

Early succession on plots with the upper soil horizon removed

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Abstract. Succession was studied on plots with the upper soil horizon removed in an area affected by acidic air pollution in the Krušné Hory Mts., Czech Republic. 10 permanent 1-m² plots were marked and vegetation recorded annually using a grid of 100 subplots from 1989 to 1995. Constrained ordination analyses showed that soil texture is the most important environmental factor influencing the course of succession. Its effect on species composition increases with successional age of the plant community. On fine-grained soils species-poor communities dominated by grasses (*Calamagrostis villosa*, *Deschampsia flexuosa*) and on coarse-grained soils species-rich communities dominated by heather (*Calluna vulgaris*) developed. Succession proceeded from communities where species composition was determined by diaspore availability towards communities where species composition depended on environmental conditions. Successional communities after 10 yr are more dependent on soil characteristics and consequently environmental determination increases over the course of succession and causes the communities to diverge.

Keywords: Convergence; Divergence; Krušné Hory Mts.; Redundancy Analysis; Soil texture.

Nomenclature: Rothmaler (1976).

Introduction

The factors affecting the course of succession and convergence/divergence in successional development have been studied for a long time (e.g. Clements 1916; McCune & Allen 1985; Prach 1985; Boerner 1988; Inouye & Tilman 1988). Chance or historical factors such as variation in the weather, disturbance intensity, and colonization potential are more important at early successional stages, whereas the importance of site characteristics usually increases with successional age (Christensen & Peet 1984; McClanahan 1986; Tsuyuzaki 1989; McLendon & Redente 1990; Myster & Pickett 1990; Lepš & Rejmánek 1991). Climatic variation is particularly important in early stages of succession on rough substrates (e.g. Tsuyuzaki et al. 1997; Titus & del Moral 1998).

Repeated observations on permanent plots are among the most useful tools, not only for the study of succession, but also for investigating competitive relationships

(Herben 1996). Although experiments are the only reliable tools for demonstrating mechanisms (Goldberg 1995; Lepš 1995; Lepš et al. 1999), repeated observations of permanent plots provide insights into the dynamics of population processes and are probably the most reliable tools to demonstrate convergence/divergence during succession. Recent developments in multivariate methods, particularly in constrained ordination (ter Braak & Prentice 1988; ter Braak & Šmilauer 1998), provide ecologists with powerful tools for testing various hypotheses where the tests can be tailored according to the design of the observations (including repeated measurements).

During the 1980s, extensive areas in Central Europe experienced forest decline (Kubíková 1991). The Krušné Hory Mts. in NW Bohemia, Czech Republic were among the most heavily damaged areas where many km² of spruce forest (both native and planted *Picea abies*) died off. One of the remediative measures taken was to replant *P. abies* and, to a lesser extent, *P. pungens*, in so called 'bulldozer plots'. The upper part of the soil profile, roughly the humus horizon (A), usually ca. 10 cm deep, was removed by heavy machinery and spruce seedlings were planted directly into the eluvial (E) or spodic (B) horizons. The aim of the procedure was to remove the acidified upper soil and also to prevent competition from grasses, particularly *Calamagrostis villosa*. This method was rarely successful for the re-establishment of trees, but provided an opportunity for the study of succession on a mineral horizon which had developed from weathered granite. Thus, the succession started from bare plots, with the humus horizon removed. Nearly all germinable seeds and rhizomes able to regenerate vegetatively were removed with the humus horizon. As the soil removal procedure differed in severity between sites, as do parent rock characteristics, the plots enabled the testing of the effect of various soil conditions on the course of successional development.

The aims of this study are: 1. To characterize the course of succession on disturbed soil. 2. To test for differences in successional development caused by environmental differences. 3. To compare environmental determination of plant communities during succession.

Study area

The study was conducted in the southwestern part of the granitic Krušné Hory Mountains (Ore Mts., Erzgebirge), 50°23'N, 12°38'E. The region has a cold climate with a mean annual temperature of 4.5 °C and annual precipitation of ca. 1100 mm (Böer & Vesecký 1975). Study sites were located in a forested area heavily impacted by acid deposition, at an elevation of approximately 930 m above sea level in two areas where the topsoil had been removed, Rolavský vrch and the Jelení potok stream valley. These two sites are located < 1 km from each other. Before forest dieback the area was covered by natural and semi-natural spruce forests. The most common soil types in the area are podzols and pseudogleys (Němeček & Tomášek 1983). All of the plots are located on the podzol that developed on deeply weathered coarse-grained granite. After the bulldozer treatment (i.e. after removing the upper soil layers), soil conditions differed mainly by the depth of destruction of the upper part of the soil profile. Soil profiles are now characterized by the absence of organic horizons and the occurrence of a more or less developed hardpan (an impermeable horizon cemented by iron oxides) at various depths (from 30 cm to more than 1.5 m) within the B horizon.

Material and Methods

Sampling

In 1989, seven permanent 1 m × 1 m plots were established on a gentle slope (<4°) in the valley of the Jelení potok stream, and three permanent plots on the plateau of the Rolavský vrch hill. By 1989, it had been 1, 2 or 3 yr since topsoil removal. Plots were established so that they were located in unvegetated areas between spruce seedlings. In some cases, however, they were eventually slightly influenced by the growing spruce saplings. The vast majority of saplings had not reached breast height by the seventh year after planting, and in many cases had either died or remained between 0.5 - 1.0 m in height and consequently did not influence the plots. Plots were censused each year (with the exception of 1993) from 1989 to 1995. For the analysis, the 1 m × 1 m plots were further divided into a grid of 100 0.1 m × 0.1 m subplots, and the cover of each species was estimated in each subplot. This enables very precise estimates of cover in the 1 m × 1 m plots. In this way, we obtained 60 'relevés' (10 plots sampled repeatedly in six years), each based on 100 subplots. All analyses were carried out with the same set of 60 relevés.

Soil samples were collected in 1998. Soil texture

was determined after destruction of the organic matter and chemical dispersion by wet sieving (fraction of soil particles either >2 mm or >0.1 mm). The results are based on means of five soil cores close to each plot. In each soil profile, depth and thickness of the hardpan were recorded.

Data analysis

Both unconstrained and constrained ordinations were used to analyse the dependence of species composition on successional time and environmental characteristics using CANOCO for Windows package (ter Braak & Šmilauer 1998). Principal component analysis (PCA) and Redundancy analysis (RDA), ordination methods based on the assumption of a linear response were used because the data set was relatively homogeneous. (We first carried out DCA with Hill's scaling (see ter Braak & Šmilauer 1998) and observed that the lengths of the 1st and the 2nd DCA-axes were 2.8 and 2.3 respectively, which permits the use of linear methods.) In all the analyses, centring by species and no standardization by samples were used. In PCA, environmental data were fitted *ex post* to the PCA ordination axes. Note that the unconstrained and constrained analyses are complementary: in PCA, axes are first extracted purely on the basis of species composition, and are then correlated with environmental variables; whereas in RDA, the axes are extracted to maximize the species-environment correlation. Consequently, PCA axes correspond to the dominant gradients in species composition and RDA axes to gradients in species composition best correlated with measured environmental variables. RDA was followed by variance partitioning (ter Braak & Šmilauer 1998: 261), a procedure that enables one to ascribe the explained variability to particular variables.

Besides successional age, the following environmental characteristics were used: depth to the top of the hardpan, hardpan thickness and percentage weight of particles >2 mm (fraction >2), between 0.1 mm and 2 mm (fraction 0.1-2), and <0.1 mm (fraction <0.1) in the top 5 cm of soil. In coarse-grained soils the fraction >2 mm was nearly 50%, whereas in fine grained soils it was 17%. The fraction < 0.1 mm reached 36% in fine grained soil, whereas in coarse grained soils was only 20%. We conducted forward selection with all of the above variables; successional time and fraction <0.1 mm were the only significant explanatory variables. Thus, all of the other analyses were carried out with these two variables only.

In constrained ordinations various combinations of explanatory variables (environmental variables in CANOCO terminology), including their interactions and covariables, are used. Our data are in the form of

repeated observations. Within the framework of constrained ordinations, combinations of explanatory variables and covariables followed by an appropriate Monte Carlo test (i.e. with a permutation scheme adjusted to the repeated measurement design, see ter Braak & Šmilauer 1998: 106) enable testing of particular effects in a way directly comparable to repeated measures ANOVA. Whenever within plot effects are of interest (e.g., temporal changes, interaction of time with environmental characteristics), the identity of the plot (coded as several dummy variables) was used as a covariable. Various combinations of environmental variables and covariables enabled the testing of specific hypotheses. Analyses are numbered consecutively and their results are summarized in Table 1.

Percentage of particles <0.1 mm effectively characterizes soil texture and reflects the gradient from fine-grained soils, characterized by a high proportion of particles <0.1 mm, to coarse-grained soils. We prepared contour plots for changes in cover of the most important species, total cover and species richness, in relation to successional age and percentage of particles <0.1 mm. Firstly, data were smoothed by a LOESS smoother (locally weighted regression smoothing) and the resulting function was displayed using contour plots. Calculations and plots were carried out using S-plus software (Anon. 1995).

To learn whether determination of species composition by soil characteristics increases or decreases during succession, we carried out separate RDA analyses for plots of the same age with the fraction <0.1 mm being the only explanatory variable and compared the fit between particular successional ages.

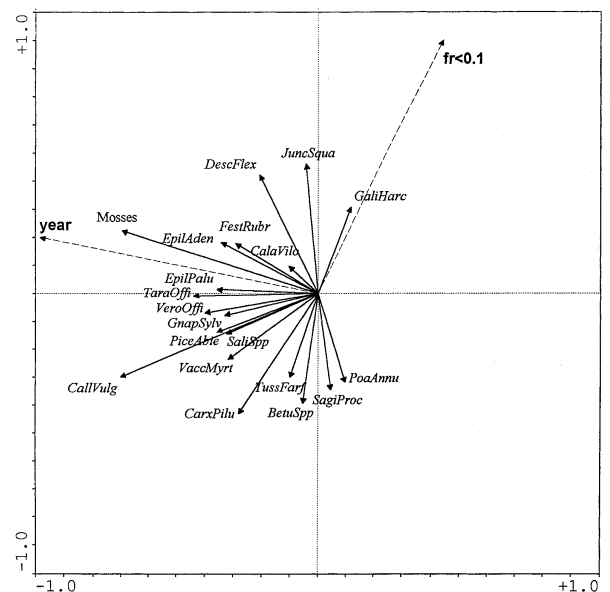
Results

In analyses of changes in species composition we first attempted to explain general patterns in species dynamics. Both the PCA (Analysis 1 in Table 1) and RDA (Analysis 2) show the same general pattern. A high value of species-environment correlation on the first PCA and RDA axes, and a similarity in patterns in the ordination diagrams reveal that the two variables are dominant determinants of species variation in our data set. Because of the similarity only RDA results are displayed (Fig. 1). The increase in total moss cover with successional age is relatively independent of the fraction of particles <0.1 mm, *Calluna vulgaris* increases with time on coarse-grained soils, whereas *Deschampsia flexuosa*, *Calamagrostis villosa* and *Juncus squarrosus* increase mainly on fine-grained soils. Many species show patterns similar to *Calluna vulgaris*, i.e. they increase in, or are associated, with coarse-grained soils.

Table 1. Summary of results of ordination analyses; 1: PCA; 2-5: RDA. *r* is species-environment correlation on the first axis, %-1st axis is percentage of species variability explained by the first axis, %-all constrained is percentage of species variability explained by all the constrained axes, *F*-trace is the value of the overall *F*-statistic and is the corresponding probability level obtained by the Monte Carlo test. Year is age of the plots, Fr0.1 is fraction of soil particles <0.1 mm; *P* in analyses 2-5 = 0.002; no values for Analysis 1.

	Explanatory variables	Covariables	<i>r</i>	%-1st axis	%-all constr.	<i>F</i> -trace
1	Yr, Fr0.1	none	0.783	46.9	-	-
2	Yr, Fr0.1	none	0.806	29.8	40.0	18.99
3	Yr	PlotID	0.875	45.6	45.6	41.13
4	Yr, Yr*Fr0.1	PlotID	0.881	46.1	56.2	30.74
5	Yr*Fr0.1	PlotID, Yr,	0.796	19.4	19.4	11.52

The main goal of this analysis was to visualize the trends (not to perform statistical tests) so consequently, the repeated measurement nature of the data was neglected. Variance partitioning revealed that of the 40% of variability explained by year (successional age) and soil texture together, 26% can be ascribed solely to year, 11% to soil texture and 3% is the shared effect.



BetuSpp	<i>Betula</i> spp.	JuncSqua	<i>Juncus squarrosus</i>
CalaVilo	<i>Calamagrostis villosa</i>	PiceAbie	<i>Picea abies</i>
CallVulg	<i>Calluna vulgaris</i>	PoaAnnu	<i>Poa annua</i>
CarsPilu	<i>Carex pilulifera</i>	SagiProc	<i>Sagina procumbens</i>
DescFlex	<i>Deschampsia flexuosa</i>	SaliSpc	<i>Salix</i> spp.
EpilAden	<i>Epilobium adenocaulon</i>	TaraOffi	<i>Taraxacum officinale</i>
EpilPalu	<i>Epilobium palustre</i>	TussFarf	<i>Tussilago farfara</i>
FestRubr	<i>Festuca rubra</i>	VaccMyrt	<i>Vaccinium myrtillus</i>
GaliHarc	<i>Galium hircynicum</i>	VeroOffi	<i>Veronica officinalis</i>
GnapSylv	<i>Gnaphalium sylvaticum</i>		

Fig. 1. Ordination biplot of analysis 1 (species = full arrows and environmental variables = dashed arrows).

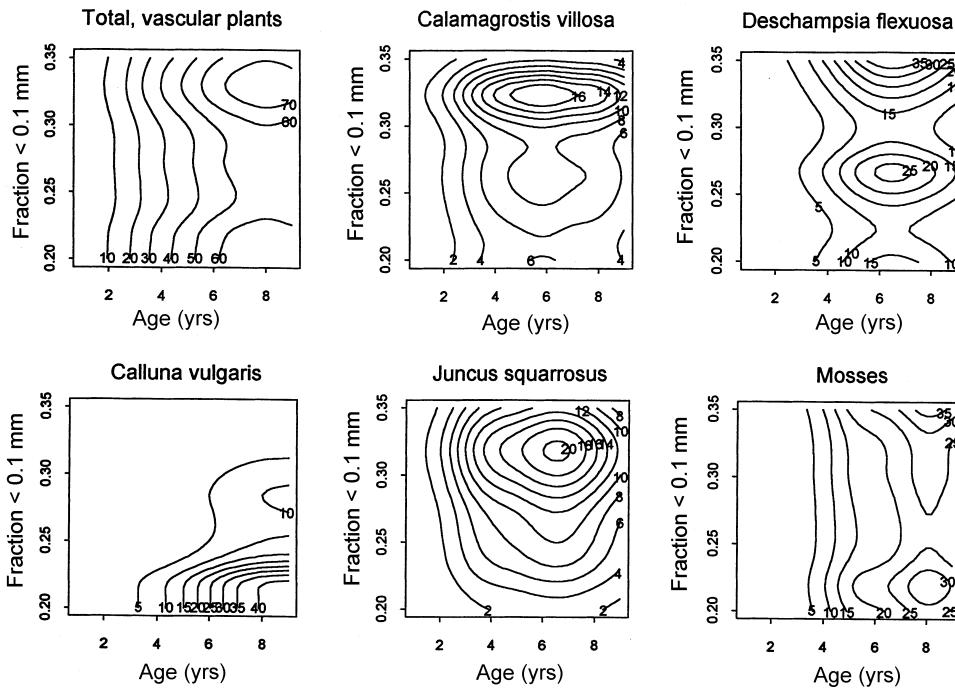


Fig. 2. Contour plots displaying temporal changes in total cover, cover of the four dominant vascular plant species and cover of mosses in relation to soil texture. Texture is expressed as weight proportion of particles < 0.1mm. Age is time since upper soil horizon removal. The data were initially smoothed by a LOESS smoother and then displayed.

In all subsequent analyses (3 to 5 in Table 1) significance tests were of primary interest, and thus plot identity is used as a covariable, and the tests correspond to repeated measures ANOVA.

Analysis 3 shows that there is a clear successional trend, common to all the plots. In analyses 4 and 5, the effect of soil texture (expressed by fraction < 0.1mm) on the course of succession was tested. From these analyses it is clear that the effect of soil texture is less pronounced than the effect of successional age, but is still highly significant, explaining nearly 20% of between-plot variability in successional development.

Species positively correlated with *Calluna*, increase with time on coarse-grained soils and form relatively species-rich communities. The other three dominant

species, *C. villosa*, *D. flexuosa* and *J. squarrosus*, are negatively correlated with this group and develop with successional age into relatively species-poor communities on fine-grained soils. Cover of both vascular plants and mosses (Fig. 2), and species richness (Fig. 3) increase with succession. The increase in cover is relatively independent of soil texture, but the increase in species richness is fastest in coarse-grained soil plots, dominated by *Calluna vulgaris*, and is considerably slower in fine-grained soil plots with high cover of *C. villosa*, *J. squarrosus* and *D. flexuosa* (Figs. 2 and 3).

Separate analyses for plots of the same age (Table 2)

Table 2. Results of RDA analyses with a single explanatory variable, fraction of soil particles < 0.1 mm, for sets of plots of the same successional age. *N* is the number of plots analyzed, *r* is species-environment correlation on the first axis, %-explained is variability in species composition explained by the explanatory variable, *F* is the value of the F-statistic and *P* is the corresponding probability level obtained by the Monte Carlo test.

Age	<i>N</i>	<i>r</i>	%-explained	<i>F</i>	<i>P</i>
3	10	0.705	17.5	1.70	0.15
4	10	0.738	21.8	2.23	0.06
6	9	0.853	30.4	3.06	0.05
8	8	0.840	34.4	3.14	0.03

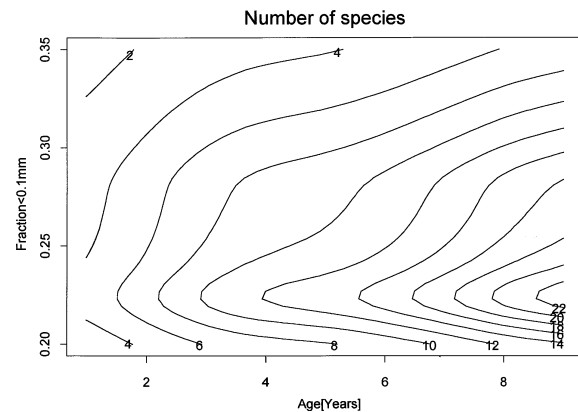


Fig. 3. Contour plot displaying temporal changes in species richness in relation to soil texture. Texture is expressed as weight proportion of particles < 0.1mm. Age is time since upper soil horizon removal. The data were initially smoothed by a loess smoother and then displayed.

show that all the characteristics of the fit (species-environment correlation on the first axis, percentage of the variability explained by the environmental variable, F -statistic, and the corresponding probability level) increase with successional age. Because no data were collected in 1993 and plots differed in age at the beginning of the study, 10 plots of the same age were not available for some ages, and subsets of eight or nine plots were used. However, all the characteristics show a concordant result and, in particular, significance increases (i.e., the probability level decreases) even though a decrease in power of the test is expected with the decreasing sample size. Thus, we can conclude that the determination of species composition by soil texture increases over the course of succession.

Discussion

Soil water regime is determined principally by soil texture and the occurrence and thickness of the impermeable horizon (Jenny 1980). The hardpan determines the duration of waterlogged conditions, which occur mainly during spring snowmelt. The proportion of fine soil particles is an important determinant of water availability in the soil, which plays an important role over the entire growing season, particularly during summer. Summer drought is probably the more serious of the two stresses and may be the reason why soil texture is more important than depth of the hardpan for influencing the course of succession and the resulting community composition. Sites with coarse-grained soils are more moisture stressed and it appears that this maintains more gaps in the community. Because of these open areas the coarse-grained soil plots are more species-rich, harbouring species such as *Carex pilulifera*, *Veronica officinalis*, *Poa compressa*, *Tussilago farfara*, *Luzula multiflora* and *Sagina procumbens*. The recruitment and survival of these species is suppressed at plots with fine-grained soil by increasing cover of the competitive grasses *Calamagrostis villosa* and *Deschampsia flexuosa*. We found strong dominants both on coarse (*Calluna vulgaris*) and fine-grained soils (*Calamagrostis villosa*, *Deschampsia flexuosa* and *Juncus squarrosus*). However, the competitive effect of graminoids on seedling recruitment is probably much more powerful. Over the course of the study many seedlings and young plants were found under *Calluna vulgaris*, but few species (e.g. *Galium hircynicum*) germinated and grew in the dense vegetation formed by the grasses. This might be at least partially caused by a mat of litter produced by these grasses. *C. villosa*, in particular, produces large amounts of slowly decomposing litter (Pyšek 1991, 1993). In general,

litter is known to decrease seedling germination (e.g. Foster & Gross 1997; Špačková et al. 1998; Simard et al. 1998).

The seedlings of trees and shrubs were found mainly in coarse-grained soil plots, e.g. *Betula pendula* and *Salix* spp. seedlings were observed in coarse-grained soils from the first year of the study. Although a few of these tree and shrub seedlings survived, their growth is extremely slow, seven-year-old seedlings were less than 10 cm tall and their cover did not exceed 1%. *Picea abies*, common in surrounding forests, was planted in the bulldozed areas. Although our plots were located so that no planted trees were inside, in a few cases the small trees' branches spread over the plots and attained some cover there. The location of *P. abies* in the ordination diagrams mainly reflects this effect. In addition, there was a mast year for spruce in 1992 (Prach et al. 1996), with seeds released in early spring 1993. Unfortunately, there were no observations in 1993, but a few seedlings were recorded in 1994, the majority of them surviving to 1995. These seedlings were restricted to coarse-grained soils, being absent from grass-dominated plots, and their growth was extremely slow (if any). This corresponds to the experimental evidence of Prach et al. (1996) on the restriction of spruce seedling recruitment by grass competition. Other woody seedlings (*Sorbus aucuparia*, *Populus tremula*) were very rare and did not survive more than one year. Clearly, the removal of the upper soil changed the course of succession considerably so that it differs dramatically from that described for clear-cut areas of mountain forests (Pyšek 1994).

Within the range of environmental conditions and time span covered by our study, environmental determination of plant community composition increases with successional age. The relationship of species composition and the most important environmental factor, soil texture, is non-significant in the early years but significant later. With increasing successional age there is divergent development, into grass-dominated species-poor communities on fine-grained soils and *Calluna vulgaris*-dominated communities with higher species richness on coarse-grained soils. The resulting view of successional dynamics can be termed divergent: the original 'donor controlled' community of stress tolerant ruderals diverged into a community dominated by species with a competitive strategy (*C. villosa*, *D. flexuosa*) in less stressed habitats, and a community of stress tolerators on more stressed habitat (water deficit stress is higher on coarse-grained soils (Jenny 1980). It seems that species composition in the early stages of succession was mainly influenced by seed availability and perhaps also weather conditions, and that environmental determination of species

composition increases with time. Similar observations have been made by, *i.a.*, Osbornová et al. (1990), McClanahan (1986), Tsuyuzaki (1989), McLendon & Redente (1990), and Myster & Pickett (1990). However, the observed divergence is valid only within the time span of our study and within the range of environmental conditions covered here (Lepš & Rejmánek 1991).

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