Community stability, complexity and species life history strategies*

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Abstract

The essence of the contradiction between traditional ecological complexity-stability hypothesis and recent theoretical results is clarified. The distinction between resilience and resistance is stressed. The possibilities of field verification of May's model are discussed. No satisfactory method for estimation of connectance and mean interaction strength in plant communities has been found. Relation between these parameters and stability in real communities remains an open question. The relation between connectance and stability (resilience) in purely competitive model communities is more complicated than May's rule predicts. The certain value of connectance having been achieved, stability increases with increasing connectance. We assessed the positive relation between species diversity and resistance, and negative relation between species diversity and resilience in plant communities during old-field succession in xeric habitat. But there is no causal relationship between species diversity and both kinds of stability. Resistance and resilience of the plant communities studied were determined primarily by life history strategies of constituent species. The results are interpreted in terms of Grimes' life history strategies and imply the validity of Gleasonian, population-centered explanation of community phenomena.

Introduction

Stability: resilience and resistance

Relationship between complexity and stability of biotic communities is a well known controversy in contemporary ecology. Until recently, many ecologists believed that increased community complexity, often expressed as 'species diversity', begets greater community stability (e.g. Elton, 1958; Odum, 1971; Andersen & King, 1978; Czarnowski, 1978). But during the past decennium, this hy-

pothesis seems to have lost ground (especially May 1972, 1973, 1976; also Goh & Jennings, 1977; Goh, 1980; Svirežev & Logofet, 1978; van Hulst, 1979; Nunney, 1980; Abrams, 1981).

May (1972) examined the complexity-stability question in model m-species ecosystems by constructing $m \times m$ community matrices with each off-diagonal element a_{ij} (interaction coefficient) assigned from a distribution of random numbers, where distribution itself has mean value zero, and standard deviation value (average interaction strength) s. The proportion of non-zero off-diagonal elements, e.g., the fraction of the pairs of species which directly interact, is called connectance, C. All diagonal elements a_{ii} are chosen to be -1. This means that each population ($i = 1, 2, \ldots, m$) in isolation will return to its equilibrium value, with the same damping time, if perturbed. The asymp-

totic stability of such community matrices was then evaluated in terms of their eigenvalues.

An equilibrium configuration in the linearized multispecies system is stable if and only if all eigenvalues of the community matrix have negative real parts (cf. Barnett & Storey, 1970).

The central feature of May's results for model ecosystems is the sharp transition from stable to unstable behaviour as soon as either the species number m, or the connectance C, or the average interaction strength s, exceeds a critical value. Only if the inequality $s < (mC)^{-1/2}$ holds, the system will certainly be almost stable: $P\ (m,\ s,\ C) \to 1$. In general, by becoming more complex a system becomes less likely to be stable. This conclusion for $m \gg 1$ comes from the fact that the largest real part, $R(\lambda)_{max}$, of the eigenvalues of the random matrix $\{a_{ij}\}$ with $a_{ii} = -1$, is asymptotically $s(mC)^{1/2} - 1$ (see Wigner's semicircular law for random matrices: Wigner, 1967; Arnold 1969; Girko 1980).

May (1972, 1973) suggested that many natural communities could be more stable than random equivalents because of concentration of interactions in small blocks of species or compartments. This point was questioned by Pimm (1979) who concluded that for systems of equal connectance, those that are completely compartmentalized are less likely to be stable than those that are not.

It should be stressed that in nonlinear systems the above mentioned procedure can only establish stability relative to small perturbations of the initial state from an equilibrium (local stability). The more relevant method for studying stability relative to realistic perturbations is the direct method of Liapunov, i.e. global stability analysis. Fortunately, for many ecologically interesting models a Liapunov function can be constructed and the global stability is then legitimately characterized by the local stability analysis (May, 1973; Goh, 1979). Differences in local stability of multispecies continuous and discrete models have been evaluated by Kindlmann & Rejmánek (1982).

Much confusion has resulted from using the same word 'stability' with several different meanings, only one of which corresponds to Liapunov's definition used by May. For further discussion two ecologically important meanings of 'stability' should be distinguished (cf. Webster *et al.*, 1975; Harrison, 1979; Rejmánek, 1979).

(1) *Resilience:* The ability of a system to return to

normal after a disturbance or stress period. Orians (1975) and Westman (1978) call this concept 'elasticity', Holling (1973) calls it 'stability'. This concept corresponds to Liapunov's asymptotic stability in theoretical studies. In empirical studies it is approached as reciprocal values of 'restoration time' of total biomass, community population structure, or other community attributes of interest (cf. Westman, 1978). However, it would be unrealistic to expect 100% restoration of the original structure or function, since such a value does not take into account natural climatic, spatial, sampling, as well as successional variation.

(2) *Resistance:* The ability of a system to avoid displacement during a stress period. Orians (1975) and Westman (1978) call it 'inertia', Holling (1973) used the term 'resilience' for the same concept. Mathematical analysis of resistance is still in an elementary stage of development (Harrison, 1979). In developing field descriptions of community resistance ecologists may usefully apply a broad scale of similarity and/or dissimilarity indices (Orlóci, 1978, Huhta, 1979, Rejmánek, 1981) besides such summarizing characteristics as differences in total biomass or in total net production. The higher difference or dissimilarity in some feature resulting from perturbation, the lower resistance in respect to the considered characteristics.

Recent theoretical investigations (Webster *et al.*, 1975; Harrison, 1979) have specified the situations where resilience and resistance are inversely related. Empirical studies are needed to determine if this is the case.

Verification

Is there any perspective for field verifications of May's model?

Although May's conclusion is widely cited, there have been only few attempts to apply it to real ecological data.

Only recently, Lawlor (1978) pointed out the urgent question: What is the true connectance and true average interaction strength in real communities? The first estimations of connectance in a considerable number of communities with several trophic levels and different species numbers were made

by Rejmánek & Starý (1979) and Yodzis (1980). Their results show that connectance may decline considerably as the number of species increases.

Connectance and interaction strength values for plant communities have recently been estimated by McNaughton (1978). He concludes, in accordance with May's criterion, that more diverse communities may be more stable (resilient) than less diverse ones because both connectance and average interaction strength decline as the number of species increases (see Figure 1 and Figure 2 in McNaughton's paper). Finally, McNaughton demonstrated a significant tendency for grazing to cause smaller changes in the plots with small values of an 'instability index' $s \sqrt{(mC)}$. A skeptical view on the essence of this coincidence has been given by May (1979).

Unfortunately, McNaughton used the point correlation coefficient V (Poole, 1974) applied to nearest-neighbour data. The coefficient V gives limits of $+1$ if the two species always occur together, -1 if they never do, and a value of zero if the species are distributed independently. We show (Fig. 1) that a random simulation by computer (IBM 370/135) of the nearest-neighbour data elaborated step by step, according to McNaughton's method (including the correction for sample size) yields essentially the same results. The main source of such behaviour lies, undoubtedly, in recording only two species at each sampling point. The calculation of the correlation significances arises from the misbelief that the null hypothesis of the test is to expect zero correlation. It seems likely that McNaughton's conclusions do not reflect much more than the statistical properties of the method. Slightly different but more rigorous analyses of shortcomings associated with contact sampling techniques, have been done by Harris (1979), Lawton & Rallison (1979) and de Jong, Arssen & Turkington (1980). Different approaches to measuring interaction strength and connectance in plant communities must be evolved (cf. Berendse, 1979; McNaughton, 1979; Snaydon, 1979). Unless we know how to measure connectance and interaction strength, we cannot test or use the theoretical results mentioned above.

Multispecies competitive systems

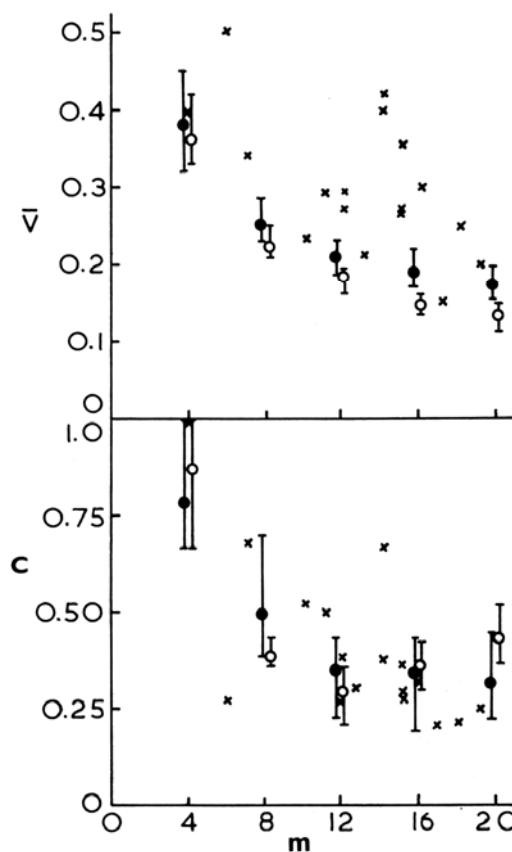Moreover, there is one crucial point which was not mentioned in previous comments to McNaugh-

Fig. 1. Effect of species number ($m = 4, 8, 2, 16$ and 20) on the average interaction strength between the species (evaluated as mean point correlation coefficient, $\bar{V}$) and on the connectance (C) calculated on the basis of randomly generated 100 'sampling points' from a 'community' with an ideal uniform distribution of species cover values ($\bigcirc$), and with a geometric series distribution (McNaughton & Wolf, 1973, p. 644) with $p = 2/m$ ($\bullet$). Each point represents the mean of 10 repeatedly generated '100-point samples'; the bars correspond to ranges of the values. The values reported by McNaughton (1979) are indicated by crosses (x).

ton's paper (MacDonald, 1978; May, 1979; Harris, 1979; Lawton & Rallison, 1979; Yodzis, 1980). It is the relevance of applying May's generalizations to communities with only one trophic level – to plant communities in our case.

For the justification of such an approach, we have determined the largest real parts, $R(\lambda)_{max}$, of eigenvalues of interaction matrices consisting of the elements

$$a_{ij} \begin{cases} -|A| & \text{for } i \neq j \\ -1 & \text{for } i = j, \end{cases}$$

where the connectance C (less than 1) was introduced by zeroing of certain number of off-diagonal a_{ij}–a_{ji} pairs. The values of A were chosen from a normal distribution with mean = 0 and standard deviation s (interaction strength in May's terminology). Such 'competitive matrices' represent models of very general multispecies competitive systems. In this study, samples of 25 matrices were generated for each selected combination of m, s and C values. Results of this analysis are presented in Figure 2 where mean largest real parts of eigenvalues, $R(\lambda)_{max}$, are plotted against $\sqrt{m}$, s and $\sqrt{C}$.

The dependence of mean $R(\lambda)_{max}$ on $\sqrt{m}$ and on s is positive, linear, and essentially in agreement with May's rule. To the contrary, the dependence of $R(\lambda)_{max}$ on $\sqrt{C}$ is surprising. It indicates a decrease in stability until $C \doteq 0.5$, or $\sqrt{C} \doteq 0.7$, and an increase in stability (decrease of mean $R(\lambda)_{max}$) with following increase of C. An attempt towards an analytical explanation of this result will be published elsewhere (Kindlmann, Lepš & Rejmánek, 1982).

It remained hidden even for Post, Shugart & DeAngelis (1978) (see also Post & Travis, 1979) that

for competitive systems defined above the stability (resilience) increases with connectance for high connectances. In their model, the diagonal matrix elements (which play a central part in setting stability) are not assigned independently of the off-diagonal elements. The construction of their model implies that as the connectance increases, the average magnitude of the negative diagonal elements becomes larger and larger, and the probability for the matrix to be stable can increase. They accepted this explanation for the continuous increase of the probability of stability with increasing connectance (from 0 to 1).

Spatial patchiness

The role that spatial patchiness can play in complexity-stability relationship has recently been the subject of reaction-dispersal model by Yodzis (1978), who has pointed out that if there is some dependence of stability (resilience) on species richness in the sessile communities, this dependence is so highly sensitive to the value of dispersal parameters of particular species that it will in practice be
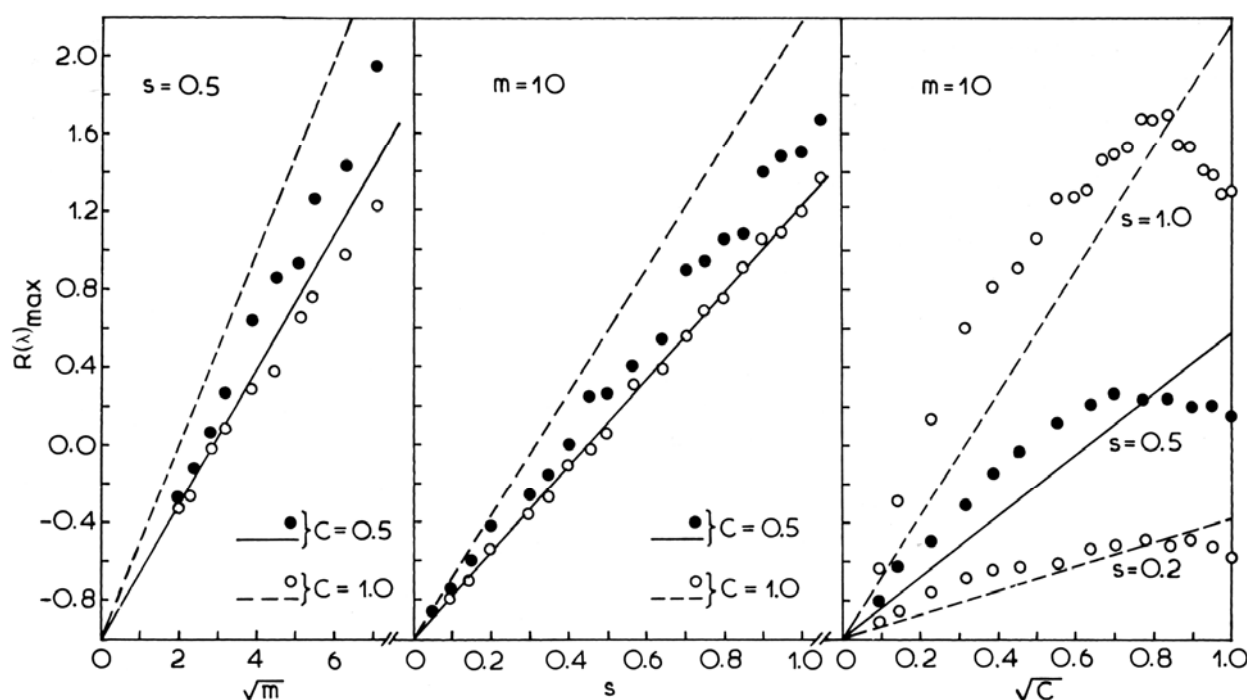

Fig. 2. The relationship between complexity and stability (resilience) of competitive systems is illustrated by plotting the mean largest real part, $R(\lambda)_{max}$, of eigenvalues of random competitive matrices against number of species *(m)*, interaction strength *(s)* and connectance *(C)*. The lines represent the respective asymptotic behaviours predicted by May's rule.

masked by random effects. It can be the case when community stability depends primarily on the adaptive characteristics of organisms in the community (cf. Orians, 1975).

Regarding the crudities of May's and related models and difficulties of field studies, the predictive value of contemporary stability theory remains an open question. The following case study shows how empirical data on the community level can be explained by different kinds of theories, namely those dealing with bionomic strategies of plant species replacing each other in communities during succession.

Resilience versus resistance: A lesson from old-field succession

Material and methods

In order to gain more insight into the successional development of plant communities and the possible rules governing it, the authors and their coworkers started intensive ecological studies of 8 abandoned fields forming a part of the Bohemian Karst protected area, Central Bohemia, Czechoslovakia (Fassatiová, 1978; Huml, 1978; Kosinová & Rejmánek, 1979; Klimková, 1977; Lepš, 1977; Lepš & Prach, 1981; Mestenhauserová, 1979; Michálek, 1979; Prach, 1981; Rambousková, 1980; Rauch, 1978; Baumová, 1981, etc.).

The xeric successional series was represented by two adjacent old-fields of different ages, 7 and 50-yr in 1976, which were situated on the terrace of the Berounka river near the village of Srbsko. The substrate consists of brown soil on mainly acid sediments. The vegetation of the younger field could be included in the alliance *Convolvulo-Agropyrion repentis* Görs 1966. The plant community of the older field represents the locus classicus of the association *Fragario-Festucetum rupicolae* Bureš 1976 (*Festucion valesiacae* Klika, 1931).

In 1975 and 1976, the fields were visited at intervals of ca. 3 weeks during the growing season, and on each occasion vegetation samples were collected at random, all aboveground living and dead plant material was removed in 5 (occasionally 10) quadrats of 0.25 m². The risk of sampling the same plot more than once was avoided by marking quadrats

in the map. In the laboratory the living material in each sample was sorted into its constituent species, oven-dried and weighed. In 1977 and 1978 only the maximum aboveground biomass was sampled by the same method. In 1974 only the total aboveground biomass from the younger old-field was sampled without sorting into species.

Species diversity was measured on the basis of species biomass units by the use of two indices: $N_1 =$ the antilogarithm of the Shannon's index and $N_2 =$ the reciprocal of the Simpson's dominance index (see Hill, 1973). Values for the younger field achieved $N_1 = 6.6$ and $N_2 = 4.5$ at the time of maximum biomass in the year 1975. Respective values for the older field were $N_1 = 9.7$ and $N_2 = 5.6$.

Community dissimilarity was expressed 1) as Euclidean distance:

$$ED = \sqrt{\sum_{i=1}^{m} (W_{ia} - W_{ib})^2} \, ,$$

where W_{ia} and W_{ib} are biomasses of species i in the sample a and b respectively, and m is the number of species presented in at least one of the samples; or 2) by ad hoc defined 'mean relative change of species importance':

$$RC = \frac{1}{m} \sum_{i=1}^{m} \left(\frac{\max (W_{ia}, W_{ib}) + 1}{\min (W_{ia}, W_{ib}) + 1} - 1 \right) \, .$$

Results

The extreme drought of 1976, effects of which were reported from many parts of Europe (cf. Knapp, 1977; Hopkins, 1978; Sykora, 1979; Willems, 1980), caused severe external perturbation of the two old-fields under consideration. Figure 3 demonstrates the effect of the drought on the maximum above ground biomass of fields studied in 1976 and following two years. Figure 4 shows the effects of the 1976 drought on the community dissimilarity of both old-fields to their 1975 state. The younger field, with a lower species diversity (see previous chapter), seems to be more resilient but less resistant with regard to the changes of the characteristics mentioned. On the other hand, the older field, with higher species diversity exhibited higher resistance but lower resilience. Detailed descriptions and interpretations of seasonal and year-to-year development of community population struc-
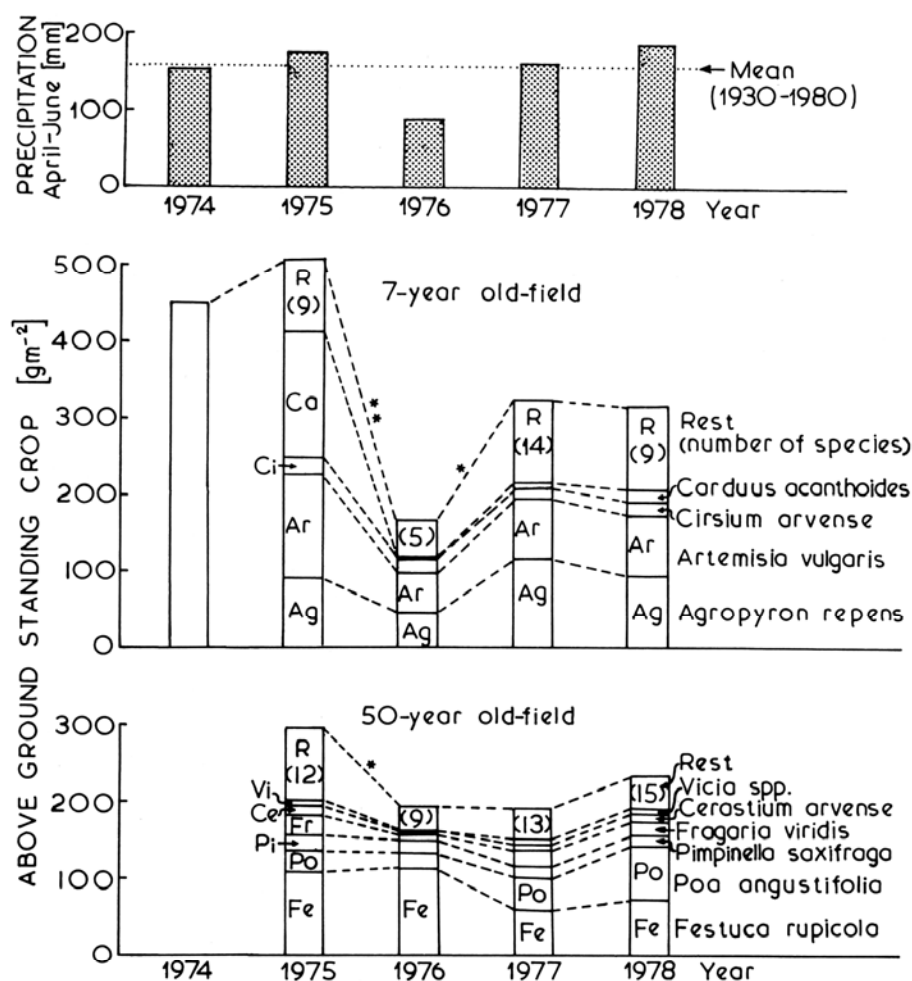
Fig. 3. Course of the 1974–1978 spring precipitation and effects of the 1976 drougth on the maximum above ground standing crop at two old-fields of different ages. Significant changes of mean above ground biomass in 0.25 m² quadrats are indicated (tested by the *t*-test: * = $p < 0.05$, ** = $p < 0.01$). The number of species constituting the 'rest' has indicative meaning only because of variability of species-area relation.

tures (sensu Whittaker, 1970 and Rejmánek, 1977) will be presented in a more comprehensive paper.

The main difference between the two communities under investigation lies in the reaction of the dominant species to stress. In the first community *Artemisia vulgaris* and *Agropyron repens* represent dominant constituents with a very flexible response to moisture conditions. The nearly total disappearance of *Carduus acanthoides* after 1975 can be considered as successional change, caused by both the biennial character and selfinhibition of this dominant (Huml, 1978). However, a large number of dominants in the second community (e.g., *Festuca rupicola, Pimpinella saxifraga*) represent species

with rather rigid reactions to changing moisture conditions. The important process, in the period following the 1976 drought, was the remarkable decay of *Festuca rupicola* turfs. This enabled *Poa angustifolia* and other species in the community to expand (see Fig. 3). Recovery of *Festuca rupicola* turfs proceeded very slowly.

Our results can be interpreted in terms of Grime's (1979) life-history strategies. According to his concept and terminology, the younger old-field community consists mainly of 'competitive-ruderals' *(Artemisia vulgaris, Carduus acantho-ides, Cirsium arvense, C. vulgare, Agropyron repens, Trifolium repens)* and 'ruderals' *(Galium*
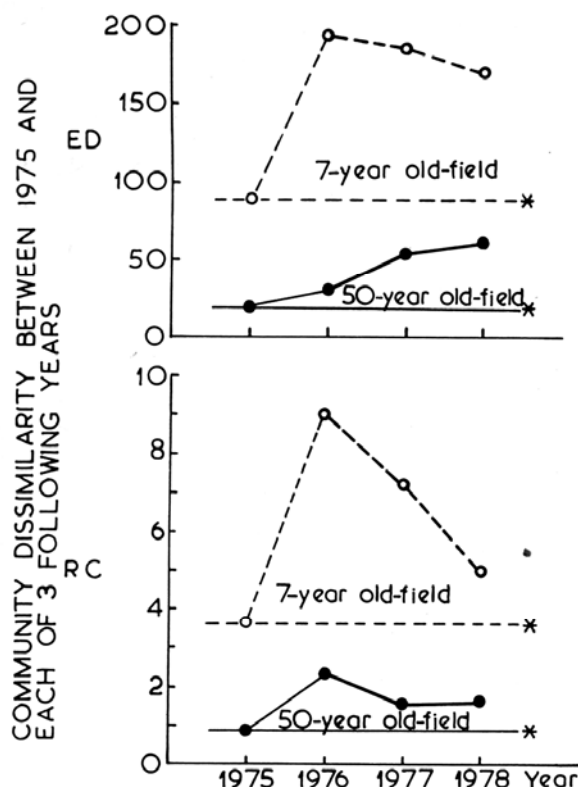
Fig. 4. Effects of the 1976 drought on the community dissimilarity of early (7-year) and late (50-year) old-field to their 1975 state. *ED* – Eclidean distance based on species biomasses, *RC* – mean relative change of species biomass (see the text). Levels of mean dissimilarity between three successive samples in the top of 1975 growing season (6–10, 7–2, 7–24) are indicated by lines with asterisks.

aparine, Stellaria media, Medicago lupulina, etc.). The older community consists mainly of 'stress-tolerators' *(Festuca rupicola, Pimpinella saxifraga, Thymus pulegioides, Teucrium chamaedrys, Dianthus carthusianorum),* and 'C-S-R strategists' *(Poa angustifolia, Lotus corniculatus, Festuca rubra, Fragaria viridis).* The responses of the communities as a whole, during and after the stress period, seem to be disposed by constituent species (see Grime, 1979).

Discussion

Once again: Clements or Gleason? There is a remarkable parallel with the old Clements vs. Gleason controversy in contemporary ecology (cf. van der Maarel & Werger, 1978; McIntosh, 1980). Cle-

ments' organismic, holistic concept of communities and succession is implicitly or explicitly rejuvenated by Margalef (1968, 1974) and Odum (1969, 1971). The Gleasonian individualistic, population-centered approach is represented, for example, by Drury & Nisbet (1973) and Miles (1979).

Our conclusions about one series of old-field succession are in agreement with the theoretical analysis of Harrison (1979) and with the general statement of van der Maarel & Werger (1978): '... relatively late stages in succession are more resistant than earlier ones, but they are less resilient.' But according to experimental studies of resistance by Hurd *et al.* (1971), this kind of stability increases during succession only at the primary trophic level.

Interpretation of results

The interpretation of our results is summarized in Figure 5 and supports rather the 'Gleasonian' explanation of described community phenomena.

We found a positive relationship between species diversity and resistance, and a negative relationship between species diversity and resilience. Consistent conclusions were achieved by both Rauch (1978, and pers. comm.) who perturbed old-fields experimentally with fly ash, and Michálek (1979, and pers. comm.) who used three herbicides as stress agents.

However, there are perhaps no direct causal relationships. Both kinds of community characteristics, (1) species diversity and (2) two different types of stability, seem to be determined by the bionomic strategies of the dominant species involved and by external variables (time, soil fertility).

The remarkable immobilization of available forms of soil phosphorus, aluminium, iron and calcium phosphates was detected during the described successional series (Klimková, 1977; Rejmánek & Jeník, 1978). This trend is, at least partly, responsible for the exchange of the 'ruderal-competitors' for 'stress-tolerators'. The causal chains:

Low level of available P in soil → low productivity → low competition → high species diversity

and

High level of available P in soil → high productivity → high competition → low species diversity
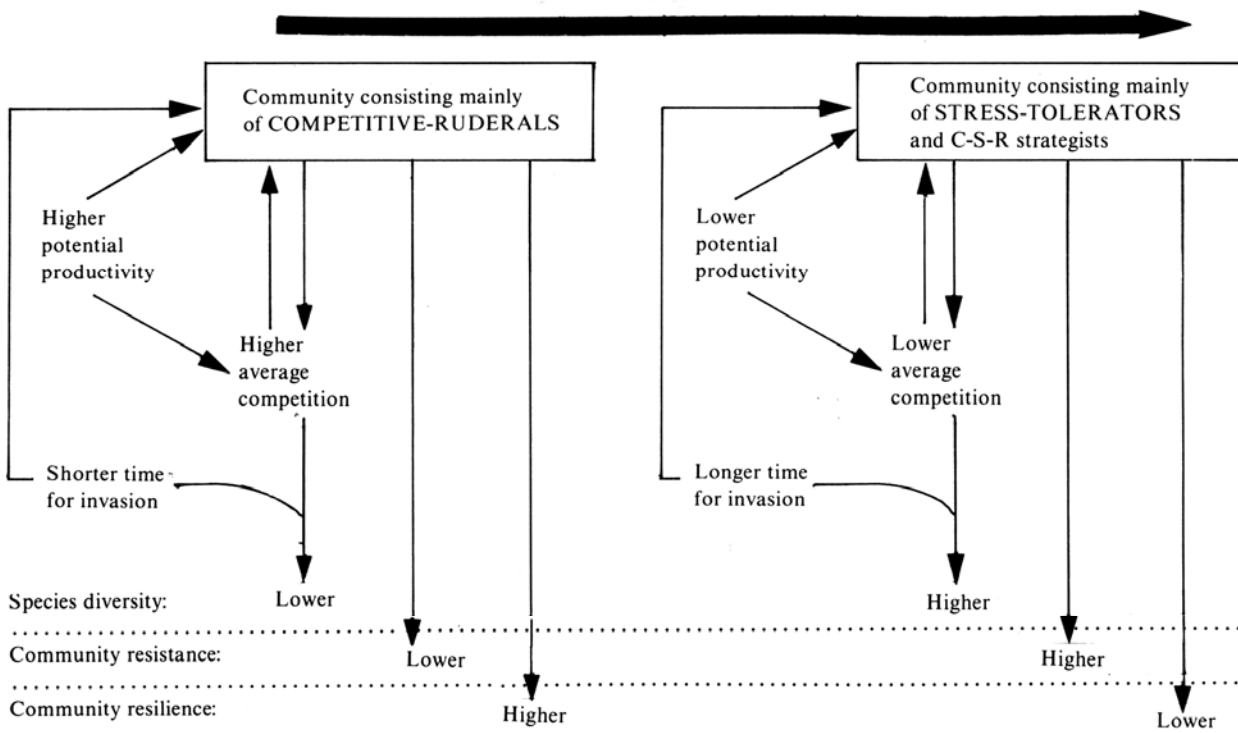
Fig. 5. Relationships between species strategies (sensu Grime, 1979), species diversity, community resistance, and community resilience during old-field succession in a xeric habitat.

were described by Auclair *et al.* (1976) and form part of our explanatory scheme (Fig. 5). Mellinger & McNaughton (1975) reported consistent trend for old-field succession in central New York and Willems (1980) from chalk grasslands in the Dutch province of Limburg.

The most important part of our scheme is based on explicit characteristics of different 'strategists' (Grime, 1979). Secondary succession usually starts with communities consisting of opportunistic species, so called R-strategists or ruderals. The common feature of ruderals is the tendency for a short life-cycle, rapid relative growth rates of biomass, and high seed production. It is difficult to follow long-term responses of such communities to stress because they are quickly overgrown by better competitors, 'competitive-ruderals'. Communities consisting of these strategists exhibit longer duration and their responses to stress period can be followed for a few years without undesirable interference of successional changes. This was our case. Competitive-ruderals feature a relatively longer period of vegetative growth, and a considerable biomass may

be attained before the onset of flowering. Responses to stress, as well as regeneration are rapid. Regenerative strategies proceed by vegetative expansion, by seasonal regeneration in vegetation gaps, by numerous wind dispersed seeds, and by persistent seed bank (cf. Grime, 1979).

Under conditions of decreasing potential productivity, a succession is directed towards communities with prevailing 'stress-tolerators' (Grime, 1979). This kind of strategy is characterized by slow rate of growth, long-lived organs, slow turnover of nutriens, low morphogenetic plasticity, and slow rate of recovery. These features are, in general, in agreement with the response of older abandoned field community to stress the period of 1976. But in this community there are also some species that exhibit an intermediate character among ruderals, competitors and stress-tolerators – 'C-S-R strategists'. These combined strategists recover gaps of dead stress-tolerators more quickly than stress-tolerators themselves do (e.g. *Poa angustifolia* temporarily substituting *Festuca rupicola*).

Our results can be explained completely by

means of Grime's theory. But we may ask: Is it really a 'Gleasonian' explanation? One may object that some characteristics of different 'strategists' were derived from their behaviour within communities. Feedback between the community as a whole and particular populations may be stressed here; only certain types of strategists are allowed to join the community. A full explanation of our results is, of course, impossible by examining isolated populations only. In spite of such 'holistic' elements, our interpretation of achieved results is strongly reductionistic, i.e. Gleasonian. The compliancy of holistic and reductionistic population-centered approaches in community ecology has been stressed by Lane *et al.* (1974), Braakhekke (1980), and others. Our case study represents simple kinds of plant communities only, and conclusions must therefore be taken with caution. Nevertheless, presented interpretation is in agreement with recent critical reevaluations (see Marks, 1974; Sousa 1980; Smedes & Hurd 1981) of the trends and mechanisms of successional changes in plant and animal communities.

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