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A MODEL AND EXPERIMENTAL DATA ON CHANGES IN PLANT

COMMUNITY STRUCTURE DURING A GROWING SEASON

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ABSTRACT

There is theoretical and practical interest in understanding the dynamic aspects of competition and resource use in grassland plant communities. Perturbations of these systems (those induced by intense grazing, exclosure, irrigation, and fertilization) could be evaluated more accurately if a better knowledge of the ecological processes involved were available. Two approaches are used here to study these problems: a deterministic matrix model based on some broad ecological principles is used to generate sets of data describing the seasonal dynamics of perturbed and non-perturbed hypothetical communities and information available on seasonal dynamics under different treatments of a shortgrass prairie in eastern Colorado (US) is analyzed. The rationale of a previous model of the dynamics of a plant community during a growing season, which related changes of species biomass to changes in the availability of resources for plant growth, is here utilized and extended on the basis of the information obtained from the model behavior and the data.

INTRODUCTION

The evaluation of the effects of grazing strategies, fertilization
of grasslands, etc., is usually done on the basis of certain criteria,
e.g., maximizing dry matter production of one or several species, maintaining
soil cover, etc. (Lewis 1969). The knowledge of ecological processes,
such as resource use, plant competition, etc., associated with these
management practices would help to evaluate their effects on a more sound
basis. The ability to express that knowledge in synoptic terms, i.e.,
not depending on the floristic composition of the grassland, will allow
us to apply it to a wide range of management situations.

The way in which biomass is apportioned between the species composing
a plant community has been recognized as a structural characteristic of
the community which is the consequence of ecological relations between
the community and the abiotic environment (Whittaker 1972).

It has been shown (Ares 1972) that variations in the amount of resources
such as water in the soil and light during a growing season induce modifica-
tions in the apportionment of total biomass between species in a community
of weeds accompanying the alfalfa crop. This also allowed us to formulate
a tentative model on seasonal succession in the plant community. In this
community which was a pioneer of a secondary succession, very drastic
changes occur in time, both in the resources available for plant growth
and in the botanical composition of the system.

There are other plant communities in which changes of this sort are
not so drastic. In a grassland plant community which has been submitted
to regular grazing for several years, for instance, no major floristic
changes occur during the growing season, and changes in relative biomass

of species are almost cyclic according to the improvement and decayment of environmental conditions favorable for plant growth.

In these communities, other factors affect the apportionment of biomass between species, one of the most important being the selective effect of the grazing animal; whenever grazing is intense and continuous, as is the case in many grasslands in the world, it constitutes a selective factor of prime importance which may determine by itself the ecological success or failure of plant species.

Usually, man's strategies for the utilization of the grasslands as a natural resource involve the alternation of grazing and exclosure periods; the sequence, time duration, and periodicity of these manipulations constitute ecological variables which modify the structure of the plant community. Fertilization and irrigation also induce temporary or definite changes either in relative importance of species, floristic composition, or both.

The concept of a perturbed community is used here to describe a situation following some major change in the environment, e.g., deferment after grazing for a long time, fertilization of an old grassland for the first time, etc. A non-perturbed community is one in which the environment has not changed drastically as a result of human activities at least in the near past; this is reflected both in a stable floristic composition and a stable apportionment of biomass between species.

The attempt is done here to relate changes in biomass of species to some ideas in ecological theory about fitness, dominance, and use of resources. To this end, a model of a hypothetical community of ten species has been built and its behavior used to explore the changes in biomass of species produced when the environment is somehow perturbed as mentioned above.

Then, data on plant species biomass obtained by extensive sampling of grasslands on the Pawnee Site, eastern Colorado (US) have been analyzed. This analysis and the similarities of behavior of the real and the hypothetical community of the model suggest an improvement of the ideas on seasonal succession previously developed by this author.

METHODS

A matrix model based on general ecological theory

There are several good reasons for developing a deterministic, discrete matrix model to simulate some ecological situations. By adequate selection of matrix elements, it is possible to imitate continuous situations with considerable accuracy. Leslie (1948) drew attention to the fact that his basic matrix model was conceptually equivalent to an exponential growth equation. Considerable flexibility may be attained when some of the elements of the operational matrix of a model are replaced by functions of time or of the vectors defined in each simulation step (Pennycuick, et al. 1968). Also, it is possible to formulate general, flexible, and simple matrix models of many ecological situations other than those classically explored (Usher 1972).

The model here described consists of a FORTRAN IV simulation by iterative matrix operation on a vector X_i which describes the composition of the plant community at each of 50 simulation steps covering the growing season. The plant community is supposed to be composed of ten species, and X_i represents the live biomass in g/m^2 of each.

The following operations define what the model does at every simulation step, given the composition of plant community at the beginning of the growing season:

$$
\begin{bmatrix}
f(X_i,s,t) & \alpha_{21} & 0 & . & 0 \\
\alpha_{12} & f(X_2,s,t) & \alpha_{32} & . & . \\
0 & \alpha_{23} & . & . & . \\
. & . & . & . & . \\
. & . & . & . & \alpha_{n,n-1} \\
0 & . & . & \alpha_{n-1,n} & f(X_3,s,t)
\end{bmatrix}
\times
\begin{bmatrix}
X_1(t) \\
X_2(t) \\
. \\
. \\
. \\
X_n(t)
\end{bmatrix}
=
\begin{bmatrix}
\Delta X_1 \\
\Delta X_2 \\
. \\
. \\
. \\
\Delta X_n
\end{bmatrix}
$$

$$
\begin{bmatrix}
X_1(t) \\
X_2(t) \\
. \\
. \\
. \\
X_n(t)
\end{bmatrix}
+
\begin{bmatrix}
\Delta X_1 \\
\Delta X_2 \\
. \\
. \\
. \\
\Delta X_n
\end{bmatrix}
=
\begin{bmatrix}
X_1(t+1) \\
X_2(t+1) \\
. \\
. \\
. \\
X_n(t+1)
\end{bmatrix}
$$

where $f(X_i,s,t)$ is a function of species biomass X_i at time t, site s, characteristics defined with respect to one critical environmental variable, and time of simulation t; and ΔX_1 represents the positive or negative modifications of biomass as a consequence of matrix operation in each time step.

The following describes the explicit form of functions in the diagonal of the matrix:

$$
\text{(a)} \quad f(X_i) = \text{SATFAC} = (X_{isat} - X_i)/X_{isat}
$$

where X_{isat} is a saturation value of population size for each species which is set as $10X_i$ at the beginning of simulation.

The assumption is made that the community distribution of relative biomass among species fits an equitable distribution as that described

by MacArthur (1957), and that the potential maximum increase of biomass of each species is determined by the abundance of resource or microenvironments suitable for that species. It is also assumed that the order of dominance in the community is determined by the amount of resources available in the environment for each species (McNaughton and Wolf 1970).

(b) $f(s) = DISFAC_i = 1 - (|OPTFAC_i - SITFAC|/100)$

where SITFAC is either constant = 100 or varies between 100 and 0 according to variation in total biomass of the community and represents the value of a critical resource. $OPTFAC_i$ is an optimum value for each of the i species defined in the range $0 \leq OPTFAC_i \leq 100$ at the beginning of simulation. These definitions result in $0 \leq DISFAC_i \leq 1$ and increasing as the value of the critical variable in the site approaches the optimum of species i.

The assumption behind this procedure is that the difference between the physiological optimum of one species with respect to a critical resource and the actual value of the resource is one of the causes determining dominance or scarcity of that species in the environment. This characteristic of the model has been inspired by Levins' (1962, 1966) treatment of fitness of different phenotypes in a specific population. According to his reasoning, fitness can be expressed as a function of $W(S - S_i)$ where S is the actual environment value of a variable and S_i is a value optimum for that species. The treatment used here applies a similar reasoning to fitness between different subpopulations of a multi-specific community, instead of different subpopulations inside a unispecific population.

(c) $f(t) = TFAC = \frac{1}{2} \sin (0.628 \times TIME)$

This definition implies $-1 \leq$ TFAC ≤ 1 in the interval $0 \leq$ TIME ≤ 50. This is intended to describe in a deterministic way the combined effects of growth and decay of green material during the season. The explicit form of the total function occupying the diagonal elements of the matrix is thus:

$$f(X_i, s, t) = \text{TFAC} \times \text{SATFAC}_i \times \text{DISFAC}_i \qquad (1)$$

The model was operated by omitting DISFAC_i from equation (1), and it was verified that all species keep their relative proportions constant throughout the season only when TFAC and SATFAC_i are included and when saturation is defined as a proportional function of each species biomass.

The off-diagonal elements α_{ij} of the operational matrix are coefficients with the negative sign describing the competitive effect upon any species caused by other species with a similar amount of biomass in the community. Their values can be defined in the range $0.01 \leq \alpha \leq 0.1$, but they have all been assumed to be identical to 0.01 in the versions of the model described in this paper.

The following describes the explicit form of ΔX_i resulting from matrix operation:

$$\Delta X_i = X_i \left((\text{TFAC} \times \text{SATFAC} \times \text{DISFAC}) - \sum_1^2 \alpha_{ij} X_j \right)$$

where j in the summation term is either $i - 1$ or $i + 1$, if defined.

The model also computes two indices describing plant community structure at each simulation step. These are e_1, the equitability index of Lloyd and Ghelardi (1964), and e_2 defined as:

$$e_2 = \sum_1^n (X_i - \overline{X})^2/n - 1$$

Output of two versions of the model are described in this paper. In the first version (i) the value of the hypothetical resource remains constant throughout the season and near the optimum of dominant species. Optimum values for each species with respect to that resource are computed by means of a function of rank of species abundance at the beginning of the season. The underlying assumptions are that dominance ranking does not change during the growing season and also that conditions suitable for growth improve gradually for all species, the success of each at any time being determined by the proximity of physiological optimum to environmental characteristics. The equation which describes the function is:

$$OPTFAC_i = 100/R \tag{2}$$

where $10 \leq OPTFAC_i \leq 100$ and $1 \leq R \leq 10$ describes the rank position of species i in the community at the beginning of simulation, $R = 1$ being the most abundant or dominant. The second version (ii) of the model differs in that the value of the resource is allowed to change during the growing season, continually approaching the optima of dominated species. This is conceptually equated to a situation in which a critical factor or resource which was available at a level which was optimum for the dominant species becomes scarce and another resource, not necessarily one which the dominant species are best adapted to utilize, becomes limiting and constitutes a new factor modifying plant community structure. Examples of this situation could be the deferment of a community after intense and conspicuous grazing during many years and fertilization or irrigation in native grassland not previously submitted to that treatment.

Experimental data

The data presented refer to an investigation made in the context of the US/IBP Grassland Biome program at the Pawnee Intensive Site on a shortgrass prairie dominated by *Bouteloua gracilis* (H.B.K.) Lag. (blue grama). The pasture of the site has been described in detail by Klipple and Costello (1960).

Intensive sampling of aboveground green biomass by species was made during 1970 and 1971 in plots that differed with respect to the treatments applied to them. The sampling techniques are described in French (1970), and Table 1 describes the pattern of treatments applied to the plots. The interval between samples ranged from 15 to 40 days.

Structural changes in the plant community in these plots are evaluated by means of e_1 and e_2 indices as described in the model section above. These indices have a nearly inverse relationship, so that e_1 decreases as dominance increases, while e_2 increases in the same circumstance. The index e_1 is strictly a comparison between two community structures, one which is assumed equitable and the other the actual structure represented by the sample data; e_2 is independent of any distribution as it is only a function of relative biomass dispersion around a mean.

RESULTS

Model output

(i) Model version which holds the critical resource level near the optimum for the dominant species:

In this version of the model the value of the critical environmental factor has been set equal to 100 during the whole growing season. The

Table 1. Past and present treatments applied to plots on a blue grama shortgrass prairie[a/]

Plot	Previous 20 Years	1969	1970	1971
A	Heavy grazing	Heavy grazing	Heavy grazing	Heavy grazing[b/]
B	Moderate-light grazing	Moderate-light grazing	Moderate-light grazing	Moderate-light grazing[b/]
C	Moderate-light grazing	Moderate-light grazing	Exclosed[b/]	Exclosed[b/]
D	Moderate-light grazing	Moderate-light grazing	Exclosed + Nitrogen fertilizer + Irrigation[b/]	Exclosed + Nitrogen fertilizer + Irrigation[b/],[c/]

[a/] All plots are on Ascalon soil series.

[b/] Data used for this paper.

[c/] Not refertilized in 1971.

optimum values with respect to that factor for each species were assigned by equation (2).

Fig. 1 shows the variation of species biomass during the growing season generated by the model under the assumption that the level of critical variable or resource does not change during the growing season.

Fig. 2 shows the change in plant relative biomass distribution as estimated by e_1 and e_2 indices. Though derived from different concepts, the behavior of both indices is consistent and comparable in showing a high dominance in the middle part of the growing season.

(ii) Model version in which the critical resource level varies during the growing season, approaching the optima of minor species:

In this version (Fig. 3) the value of the critical resource has been allowed to vary during the growing season, approaching the optima of dominated and scarce species. This results in a diminishing dominance as the growing season proceeds, as those species that were dominant at the beginning of it are no longer able to maintain their relative importance in terms of biomass values as a consequence of poorer ability to utilize the changing environment.

Fig. 4 shows the corresponding e_1 and e_2 variations. It is apparent that the introduction of a variable level for the critical factor causes a change from a concave to a convex trend of variation or reciprocally, depending on which of the two indices is considered, indicating a minimum of dominance in the middle of the growing season.

Experimental data

Values of e_1 and e_2 were computed using data on ash free dry plant biomass obtained by sampling the plots during the growing season of 1970 and/or 1971.
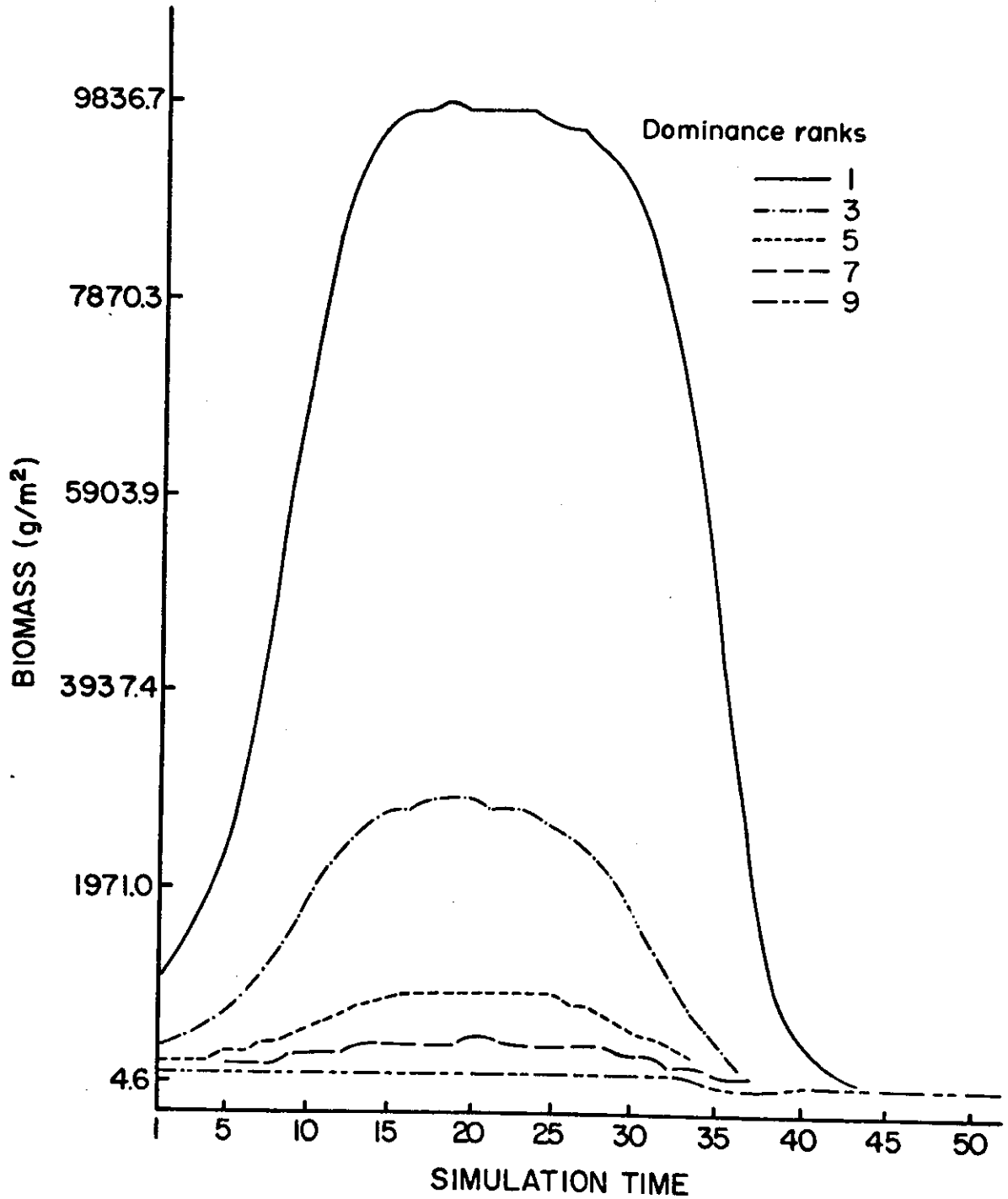
Fig. 1.   Variation of biomass of five of the ten species composing the
hypothetical community in the model; plant species have been
selected to cover the range from the most to the least abundant.
The value of the environmental factor was maintained at a level
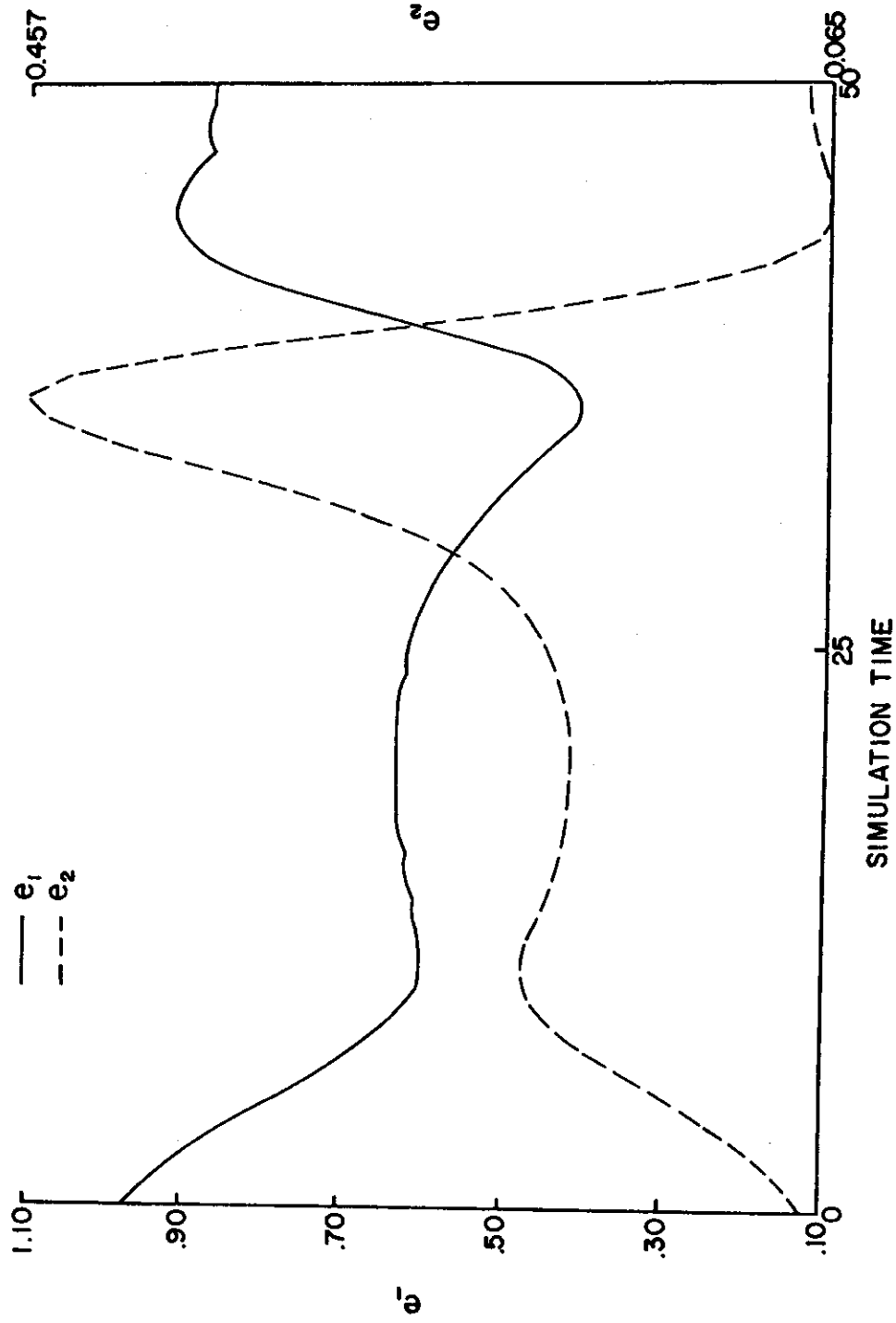equal to the optimum of the dominant species.

Fig. 2. The variations in species equitability during the growing season corresponding to the situation described in Fig. 1, as estimated by e_1 and e_2 indices.
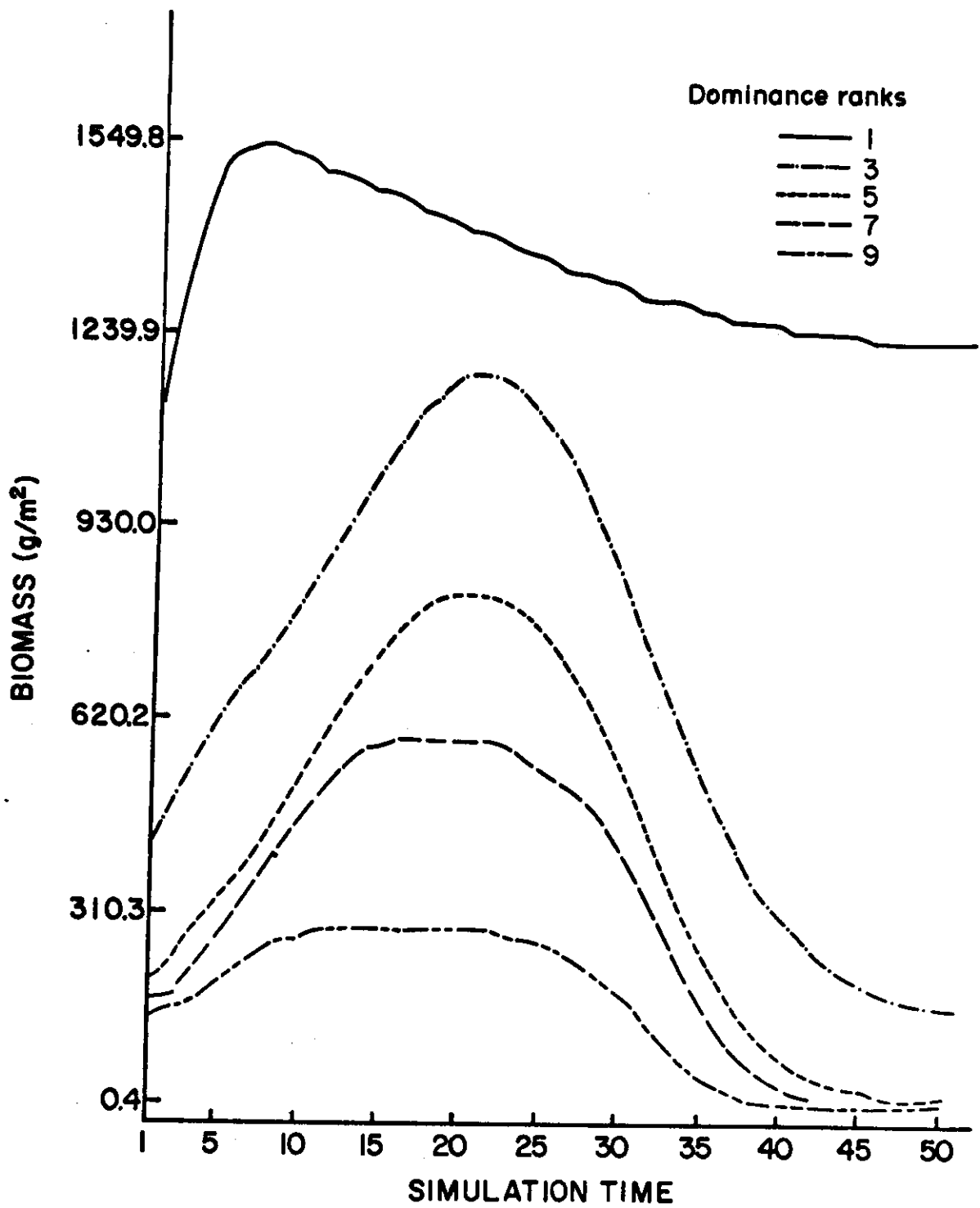
Fig. 3. Same as Fig. 1, but in this case the value of the resource is allowed to vary from the value which is optimum for dominant species to the optima of dominated species.
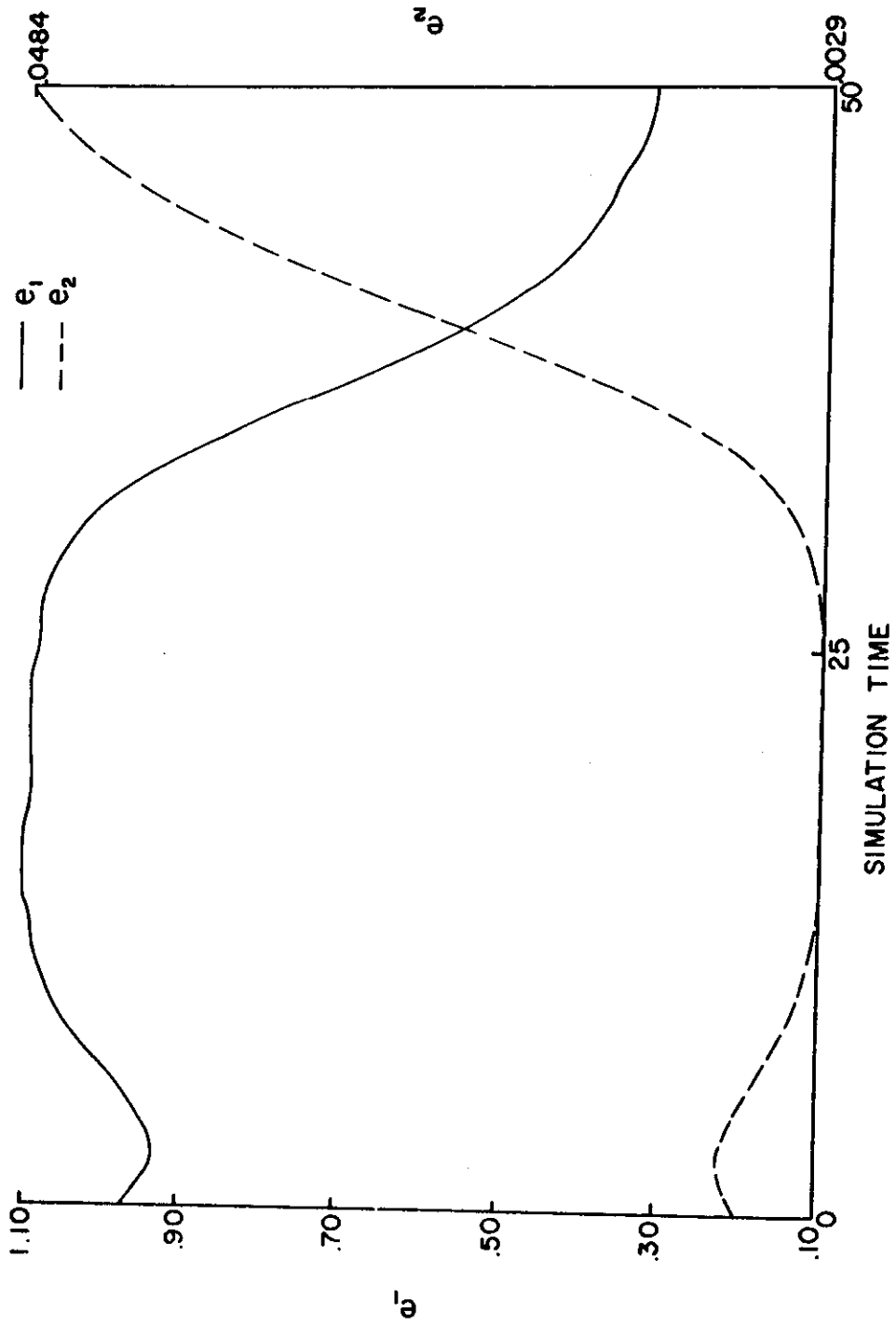
Fig. 4.   Same as in Fig. 2, corresponding to the situation in which the level of resource is allowed to vary in the direction of dominated species optima (e_1, e_2).

Plot A (Fig. 5) may be considered as the situation most similar to the (i) version of the model. It is a plant community that has been submitted for a long time to a selective force of prime importance such as intensive grazing. Species which are dominant are well adapted to the prevailing conditions.

Plot B (Fig. 6) is a very similar situation with the difference that grazing is a less important selective factor when compared with A, thereby allowing for the possibility that some other environmental factor may also be important in structuring the relations between species. Both of these plots represent ecological situations which may be quali- tatively compared with the first version of the model shown.

The reciprocal relationships between indices e_1 and e_2 are apparent when observing Fig. 5 and 6. The concave and convex variations during the growing season closely resemble those produced by the model under assumptions which are consistent with the treatment received by plots A and B; the magnitude of the inflections is less marked in plot B than in plot A, which is also consistent with model assumptions.

Plot C may be thought of as a situation more similar to version (ii) of the model shown in which there is a defined structure, but the ranking of species bears no ecological relation with the selective characteristics of the environment, since those qualities that rendered species more adapted to grazing conditions are not necessarily the most appropriate to compete under deferment conditions. It is reasonable to think that the changes in structure should indicate the perturbation imposed on the community.

Fig. 7 shows e_1 variation during the growing season in plot C in 1970 and 1971 growing seasons. Change from a concave shape with a minimum
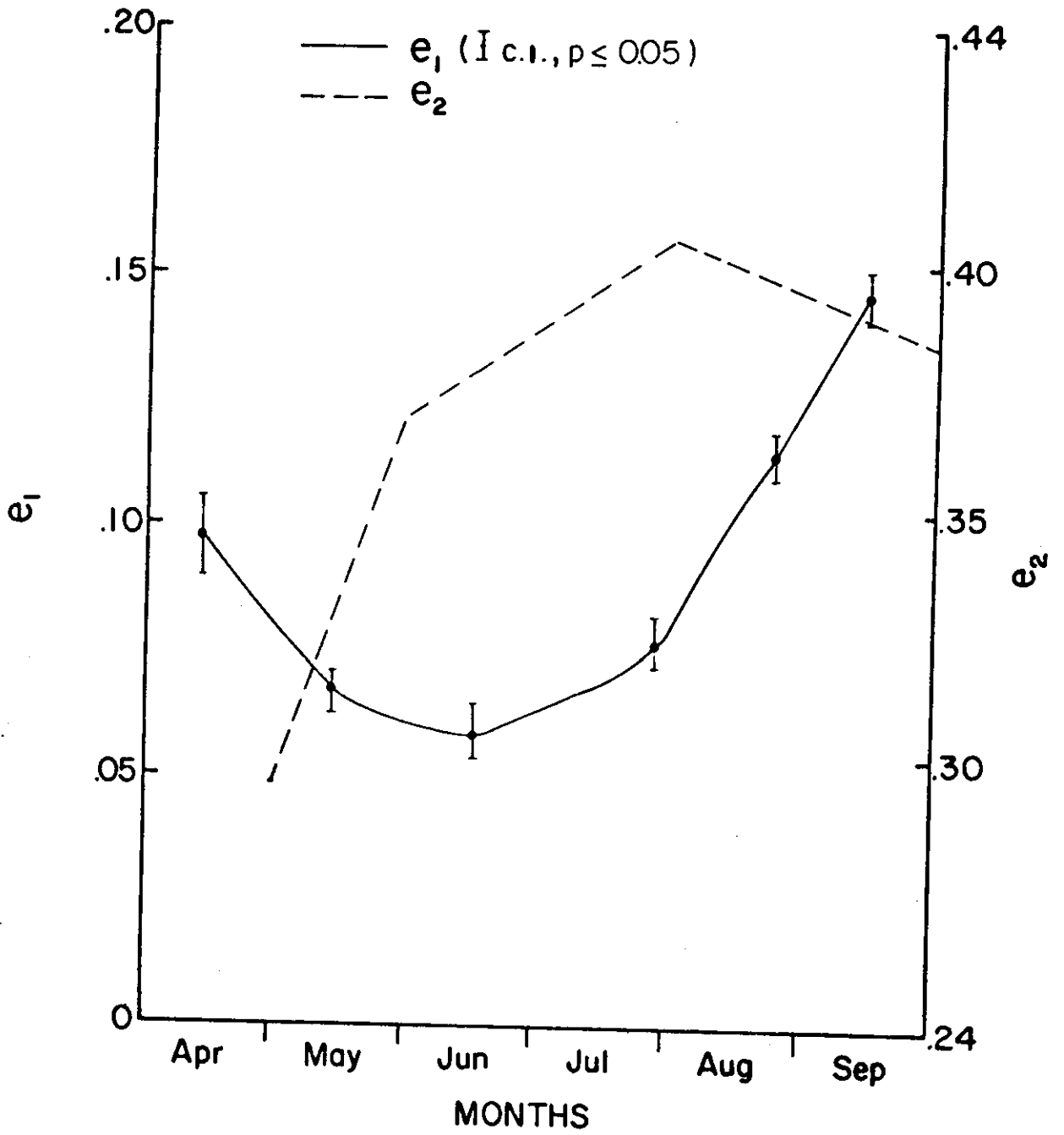
PLOT A

Fig. 5. Variations in plant community structure as described by e_1 and e_2 indices, evaluated from samples taken during the growing season in plot A.
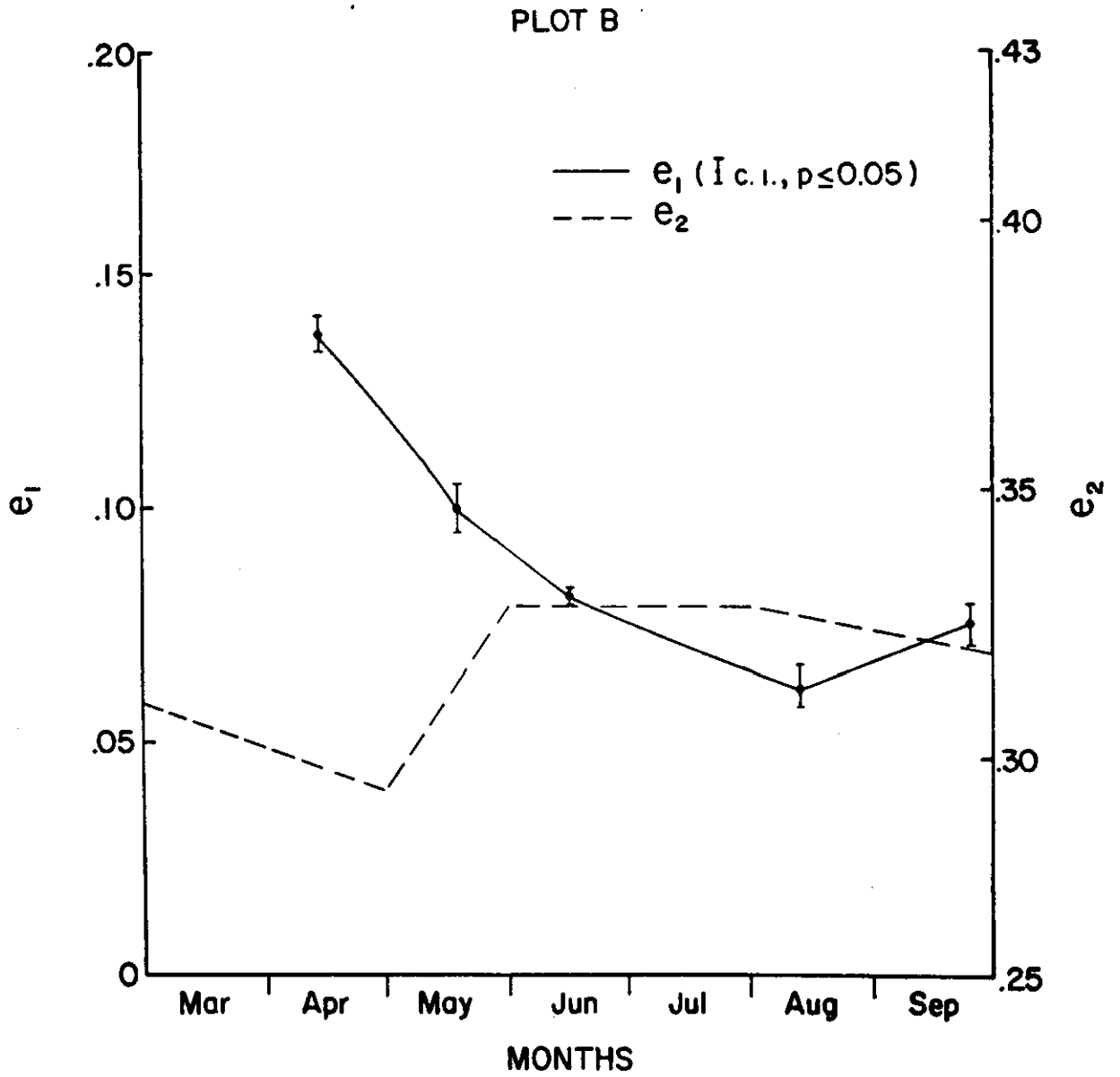
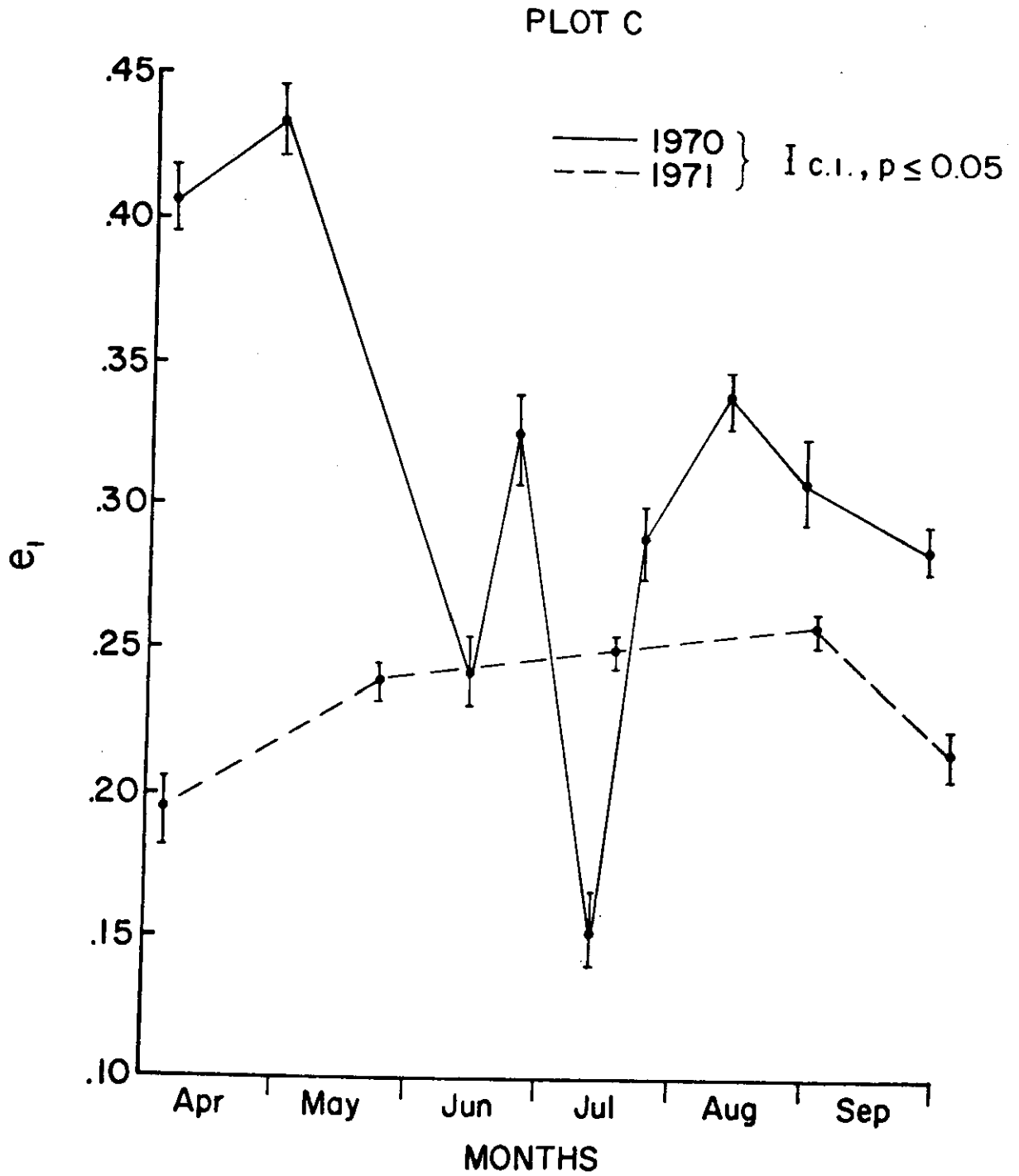Fig. 6.   Same as in Fig. 5 for data obtained from plot B.

Fig. 7.   Variations in plant community structure (e_1) in plot C in two successive years after perturbation of the environment by exclosure.

around the mid-growing season to a convex curve which might be characteristic of disturbed communities is evident during the second growing season after exclosure. This may imply the existence of a lag time during which the effects of the perturbation are not evident. These considerations are also supported if e_2 indices are considered, although the corresponding graphs are not shown here.

Plot D shows the most extreme situation in the sense that the perturbation of the plant community is maximal, since elements which are known to modify plant growth, such as nitrogen and water, are added to a pasture which has been deferred after many years of grazing (Fig. 8). The same tendency of e_1 changes from a concave curve with a minimum in the middle of the growing season to a convex curve with a maximum in the mid-growing season is observed, and the inflection in plot D is more marked than in plot C.

DISCUSSION

Perturbed and non-perturbed adjustments of a plant community to the environment can be explored by looking at the apportionment of total biomass between species.

Both e_1 (equitability index of Lloyd and Ghelardi (1964)) and e_2 can be used to characterize biomass distribution. The rationale behind e_1 is a comparison between the dominance-rank relation of the community and that of MacArthur's (1957) model, though the value of the index does not depend on any of the assumptions of the model. It is desirable, however, to describe equitability without reference to any particular biomass distribution (Whittaker 1972); e_2 is preferable from this point
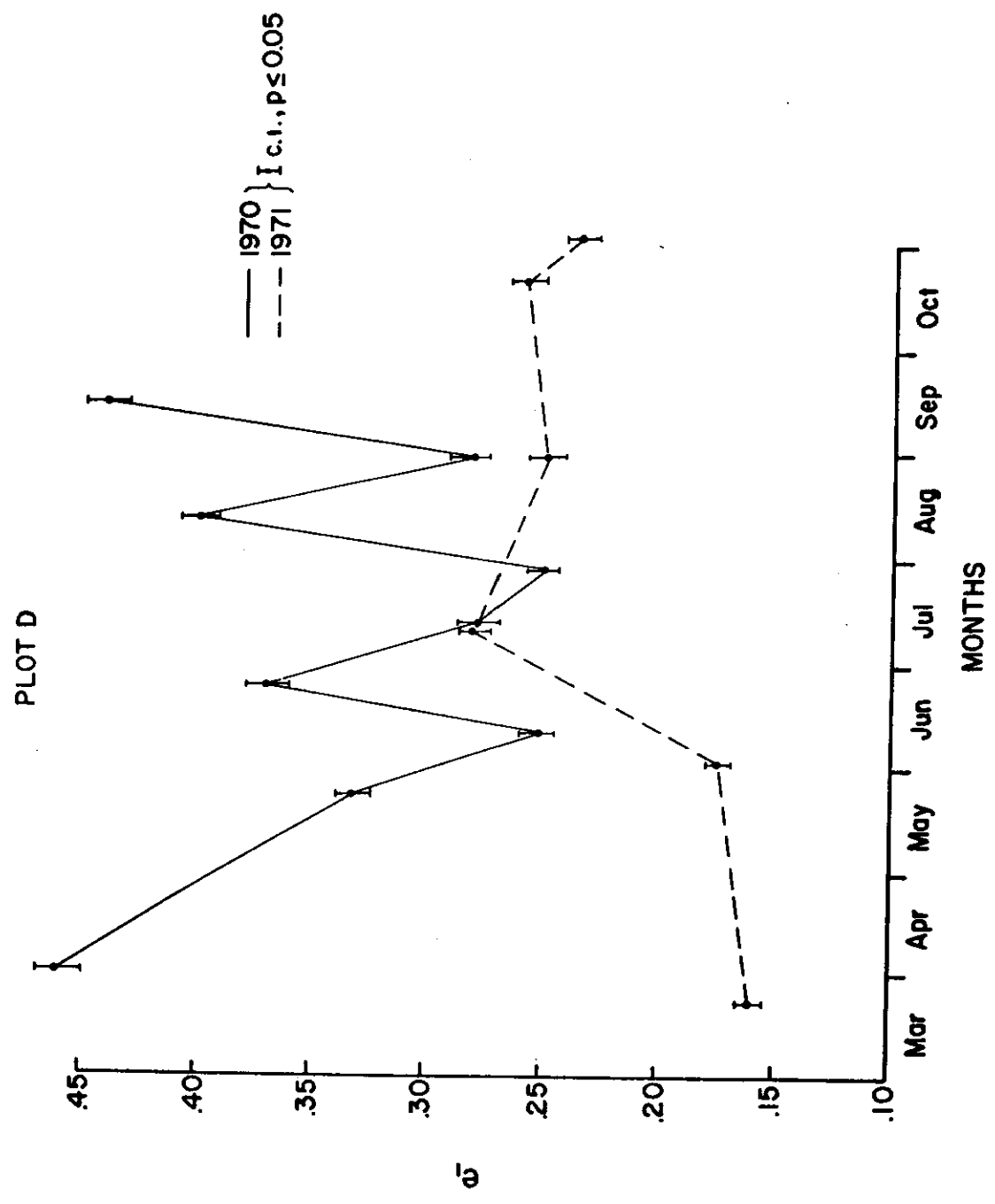
Fig. 8. Variations in plant community structure (e_1) in plot D in two successive years after perturbation by exclosure and fertilization.

of view, since it is just a measure of dispersion of biomass values around their mean value (Fig. 9).

According to the results shown here, both indices are able to show changes in dominance produced as a consequence of modifications of the environment.

In a previous experiment (Ares 1972) it was shown that competitive exclusion determined a decrease of dominance as measured by e_1 during the growing season. This was interpreted as the consequence of use of resources (water, light, etc.) which determined the partial exclusion of some species by the end of the growing season.

The behavior of the model presented in this paper suggests, and the trends in the data shown seem to confirm, that variations of dominance during the growing season depend on the perturbations to which the plant community has been submitted (Fig. 10). When the community has not been perturbed, e.g., in version (i) of the model or plot A, the trend of variation of dominance as measured by e_1 is concave (or convex, if measured by e_2), indicating a maximum of dominance at the middle of the growing season.

In a perturbed situation, e.g., version (ii) of the model or plot C and D, the trend is convex if measured by e_1 (or concave if measured by e_2), corresponding to a minimum of relative biomass of the dominant species at the middle of the growing season.

It should be born in mind that the data shown here do not validate the model proposed, but rather the model constitutes a feasible explanation of the trends of variation of biomass during the growing season observed. The model proposed here constitutes perhaps a crude simplification and is not unique with respect to the real situation which describes, a fact that is common to all simulation models.
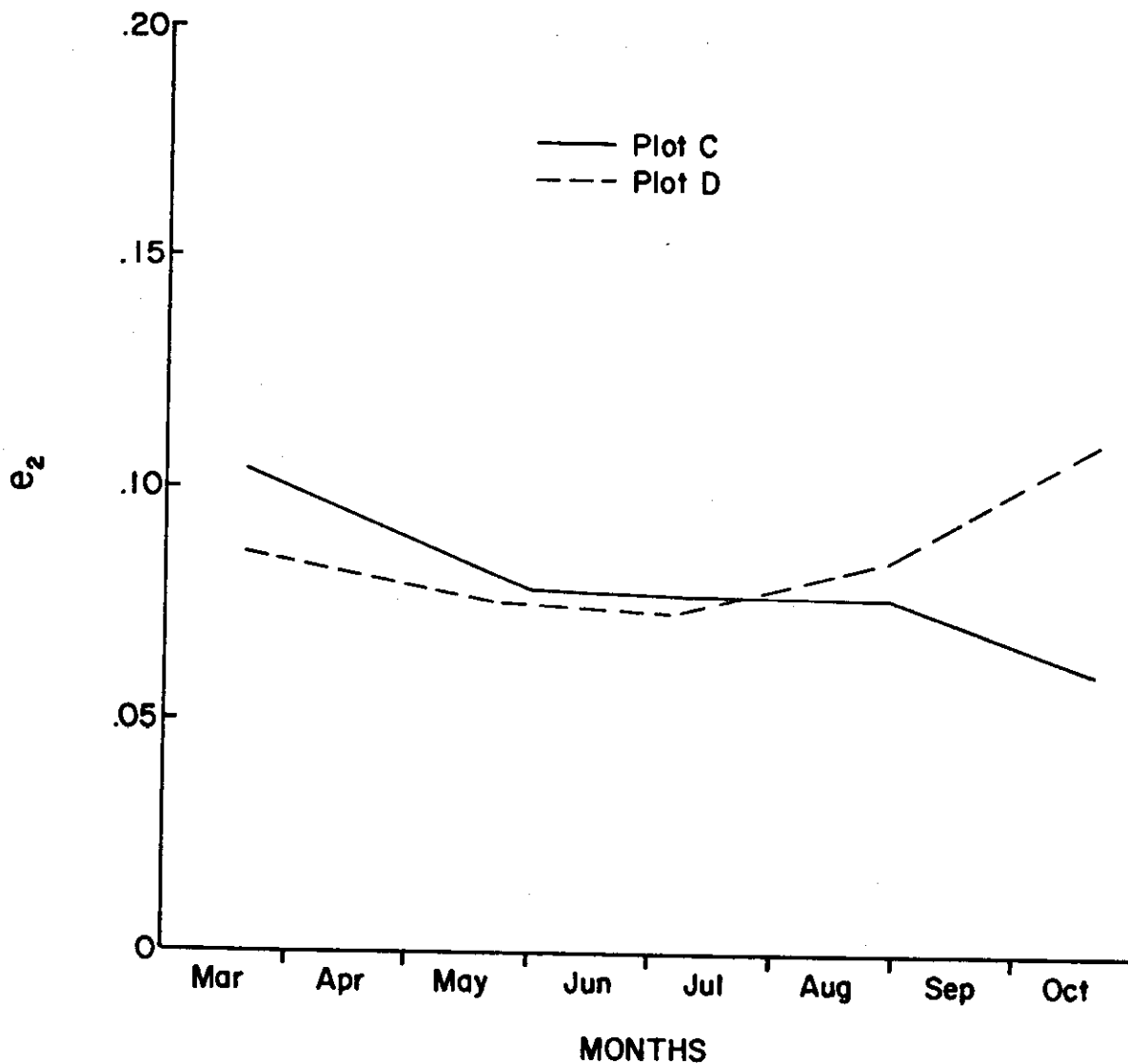
Fig. 9.   Comparison between structural variations in plots C and D
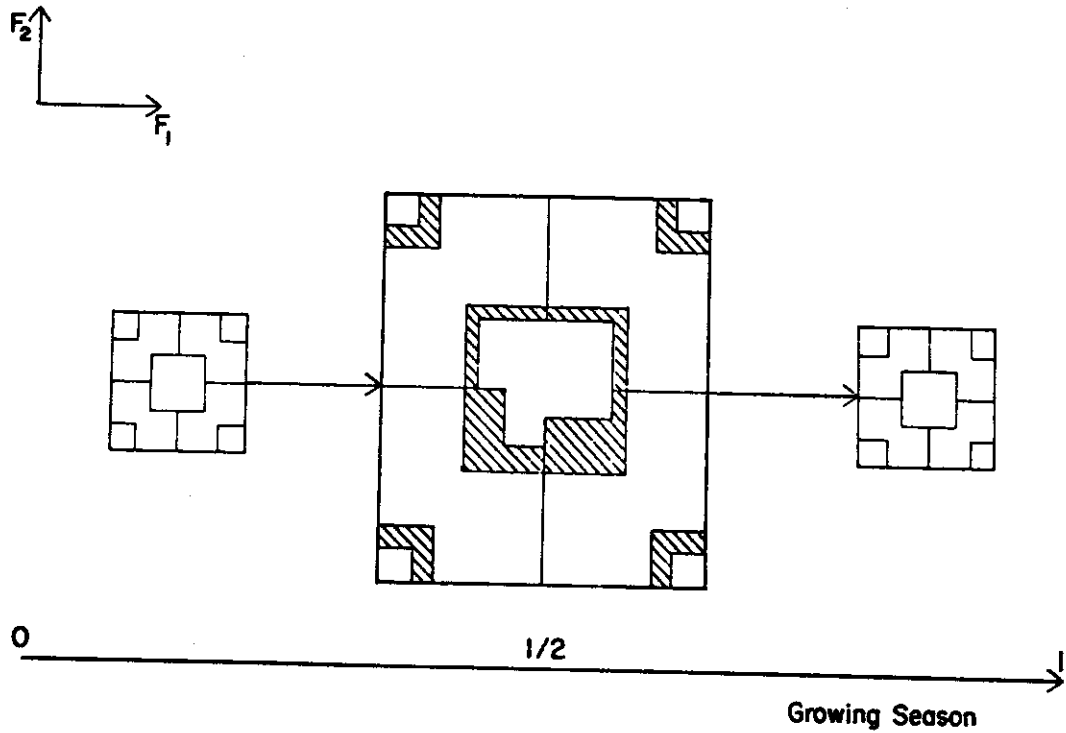in 1971 growing season, estimated by means of e_2 indices.

Fig. 10. A pictorial synthesis of several concepts regarding plant community intraseasonal dynamics. The external boundaries of the boxes represent the maxima and minima of two environmental critical factors (Fig. 1 and 2) that define the total fundamental niche or habitat available to the community. The internal boundaries represent the fractions of space that are occupied by each species. The shaded area is a representation of the intensity of competition and overlap between the species. The competition determines exclusion and return to a stable situation similar to that existing at the beginning of the growing season as habitat width shrinks again at the end of the growing season. A variation of the level of a factor for which competition could be established increases the level of competition and overlap. This rearrangement determines a lower equitability in biomass distribution. When the variation in equitability is described by means of e_1 and e_2 indices, a change from concave to convex tendencies (or vice versa, depending on the index chosen) indicates a rearrangement of the dominance order in the community.

ACKNOWLEDGMENTS

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