Climate and pH as determinants of vegetation succession in Central European man-made habitats

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Abstract

Questions: (1) What are the most important abiotic environmental variables influencing succession in central European man-made habitats? (2) How do these variables interact with one another and with variation in community properties?

Location: Central, western and southern parts of the Czech Republic. Habitats included old fields, urban sites, spoil heaps after coal mining, sites at water reservoirs, extracted sand pit and peatland and reclaimed sites in areas deforested by air pollution.

Methods: We investigated vegetation patterns on 15 successional seres, sampled by the same methods. Time of succession over which the data were available ranged from 12 to 76 years. The cover of vascular plant species (in %) was estimated in 5 m × 5 m plots. The relationships between vegetation characteristics (species composition, total cover, cover of woody species, species number and rate of dominant species turnover) and 13 abiotic site factors, including climatic and soil variables, were tested using CCA ordination and regression models.

Results: Substratum pH, the only substratum characteristic, and climate were the environmental variables significantly affecting the vegetation patterns in the course of succession. The rate of succession, measured as the turnover of dominant species, was significantly more rapid in lowland than in mountain climates. On alkaline soils, species numbers in succession increased towards warmer climates. However, acid soils prevented any increase in species numbers, regardless of the climate. Surprisingly, forms of nitrogen and contents of C, P and cations did not exhibit any significant effect on the vegetation characteristics studied.

Conclusions: Our approach, to compare a number of seres, can contribute not only to our understanding of succession, but also to help restoration projects to predict vegetation change because the crucial environmental variables, as identified by this study, are easy to measure.

Keywords: Ordination; Soil property; Species number; Succession rate; Vascular plant.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Due to global changes in land use, the importance of man-made habitats in modern landscapes has been increasing. This drives a need for studies on succession in these habitats. Research in vegetation succession yielded conclusions on the direction of succession, its rate, convergence or divergence among seres, changes in diversity and productivity, the role of abiotic conditions, diaspore availability, competition, herbivory and importance of life-history traits (Glenn-Lewin et al. 1992; van Andel et al. 1993; Walker & del Moral 2003; Prach & Řehounková 2006). However, most studies have considered only one type of succession in one or a few sites and employed various methodologies (Burrows 1990; Walker & del Moral 2003). These factors limit succession theory because the results cannot be directly compared across seres and rigorously tested and many generalizations remain speculative. Little attention has been paid to quantitative analyses of patterns of succession over a larger number of seres. The main reason is the lack of data sampled in a comparable way (Prach et al. 2001).

In previous papers, long-term data from 15 successional seres, developing in a variety of man-made habitats in central Europe and sampled in the same way, were analysed. This enabled us to explore the rate of succession (Prach et al. 1993), participation of woody species (Prach & Pyšek 1994), changes in species traits (Prach et al. 1997) and differences between successional dominants, other species participating in succession and local flora (Prach & Pyšek 1999). Prach et al. (2001) have shown that spontaneous successions on bare ground in central European vegetation diverge: seres occurring in agricultural, industrial or urban landscapes tend to develop differently from those occurring in less human-altered, mostly forested landscapes. The two groups of seres were termed 'ruderal' and 'non-ruderal' successions, reflecting the degree of representation of 'so-called' ruderal species (Ellenberg 1988; Grime 2001), associated with

intensively disturbed habitats.

The above mentioned papers described the pattern of succession but did not relate observed dynamics of vegetation development to environmental factors. Although the influence of climate and substratum on the course of succession is generally important (Walker & del Moral 2003), quantitative assessments across different seres are missing. In this study, vegetation patterns in the successions are related to climate and soil characteristics at the beginning of succession. We have two questions: 1. What are the most important abiotic variables influencing succession in central European man-made habitats? 2. How do these variables interact with one another and with variation in several successional vegetation properties, including species composition?

Material and Methods

Study sites

We studied 15 seres in the central, western and southern parts of the Czech Republic, in the temperate zone of Europe. All seres that were available in sufficient numbers of differently aged stages in that region at the time were included. All seres started on bare ground immediately after disturbance. Time of succession over which the data were available ranged from 12 to 76 years. Location of the seres and the sequence of dominant species with the period of their dominance in years since the onset of succession for which data were available and sources of primary data are indicated in Table 1.

Data collection

Successional pattern in the seres was studied by combining permanent plots and the space-for-time substitution approach (Pickett 1989). The cover of vascular plant species was visually estimated in 5 m × 5 m sampling plots in sample years. The plots were located in particular spontaneous successional stages, avoiding those of unclear history or those subsequently disturbed. Because many of the representative stages were small, one sampling plot was used per stage. Soil analyses of the bare material (using standard methods, ten samples in each sere) on which the succession started were used to obtain initial soil characteristics. Each sere was also characterized by altitude, mean annual temperature and annual precipitation (Table 2). Climatic data were obtained from Moravec & Votýpka (1997).

The following characteristics were calculated from vegetation records for each sere: maximum attained *total cover*, maximum cover of woody species (termed *woody cover*), mean number of species per sampled plot (*spe-*

cies number) and *rate of succession* expressed as mean annual change of dominant species cover (in % cover). The dominant species was defined as the single species with the highest cover in the respective year (see Prach et al. 1993 for details). Because of different sere durations, all these community characteristics were expressed for the first 12 years of succession, i.e. the period for which data were available in all seres. This approach is justified since the long-term course of succession is largely determined by successional development in the early years (Prach et al. 1997; Walker & del Moral 2003).

Statistical analysis

Vegetation records, based on species covers sampled in each year, were used as input data for a Canonical Correspondence Analysis (CCA) (ter Braak & Šmilauer 1998). Only species with at least 1% cover in at least one year were included; this yielded a matrix of 177 samples (stage/year records) and 247 species. Each vegetation record was characterized by age (years since the beginning of succession). Data on cover and age were log transformed. Age was included as the only explanatory variable and its significance was tested by the distribution free Monte Carlo test (1000 permutations). Environmental and community characteristics could only be used as passive variables, without any impact on the pattern of species or samples in the ordination diagram, because they characterized whole seres (not particular stages) or were derived from the vegetation data.

Those environmental and community characteristics that were significantly correlated with the mean sample (1-12 years) scores of each sere on the second CCA axis were used in multiple regression models. Community characteristics were the response variables, while environmental characteristics were the explanatory variables.

Because the regression models were multiplicative, i.e. they included interactions between the explanatory variables, significant interactions were analysed with simple slopes of one variable on another, to arrive at three specific values of the changing variable: mean and mean plus and minus its sample standard deviation (Quinn & Keough 2002).

The aim of each analysis was to determine the minimum adequate model where all explanatory variables and their interactions were significantly ($P < 0.05$) different from zero and from one another; all non-significant terms were removed. This was achieved by a step-wise process of model simplification, beginning with the maximal model (containing all explanatory variables and their interactions) and then proceeding with elimination of nonsignificant terms (through deletion tests from the maximal model) and retention of significant terms (Pyšek

Table 1. Survey of the 15 sites involved in the study with dominant species and years of their dominance since the onset of succession for which data were available.

Symbol	Site description	Coordinates	Sources	Important species
1. Ow	Wet old fields Bohemian Karst near Prague	49°54' N, 14°07' E	Osbornová et al. (1990) K. Prach, unpubl.	*Polygonum lapathifolium* 1; *Ranunculus repens* 2-5; *Arctium tomentosum* 7; *Petasites hybridus* 13-28; *Phragmites australis* 30-32.
2. Om	Mesic old fields Bohemian Karst near Prague	49°58' N, 14°12' E	Osbornová et al. (1990) K. Prach, unpubl.	*Glechoma hederacea* 1-2; *Brachypodium pinnatum* 8; *Arrhenatherum elatius* 15; *Crataegus* spec. div. 28-57.
3. Ox	Xeric old fields Bohemian Karst near Prague	49°57' N, 14°08' E	Osbornová et al. (1990) K. Prach, unpubl.	*Papaver rhoeas* 1; *Artemisia vulgaris* 4; *Agropyron (= Elymus) repens* 6-8.
4. Up	Urban ruderal sites, town of Plzeň, nutrient-poor, mineral soil	49°45' N, 13°23' E	Pyšek (1978)	*Chenopodium album* 1-3; *Sisymbrium loeselii* 4-5; *Melilotus alba* 6; *Tanacetum vulgare* 7-9; *Calamagrostis epigeios* 10-12.
5. Um	Urban ruderal sites, town of Plzeň, moderate in nutrients, mineral soil	49°44' N, 13° 22' E	Pyšek (1978)	*Chenopodium suecicum* 1-3; *Artemisia vulgaris* 4-11; *Salix caprea* 12.
6. Ur	Urban ruderal sites, town of Plzeň, rich in nutrients, organic soil	49°44' N, 13 22' E	Pyšek (1978)	*Chenopodium album* 1-3; *Ballota nigra* 5-6; *Urtica dioica* 4 and 7-10; *Sambucus nigra* 11-12.
7. Sh	Large spoil heaps from open-cast brown coal mining, NW part country dry sere on tops and slopes of hills	50°34' N, 13°37' E	Prach (1987) Hodačová & Prach (2003)	*Polygonum lapathifolium* 1-2; *Atriplex nitens* 6-7; *Carduus acanthoides* 8-12; *Tanacetum vulgare* 15-16; *Arrhenatherum elatius* 24-32; *Calamagrostis epigeios* 37;
8. Shw	Large spoil heaps from open-cast brown coal mining, NW part country wet sere in depressions	50°34' N, 13°37' E	K. Prach unpubl.	*Tussilago farfara* 2; *Typha latifolia* 5; *Phragmites australis* 14-38.
9. Eb	Exposed bottom of a destroyed water reservoir, NW part country	50°33' N, 13°32' E	K. Prach unpubl.	*Rumex maritimus* 1; *Carex gracilis* 2; *Juncus effusus* 3; *Calamagrostis epigeios* 4-12.
10. Sp	Sand pit abandoned after sand and gravel extraction, S part country	48°50' N, 14°56' E	K. Prach unpubl.	*Rumex acetosella* 2; *Pinus sylvestris* 4-24.
11. Pe	Peatland abandoned after peat extraction and drainage, S part country	49°03' N, 14°57' E	M. Bastl & K. Prach unpubl.	*Polygonum persicaria* 1; *Glyceria fluitans* 2-4; *Juncus effusus* 5-8; *Agrostis canina* 9; *Carex rostrata* 10-12.
12. Ds	Dumps around a newly constructed fishpond formed by sandy subsoil	49°03' N, 14°49' E	K. Prach unpubl.	*Molinia coerulea* 1-3; *Calamagrostis epigeios* 4-10. *Betula pendula* 11-15.
13. Dp	Dumps around a newly constructed fishpond formed by organic, peaty topsoil	49°03' N, 14°49' E	K. Prach unpubl.	*Galium palustre* 1-2; *Phalaris arundinacea* 3-14. *Alnus glutinosa* 15.
14. Bp	Bulldozed sites in areas of former *Picea abies* plantations deforested due to air pollution in mountains at NW border country, scraped sites with grass cover and topsoil removed	50°41' N, 13°35' E	Pyšek (1992) and P. Pyšek unpubl.	*Calamagrostis villosa* 1-6; *Deschampsia flexuosa* 10-15.
15. Bm	Bulldozed sites in areas of former *Picea abies* plantations deforested due to air pollution in mountains at NW border country, mounds formed by dumped material	50°41' N, 13°35' E.	Pyšek (1992) and P. Pyšek unpubl.	*Calamagrostis villosa* 1-15.

et al. 2005). To prevent biases to model structures caused by correlation between variables, we simplified by a backward elimination from the maximal models using step-wise analysis of deviance tables (Crawley 1993). In this way the results were not affected by the order in which the explanatory variables were removed in the step-wise process of model simplification.

Because the explanatory variables were measured on different scales, they were standardized to zero mean and unit variance to achieve comparable influence for all. The interactions among the explanatory ones were then analysed on centred variables. Using the standardized values, collinearity of the explanatory variables was checked with a matrix of correlation coefficients and by calculating tolerance values. To achieve the latter, the regression of the explanatory variable in question

Table 2. Successional seres studied and their environmental and community characteristics. See Table 1 for further details. Soil characteristics relate to the beginning of succession, community characteristics (cover, species number, rate of succession) are expressed for the first 12 years (see text for details). The rate of succession was expressed as average annual change of dominant species cover (in %) during the first 12 years of succession.

Sere	Code	Duration [yrs]	Altitude [m a.s.l,]	Mean annual temperature [°C]	Mean annual precipitation [mm]	pH (H$_2$O)	Conductivity [μS.cm^{-1}]	Ca [ms/1000 g]	Mg [ms/1000 g]	N- total [%]	N-NH$_4$ [mg/1000 g]	N-NO$_3$ [mg/1000 g]	C- total [%]	C:N	PO$_4$ [mg/1000 g]	Maximum total cover [%]	Maximum cover of woody species [%]	Mean species number per plot	Rate of succession [% per year]
Wet old fields	Ow	32	200	8.5	525	7.7	104	4007	98	0.44	1.05	1.42	2.2	8.1	0.23	93	0.0	18.8	24.1
Mesic old fields	Om	57	371	7.5	575	7.8	138	3980	81	0.31	1.14	0.84	3.1	9.4	0.21	90	16.0	22.0	14.2
Xeric old fields	Ox	76	249	8.5	475	7.4	95	3122	69	0.24	1.35	1.24	3.7	9.1	0.20	90	0.0	38.8	17.2
Urban sites – poor[1]	Up	12	338	7.5	525	7.9	454	3945	288	0.09	1.15	0.26	2.9	14.0	0.27	98	0.2	23.9	27.2
Urban sites – moderate[2]	Um	12	338	7.5	525	7.8	718	7597	314	0.20	1.70	0.97	4.8	18.3	0.12	98	22.0	20.6	26.1
Urban sites – rich[3]	Ur	12	338	7.5	525	7.5	507	6035	174	0.32	1.95	0.70	5.4	15.9	0.16	91	18.0	19.9	18.7
Spoil heaps[4] – dry	Sh	38	277	7.5	625	7.5	313	780	592	0.16	3.58	18.4	2.5	15.6	0.08	42	0.0	12.4	8.2
Spoil heaps[4] – wet	Shw	38	277	7.5	625	7.5	313	780	592	0.16	3.03	9.06	2.5	15.6	0.13	55	0.0	10.5	9.3
Exposed bottom[5]	Eb	12	242	7.5	625	4.3	1855	4038	702	0.96	0.95	0.52	10.7	11.2	0.12	91	22.0	6.7	12.9
Sand pit	Sp	24	471	7.5	675	5.3	18	31	5	0.04	0.02	0.09	0.5	10.2	0.01	43	34.0	5.8	2.3
Extracted peatland	Pe	12	446	7.5	625	4.0	256	1373	231	1.84	0.30	1.20	47.5	25.8	0.03	38	1.9	7.0	1.8
Dumps[6] – sandy	Ds	15	426	7.5	625	4.8	167	90	34	0.04	0.03	0.11	0.4	9.3	0.02	88	29.0	16.4	16.1
Dumps[6] – organic	Dp	15	426	7.5	625	4.7	91	168	24	0.39	2.63	0.13	4.5	11.6	0.20	91	20.0	14.5	11.8
Bulldozed plots[7]																			
– without top soil	Bp	20	837	5.5	950	4.9	43	58	9	0.16	1.87	0.12	3.3	20.7	0.01	76	2.0	14.6	1.6
– dumped material	Bm	20	834	5.5	950	4.8	81	1856	28	0.56	4.34	3.23	11.2	20.0	0.56	77	0.1	13.2	1.8

[1] On mineral substrata poor in nutrients such as industrial waste; [2] On mixed, mineral and organic substrata; [3] Nutrient rich sites on organic substrata; [4] Large-scale spoil heaps from brown coal mining; [5] Exposed bottom of a destroyed water reservoir; [6] Dumps around a newly constructed fishpond; [7] Reclaimed sites in areas of former *Picea* plantations deforested due to air pollution, with two distinguished seres: on bulldozed plots with top soil removed, and on mounds formed by the removed soil.

was compared against all of the remaining explanatory variables in the model. The tolerance values for each explanatory variable were considered unacceptably low if their values in the expression $1-r^2$ (where r^2 is the variance explained by the remaining explanatory variables) were < 0.1. The number of correlated variables was reduced by principal component analysis (PCA). To decide which PCA scores should be used for the reduction, we extracted unrotated components from the original explanatory variables, and evaluated their communality values and the total variance, explained by the individual axes of their PCA (Quinn & Keough 2002).

The appropriateness of the models was checked by plotting standardized residuals against fitted values and by normal probability plots (e.g. Crawley 1993). Their explained variance was expressed by r^2 based on mean squares, instead of sum of squares as with the usual r^2 (Quinn & Keough 2002). Larger values of these adjusted r^2 indicated better fits, taking into account sample sizes and the numbers of predictors. To check for outliers, the points with the largest influence on minimal adequate models were assessed by Cook's (1977) distances. Data points with the largest Cook's distances were sorted in a descending order and weighted out of the analysis one after another. The models were re-fitted after weighting out each data point, and the points causing a significant change in deviance were considered as outliers (Gilchrist & Green 1994; Jarošík et al. 2002). The calculations were performed in software packages GLIM version 4 (Francis et al. 1994), SPSS version 13 (PCA; Anon. 2005) and CANOCO (CCA; ter Braak & Šmilauer 1998).

Results

Pattern of succession in studied seres

The first CCA axis ($\lambda_1 = 0.443$) reflected the development of particular seres over time (Fig. 1). The Monte Carlo permutation test for the first axis was highly significant ($P = 0.001$, $F = 7.552$). Among the environmental characteristics (Table 2), only pH, mean annual temperature, precipitation and altitude were significantly correlated with the mean sample scores of each sere on the second axis ($\lambda_2 = 0.828$). Therefore, these characteristics influence the pattern of vegetation development during the course of succession. The following community characteristics were correlated with the second axis: species number, rate of succession, total cover and woody cover (Fig. 1).

The seres were separated into two clusters reflecting their ruderal and non-ruderal status. The non-ruderal seres are associated with acidic substrata at higher altitudes in cooler and wetter regions and tend to have higher cover of woody species, lower total cover, a lower number of species and a slower rate of succession. No pattern was seen between primary and secondary seres (see Prach et al. 2001).

Effect of abiotic conditions on community characteristics

The three explanatory variables related to environmental conditions (altitude, temperature and precipitation) were strongly correlated: the range of absolute values of standardized Pearson's correlation coefficients was $r = 0.88$-0.97, that of tolerance values = 0.03-0.08. However, in the PCA, the first axis of precipitation, altitude and temperature in total explained 95% of the variance, while extracted components accounted for 0.91-0.98 of the variation. Thus, removing highly correlated variables of altitude, precipitation and temperature, and replacing them with a single uncorrelated variable, characterizing the climate by the PCA factor scores, reduced the total variance explained by altitude, precipitation and temperature by only 5%. The scores increased with increasing altitude (factor loadings = 0.96) and precipitation (loadings = 0.99), but decreased with increasing temperature (loadings = –0.98). Therefore, increasing scores can be interpreted as changes in climate with increasing altitude.

The original explanatory variables of altitude, precipitation and temperature were much less correlated with pH ($r = 0.45$-0.59; tolerance = 0.26) and, subsequently, there was much less correlation of pH with the climate score ($r = -0.54$; tolerance = 0.71). Hence, pH can be here thought of as an explanatory variable characterizing habitat conditions independently of climate.

The regression slopes of response variables on factor scores are usually complicated because the factor scores themselves are often difficult to interpret (e.g. Rawlings et al. 1998). Also in our case, the regression slopes for temperature, precipitation and altitude slightly differed, hence the PCA scores that are linear combinations of the three variables do not exactly correspond to a regression on any of them. However, because all three variables are easily interpretable as a change in climatic conditions from lowlands to mountains, the regression slopes of response variables on factor scores can be well interpreted, as is usually the case when factor scores reflect the effect of meteorological factors (Jarošík & Dixon 1999). With this in mind, it can be concluded that only species number ($F = 8.93$; $df = 3$, 11; $P = 0.003$; $r^2_{adjusted} = 0.76$) and the rate of succession ($F = 12.04$; $df = 1$, 13; $P = 0.004$; $r^2_{adj.} = 0.51$) were significantly affected in this analysis by the environmental site conditions (Fig. 2) but not total cover ($F = 1.33$; $df = 3$, 11; $P = 0.3$) nor woody cover (F
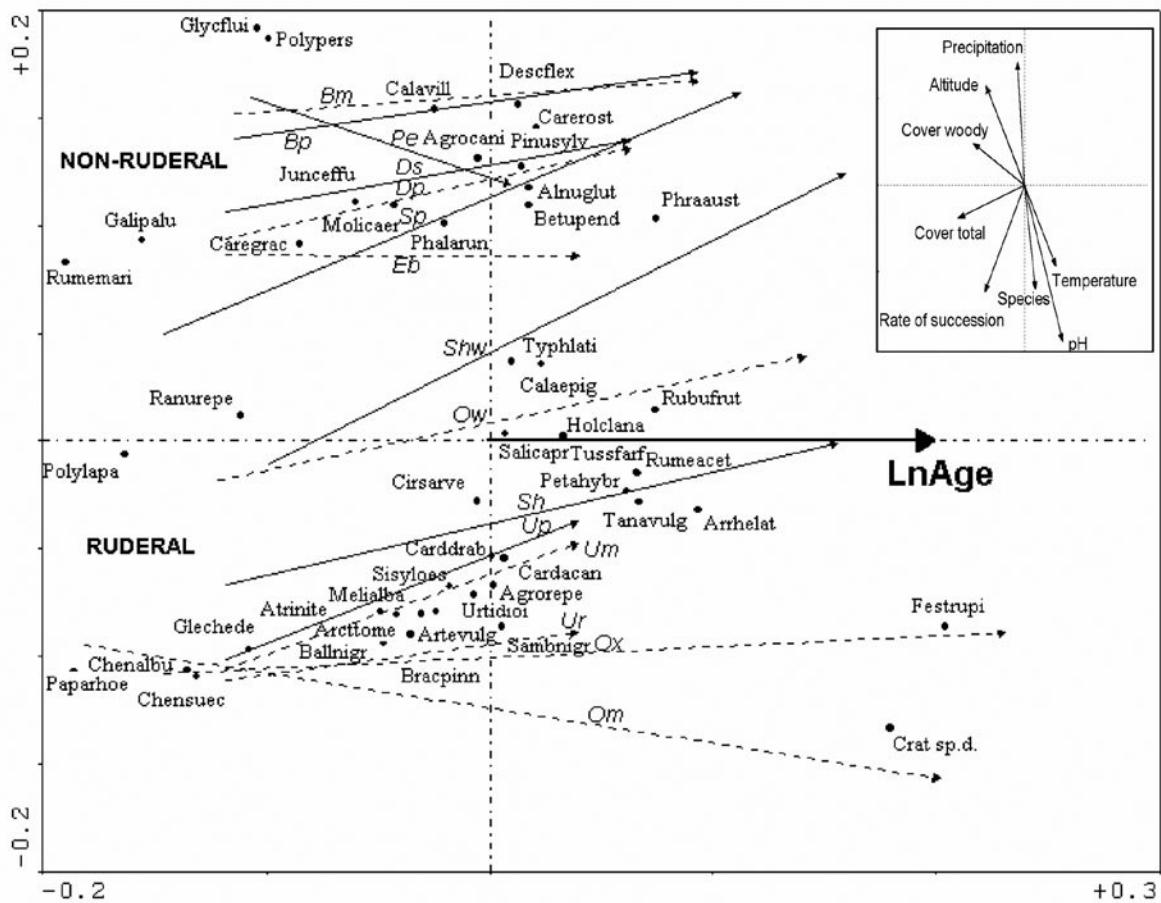
Fig. 1. Scheme of vegetation succession in central European man-made habitats based on CCA. Dashed arrows indicate *a priori* defined secondary successional seres, solid arrows indicate primary seres. Codes of seres (see Table 1) are shown. Arrows indicating the direction of succession in particular seres were fitted by connecting centroids of vegetation records from years one to five with positions of records representing the oldest stage in a given sere. The centroids from the first five years were considered to better represent the initial stages than year one because of a high variation in species composition and fluctuations usually associated with low cover in the first years of succession. Position of dominant species, abbreviated by first letters of generic and species name, is indicated (see text). Environmental and community characteristics significantly correlated with the second axis are displayed as pas□

= 1.84; df = 3, 11; P = 0.2).

Climate affected the species number differently on acid (Fig. 2A) and alkaline (Fig. 2B) soils [deletion test on interaction (climate) × (pH): F = 13.20; df = 1, 12; P = 0.003]. The effect was non-significant (F = 1.82; df = 1, 12; P = 0.2) on acid soils (mean pH plus s.d.), but highly significant (regression slope ± SE of species number on climate scores: –24.31 ± 6.68; F = 13.26; df = 1, 12; P = 0.003) on alkaline soils (mean pH minus s.d.). The non-significant result obtained for acid soils was not affected by the two climatically different mountainous seres in areas of former *Picea* plantations (Bp & Bm, Fig. 2A). These seres had small Cook's distances (Bm = 0.08, Bp = 0.03, compared to the largest Cook's distance

= 1.01 for xeric old fields; Ox) and thus small influence on the statistics. Therefore, there was no change in species numbers on acid soils regardless of the character of climate.

The rate of succession was significantly faster in lowland than mountain climates (regression slope of the rate of succession on climate scores: –6.12 ± 1.76; F = 12.04; df = 1, 14; P = 0.003) (Fig. 2C). Climatically different mountain seres on acid soils, Bm and Bp (see Table 1 for codes), had the largest influence on the statistics (Cook's distances: Bm = 0.17, Bp = 0.15). After deleting these seres, the regression slope indicated a highly significantly (t = 6.10; df = 13; P = 0.00004) faster decrease in the rate of succession (–16.88 ± 4.67;
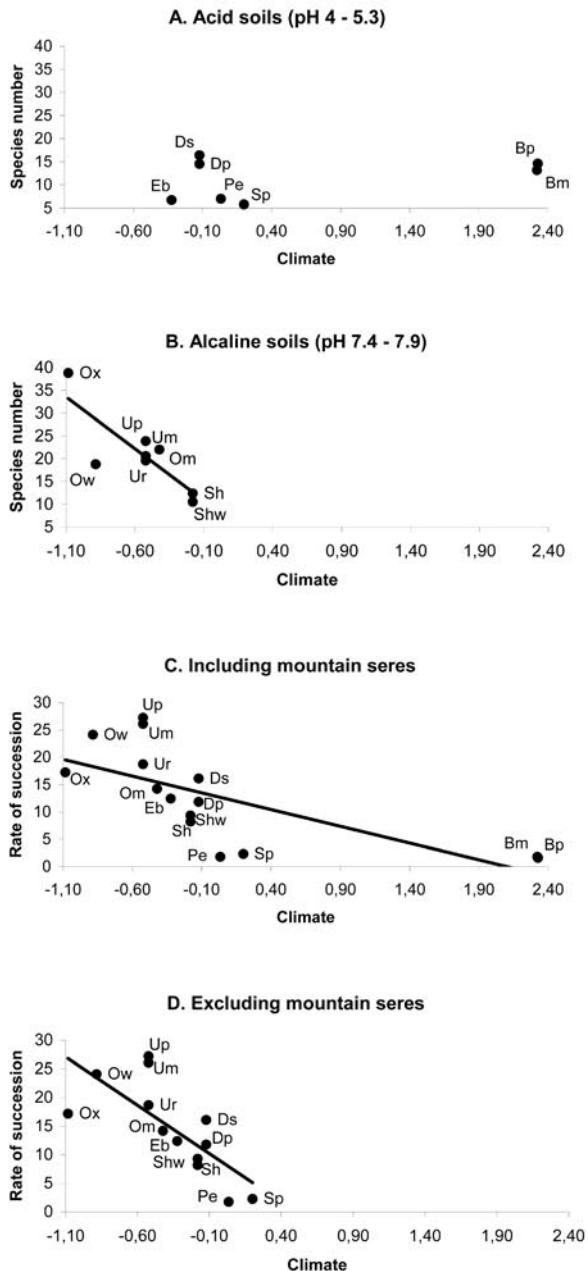
Fig. 2. The effect of climate on species numbers (**A**, **B**) and the rate of succession (**C**, **D**). Climate is defined by PCA scores along the first component and can be interpreted as climatic change with increasing altitude. Lines indicate statistically significant relationships, described in the text. Codes of seres are as in Table 1. The rate of succession was expressed as mean annual change of dominant species cover (in %) during the first 12 years of succession.

$F = 13.07$; $df = 1, 10$; $P = 0.005$) (Fig. 2D). There was no significant effect of pH on the rate of succession, neither direct ($F = 0.31$; $df = 1, 12$; $P = 0.6$) nor in the interaction with climate ($F = 1.60$; $df = 1, 12$; $P = 0.2$).

Discussion

Environmental variables and vegetation pattern

The most important environmental variables differentiating successions in central European human-made sites appear to be soil pH and macroclimate. The pH of the substratum, temperature, precipitation and altitude were the only environmental variables significantly correlated with vegetation pattern in the course of succession in our systems. The importance of pH in determining the pattern of vegetation has been well described (Ellenberg 1988). However, most successional studies dealt with changes of pH over time (Bazzaz 1996) and pH was only rarely studied as a factor determining successional pattern across stages of the same age (Christensen & Peet 1981). Instead, soil nitrogen and its forms were usually considered as the most important factor (Tilman 1988; Wilson & Tilman 2002). However, in our analyses, none of the nitrogen forms had a significant effect on vegetation pattern when community characteristics were regressed on the nitrogen forms with a significance assessed by the experiment-wise error rate based on the Dunn-Sidák method (Ury 1976; Sokal & Rohlf 1995). None of these forms significantly correlated with pH (Pearson's two-tailed correlation coefficient on standardized values). Our results do not allow any causal explanation of the fact that pH significantly influenced the successional pattern while nitrogen did not. Large-scale experiments are needed to explain these findings. For discussion on the relationships between soil characteristics see, for example, Stevenson et al. (1999).

The role of macroclimate in determining vegetation pattern is also well understood (Box 1981), but the conclusions regarding its influence on the course of succession remain largely speculative, because of the lack of directly comparable data (Walker & del Moral 2003, pp. 262-266, but see recent papers of Otto et al. 2006 and Dovčiak et al. 2005). Besides the expected direct effect on species establishment, macroclimate influences vegetation succession through the regional species pool (Settele et al. 1996), which was not directly evaluated in this study. However, it is generally known that ruderal species in central Europe are more frequent in warmer lowlands than in the uplands and moreover they prefer higher pH (Ellenberg et al. 1991). This may be the main explanation of the separation of ruderal and

non-ruderal seres (see Prach et al. 2001).

In our set of seres, there were either alkaline or acidic substrata but none between pH 5.5-7.0. However, we included all seres which were available in sufficient number of representative stages in the territory at that time. Still, the set represents the highest number of seres ever analysed in one study (Walker & del Moral 2003). In addition, the range of pH is more crucial for determining the reliability of this response variable than is the distribution of its values. This is so because the standard error of the response variable decreases with the increasing ranges of the explanatory variable, which increases the reliability of the response variable. Moreover, the reliability of the explanatory variable increases by having lots of measurements at the extreme left-hand and right-hand ends of the range of the explanatory variable, and fewer at the middle (e.g. Crawley 2002, pp. 66-68), which is exactly the case for the range of pH values in our study. Thus, the missing values in the middle of the pH range do not invalidate our analysis. Moreover, no alkaline substrata occur at high elevations (no limestone or other alkaline bedrock present) in the considered geographical area. The absence of alkaline pH at high elevations does not necessarily mean confounding of pH with climate. However, because the significant effect of interaction between climate and pH on species number appears only on alkaline soils at low elevations, while no significant interaction was recorded on acidic soils throughout the whole range of altitude, we cannot completely exclude the possibility that the presence of the interaction between climate and pH on alkaline soils may be just a consequence of the absence of alkaline substrata at high elevations.

Climate and pH as determinants of succession

On the temperate sites explored in our study, the number of plant species was higher in successional seres with higher pH and in drier and warmer climates. The rate of succession, expressed as the rate of species replacement, increased only towards the drier, warmer climates. Nevertheless, the decrease in the rate of succession with increasing climate harshness, i.e. cold, became more profound after weighting out the two mountain seres on acidic soils. This indicates that acid soils could be a constraint to species replacement. However, in our data set, pH did not directly affect the rate of succession. Species replacement is a different process than the increase in species numbers. The lower dependence of species replacement on soil pH, compared to species numbers, may result from species replacement (hence the rate of succession) being more responsive to biotic factors, interspecific competition in particular, while the higher species numbers over succession are more determined by abiotic conditions of a site. It is generally known that acidic soils harbour fewer number of species than neutral and slightly alkaline ones (Ellenberg 1988). The metric used for measuring the rate of succession is limited in its sensitivity, as it does not account for changes in the flora as a whole. A previous study has shown (Prach et al. 1993) that measure of the rate of succession based on dominant species reflects the dynamics of succession and makes it possible to relate it to environmental factors. The effects of stress on succession rate using a space/time substitution method were recently discussed by del Moral & Ellis (2004) who found declining species richness and rate of succession with elevation.

The lack of significant effects of pH and climate on total cover and woody cover in the regression models may be explained by the fact that no really extreme site was included. Moreover, establishment of woody species is largely determined by sources of diaspores and seed rain, local site moisture and direct competition from the herb layer (Dovčiak et al. 2005), which were not investigated in this study and may overwhelm the influence of pH and macroclimate.

The increasing extent of man-made habitats throughout the world accentuates the understanding of the importance of spontaneous ecological succession as a tool of ecologically sound restoration. The approach used here, i.e. to compare a number of seres, can contribute not only to our understanding of succession, but also may help restoration projects predict vegetation change, because the controlling environmental variables are easy to measure and substratum pH can be manipulated (Prach et al. 2007).

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