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ELSEVIER

Ecological Engineering 3 (1994) 39–47

ECOLOGICAL ENGINEERING

Effect of soil characteristics on succession in sites reclaimed after acid rain deforestation

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Abstract

Change in dominant species on sites reclaimed after the forest decline in the Krušné hory Mountains, Czech Republic, is explained by changes in soil characteristics. A 15-year course of succession was inferred from comparing sites of different ages. Succession was studied in two contrasting habitat types: (1) plots from which the vegetation cover with top soil and diaspores was completely removed in order to make replanting of spruce (*Picea abies*) saplings possible, and (2) mounds originating from accumulating the removed material. At the beginning of succession in the plots, *Calamagrostis villosa* was the main colonizer and retained its dominance up to 5 years, after which it was gradually replaced by *Deschampsia flexuosa*. In contrast, revegetation from *C. villosa* rhizomes occurred in mounds and no dominant species exchange was observed during the first 15 years of succession. Differences in contents of soil chemicals and in their trends over time were found between habitat types. Organic matter and nitrogen levels were higher in mounds than in plots during the whole period of succession studied. Soil acidity decreased in plots but increased in mounds. It appears that *C. villosa* is outcompeted from plots because of its high requirements for the organic matter content, a factor that was found to be the best predictor of trends in the species' successional behaviour. Occurrence of *D. flexuosa* was correlated with soil acidity and calcium and potassium contents.

Key words: Czech Republic; Forest decline; Reclaimed sites; Soil conditions; Succession

1. Introduction

In Europe, recent forest decline was studied intensively in the last few decades (Nilsson and Duinker, 1987; Krause, 1989; Fuhrer, 1990). This decline has been attributed to high SO_2 concentrations and poor forest management, namely extraction of timber without replenishment of nutrients, in particular Mg (Ulrich et al., 1980; Bosch et al., 1986). In the Czech Republic, extensive areas of Norway

SSDI 0925-8574(93)E0035-0

spruce (*Picea abies*) forests were damaged in the mountain ranges in the northwestern part of the country. Deforested areas are rapidly being colonized by grasses (Pyšek, 1990, 1991) whose cover makes the replanting of forest trees extremely difficult. Complete removal of the vegetation cover and of the upper soil layer has been carried out to cope with this problem. The subsequent replanting of trees, however, has often not been successful and the reclaimed sites have become exposed to the spontaneous colonization and revegetation.

A previous paper (Pyšek, 1992) described the course of succession in such reclaimed sites in the Krušné hory Mountains. It has been shown that succession in bulldozed plots started with certain perennials spreading by seed from the outside. Grasses contributed most to the total community biomass during the first 15 years of succession. Among these, *Calamagrostis villosa* (Chaix) J.F. Gmel. and *Deschampsia flexuosa* (L.) Trin. played the most important role. Both are rhizomatous polycarpic perennials forming extensive clones of shoots and tolerating nutrient- and base-poor, acidic habitats (Scurtfield, 1954; Conert, 1989; Foggo and Warrington, 1989). Litter produced by both species is persistent and inhibitory to plant establishment and growth (Grime et al., 1988; Pyšek, 1990). A unidirectional shift between these dominants was observed with time: the most successful colonizer of newly created habitats, *C. villosa*, was gradually replaced in the course of approximately 5 years by *D. flexuosa* (Fig. 1). In contrast, no species change occurred in mounds established from the material being removed from plots. In this habitat type, *C. villosa* regenerated from rhizomes and retained its dominance.

The present paper focuses upon the mechanisms behind the change in dominant species and addresses the following questions: (1) What are the changes of soil characteristics during succession? (2) How do these characteristics affect the shift in dominant species?

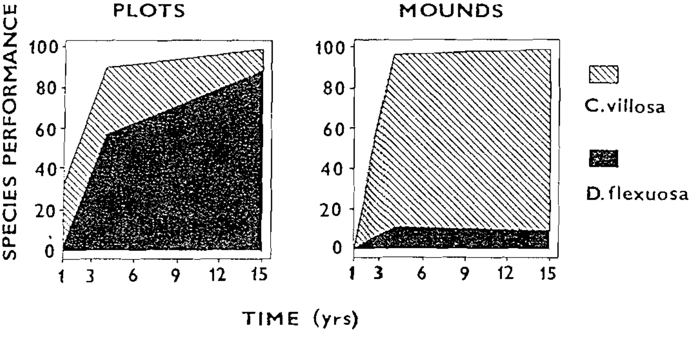

Fig. 1. Changes in performances of *Calamagrostis villosa* and *Deschampsia flexuosa* in both habitat types (plots vs. mounds) during 15 years of succession: *C. villosa* was the prevailing species from the very start, but was gradually replaced by *D. flexuosa*. Percentage contribution of each species to the total community biomass was used as a measure. Note that the data for both species are accumulated.

2. Material and methods

Study site

The research was carried out in the Krušné hory Mountains (in German: Erzgebirge), Northern Bohemia, Czech Republic, a part of the crystalline complex formed by meta-igneous and sedimentary rocks. The area has a moderately cold climate with a mean annual temperature of 5.0°C and annual precipitation of 984 mm (Fláje meteorological station, 50-year average 1901–50). Study sites were located in the vicinity of the Fláje reservoir, district of Litvínov (50.36°N, 13.37°E), at the altitude of 800–900 m.

Succession was studied in two different habitats: (a) Plots created by bulldozing away the upper soil layer (20–30 cm). These were mostly oblong in form and 20–30 × 50–70 m in size (with the exception of the oldest site which was formed by 20-m-wide stripes several hundreds of meters long). This habitat type is subsequently referred to as "plots". As the subsoil had previously been little affected by weathering and plant growth, some features of primary succession (Odum, 1971; Begon et al., 1986; Miles, 1987) were observed (Pyšek, 1992). (b) Mounds built by material removed from plots so that the mounds were bordering the plots. The mounds were 3–5 m in width, 1–2 m in height and 50–70 m in length. A course of succession different from that in plots was found in these sites: vegetation cover had been destroyed but humus-rich top soil with diaspores was present and secondary succession (Begon et al., 1986; Vitousek and Walker, 1987) was thus the case here (Pyšek, 1992). This habitat type is termed "mounds".

Sampling

The methodical approach used in this study is based on the assumption that a series of communities which currently exist in a given habitat but have been developing for a different time can be inferred to reflect succession (Begon et al., 1986). Three sites of different successional age, disturbed in 1975 (subsequently indicated as S15), 1986 (S4) and 1989 (S1), were compared in 1990 in order to reconstruct the first 15 years of succession.

Changes of population characteristics of dominant species during succession were described in detail in the previous paper (Pyšek, 1992). For the purpose of the present study, data on biomass of both dominants sampled from 0.5-m quadrats were used (see Pyšek, 1992, table 2 for values). Five quadrats were sampled in each successional stage and habitat type with the exception of plots in the S1 site where ten samples were taken because of higher vegetation heterogeneity. The quadrats sampled thus do not represent true replications but rather pseudoreplications sensu Hurlbert (1984). In the same quadrats soil samples were taken from the upper 20 cm. Atomic absorption (Ca, K), UV-VIS spectrophotometry (P), titration with $KMnO_4$ (organic C), Kjeldahlization (nitrogen) and potentiometry (pH) were used to analyse the samples.

Data analysis

The data were analysed by standard statistical methods (Sokal and Rohlf, 1981). A stepwise multiple regression was used to explain the changes in dominant

Table 1
Partial correlation coefficients between soil characteristics (see Table 2 for values). Pooled data from all habitat types and successional ages were used ($n = 45$)

	Organic carbon	Nitrogen	Phosphorus	Potassium	Calcium	pH
Organic carbon	–					
Nitrogen	0.40 **	–				
Phosphorus	0.20	−0.05	–			
Potassium	−0.52 **	0.26	0.30 *	–		
Calcium	0.38 **	−0.16	−0.11	0.03	–	
pH	−0.26	0.13	0.13	−0.10	0.71 ***	–

Significance level of the correlation coefficient: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

species performances during succession on the basis of soil characteristics to overcome the fact that some of the soil variables were mutually correlated (Table 1). Performance of each species considered was expressed as its contribution to the total community biomass.

3. Results

Effect of site and successional age on soil characteristics

Results of soil analyses are summarized in Table 2. Two-way ANOVA, analysing the effect of site (i.e., plots vs. mounds) and successional age on soil characteristics (Table 3) revealed that there was a highly significant effect of both on organic carbon content, which was higher in mounds than in plots and increased between years 1 and 4 of succession in plots (Table 2). Furthermore, significant effects of interaction between the site and age were found in Ca content and soil acidity. In both characteristics, there were opposite trends in time between plots and mounds. At the beginning, plots were more acid than mounds; in the course of succession, however, the soil acidity decreased in plots and increased in mounds (Table 2) so that the pH value was higher in plots than in mounds after 15 years of succession. Correspondingly, the trend in calcium content was opposite, starting with a higher value in mounds than in plots; after 15 years it reached a higher value in plots (Table 2), but this difference was at the border of significance ($t = 2.09$, $P = 0.056$). Moreover, there was also a significant effect of site on Ca-content and of site/age interaction on P-content (Table 3). Nitrogen levels were significantly affected by site, remaining higher in mounds from the very start till 15 years of succession, and also by age (Table 3): in both habitat types the nitrogen content increased between years 1 and 4 of succession and then decreased again (Table 2).

Relation between the dominant species exchange and soil characteristics

To investigate the effect of soil chemical characteristics on the performance of dominant grasses, stepwise multiple regression relating their contribution to the

Table 2

Soil characteristics in plots and mounds and their changes during succession. Means ±s.e. are given (weight percent). Number of samples $n = 5$, except of 1-year-old plots $n = 10$

Years of succession	1	4	15
Phosphorus:			
plots	0.125 ± 0.004	0.126 ± 0.007	0.136 ± 0.0
mounds	0.134 ± 0.006	0.150 ± 0.005	0.124 ± 0.0
Organic carbon:			
plots	4.88 ± 0.33	8.46 ± 0.72	6.28 ± 0.5
mounds	10.82 ± 1.11	11.46 ± 1.27	11.80 ± 1.1
Calcium:			
plots	0.15 ± 0.004	1.10 ± 0.34	0.35 ± 0.0
mounds	2.86 ± 1.12	0.68 ± 0.21	0.19 ± 0.0
Potassium:			
plots	1.55 ± 0.14	1.60 ± 0.06	1.91 ± 0.2
mounds	1.18 ± 0.23	1.46 ± 0.14	1.56 ± 0.1
pH:			
plots	3.96 ± 0.07	5.14 ± 0.24	5.09 ± 0.1
mounds	5.25 ± 0.69	4.35 ± 0.33	3.59 ± 0.0
Nitrogen ($\times 10^{-3}$)			
plots	29.80 ± 2.37	38.70 ± 2.06	32.30 ± 0.4
mounds	31.40 ± 1.29	45.80 ± 7.51	39.80 ± 3.2

Table 3

Summary of two-way ANOVA showing the effect of successional age and site (i.e., plots vs. mounds) on soil characteristics

	Source	d.f.	S.S.	F-ratio	P
Phosphorus:	site	1	0.00077	1.54	0.221
	age	2	0.00049	0.44	0.646
	age × site	2	0.00028	3.44	0.042 *
	error	39	0.01237		
Organic carbon:	site	1	231.87	55.18	0.000 ***
	age	2	25.38	6.04	0.005 **
	age × site	2	16.80	2.00	0.149
	error	39	163.89		
Calcium:	site	1	4.98	5.26	0.027 *
	age	2	5.16	2.72	0.078
	age × site	2	20.13	10.63	0.0002 ***
	error	39	36.94		
Potassium:	site	1	0.82	4.05	0.051
	age	2	1.04	2.59	0.088
	age × site	2	0.10	0.25	0.779
	error	39	7.89		
pH:	site	1	1.09	2.09	0.155
	age	2	1.80	1.74	0.189
	age × site	2	14.01	13.46	0.000 ***
	error	39	20.30		
Nitrogen:	site	1	291.60	4.99	0.031 *
	age	2	436.06	7.46	0.002 **
	age × site	2	36.23	0.62	0.543
	error	39	58.42		

Table 4
Results of stepwise multiple regressions relating the dominant species performances (expressed as percentage of the total community biomass estimated in 0.5-m quadrats) to soil characteristics. Data for plots and mounds from all successional stages were pooled. Only those variables that added significantly to the model are presented. The regression coefficient and its significance level for each variable considered is provided

	Coefficient	*P*-level	Analysis of variance		
			d.f.	F-value	*P*
Calamagrostis villosa					
Predictor: Constant	25.94	0.453	2,32	23.35	< 0.0001
Organic carbon	12.65	< 0.0001			
pH	− 14.12	0.048			
Deschampsia flexuosa					
Predictor: Constant	− 149.87	0.0001	3,31	10.73	< 0.0001
pH	30.28	0.0002			
Calcium	− 15.89	0.008			
Potassium	33.21	0.009			

total community biomass to the contents of soil chemicals was used (Table 4). For *C. villosa*, there was a highly significant positive effect ($P < 0.0001$) of organic matter content on the species performance and 56.8% of variance within the data set was explained by the predictors included. The relationship between dry weight

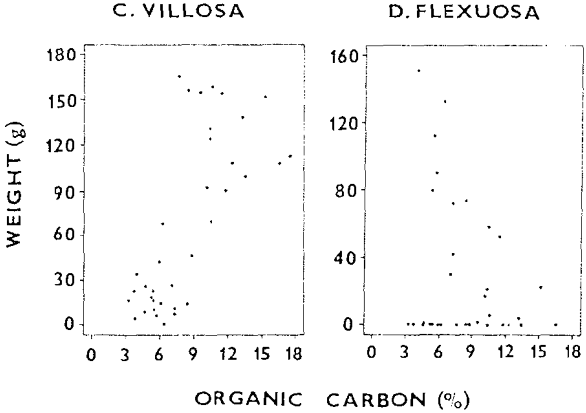

Fig. 2. Scatter plots showing the relationship between the dominant species performance and organic carbon content, which was found (Table 4) to be the most important predictor of the species role in the community. Linear model WEIGHT = $a + b \times$CARBON CONTENT provided a significant fit to the data in the case of *Calamagrostis villosa* ($r = 0.73$, $P < 0.001$, $n = 35$), whereas for *Deschampsia flexuosa* it turned out to be nonsignificant ($r = -0.23$, $P = 0.17$, $n = 35$). Data pooled over time and habitat type were used.

of *C. villosa* and amount of organic matter in the soil was linear (Fig. 2). Correspondingly, a negative although non significant effect of carbon content on the performance of *D. flexuosa* was found. Contribution of this species to the community biomass was, however, positively related to the pH value ($P < 0.001$) and potassium content ($P < 0.01$) and negatively to the calcium content ($P < 0.01$). Also in this species, the multiple regression yielded a significant result ($P < 0.001$) and 50.9% of variance was accounted for by the predictors considered (Table 4).

4. Discussion

The successional replacement of *C. villosa* by *D. flexuosa* may be explained by soil characteristics. In natural conditions, *C. villosa* as an understory species of spruce forests is confined to deep, humus-rich soils (Conert, 1989). Humus soil layer was, however, completely removed from plots. Nevertheless, *C. villosa* was the main colonizer due to its stands being present in the vicinity of these newly created sites and serving thus as a diaspore pool, and to its capability to spread easily by seed (Pyšek, 1992). At the beginning of succession, the species is probably able to dominate because of its higher growth rate and intensive vegetative spreading. Later on in succession, *C. villosa* appears to be limited by low organic matter content and is eventually replaced by *D. flexuosa*. On mineral soils, trends to *D. flexuosa*-dominated stands are common (Miles, 1985; Grime et al., 1988). Low content of organic matter in plots is the principal difference in comparison with mounds (see Tables 2 and 3), where *C. villosa* retained its dominance over *D. flexuosa*. However, one must bear in mind that a significant correlation never means a definite causal relationship. Even though organic carbon correlates significantly with the occurrence of *C. villosa*, there may be other factors of more importance, i.e., biological traits of both dominant species involved in succession or the internal dynamics of their clones. However, data obtained from an other part of the Krušné hory Mountains suggest that under different soil conditions (namely on soils with higher content of organic matter), the shift of dominance between both species may be reversed, i.e., *C. villosa* replacing *D. flexuosa* (Lepš, Michálek and Pyšek, unpublished data).

Vegetation cover usually accelerates acidification but changes making the soil less acid can also occur (Miles, 1985). Decrease of soil acidity which occurred in plots between years 1 and 4 appears to have stopped after *D. flexuosa* became the dominant species (compare Fig. 1 with Table 2). This corresponds to the report that grasslands associated with *D. flexuosa* provide more humus and promote podzolization (Piggott, 1970).

Some practical conclusions in terms of reforestation may be derived from the results presented here. In the region studied, the main disadvantage of sites occupied by *C. villosa* is that the spontaneous revegetation by trees is prevented because of dense grass cover. In reclaimed plots, replacement of *C. villosa* by *D. flexuosa*, associated with changes in soil features (especially the decrease of soil acidity, increase in Ca, K and nutrients), appears to promote the spontaneous establishment of trees (*Betula pendula, Sorbus aucuparia*) and therefore to speed up the succession to the forest.

5. Acknowledgments

My thanks are due to Dana Čížková for help with the field work, Petr Artner for carrying out the soil analyses and Pavla Kotková for comments on statistical treatment of data. I thank two anonymous reviewers for their comments on the manuscript. Eva Švejdová kindly drew the figures.

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