fig. 5. Average of all competition coefficients between 20 species in plots with different soil depths. Relation between mean of competition coefficients and habitat: Increasing habitat width corresponds to increasing soil depth. Example no. 2.

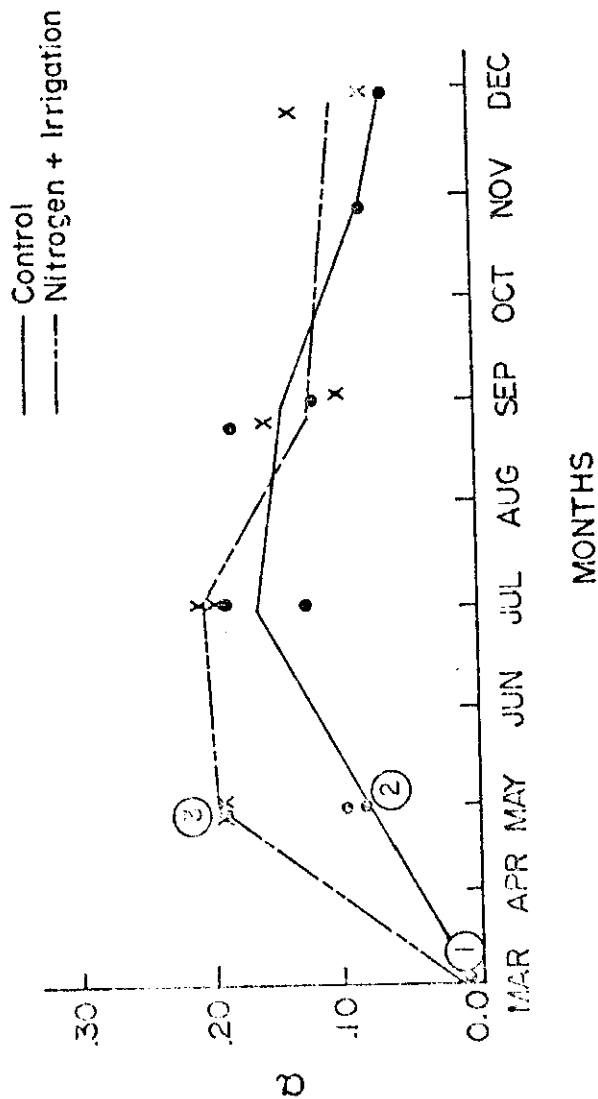


Fig. 6. Mean of competition coefficients of species over time in control and irrigated plus fertilized plots. Numbers encircled refer to points selected for detailed analysis of individual species response to increase in resource level as a consequence of the development of growing season or of artificial management.

instead of considering each individual species from the most abundant to the least abundant, groups of species have been formed in such a way that group no. 1 is composed of the four most abundant species, group no. 2 of the following four species, and so on.

Table 3 shows the result of five linear regression analyses (with respect to habitat width) of the average competition coefficients of five groups of four species each in decreasing order of importance. The slope of the regression diminishes as we consider groups of species of lower representation in the community, with the exception of group 4. This indicates that minor species are less sensitive to changes in the amounts of resources, which poses the question of whether this is so because they depend greatly on the effect of competition of dominant species. Table 4 shows a similar analysis for the data of example no. 2 which are consistent with the results of the previous example.

Before examining the corresponding analysis for example no. 3, it seems worthwhile to make some comments on different types of variations in the amount of resources available to the grassland plant community which are underlying the examples shown.

(1) There is a variation of resource level which is caused by habitat changes over space (as in example no. 2) or over time (as in example no. 3). This variation may be termed "expected" or "natural," meaning that it constitutes a factor of natural selection over the community succession; therefore, the changes induced by it in the community should be regarded as relatively stable. This item should be compared with item (2).

TABLE 3. Results of linear regression analysis of average of competition coefficients of all species with respect to habitat width in example no. 1. Species were grouped in five categories in order of decreasing importance as measured by biomass quantity through the whole gradient.

Group rank	Correlation coefficient (r^2)	Regression slope (m)
1	.866	.0057
2	.873	.0055
3	.957	.0050
4	.791	.0053
5	.993	.0035

TABLE 4. Results of linear regression analysis of average of competition coefficients of all species in example no. 2. Species were grouped in five categories of decreasing importance as measured by biomass quantity through the whole gradient.^{a/}

Group rank	Correlation coefficient (r ²)	Regression slope (m)
1	.872	.053
2	.709	.022
3	.772	.023
4	.652	.014
5	.590	.004

^{a/}Regression analysis of correlation coefficients in relation with the slope produced $r = .954$ and a slope $m = 5.7003$. Regression of slope m in relation with group numbers produced $r = -.914$ and a slope $m = -.0106$.

(2) Changes in level of resources induced artificially ("unexpected") by irrigation or fertilization (examples no. 1 and 3). These changes may be reflected also in the community structure by a change in the competitive interaction between species. These may not be as stable as (1).

The analysis which follows is directed to see whether there is a different interaction between different groups of species in one case as compared with the other which might help to understand the different nature of responses to natural vs. artificial increases of resource levels.

Three critical points have been selected in the data of Fig. 6. The comparison of points 1 and 2 should give some insight into which species show an increment of competitive ability under normally-improving conditions. The comparison of points 2 and 3 should give some understanding of the improvement of competitive ability in different groups of species as the level of resources is artificially increased.

It is not possible to present the data along this conceptual gradient in the same form as for the previous examples since only the extreme points of the gradient are defined and it is of little interest to fit a straight line between two points. Instead, the average values of competition coefficients for the species taken in three different groups of decreasing importance are shown for the extreme points of the conceptual gradient defined (Table 5). The inspection of the column where net differences are computed shows that the pattern of variation observed in correspondence with the "natural" or "expected" variation is one in which major species increase their competitive activity more than the rest; the contrary trend is observed when the variation is "unexpected" or "artificial" in nature.

TABLE 5. Comparison of competition coefficients at extreme points of two conceptual gradients defined over the data of Fig. 6: A "natural or expected gradient" (points 1 and 2) and an "artificial or unexpected gradient" (points 2 and 3). Mean values and increments are shown.

Group of species	Kind of resource variation				Differences	
	Natural (Points 1 & 2)		Artificial (Points 2 & 3)		Natural	Artificial
	Low	High	Low	High		
1	.09	.29	.29	.44	.20	.15
2	.05	.16	.16	.30	.11	.14
3	.00	.03	.03	.22	.03	.18

Discussion

Fig. 1a, 1b, 2a, 2b, and 3a suggests that changes in the level of resources in the plant community can be detected by changes in the "evenness" of species distribution. Whether this change represents increases in dominance in the classical ecological sense that is given to this word (Whittaker 1965), that is, a relative increase in abundance, cover, or weight of those species already abundant at the lower level of resource, is not very clear. Sometimes (Fig. 1b and 3a) dominance increases with what may be supposed to represent an increase in habitat width, and sometimes it decreases (Fig. 1a and 2a). Also, the estimation of dominance may change depending on the index used to estimate it (compare Fig. 3a and 3b). I have attempted to analyze and characterize the shape of abundance-rank function for many sets of data by means of χ^2 tests and least-square polynomial curves, but I have not found a clear trend in the information available to me which would indicate whether there is a group of species ranks that consistently is promoted or depressed when habitat width increases. Some other facts surrounding this question are suggested by analysis of competitive activity.

Some of the modifications of the "evenness" of species distributions observed in the different ecological situations analyzed in this paper are consistent with previous experimental information (Ares 1972). In fact, the analysis of Fig. 3a suggests that e_1 could be a tool for ascertaining variations in level of resources. Note that the plots treated with nitrogen fertilizer show lower index values at the beginning of the growing season while the irrigated plots show the lower values at the end of the same period. This is consistent with the way in which both

resources are used. Nitrogen is known to be an important factor controlling vegetative growth (Salisbury and Ross 1969) which occurs during the first part of the growing season, while it is relatively unimportant after maximum vegetative growth is attained. On the other hand, competition for water is greater in the drier part of the growing season, which is the second part of the growing season at the location of the experiment.

When looking at the competition between all species in relation to habitat width (Fig. 4, 5, and 6), an increase in habitat width seems to determine an increase in competition activity in the plant community. This holds true for both types of resource increase [(1) and (2)], and the response is very consistent for all species, as shown by the fact that all the regression slopes are positive in Tables 3, 4, and 5.

Throughout this paper there has been the assumption that there is a certain behavioral characteristic of each species in the community, that behavior is dependent on the *rank* situation of the species in the community. In other words, we are restating the idea that certain species behave as dominants, subdominants, or dominated, and that this "role" is more or less independent of the taxon that plays it. If this is the case, it is logical to expect that competitive interaction as estimated by competition coefficients is different for different groups of species in the community.

All of the species have been divided into a number of groups ordered according to decreasing quantity of biomass along the whole gradient. It appears that in the examples shown (Table 6), the dominant groups show the higher mean of competition coefficients, which is consistent with what we expect from those groups and from the competition coefficients.

TABLE 6. Averages of competition coefficients for species composing groups of decreasing dominance in the community.

Example	Groups of decreasing dominance				
	1	2	3	4	5
1	1.00	0.93	0.80	1.00	0.75
2	0.48	0.26	0.18	0.20	0.01
3	0.26	0.39	0.18	0.12	--

This may eventually be a way to characterize dominance, which has the advantage of taking into account patterns of biomass distribution in the field since competition coefficients depend strongly on the composition, size, location of samples, and interaction between species.

Another fact arising from inspection of regression slopes in Tables 3 and 4 and the differences in Table 5 is that the *increase* of competition coefficients corresponding to an increase in habitat width is different for each of the groups. In fact, it always happens that the dominants increase their competitive interaction with the rest of the species more than the lower ranks. The situation is partially or completely reversed when the increase in resources is artificial or unexpected, as in examples no. 1 and 3.

In Table 4, correlation coefficients are shown, as well as slopes of regression for different groups with respect to habitat width. If the regression analysis of these quantities is made, as shown in the bottom of the table, a positive correlation between m and r is found. This would indicate that those ranks of species which are able to modify their competitive ability in a close adjustment with the changes in the environment are less sensitive to other disturbances, namely, the effects of other species. This may be particularly useful for a mechanistic approach when modeling multispecies interactions. Note that this does not seem to hold for example no. 1 (artificial perturbation), Table 3.

Returning to the distinction between "natural" and "artificial" variations in habitat width, we note that when looking at the first kind of situation, as in examples no. 2 and 3 (points 1 and 2), the group

which shows the greater increase in competitive action against the rest of species is the first, i.e., the dominant; but when the perturbation is of an artificial nature, as in examples no. 1 and 3 (points 2 and 3), some subdominant or dominated group takes more relative or absolute advantage of the increase of resource.

Thus, under "natural" or "expected" conditions, the species which take most advantage of the increasing resource are the usual dominants of the community, while under "artificial" or "unexpected" conditions a subdominant or even a dominated group may take greater advantage of the increasing resource.

The above statement is related to the question posed by McNaughton and Wolf (1970) that the dominant species are so because they are specialists in use of an abundant resource in the environment. The results here suggest that whenever a critical resource increases according to usual patterns, the dominants take more advantage of the situation than other species. However, when the fluctuation is "artificial," "man induced," or "unexpected" in nature, some other group makes the modification more profitable for their own use. However, this is not stable over time, probably because there are still habitat characteristics which make the dominants the best fitted, and in the long term they will regain their relative place in the community if the conditions prevailing before the modification are partially or completely restored.

A subjective picture of species function along an environmental gradient, which is qualitatively supported by the information here, can be formulated at this point. In this conception (Fig. 7), species are supposed to compete with each other more intensively as the total

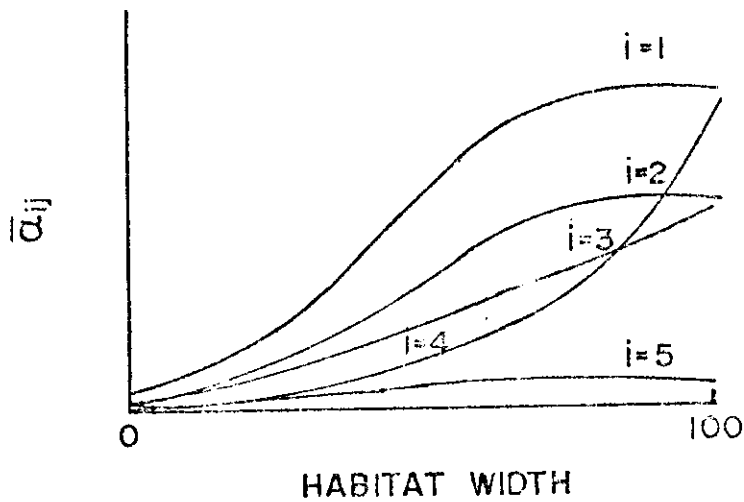


Fig. 7. Conceptual relations between the changes in habitat width and the interaction between species estimated by the average of second-order competitive coefficients between species i and the remaining species in the community. All species increase their competitive action as the habitat width increases, though the rate may be different depending on the rank of the species in the community and the nature of the habitat perturbation.

habitat width increases. Note that all of the species are supposed to be found through the whole gradient, which limits this discussion to a very narrow range of heterogeneity between samples of the defined community. The slope of curves is supposed different for each species; dominant species show the greater competitive effect and also the greater slope of change as habitat width increases. However, there may be some permutations of either one depending on the kind of habitat variation. These permutations may, in fact, mean that the rank order suffers "permutations" from one place in the gradient to another. The data shown here suggest that the way in which this rearranging in the community order takes place is in association with the kind of perturbation of the habitat width. These structural and functional variations seem adequate to depict several different situations in grassland communities.

Conclusions

The particular way in which biomass is partitioned between the species composing grassland plant communities is related to functional characteristics of the community, which refer to the amount of resources made available to it, either by spatial heterogeneity of the environment, time variations of the growing conditions, or through irrigation and fertilization.

Though an increase in habitat width does not always increase dominance, it consistently increases the level of competition, as estimated by the mean of off-diagonal elements of community matrices.

The analysis of the competitive ability of different groups of species of decreasing ranks of abundance within the community suggests

that when the variation of habitat is of a type described as "natural" or "expected" in nature, the dominant groups take more advantage of it than the rest of the species, and they show a relatively greater increase in competitive ability. When the variation of habitat is "artificial," "man-induced," or "unexpected," some subdominant or dominated group may greatly increase its competitive ability.

These data provide some insight into the effect that different types of habitat perturbations have on the plant community function and may be used when modeling interactions between species at varying levels of critical resources.

Acknowledgments

Dr. Norman French, Dr. John Marshall, and Dr. Robert H. Whittaker read the manuscript at different stages of its preparation and made valuable comments. Dr. P. Sims and Dr. W. Lauenroth generously allowed me to use some unpublished data.

This research was conducted during a leave at the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins. The author is a fellow of the Consejo Nacional de Investigaciones Científicas y Técnicas, República Argentina.

Literature Cited

- Ares, J. 1972. Equitability, competition and seasonal succession in a plant community. *Ecology* 60:325-331.
- Ares, J. O., and R. C. Leon. 1972. An ecological assessment of the influence of grazing on plant community structure. *Ecology* 60:333-342.
- Buzas, M. A. 1972. Patterns of species diversity and their explanation. *Taxon* 21(213):275-286.
- Colwell, R. K., and D. J. Futuyuma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52(4):567-576.
- Hanson, H. C., and E. D. Churchill. 1961. *The plant community*. Reinhold Pub. Corp., New York. 218 p.
- Klippel, G. E., and D. F. Costello. 1960. Vegetation and cattle response to different intensities of grazing on short-grass ranges of the Central Great Plains. U.S. Dep. Agr. Tech. Bull. 1216. 82 p.
- Levins, R. 1968. *Evolution in changing environments*. Princeton Univ. Press, New Jersey. 120 p.
- Lloyd, M., and R. J. Ghelardi. 1964. A table of calculating the "equitability" component of species diversity. *J. Anim. Ecol.* 33:217-225.
- MacArthur, R. H. 1957. On the relative abundance of bird species. *Nat. Acad. Sci., Proc.* 43:293-295.
- Margalef, R. 1963. One certain unifying principle in ecology. *Amer. Natur.* 97:357-374.
- McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.
- Odum, E. 1969. The strategy of ecosystem development. *Science* 164:262-270.
- Pielou, E. C. 1965. The use of information theory in the study of the diversity of biological populations. *Fifth Berkeley Symp. Math. Statist. Probability, Proc.* 4:163-177.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity. I. *Ecology* 43:185-215.
- Price, L. W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. *Ecology* 52(4):638-647.

- Pulliam, H. R., E. Odum, and G. W. Barrett. 1968. Equitability and resource limitation. *Ecology* 49:772-774.
- Risser, P. G., and E. L. Rice. 1971. Diversity in the species in Oklahoma upland forests. *Ecology* 52(5):876-880.
- Salisbury, F. B., and C. Ross. 1969. *Plant physiology*. Wadsworth Publ. Co., California. 747 p.
- Singh, J. S., and R. Misra. 1969. Diversity, dominance, stability and net production in the grasslands at Varanasi, India. *Can. J. Bot.* 47:425-427.
- Slobodkin, L. B. 1961. *Growth and regulation of animal populations*. Holt, Rinehart and Winston, New York. 184 p.
- Van der Sluij, D. H. 1971. Native grasslands of the Mesopotamia region of Argentina. *Neth. J. Agr. Sci.* 19:3-22.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147:250-260.
- Whittaker, R. H. 1971. Evolution of natural communities, p. 137-159. *In* *Ecosystem structure and function*. 31st Annu. Biol. Colloquium, Proc., Oregon State Univ. Press, Corvallis.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21(2/3):213-251.