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Changes in species traits during succession: a search for pattern

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Cover data from 13 successional seres starting on bare ground in the western part of the Czech Republic were analysed. The following questions were addressed: (1) whether the participation of species with particular traits exhibits some trends, and (2) whether primary and secondary seres differ from each other in the course of the first 10 yr of succession. Primary seres were distinguished from secondary ones a priori on the basis of absence or presence of (a) organic topsoil, and (b) soil seed bank at the onset of succession. Traits important for the course of succession were considered, their relative importance expressed for each sere and year on the basis of species quantities, and tested for trends (increase, decrease, unimodal response, no evident trend or absence). The majority of traits considered exhibited some trends in the course of succession. Participation of C-strategists, phanerophytes, intensity of lateral spread, presence of VA mycorrhizae, dispersal by animals and wind, and height of plants significantly increased during the first 10 yr of succession, whereas the participation of R-strategists, therophytes, propagule weight, and capability of forming persistent seed bank decreased. Participation of S-strategists, geophytes, hemicryptophytes, and all relevant types of pollination did not exhibit any significant trend. Primary and secondary seres differed from each other neither in trends in life-history characteristics of constituent species nor in their relative importance after the first 10 yr of succession.

It is generally accepted that life-history characteristics and autecology of species involved in succession change during the process (Noble and Slatyer 1980, Huston and Smith 1987, Walker and Chapin 1987, Brown 1992, Glenn-Lewin et al. 1992). However, conclusions on the pattern of changes in species traits during succession are often rather speculative. So far, only a few studies have provided rigorous quantitative analyses of a larger set of species traits (Rydin and Borgegård 1991) and we are not aware of any quantitative study comparing more successional seres with regard to species characteristics.

In previous studies, we analysed plant species dynamics in a number of successional seres in various man-disturbed sites in central Europe (Prach et al. 1993, Prach and Pyšek 1994a, b). In the present paper, we address the question whether or not (1) the traits of constituent species exhibit trends among the seres, and (2) primary seres differ from secondary ones in this respect.

Methods

Seres studied

Cover data were obtained from published case studies and unpublished records for 13 successional seres. In the majority of cases, the cover of each species present was estimated annually in 5 × 5 m permanent plots fixed immediately after creation of the site. In some seres (nos. 2, 3, 4, 11, 12, 13) comparable stages of different age were considered or both approaches were combined to infer the course of succession. Only the first 10 yr of succession were analysed in the present paper because of incomplete data from later successional stages and various length of the recording period.

All the seres started on bare ground and were located in the western part of the Czech Republic. The primary seres were distinguished a priori on the basis of (a) absence of organic topsoil, and (b) absence of soil seed bank at the onset of succession. Those seres with organic topsoil and seed bank present were considered as secondary. The following seres were analysed (P indicates primary, S secondary seres):

1. Large spoil heaps from open-cast brown coal mining. Data from Prach (1987) and unpubl. (P).
2. Abandoned sand pit. Data Kočár and Prach (unpubl.) (P).
3.–4. Reclaimed sites in areas deforested due to air pollution. To make the replanting of spruce easier, the sites were bulldozed creating plots with grass cover and topsoil removed (P) and mounds formed by the dumped material (S). Data from Pyšek (1992).
5.–6. Barriers around a newly constructed fishpond formed by sandy subsoil (P) or organic (peaty) topsoil (S). Data Prach (unpubl.).

7.–9. Ruderal urban sites in the town of Plzeň. Three particular seres were distinguished according to the substratum: nutrient poor, mineral (P); moderate in nutrients, mineral (P); nutrient rich with organic topsoil (S). Data from Pyšek (1978).

10. Exposed bottom of a destroyed water reservoir. Data Frantík, Osbornová and Prach (unpubl.) (S).

11.–13. Abandoned fields (S). Three seres were distinguished according to the soil moisture conditions: xeric, mesic and wet. Data from Osbornová et al. (1989) and Prach (unpubl.).

For a detailed description of the seres see Prach et al. (1993), Prach and Pyšek (1994a, b) and the sources mentioned.

Species traits considered

Those traits were considered which are important in succession (Noble and Slatyer 1980, Huston and Smith 1987, Walker and Chapin 1987, Brown 1992, Glenn-Lewin et al. 1992) and, at the same time, the information is available for a large set of species (taken mostly from Grime et al. 1988, and Frank and Klotz 1990). For each sere, the following characteristics were attributed to each species which attained at least 1% cover in at least one year of succession:

(a) Life strategy (C, S, R) according to Grime (1979). For combined strategies, the respective cover value was shared between the combined types. CSR-strategists were excluded from the analysis as being useless in evaluating the trends in the basic three strategies.

(b) Life forms (Raunkiaer's scheme, see, e.g., Mueller-Dombois and Ellenberg 1974): T – therophytes, G – geophytes, H – hemicryptophytes; Ph – phanerophytes (chamaephytes were not considered because of too low representation).

(c) Intensity of lateral spread: perennials attaining more than 1 m (degree no. 5 in Table 6.2 in Grime et al. 1988) were considered.

(d) Presence of VA mycorrhizae (Table 6.2 in Grime et al. 1988).

(e) Formation of persistent seed bank (as characterized by the symbol Bs in Table 6.3 in Grime et al. 1988).

(f) Propagule weight: participation of species with seeds lighter than 0.5 mg (the degrees 1 and 2 on the scale given in Grime et al. 1988).

(g) Dispersal by wind and animals (others were not relevant).

(h) Pollination mode: wind, insect (others not relevant).

(i) Maximum height (as given in Dostál 1950). Woody plants were not considered.

The importance of particular characteristics was weighed by the respective species cover for each observed year and sere.

Data analysis

In each sere, the change over time in the relative importance of particular traits (expressed as a percentage contribution of species possessing the given trait) was modelled with a generalized linear model (Gamma distribution, log link function – McCullagh and Nelder 1989). The cases where the trait was present in less than 25% of observations and with maximum relative frequency less than 5% were excluded from fitting and marked as not present. Otherwise, the significance of a linear model was tested (against the null model of constancy of the trait frequency throughout the 10-yr period), using analysis of deviance. The threshold for a trend significance was set rather high, namely at a Type I Error probability of 0.10, for various reasons (only asymptotically valid test, low resolution of the test because of low number of observations, and the overall goal being the identification of the underlying trend in the data). When a significant linear trend was found, the "slope" of the dependence was noted and the trend was marked either "up" or "down". If the form of linear dependence was not accepted, a second-order polynomial was fitted and the model was tested against the null model. If significant, the actual shape was checked and when the fitted curve had a bell-like shape, the trend was called a "peak". The other case (with a "valley"-shape) and the cases where the pattern of change was too complicated were marked as "xx". Using the same approach, a generalized linear model was fitted for all the seres combined, corresponding to the hypothesis that all the seres have approximately the same behaviour as far as the considered traits are concerned.

For each logical group of traits (strategies, life forms, dispersal, and pollination – see the previous section), a contingency table was created with two or three explanatory ("stimulus") factors: type of succession (primary or secondary), type of the change during succession (up, dn, pk, no, xx), and – where appropriate – the level of the considered trait (e.g. C, S and R for Grime's strategies).

The contingency tables were analysed using a generalized linear model with the response variable being the number of occurrences of a particular combination of factor levels (Poisson distribution, log link function). The base-line model included all the factors and their interactions, except the one classifying the sere as primary or secondary. This base-line model was tested against the alternative one, which included the factor describing whether or not the sere is a primary one (Venables and Ripley 1994). The test was based on a χ^2 test as the correctness of the *F*-test is questionable in this case (McCullagh and Nelder 1989).

Results

Trends in plant characteristics (i.e. increase, decrease, unimodal response, and no evident trends or absence) during the first 10 yr of succession are shown in Table 1 for particular seres as well as for all the seres together. Participation of C-strategists and that of phanerophytes, intensity of lateral spread, presence of VA mycorrhizae, dispersal by animals and wind, and height of plants significantly increased during the first 10 yr of succession, whereas the participation of R-strategists, that of therophytes, propagule weight, and capability of forming persistent seed bank decreased. Participation of S-strategists, geophytes, hemicryptophytes, and all relevant types of pollination did not exhibit any significant trend. With respect to the trends, primary and secondary seres did not differ significantly from each other in any of the characteristics considered.

The relative importance of the particular life-history characteristics in the 10th yr of succession is given in Table 1 for all the seres analysed. Primary (6 cases) and secondary (7) seres did not differ significantly from each other in any of the traits considered.

Discussion

The results of our study indicate that despite great variability in species traits among successional seres, general trends can be found by comparative studies. We are less sceptic in this matter than, e.g. Gibson and Brown (1991) who found that species colonized an abandoned field irrespective of plant life-history traits, including dispersal mechanisms.

The majority of traits considered in this study exhibit some trends in the course of succession. It should, however, be taken into account that rather robust statistics were used. The relevant limitation to our data is that only the first 10 yr of succession were analysed, and some of the trends may potentially have a different pattern in a longer perspective.

Some of the trends detected in the present paper are not surprising. The increase and decrease of C- and R-strategists, respectively (Grime 1979), as well as the increase of phanerophytes and decrease of therophytes have been repeatedly reported, especially from the temperate zone (Burrows 1990, Glenn-Lewin et al. 1992). These integral categories of species' life-histories evidently show the clearest trends (e.g. Grime 1979, Inouye et al. 1987, Rydin and Borgegård 1991). Surprisingly, hemicryptophytes and geophytes did not exhibit any clear general trend in our data set.

Among the particular life-history traits pollination mode exhibited a chaotic pattern (see Table 1), in a certain contrast to several earlier studies (Rydin and Borgegård 1991). Increasing importance of extensive lateral spread and decreasing persistent seed bank are in accordance with successional theory since annuals, prevailing in initial stages of succession and retreating later on, do not spread vegetatively, but usually produce a large number of persistent seeds (Fenner 1987; Huston and Smith 1987). Modes of seed dispersal and seed weight are related to each other as a result of evolutionary adaptations (Harper et al. 1970). The role of wind dispersal is usually reported to decrease in succession, whereas that of animal dispersal and seed weight increases (Fenner 1987, Huston and Smith 1987, Rydin and Borgegård 1991). However, we found an increase in both dispersal categories and a decrease in seed weight. The increase of the former ones can be explained by the fact that many species typical of initial stages of succession do not posses specific modes of dispersal (see Table 6.3 in Grime et al. 1988). The decrease of seed weight corresponds to some earlier findings that first colonizers possess heavier seeds than other species typical of early stages of succession (Prach 1988; Rydin and Borgegård 1991). Mycorrhizal infection has been reported to increase during succession in favourable sites, and to be very important in any seral stage under unfavourable environmental conditions (Huston and Smith 1987, Allen and Allen 1990). The general increase of potentially VA mycorrhizal plants in our study is in accordance with this expectation. However, no relation to the severity of a site was found. The height of a species can be related to its competitive ability (Grime 1979) and it is generally expected to increase during succession (Huston and Smith 1987; Rydin and Borgegård 1991) as it does in our case. However, it can decrease in nutrient-poor sites (Gleeson and Tilman 1990), which can be seen in the nutrient-poorest sere of our data set (sere no. 3 – scraped plots; see Prach et al. 1993).

Obviously, primary and secondary seres differ from each other neither in trends in life-history characteristics of constituent species nor in their relative importance after the first 10 yr of succession. Similarly, there was no difference between the same sets of primary and secondary seres in the participation of woody species (Prach and Pyšek 1994a). The course of succession thus appears to be related to other factors than its primary or secondary status. The pattern of species traits may be correlated rather with site conditions such as soil fertility (van der Valk 1992, van Andel et al. 1993). Moreover, the differences between both types are arbitrary and often it is difficult to state unambiguously if a particular sere is primary or secondary (Glenn-Lewin and van der Maarel 1992, van Andel et al. 1993). We suggest to restrict the use of these terms only to whether or not the site was previously vegetated, without any direct implications for the course of succession to follow. Such a meaning is even closer to the original concept (Clements 1916), discarding many later unproven ideas.

Table 1. Trends in the life-history characteristics during the first 10 yr of succession shown for particular primary (P) and secondary (S) seres. C, S, R – life strategies according to Grime et al. (1988); G – geophytes, H – hemicryptophytes, Ph – phanerophytes, T – therophytes; for the definition of the other traits considered, see the text; up – increase in importance of the respective characteristic; dn – decrease; pk – unimodal response with a peak during the period; xx – no evident pattern; 0 – absence or negligible importance. The significance of differences in trends between primary and secondary seres is shown in the middle; the significant prevailing trend considering pooled data from all seres is given at the bottom of the table (N.S. – non-significant, see text for details on the statistics used). Relative importance of particular traits (expressed as the percentage contribution of species possessing the given trait) in the 10th yr of succession is shown in parentheses. At that time, the differences between primary and secondary seres in the relative importance of particular traits were all non-significant.

SERES	Type	C	S	R	G	H	Ph	T	Ex. lat. spread	VAM	Ext. seed bank	Disp. anim.	Disp. wind	Low disp. W.	Polin. insect	Polin. self	Polin. wind	Tall plants
Spoil heaps	P	up (17)	up (02)	dn (17)	pk (34)	up (49)	0 (00)	dn (17)	pk (36)	up (54)	dn (56)	up (00)	up (20)	up (68)	pk (47)	pk (47)	xx (07)	up (69)
Sandy barrier	P	up (64)	dn (36)	0 (00)	up (49)	dn (01)	up (50)	0 (00)	up (100)	dn (00)	pk (00)	pk (01)	up (99)	xx (85)	dn (01)	dn (01)	up (97)	up (100)
Urban poor	P	up (26)	pk (01)	dn (03)	up (38)	pk (57)	0 (01)	dn (03)	up (75)	pk (39)	dn (05)	pk (01)	up (28)	pk (67)	pk (24)	pk (22)	xx (54)	xx (62)
Urban moder.	P	up (26)	up (01)	dn (05)	up (01)	pk (76)	up (21)	dn (01)	up (33)	pk (57)	dn (53)	up (28)	up (14)	up (73)	up (52)	pk (31)	dn (17)	up (78)
Scriped plots	P	xx (02)	up (60)	0 (00)	dn (31)	up (67)	xx (03)	0 (00)	xx (96)	up (46)	dn (40)	up (52)	dn (33)	xx (100)	dn (08)	dn (07)	up (85)	dn (38)
Sand pit	P	xx (65)	xx (31)	dn (00)	dn (00)	xx (22)	pk (69)	dn (00)	xx (100)	xx (22)	dn (00)	xx (22)	xx (78)	xx (34)	dn (03)	dn (00)	up (93)	pk (78)
DIFFERENCE (P vs S)		N.S.			N.S.				N.S.	N.S.	N.S.	N.S.		N.S.	N.S.			N.S.
Oldfields wet	S	xx (71)	pk (04)	dn (00)	xx (74)	pk (26)	0 (00)	dn (00)	up (98)	pk (15)	pk (18)	pk (14)	xx (70)	up (78)	xx (48)	up (47)	dn (05)	xx (13)
Urban rich	S	up (52)	xx (03)	dn (09)	pk (01)	pk (66)	up (20)	dn (13)	up (75)	up (35)	dn (44)	up (58)	pk (01)	pk (53)	up (38)	pk (15)	dn (47)	xx (69)
Peaty barrier	S	up (85)	pk (14)	dn (00)	up (18)	pk (54)	up (28)	dn (00)	up (100)	up (71)	xx (53)	up (13)	up (32)	xx (55)	xx (24)	xx (24)	pk (52)	up (100)
Oldfields mesic	S	xx (23)	pk (53)	dn (01)	dn (00)	xx (71)	up (27)	dn (01)	up (92)	xx (51)	pk (20)	up (46)	dn (09)	xx (21)	dn (30)	dn (19)	up (52)	xx (66)
Mounds	S	xx (02)	up (89)	0 (00)	xx (55)	xx (37)	xx (09)	0 (00)	up (90)	xx (72)	up (35)	pk (24)	xx (63)	xx (96)	dn (13)	xx (24)	up (63)	xx (68)
Emergent bottom	S	up (65)	xx (35)	dn (00)	up (65)	pk (00)	up (35)	dn (00)	up (100)	pk (00)	dn (00)	pk (00)	up (100)	up (100)	dn (00)	dn (00)	up (100)	up (100)
Oldfields xeric	S	up (12)	xx (03)	dn (10)	pk (03)	up (77)	up (01)	dn (18)	up (51)	pk (66)	xx (19)	xx (16)	dn (07)	xx (37)	dn (36)	dn (30)	up (33)	up (81)
SERES TOGETHER		up	xx	dn	xx	xx	up	dn	up	up	dn	up	up	up	xx	xx	xx	up

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References

Allen, E. B. and Allen, M. F. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, San Diego, CA, pp. 367–389.

Brown, V. K. 1992. Plant succession and life history strategy. – Trends Ecol. Evol. 7: 143–144.

Burrows, C. J. 1990. Processes of vegetation change. – Unwin Hyman, London.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. – Carnegie Inst. Publ. no. 242, Washington.

Dostál, J. 1950. Flora of Czechoslovakia. – Czech Academy of Sciences, Prague.

Fenner, M. 1987. Seed characteristics in relation to succession. – In: Gray, A. J. et al. (eds), Colonization, succession and stability. Blackwell, Oxford, pp. 103–114.

Frank, D. and Klotz, S. 1990. Biologish-ökologische Daten zur Flora der DDR. – Wiss Beitr. Martin Luther University, Halle-Wittenberg.

Gibson, C. W. D. and Brown, V. K. 1991. The effects of grazing on local colonization and extinction during early succession. – J. Veg. Sci. 2: 291–300.

Gleeson, S. K. and Tilman, D. 1990. Allocation and the transient dynamics of succession on poor soils. – Ecology 71: 1144–1155.

Glenn-Lewin, D. C. and van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. – In: Glenn-Lewin, D. C., Peet, R. K. and Veblen, T. T. (eds), Plant succession. Theory and prediction. Chapman & Hall, London, pp. 11–59.

, Peet, R. K. and Veblen, T. T. 1992. Plant succession. theory and prediction. – Chapman & Hall, London.

Grime, J. P. 1979. Plant strategies and vegetation processes. – Wiley, Chichester.

, Hodgson, J. G. and Hunt, R. J. 1988. Comparative plant ecology. A functional approach to common British species. – Unwin Hyman, London.

Harper, J. L., Lovell, P. H. and Moore, K. G. 1970. The shapes and sizes of seeds. – Annu. Rev. Ecol. Syst. 1: 327–356.

Huston, M. and Smith, T. 1987. Plant succession: life history and competition. – Am. Nat. 130: 168–198.

Inouye, R. S., Huntly, N. J., Tilman, D., Tester, J. R., Stillwell, M. and Zinnel, K. C. 1987. Old-field succession on a Minnesota sand plain. – Ecology 68: 12–26.

McCullagh, P. and Nelder, J. A. 1989. Generalized linear models. 2nd ed. – Chapman and Hall, London.

Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. – Wiley, New York.

Noble, I. R. and Slatyer, R. O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. – Vegetatio 43: 5–21.

Osbornová, J., Kovářová, M., Lepš, J. and Prach, K. (eds) 1989. Succession in abandoned fields. Studies in Central Bohemia, Czechoslovakia. – Kluwer, Dordrecht.

Prach, K. 1987. Succession of vegetation on dumps from strip coal mining, N.W. Bohemia, Czechoslovakia. – Folia Geobot. Phytotax. 22: 339–354.

1988. Life-cycles and temporal changes in plant populations and communities. – Preslia 60: 23–40 [in Czech with English summary].

and Pyšek, P. 1994a. Spontaneous establishment of woody plants in Central European derelict sites and their potential for reclamation. – Restoration Ecol. 2: 190–197.

and Pyšek, P. 1994b. Clonal plants – what is their role in succession? – Folia Geobot. Phytotax. 29: 307–320.

, Pyšek, P. and Šmilauer, P. 1993. On the rate of succession. – Oikos 66: 343–346.

Pyšek, A. 1978. Ruderal vegetation of the city of Plzeň. – Thesis, Botanical Inst. Czech Acad. Sci., Průhonice.

Pyšek, P. 1992. Dominant species exchange during succession in reclaimed habitats: a case study from areas deforested due to air pollution. – For. Ecol. Manage. 54: 27–44.

Rydin, H. and Borgegård, S.-O. 1991. Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. – Ecology 72: 1089–1101.

van Andel, J., Bakker, J. P. B. and Grootjans, A. P. 1993. Mechanisms of vegetation succession: a review of concepts and perspectives. – Acta Bot. Neerl. 42: 413–433.

van der Valk, A. G. 1992. Establishment, colonization and persistence. – In: Glenn-Lewin, D. C., Peet, R. K. and Veblen, T. T. (eds), Plant succession. Theory and prediction. Chapman & Hall, London, pp. 60–102.

Venables, W. N. and Ripley, B. D. 1994. Modern applied statistics with S-Plus. – Springer-Verlag, New York.

Walker, L. R. and Chapin III, F. S. 1987. Interactions among processes controlling successional change. – Oikos 50: 131–135.