

The effect of spatial pattern on community dynamics; a comparison of simulated and field data

T. Czárán¹ & S. Bartha²

¹*Department of Plant Taxonomy and Ecology, L. Eötvös University, Budapest, Kun B. tér 2, Hungary-1083;* ²*Research Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, Hungary-2163*

Accepted 8.5.1989

Keywords: Dispersal, Local competition, Pattern and process, Species coalition, Succession, Vital attribute

Abstract

The effect of the spatial limits of dispersal and competition on plant community dynamics was studied using Monte-Carlo simulation. The model generates community point patterns, using life-table data, dispersion parameters and radii of competitive effects. These data have been estimated in a field situation, for the 11 most abundant weed species growing on the refuse soil dumps of a strip coal mine. In a simulation experiment, the patterns produced by two versions of the model were compared. The first was based on the field situation as much as possible; the other used the same input parameters except for dispersal, which was randomized in this case. We found considerable differences regarding the temporal changes of species abundances, the realized competitive abilities and the spatial patterns generated by the two versions. An important conclusion of this comparison is that the realized competitive effect (both intra- and interspecific) of a species is dependent not only on constant competition parameters, but on the abundance relations and on the spatial patterns of the competing populations as well. It is concluded that the spatial limits of dispersal and competition may result in the increased persistence of weak competitors, moderate the realized competitive effects of strong species, and shape the spatial coalition structure of the community.

Nomenclature: Soó, R. & Jávorka, S. 1951. A magyar növényvilág kézikönyve I-II. (Manual of the Hungarian flora) Akadémiai Kiadó, Budapest.

Introduction

Since the classical paper on pattern and process in the plant community by Watt (1947), many theoretical and field studies have appeared under similar titles. The pair of concepts 'pattern and process' has become an accepted *terminus technicus* in ecology. The term 'pattern' is not always

used in a topographical sense. (Occasionally, even physiological 'character sets' are called patterns). Watt's original interpretation of the word is strictly topographical and stochastic: he showed that the spatially determined dynamical features like the patch-forming growth of clonal plants, canalize community dynamical processes in an inherently stochastic (statistical) manner.

This means that the dynamics of a community cannot be understood without taking the spatial aspects of e.g. dispersion and population interactions into account. Only very simple, and in many respects very special, cases can be explained by pure demographical features of the populations present in the community (e.g. fecundity, mortality, age structure).

From the 1960's onwards, the topographical aspects of population interactions have been considered in diffusion models (for reviews, see e.g. Okubo 1980, Nisbet & Gurney 1982). The sets of partial differential equations of these models covered mostly oversimplified cases (e.g. population growth and dispersion in one-dimensional space only), and did not involve the stochastic character of pattern formation. Attempts to make them more realistic led to the rapid proliferation of algebraic problems, usually making the equations analytically insoluble.

Computer simulation, especially of the Monte Carlo type, has helped to avoid these analytical difficulties. Some of the simulation models account for the pattern dependent behavior of either a single population (Auld & Coote 1980), or of two competing species (Weiner & Conte 1981). Only a small part of the literature on this problem concentrates on the community-dynamical consequences of the local dispersion and interaction of several populations, for example Karlson & Jackson (1981). Pacala & Silander (1985), and Pacala (1986, 1987) constructed a series of simulation models for studying annual plant population dynamics.

On the empirical side, several case studies have analyzed relatively simple community-dynamical processes, like changes in the dominance rank order of species during the early stages of primary succession (e.g. Prach 1984, 1986, 1987; Gibson *et al.* 1985; Hogeweg *et al.* 1985; Wood & del Moral 1987) and secondary succession (Hayashi & Numata 1967, 1968; Bazzaz 1968; Pickett 1982; Humphrey 1984; Turner 1985). These studies focused on the relationships between the dynamical status of species and their population-biological characteristics (vital attributes). The mechanistic standpoint was emphasized by

Bazzaz (1979); Noble & Slatyer (1980); Numata (1980, 1982); Pickett (1982); Price (1986); Brown & Southwood (1987). Many authors consider the role of spatial relations in succession (e.g. Hogeweg *et al.* 1985; O'Connor & Aarssen 1987). Klemow (1984), Klemow & Raynal (1981, 1983, 1985) and Thompson (1985) found that demographical features of the same species may be very different on different sites. Numata (1982) and Game *et al.* (1982) concluded that the rate of succession is variable in space. According to Pickett (1980) and Pickett & White (1985), the non-equilibrium dynamics of patches that are in different successional phases may contribute to the coexistence of the participant species.

The present study concerns a simulated, pattern-dependent succession process, generated by a Monte-Carlo competition model. Besides fecundity, age-dependent survivorship and competition, there are two important assumptions in the model, both regarding the spatial dependence of population dynamics: a) plant propagule dispersion is limited in space, that is, offsprings have different chances to reach any distance from their parents; b) competition is local, that is, distant individuals do not affect each other.

The following theoretical questions are addressed:

1. How much do assumptions a) and b) affect the changes of species abundances in the course of succession?
2. How much does assumption a) affect the intensity of competition between the species?
3. How are these aspects expressed in the spatial coalition structure of the simulated community?

The parameters for simulation have been estimated so that they reflect the population-dynamical features of certain weed species as much as possible.

Materials and methods

The model

The simulation model generates community point patterns (the points representing positions of indi-

viduals) within a rectangular, continuously scaled plot. Time is measured in discrete units (say, generations).

Invasion: The plot is assumed to be invaded by propagules of the potential flora in every generation. I_i is the number of the invading seeds of species i . Invasion is represented by a Poisson point process, i.e., the spatial arrangement of the invaders is randomized within the plot. They germinate and grow up to produce offspring.

Survival: The age group structure of the species is considered in the model by specifying the probability p_{ij} of the survival of an individual from age group j of species i to the $j + 1^{\text{th}}$ age group. p_{i0} is set to the value 1.0, that is, only viable propagules are considered, which all germinate for sure if there are no interactions. Competition affects p_{i0} values as described later in this section.

Fecundity and dispersal: Φ_{ij} is the offspring number of an individual from age group j of species i (age specific fecundities). They disperse around their parents. Two different mechanisms for dispersal can be considered in the model. In the first one, the distance of dispersion is a random variable of a Gaussian distribution with zero mean; the dispersive potential is represented by the standard deviation σ_i of the Gaussian, given for each species. This case is referred to as Gaussian in the sequel. In the second kind of simulation, referred to as the Poisson case, offspring positions are independent of the location of their parents, i.e., they are randomly arranged within the plot. The temporal order of seedling recruitment is given by ranks assigned to each species.

Competition: The survival probabilities of the seedlings (p_{i0} values) are supposed to be reduced by the competitive effect of neighbouring individuals. The measure of the reduction of p_{i0} depends on which age group of which species the competitor belongs to, and how far it is situated from the seedling in question. To see this in detail, suppose there is a seedling of species i_1 and an individual from age group j of species i_2 . Let the

distance between them be d . Let further $A_{i_1, i_2, j}$ be the radius of the competitive action of an individual from age group j of species i_2 upon a seedling of species i_1 . If d is greater than this value, no competitive effect is exerted on the seedling by that individual. If $d \leq A_{i_1, i_2, j}$, then the probability of survival for the seedling is

$$P = d/A_{i_1, i_2, j}.$$

If there are other competitors in the neighborhood of the seedling, their effects are multiplicative. If $j = 0$, that is, if the competitor is another seedling, the competitive effect is bilateral, but the same rules apply otherwise.

The course of the pattern generating process is illustrated in Fig. 1. It shows that at the beginning, when the plot is unsaturated, few seedlings die because of competition. When there are many

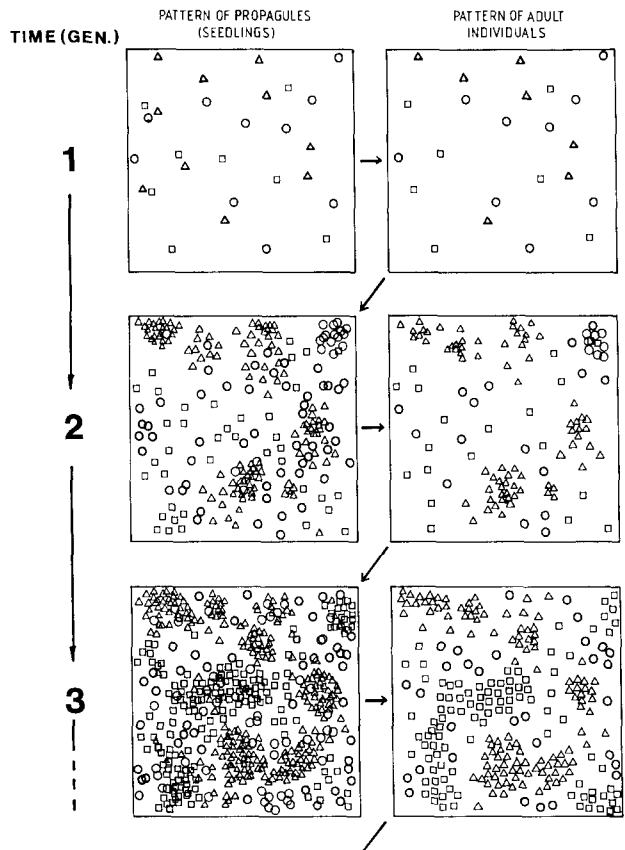


Fig. 1. Schematic illustration of the pattern generating mechanism of the simulation model. See text for details.

seedlings, close to each other and to adult competitors, only a smaller proportion survives. Monospecific aggregates (patches) are the results of small dispersal values (σ -s).

Table 1 lists and defines all the input parameters used. Fig. 2 is a schematic flow diagram of the computer program PATPRO that performed the simulations. It was written in FORTRAN IV, compiled by Microsoft Fortran, and run on an IBM PC AT machine. A previous version of the model, constructed for annuals only, was described in Czárán (1984).

Study site and sampling

Field data have been collected on the refuse soil dumps of a strip coal mine, from sites of different ages between 1 and 10 yr. The mine is located in the northern part of Hungary, at the foot of the Mátra Mountains. The dumps offer an ideal substratum for rapid spontaneous recolonization by weed species and subsequent community development (Szegi *et al.* 1988). Field vole (*Microtus arvalis*) activity was observed from the 6th year of succession. The voles disturb small areas, which enable the pioneer species to reestablish on relatively old sites.

We determined percentage frequencies for the 11 most abundant weed species occurring on the dumps, within 6 plots of age 1, 2, 3, 4, 7 and 10 yr. The sizes of the plots were different, ranging from

Table 1.

Parameter	Definition
I_i	Invasion rate for species i : the number of propagules invading the plot in each generation
ϕ_{ij}	Fecundity (<i>per capita</i> number of propagules) for age group j of species i
σ_i	Dispersal for species i : deviation parameter of the Gaussian distribution determining dispersion distances
p_{ij}	Survival probability of a member of age group j to $j + 1$ for species i
$A_{i_1, i_2, j}$	The radius of the competitive effect of a member of age group j of species i_2 upon a seedling from species i_1

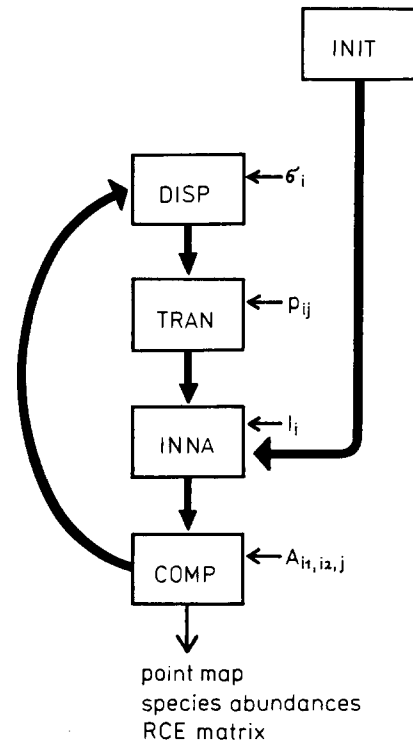


Fig. 2. Flow diagram of the simulation program PATPRO: INIT: Initializing module; DISP: Dispersal module; TRAN: Age class transformation module; INNA: Invasion module; COMP: Competition module.

10 × 10 m to 15 × 30 m. It was necessary to choose plots of different size for the frequency estimates in order to be accurate enough in each stage of the succession process. Square lattices were used for sampling; the size of the units was 20 × 20 cm. Presence/absence data were recorded in each unit, for each species; these were transformed to percentage frequencies within the lattice.

Simulations; sampling and data analysis on the simulated maps

The input parameters for the first run (Gaussian case) of the simulation program were chosen according to Table 2, presenting some estimated population biological attributes of the 11 species. The different recovery potential of each species on sites disturbed by field voles was also included in the vital attribute set of Table 2. The disturbance

caused by the voles is incorporated in the simulation model, in the form of local disturbances.

As we could not find precise data in the literature on the fecundity, survival rates, pairwise competition coefficients and dispersal abilities of our species, we decided to use broad categories – like ‘large’ (L), ‘medium’ (M) and ‘small’ (S) – for each variable. We quantified these qualitative data by assigning them to the L, M and S categories of each variable. The choice of concrete values within a category depended on our rank estimates for the species falling within that category, which is a somewhat arbitrary procedure. Thus the simulations should not be thought of as attempts to imitate the real field situation; the species codes in Table 2 and the genera names used throughout the text should be regarded as labels for the parameter sets we used for simulation, rather than real taxonomical indications. The approximate character of both our hypothesis on the mechanism of succession and the estimation of parameter values is emphasized.

The second run of the program used the same input values for all attributes of the species as the first one, except for dispersal, which was randomized in this case (Poisson version). We considered the Poisson case as a hypothetical experiment with the propagules of all individuals randomly arranged within the plot.

The output was a series of maps of the point patterns for both the Gaussian and the Poisson case simulations, one map for each year. We analyzed and compared these maps for 1) species abundances, 2) realized competitive effects and 3) spatial structure.

The maps were sampled, using a 50×50 square lattice of arbitrary units laid over them. Binary data were recorded and transformed to percentage frequencies the same way as it was done for the field situation, in order to make the simulated and the field data comparable.

The simulation program stores the competition mortality matrix for each generation (this matrix gives the proportion of propagule mortality of species A caused by the competitive effect of species B, for all [A, B] ordered pairs). We call these data ‘Realized Competitive Effects’ (RCE)

Table 2.

Species (field reference)	Code for simulation	Life form	Life span	Invasive ability	Dispersive ability	Reproductive potential	Survival rate of adults	Competitive potential	Recovery potential on disturbed sites
<i>Lactuca scariola</i>	LAC	T4	annual	L	L	L	-	S	L
<i>Matricaria inodora</i>	MAT	T4	annual	L	L	L	-	S	L
<i>Atriplex nitens</i>	ATR	T4	annual	L	L	M	-	S	L
<i>Tussilago farfara</i>	TUS	G1	perennial	L	L (seeds) M (rhizomes)	M	M	M	M
<i>Bromus japonicus</i>	BRJ	T2	winter annual	M	M	M	-	M	M
<i>Medicago lupulina</i>	MED	T4	perennial	M	M	M	M	M	M
<i>Melilotus officinalis</i>	MOF	HT	biennial	M	M	L	M	M (1 yr old) L (2 yr old)	S
<i>Picris hieracioides</i>	PIC	HT	biennial	M	M	M	M	S (1 yr old) M (2 yr old)	M
<i>Agropyron repens</i>	AGR	G1	perennial	S	S	S (seeds) M (rhizomes)	L	L	M
<i>Lathyrus tuberosus</i>	LAT	G1	perennial	S	S	S	M	L	S
<i>Rubus caesius</i>	RUB	H3	perennial	S	S	S	L	L	L

in the sequel. Average RCE-s were calculated for all species, according to the proportion of total seedling mortality attributable to each of them.

To analyze the spatial relations of the 11 species, each map was sampled once more with the program ELSAM2 (Podani 1988). This sampling process was different from the one performed on the same maps using a square lattice, because in ELSAM2 the sampling units are positioned at random. Binary (presence/absence) data were recorded from 500 square units placed on the maps of each generation (year), for both runs. In order to get dynamically interpretable results, we chose the length of the edges of the sampling units so that it matched the average of the radii of competition, $A_{i1,i2,j} - s$. Chi-square values were calculated for each pair of species (see e.g. Greig-Smith 1983, Kershaw & Looney 1983). Associations exceeding the significance levels of $P < 0.01$ and $P < 0.001$ were accepted as signifi-

cant (McIntosh 1973). Both positive and negative associations were visualized on plexus graphs.

Results and discussion

Neighbourhood effects and species abundances

The Gaussian simulation produced results quite similar to the field case regarding abundance trajectories, but the Poisson version differed markedly (Fig. 3). However, in the first 2–3 generations the abundance rank order of the species is the same for the Gaussian and the Poisson case, suggesting that spatial aspects do not much affect the initial dynamics of the community. This period is dominated by annuals with high dispersal and fecundity values, and weak competitive abilities (*Lactuca*, *Matricaria*, *Atriplex*) which may be regarded as r-strategists.

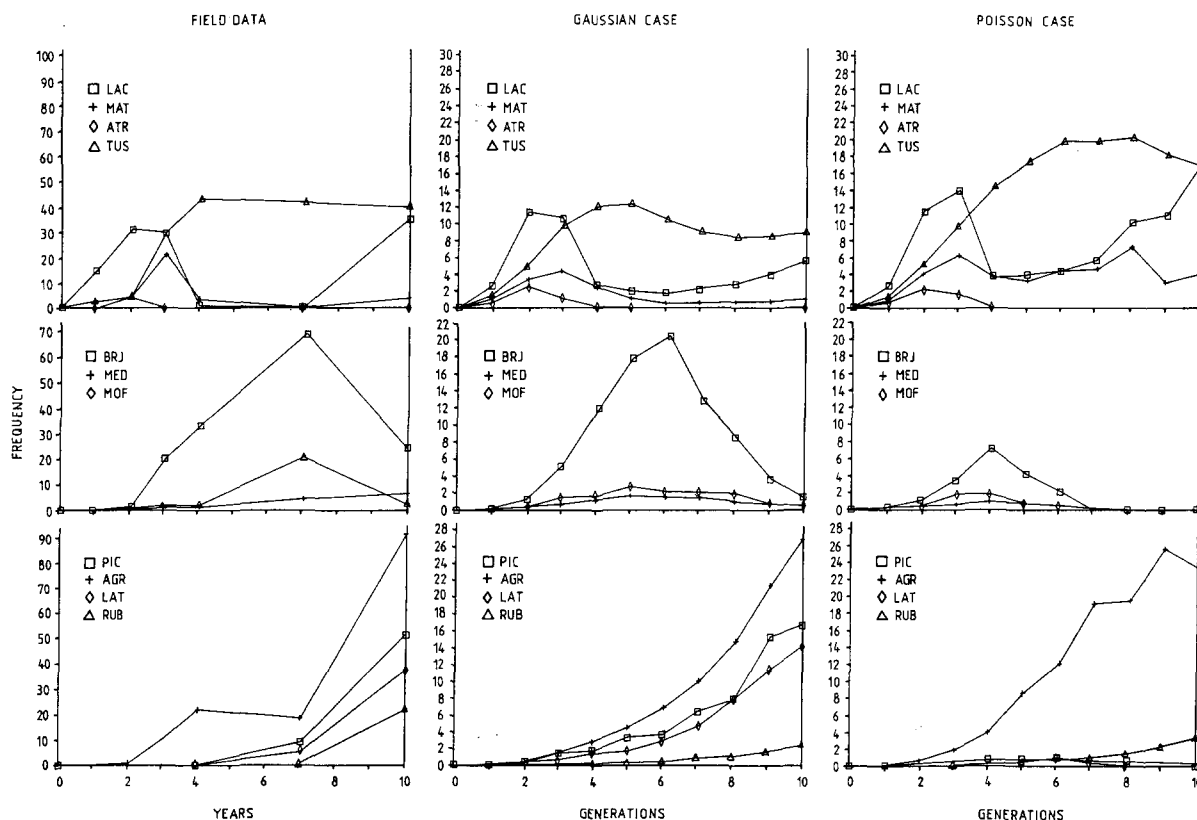


Fig. 3. Temporal changes of abundance for 11 species – data for the field reference and the two simulated cases.

From the third generation onwards, as the site becomes saturated, and the importance of competitive interactions increases, the structuring (patch forming) effect of limited propagule dispersion and neighbourhood-competition is manifested in the abundance relations. In the field case and the Gaussian simulation, this period is dominated by more competitive species; interaction is the decisive dynamical feature, strongly affected by spatial limitations. As a result of randomized propagule dispersion, some weak species like *Lactuca* and *Matricaria*, become abundant on disturbed sites to the end of simulation, but *Bromus*, not able to re-establish itself quickly enough, cannot perform as well as it could in the Gaussian case. *Medicago* and *Melilotus*, subordinated but persistent in the Gaussian version, go extinct by the eighth generation of the Poisson case. *Picris* and *Lathyrus*, both present with many individuals in the Gaussian version, become sparse. The strong competitor *Agropyron* is not too much affected, except that another strong species, *Tussilago* occupies part of its 'territory', which it could not do in the Gaussian case.

Pattern and the intensity of competition

The difference in the abundance relations of the species between the two simulated cases is a result of changing the mode of propagule dispersion. Although the competition parameters did not differ in the two runs, the RCE values of the species were very different (Fig. 4). RCE is dependent not only on the pre-defined competition parameters, but on the abundance relations and, most importantly, on the spatial patterns of the competing populations as well.

Thus, species with small dispersal values (weak dispersers) suffer the most from intraspecific competition in the Gaussian simulation version. But eliminating the structuring effect of limited dispersion (in the Poisson case) results in different dynamical consequences for strong competitors and for weak ones. For example, for *Agropyron*, and aggregating competitor (small dispersal, large radii of competition) realized intraspecific competition decreases when dispersal is randomized, and the interspecific effect increases

against all other species. *Melilotus*, a somewhat weaker species, with an intermediate dispersive potential, did not change its RCE against any of the species, including itself. The same seems to apply to *Lactuca*, a weak competitor and good disperser species, despite the fact that its temporal abundance trajectories are very different in the two simulations. *Tussilago* is an aggregating species (σ_i small), quite a strong competitor, and it has relatively great fecundity. Thus it can exclude the dominant species of the initial period of succession. In the Poisson case, it beats *Bromus* as well, and becomes the second most abundant species. As *Bromus* is suppressed, its realized competitive ability is reduced against all species. *Picris* is associated to and protected by *Agropyron* clumps, but since in the Poisson version no *Agropyron* patches appear, in the absence of refuges it goes extinct in generation 7.

More generally, random propagule dispersion makes strong competitors even stronger, and weak ones weaker, which in turn tends to reduce the diversity of the community (Fig. 5). In other words, aggregation contributes to the coexistence of species within the community by increasing the intensity of intraspecific and decreasing that of interspecific competition.

Spatial associations

According to our own field experience and the population biological features of the 11 species, the emergence of the following coalitions can be expected:

1. The group of the first colonizers (*Lactuca*, *Matricaria*, *Atriplex*, *Tussilago*); each of these species are characterized by good invasive and dispersive abilities (large I_i and σ_i values), short life span, large reproductive potential. With the exception of *Tussilago*, they are weak competitors.
2. The second coalition of stronger competitors, with more limited invasive and dispersive potential, longer life span and smaller fecundity (*Bromus*, *Medicago*, *Melilotus*). They appear abundant in the middle of the succession gradient, and are outcompeted later.
3. The third group consists mostly of strong

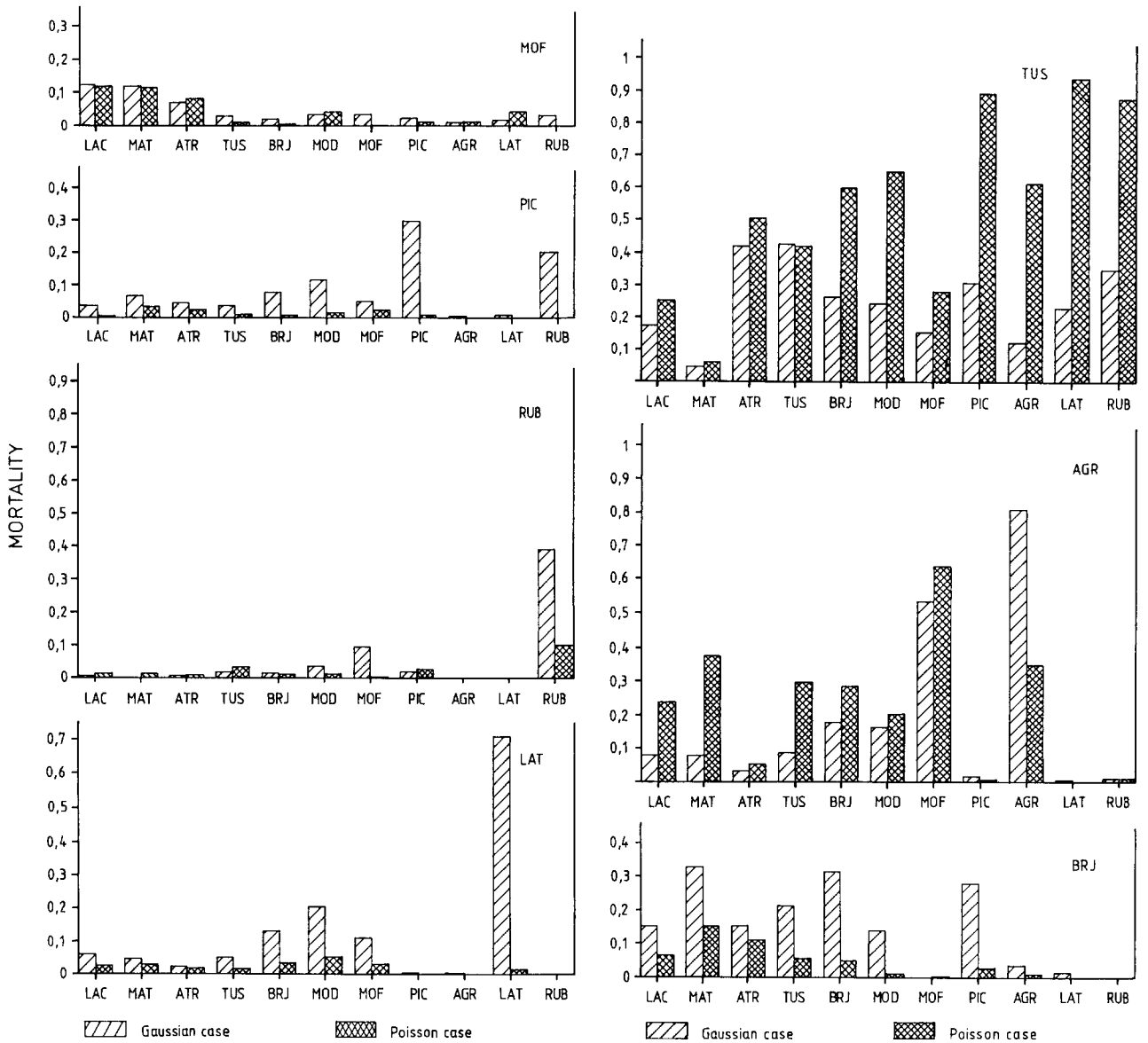


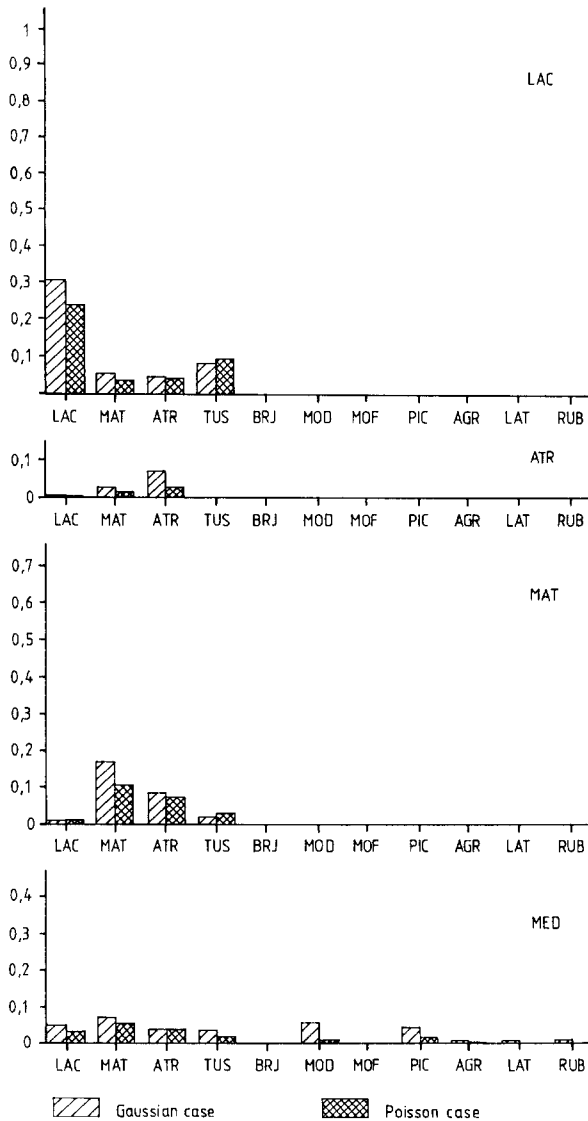
Fig. 4. Realized competitive relations of species; codes on the horizontal axes represent the species undergoing the competitive effect from the species indicated in the upper right corner of diagrams. Mortality ratios for the Gaussian and Poisson cases on the vertical axis.

perennial species (*Agropyron*, *Picris*, *Lathyrus*, *Rubus*), dominating the last generations. They invade by relatively small numbers of seeds, and gain territories by vegetative propagation mostly.

These coalitions differ regarding their recovery potential on sites disturbed by field voles as well: the pioneer species (as r-strategists) perform the

best; the perennials are the worst in this respect.

The pairwise dependance relations found for the two runs are shown on the plexus graphs of Fig. 6. There are no detectable associations in the first generations of either the Gaussian, or the Poisson case. Both produce fragments of the expected coalitions in the third generation. These structures collapse later in the Poisson case, whilst a weak trend of increasing spatial depend-



ence appears in the Gaussian version (significant correlations in generations 7 and 10). This supports the conclusion that the succession process can be divided into two quite distinct phases, the first characterized by weak competitors and a random pattern, the second by strong species, arranged in a patchy structure. Besides these factors, the temporal change of the intensity of particular associations reflects the changing domi-

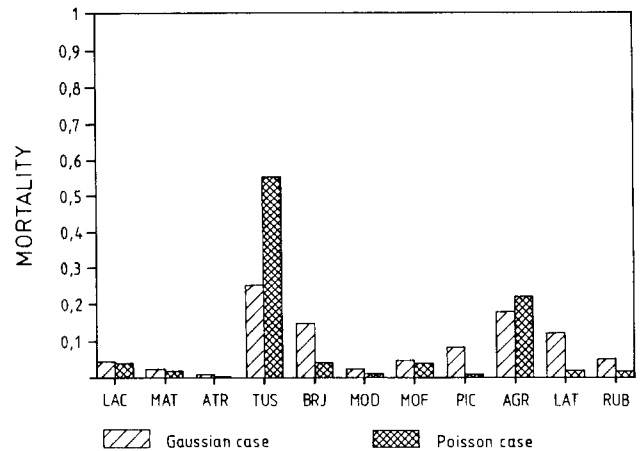


Fig. 5. Realized average competitive abilities of species; total seedling mortality caused by the species on the horizontal axis.

nance-diversity relations and the inherent stochastic character of pattern development as well.

In the third generation of the Poisson version, the number of strong positive and negative dependences on the plexus graph is strikingly great, although the positions of the propagules are determined independently of each other. This is in part a result of our choice of sampling unit size: as it corresponds to the competition radii, strong competitors are rarely found in the same sampling unit, and weak species are forced to grow together on areas they did not occupy. These relations are expressed only if both weak and strong species are present with relatively great abundances, which is the case in the third generation (*Lactuca*, *Matricaria*, *Atriplex* at or near to their peaks, *Tussilago*, *Agropyron*, *Melilotus* quickly rising). This network of positive and negative dependences vanishes with decreasing community diversity, whilst the Gaussian version produces an obvious coalition structure of the simulated community.

Conclusion

It has been showed that the spatial limits of dispersal and competitive interactions have important consequences regarding the abundance rela-

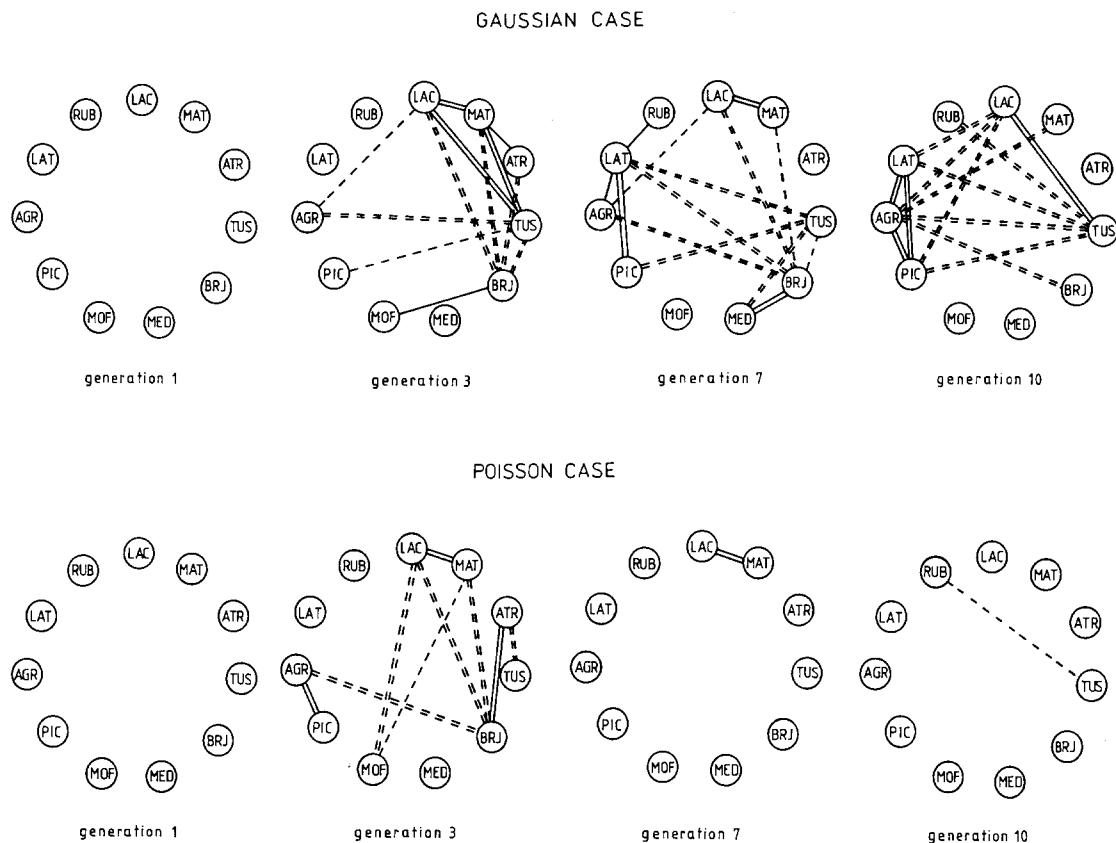


Fig. 6. Comparison of chi-square plexus graphs for the simulated succession processes; continuous lines: positive associations; broken lines: negative associations; simple lines: $P < 0.01$; double lines: $P < 0.001$.

tions, the realized competitive effects and the spatial patterns of plant populations in simple successional processes. These limits enable relatively weak competitor species to exist longer and get more abundant within the community by decreasing the RCE of stronger species against them. These relations are reflected in the spatial pattern and the coalition structure of the community.

Acknowledgements

We thank P. Juhász-Nagy, G. Fekete, J. Podani, E. Molnár, K. Virágh and B. Oborny for their comments on the manuscript. The constructive critics and suggestions by O. Wildi and three reviewers are also acknowledged.

References

- Auld, B. A. & Coote, B. G. 1980. A model of spreading plant populations. *Oikos* 34: 287–292.
- Bazzaz, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, Southern Illinois. *Ecology* 49: 924–936.
- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Ann. Rev. Ecol. Syst.* 10: 351–371.
- Brown, V. K. & Southwood, T. R. E. 1987. Secondary succession: patterns and strategies. In: Gray, A. J., Crawley, M. J. & Edwards, P. J. (eds), *Colonization, succession and stability*. Blackwell Oxford.
- Czárán, T. 1984. A simulation model for generating patterns of sessile populations. *Abstr. Bot.* 8: 1–13.
- Game, M., Carrel, J. E. & Hotrabhavadra, T. 1982. Patch dynamics of plant succession on abandoned surface coal mines: a case history approach. *J. Ecol.* 70: 707–720.
- Gibson, D. J., Johnson, F. L. & Risser, P. G. 1985. Revegetation of unreclaimed coal strip mines in Oklahoma II. *Plant communities. Reclam. Reveget. Res.* 4: 31–47.
- Hayashi, I. & Numata, M. 1967. Ecology of pioneer species of early stages in secondary succession I. *Bot. Mag. Tokyo* 80 (942): 11–22.

- Hayashi, I. & Numata, M. 1968. Ecology of pioneer species of early stages in secondary succession II. The seed production. *Bot Mag Tokyo* 81 (956): 55–66.
- Hogeweg, P., Hesper, B., van Schaik, C. P. & Beeftink, W. G. 1985. Patterns in vegetation succession, an ecomorphological study. In: White, J. (ed.), *The population structure of vegetation*. Junk, Dordrecht.
- Humphrey D. L. 1984. Pattern and mechanisms of plant succession after fire on *Artemisia*-grass sites in South-eastern Idaho. *Vegetatio* 57: 91–101.
- Karolson, R. H. & Jackson, J. B. C. 1981. Competitive networks and community structure: a simulation study. *Ecology* 62: 670–678.
- Kershaw, K. & Looney, J. H. H. 1983. *Quantitative and dynamic plant ecology*, 3rd, ed. Edward Arnold, London.
- Klenow, K. M. 1984. Plant community development in an abandoned limestone quarry; a demographic assessment. In: Veziroglu, T. N. (ed.). *The biosphere: problems and solutions*. Elsevier Science Publishers B. V., Amsterdam.
- Klenow, K. M. & Raynal, D. J. 1981. Population ecology of *Melilotus alba* in a limestone quarry. *J. Ecol.* 69: 33–44.
- Klenow, K. M. & Raynal, D. J. 1983. Population biology of an annual plant in a temporally variable habitat. *J. Ecol.* 71: 691–703.
- Klenow, K. M. & Raynal, D. J. 1985. Demography of two facultative biennial plant species in an unproductive habitat. *J. Ecol.* 73: 147–167.
- McIntosh, R. P. 1973. Matrix and plexus techniques. In: Whittaker, R. H. (ed.), *Ordination and classification of communities*. Junk, The Hague.
- Nisbet, R. M. & Gurney, W. S. C. 1982. *Modelling fluctuating populations*. Wiley, NY.
- Noble, I. R. & Slatyer, R. O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. *Vegetatio* 43: 5–21.
- Numata, M. 1980. Facts, causal analyses and theoretical considerations on plant succession. In: Miyawaki, A. & Okuda, S. (eds), *Vegetation und Landschaft Japans*. Festschrift für Prof. Dr. R. Tuxen, Yokohama.
- Numata, M. 1982. Experimental studies on the early stages of secondary succession. *Vegetatio* 48: 141–149.
- O'Connor, I. & Aarssen, L. W. 1987. Species association patterns in abandoned sand quarries. *Vegetatio* 73: 101–109.
- Okubo, A. 1980. Diffusion and ecological problems: mathematical models. *Biomathematics*, Vol. 10.
- Pacala, S. W. 1986. Neighborhood models of plant population dynamics 2. Multispecies models of annuals. *Theor. Pop. Biol.* 29 (2): 262–292.
- Pacala, S. W. 1987. Neighborhood models of plant population dynamics 3. Models with spatial heterogeneity in the physical environment. *Theor. Popul. Biol.* 31 (3): 359–392.
- Pacala, S. W. & Silander, J. A. Jr. 1985. Neighborhood models of plant population dynamics I. Single-species models of annuals. *Am. Nat.* 125: 385–411.
- Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. *Bull. Torrey Bot. Club* 107: 238–248.
- Pickett, S. T. A. 1982. Population patterns through twenty years of oldfield succession. *Vegetatio* 49: 45–59.
- Pickett, S. T. A. & White, P. S. (eds) 1985. *The ecology of natural disturbance and patch dynamics*. Acad. Press, NY.
- Podani, J. 1988. SYN-TAX III. A package of programs for data analysis in ecology and systematics. *Coenoses* 3.
- Prach, K. 1984. Selected results of the study of succession on dumps from brown coal mining (most Region, N.W. Bohemia). *Acta Bot. Slov. Acad. Sci. Slov., Ser. A., Suppl.* 1, 257–261.
- Prach, K. 1986. Colonization of dumps from coal mining by higher plants. *Ecologia, Bratislava*, 5: 421–424.
- Prach, K. 1987. Succession of vegetation on dumps from strip coal mining, N.W. Bohemia, Czechoslovakia. *Folia Geobot. Phytotax.* 22: 339–354.
- Price, M. V. 1986. Introduction to the symposium: mechanistic approach to the study of natural communities. *Amer. Zool.* 26: 3–4.
- Szegi, J., Oláh, J., Fekete, G., Halász, T., Várallyay, Gy. & Bartha, S. 1988. Recultivation of the spoil banks created by open-cut mining activities in Hungary. *Ambio* 17 (2): 137–143.
- Thompson, J. N. 1985. Within-patch dynamics of life histories, populations, and interactions: selection over time in small spaces. In: Pickett, S. T. A. & White, P. S. (eds) 1985. *The ecology of natural disturbance and patch dynamics*. Acad. Press, New York.
- Turner, D. P. 1985. Successional relationships and a comparison of biological characteristics among six north-western conifers. *Bull. Torrey Bot. Club* 112 (4): 421–428.
- Watt, A. S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1–22.
- Weiner, J. & Conte, P. T. 1981. Dispersal and neighbourhood effects in an annual plant competition model. *Ecol. Modelling* 13: 131–147.
- Wood, D. M. & del Moral, R. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68: 780–790.