On the rate of succession

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What is the rate of succession? In vegetation ecology, this term is usually understood as (a) time required for recovery of a terminal stage (Major 1974a, Numata 1982, Burrows 1990, etc.), or (b) rate of changes in vegetation (Major 1974b, etc.). Whereas an extensive body of published data exists concerning the first meaning, the latter one, which is considered in the present paper, has been only rarely examined. Species turnover has been usually adopted as a measure of change in vegetation and its rate has been evaluated by various (dis)similarity indices between samples taken in successive years (Bornkamm 1981).

We investigated the relationship between the rate of succession and crucial environmental factors. Preliminary comparison of several successional seres (Prach 1990) lead to the hypothesis that the rate of succession is higher in fertile sites than under unfertile conditions. This hypothesis is examined here using field data from studies of several successional seres in central European man-made habitats. For the purposes of this paper, we define the soil fertility as a combination of moisture and nutrient availability. We suggest a new method of expressing the rate of succession, which makes it possible to compare data sets of various origin.

Methods

Expressing the rate of succession

To express the rate of succession, changes only in cover of dominant species were used. The species that attained the highest cover value among all species present in the respective year was considered as dominant.

The computation of annual change in cover of the dominant species was based on models fitted to the original data. This made it possible to compare data collected with various degree of precision and complexity. Changes in species cover during succession were predicted by means of generalized linear modelling (GLM), assuming binomial distribution of response variables (percentage cover of considered species) and using exponential link function (see McCullagh and Nelder 1983). The explanatory variable used was time from the onset of succession (in years). The null model (i.e. hypothesis that the cover of a species is constant in time) was tested against the model with time as a linear predictor. Such a linear predictor was found to be a significant model in all cases. An extended model, including the second power of time, was also tried for all the species in all seres. It was adopted in those cases when it represented a significant increase of the explanatory power of the regression model. Under some conditions (see ter Braak and Looman 1986), this model may be interpreted as unimodal response of a species cover to the change of position on the successional gradient (represented here simply by a change in time). Unimodal form of species response was accepted mainly for species with abundance culmination in the middle of the observed period of succession, as expected.

The predicted cover values were used to calculate the rate of change. The basic measure was the difference in cover between two successive years. For a species being dominant in the respective year, difference in cover was calculated comparing the current and previous year. We can express the statistics used to evaluate species turnover rate in each year as:

$$V_i = \max_{j=1}^{n} \left(|P_{ij} - P_{(i-1)j}| \right)$$

for years $i = 2, ..., N$ and species $j = 1, ... n$. The n is number of species considered in the respective sere
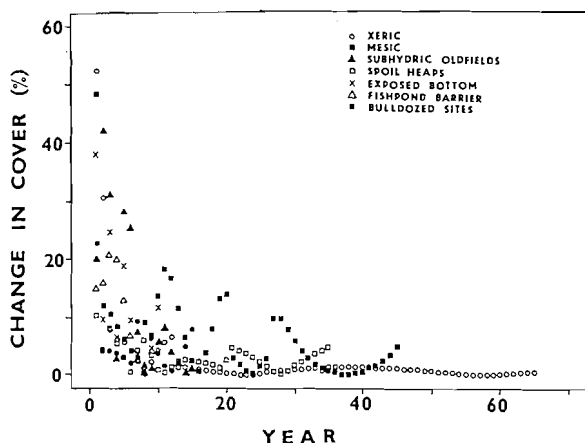
Fig. 1. The rate of succession and its changes in time. Succession rate was expressed as a difference between cover of a dominant species in the current and previous years (see text).

(being dominant at some time) and N is number of years. Values P_{1j} refer to the cover of a species in the first year and P_{ij} generally to the cover of a species j in the i-th year.

Characterizing habitat conditions

As direct measurements of habitat factors were either not available in original studies or obtained by methods with different precision, indicator values (Ellenberg 1974) were used to evaluate substrate conditions indirectly. Soil moisture (F) and contents of total nitrogen (N) were considered as factors decisive for the fertility of the site. Using the Ellenberg indicator values is justified in this case because of the wide range of habitats included, providing steep gradients of both factors considered (Klimeš 1987, ter Braak and Gremmen 1989). Only those species that occurred in the site in any of the first five years of succession with cover of at least 5% were included in the calculation of the mean indicator value.

Seres studied

Cover data were obtained from the following studies carried out in Czechoslovakia on seven seres, both primary and secondary (for summary of dominant species see Prach 1990):

(1–3) Succession in abandoned fields in the Bohemian Karst near Prague (Osbornová et al. 1989): Three particular seres were distinguished in xeric, mesic, and subhydric fields. The study was conducted from 1974 to 1987 in differently aged fields. Cover data were recorded using either point-quadrat method (in early successional stages) or phytosociological relevés (in later stages).

(4) Succession on spoil heaps from brown coal mining in NW Bohemia (Prach 1987): The study was carried out between 1977 and 1989 using point-quadrats and micromaps in permanent plots.

(5) Succession on exposed bottom of a destroyed water reservoir at Dřínov (NW Bohemia): The study was conducted from 1983 to 1990 using point-quadrats along two parallel transects.

(6) Succession on a barrier along a newly constructed Novy rybník fishpond near the town of Třeboň, S Bohemia: Sampling by point-quadrats was used in 1984–91 along a transect across the barrier. The barrier was formed by autochtonous organic material of peaty topsoil.

(7) Succession in reclaimed sites in areas previously covered by spruce forests in the Krušné hory Mts. in NW Bohemia (Pyšek 1992). Sites were bulldozed to remove grass cover with topsoil in order to make the replanting of forest trees easier. The course of the first 15 years succession was inferred by comparing sites reclaimed at different times. Cover values (visually estimated) served as input data.

Results

The rate of succession decreased with time (Fig. 1). From the visual comparison of particular seres it is obvious that the dominant species exchange was faster in those seres characterized by higher soil fertility (expressed as a sum of F+N indicator values which was: exposed bottom 14.4, subhydric old fields 13.9, fishpond barrier 13.8, mesic oldfields 11.9, xeric oldfields 11.6, spoil heaps 10.8, and bulldozed sites 9.6)
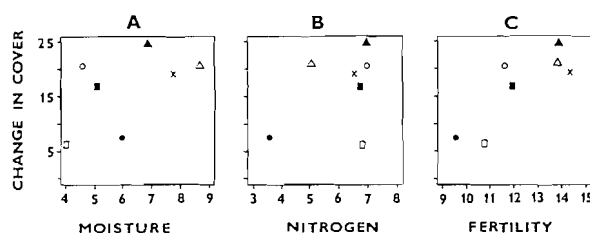

Fig. 2. Initial rate of succession related to the substrate conditions of the site. Rate of succession is expressed as a mean annual change in cover of dominant species during the first five years from the onset of succession. To quantify habitat conditions, Ellenberg indicator values were used for soil moisture (A) and nitrogen (B). Sum of both values for moisture and nitrogen is used to express the site fertility in C. The symbols correspond to those used in Fig. 1: xeric (O), mesic (■) and subhydric (▲) oldfields, spoil heaps (□), exposed bottom (X), fishpond barrier (△), bulldozed sites (●). To test a hypothesis of (monotonic) relationship between the initial rate of succession and soil fertility, Kendall's coefficient of rank correlation (Sokal and Rohlf 1981) was used which turned up to reveal a non-significant result ($\tau = 0.52$, significance level $\alpha = 0.09$, n = 7). Note, however, that the significance level given is only of an approximate character.

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Mean annual change in cover of dominant species, calculated for the first 5 years of succession, was used to examine the relationship between the initial rate of succession and substrate conditions (Fig. 2). We did not reveal any clear trends in the initial rate of succession with respect to the moisture (Fig 2A) and nitrogen status of the site (Fig. 2B). However, if both moisture and nitrogen indicator values were combined, the initial rate of succession shows an increase with soil fertility expressed in this way (Fig. 2C).

Discussion

Decrease in the rate of species exchange during succession is generally accepted (Whittaker 1975, Grime 1979, Burrows 1990, etc.) and it has been supported by quantitative data (Bornkamm 1981). This decrease is not monotonic as the rate can temporarily increase (see Fig. 1) in periods of exchange of distinct edificators or entire seral communities (Numata 1982). Concerning the relation between the rate of species turnover and site conditions, there is a lack of data and usually only vague statements have been presented so far: Drury and Nisbet (1973) wrote that "soil development, external supply of nutrients, exposure, and seed immigration in controlling the rate of development [succession] remain largely hypothetical". Major (1974b) expected that a more humid climate would result in more rapid plant succession, and Luken (1990) suggested artificial fertilization to speed up succession. Only Tilman (1988) discussed in detail species displacement in relation to site fertility. Olson (1958) demonstrated that the availability of water and nutrients "may be more important limiting factors to the rate of species establishment than the age, thickness, or organic content of the soil".

Generally, a slow rate of succession, both in terms of recovery time and species turnover, is typical of extreme habitat conditions, e.g. in nutrient-poor arctic tundra (e.g. Burrows 1990). Under very wet and nutrient-rich conditions in certain hydroseres, the rate of succession is also expected to be low (Krahulec et al. 1980). Our results suggest that there is an additive effect of soil moisture and nutrient availability on the rate of succession. This may be demonstrated by similarly slow rate of succession in wet and nutrient poor reclaimed sites after spruce forest (sere no. 7) and in dry and nutrient rich spoil heaps (sere no. 4) (Fig. 2C).

To explain our results, some conclusions of Tilman (1988) can be exploited. Transient dynamics seems to be the probable mechanism to operate, at least for a certain period, during initial stages of all seres analysed in the present study (see Tilman 1988: p. 239). Transient dynamics are defined as competitive displacement of successive species determined by differences in their growth rates. It is based on the assumptions that (a) the growth rates decrease during succession, i.e. the early

species are replaced by other species with lower growth rates in these conditions (b) competitiveness of a species for light, given by its height, increases, and (c) the higher the site fertility, the higher the growth rate. Hence the rate of species turnover is expected to increase with site fertility and decrease with time which conclusions correspond to our results. However, the rate of species turnover can also be influenced by other factors, e.g. colonization processes, disturbance regime of the site, life-span and other life history characteristics of species (Grime 1979).

In studies measuring the rate of succession on the basis of considering all the species present in a community (Bornkamm 1981), the species richness and diversity are stressed whereas taking only the dominant species into account relates the rate of succession rather to the biomass partitioning within a community. Use of similarity indices is more limited by nature of data sets available; more complete floristic lists are needed. Furthermore, similarity indices are dependent on the size of sampling plots and year-by-year sampling is required (Bornkamm 1981).

Recent studies on succession are mostly focused upon explaining underlying mechanisms and studies comparing different successional seres are rather rare. To recognize more general pattern of changes in the rate of succession and assess the importance of factors this pattern is governed by, comparisons of successional seres from various habitats are needed. Such an approach, however, must necessarily rely on data provided by authors from various geographical regions using various methodical approaches which fact makes the comparisons between seres difficult. The method suggested in this paper partly overcomes this problem as it allows the use of diverse data sets obtained in the field by various sampling procedures. The effects of irregular sampling and short term fluctuations in species performances are diminished by (a) including only dominant species, and (b) interpolating and smoothing species cover values by means of models fitted to the data. Hence, the method can be used for comparing rather heterogeneous data sets.

Comparative studies of succession can undoubtedly provide new ideas on vegetation dynamics over a large range of environmental conditions, and results on the basis of which effective management of spontaneous successional vegetation may be suggested.

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