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Pattern of species dominance and factors affecting community composition in areas deforested due to air pollution

Petr Pyšek
Institute of Applied Ecology, University of Agriculture Prague, CZ-281 63 Kostelec nad Černými lesy, Czech Republic

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Abstract

Vegetation of mountain areas affected by SO_2 pollution (Krušné hory Mts., Czech Republic) was analysed using multivariate methods. Communities with prevailing species *Calamagrostis villosa*, a rhizomatous grass expanding into deforested sites, were sampled by Braun-Blanquet relevé method. Canonical correspondence analysis was used to assess the effect of environmental variables (soil removal, deforestation, and shading). To test the effects of light, moisture, soil acidity and nitrogen, mean sample indicator values were correlated a posteriori with sample axes on ordination scores. Light, soil acidity, moisture, and site history (in terms of past deforestation and soil removal applied in reclamation procedures) were found to be the main factors responsible for the community composition. Nitrogen level had not a significant effect on the community composition. When analyzing the whole data set, i.e. including also remnants of natural spruce forests, light was the factor affecting at most the composition of communities. Within the bare spot vegetation, if treated separately, the highest variation was found along the soil acidity/moisture gradient. The effect of soil removal was only obvious at early successional stages. Species diversity increased with moisture and decreased with soil acidity. Species exhibiting S- and/or R-strategy are successful on extremely acid soils whereas forbs present in bare spots appear to be supported by disturbances.

Introduction

In central Europe, forest decline attributable to SO_2 air pollution became a striking ecological phenomena in the several last decades (see e.g. Klein & Perkins 1988; Krause 1989; Fuhrer 1990 for review and discussion on possible causes) and as such it has attracted considerable research attention (Moldan 1990). Vast areas originally covered by Norway spruce (*Picea abies*) forests were, and still are being replaced by non-forest communities dominated by expansive perennial grasses. In northern Bohemia (Czech Republic) *Calamagrostis villosa*, a rhizomatous grass is the most frequent invader of such sites (Pyšek 1992a); being a strong competitor under such extreme ecological conditions due to (1) easy distant spread due to low caryopsis weight (Pyšek 1992a),

(2) capability of producing large amount of biomass (Fiala *et al.* 1989; Pyšek 1991), (3) accumulation of litter on the soil surface which contributes to suppression of other species (Pyšek 1990), (4) rapid vegetative spread by extensive rhizome system (Fiala 1989), (5) low nutrient requirements (Conert 1989), and (6) tolerance to air pollution, *Calamagrostis villosa* may be at present considered the most abundant herbaceous species in the region studied.

It may be suggested that the vegetation changes having occurred in these areas are associated with changes in mutual relationships between species, even at different trophic levels (Pyšek 1992b) and, considering the extreme soil conditions (high acidity, low nutrient level) also factors governing the pattern of species occurrence might differ from those usually operating in less extreme situations. Consequently, species responses to environmental variables may differ from those commonly found under non-stressed conditions. The present paper thus addresses the following question: Which are the main environmental factors affecting the vegetation pattern in deforested areas and how do they differ from those one could expect to act in comparable habitats under less extreme conditions?

Methods

Habitats studied

The research was conducted in the Krušné hory Mts., a crystalline complex formed by meta-igneous and sedimentary rocks, located in the northern part of the Czech Republic. 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-years average 1901–50). Study sites were located in area of approximately 20 km^2 in size surrounding the Fláje reservoir, district of Litvínov (50.36 N, 13.37 E), at the altitude of 800–900 m.

Seven habitat types in which *Calamagrostis villosa* was a dominant species were distinguished in the studied region. Species composition of each particular habitat is summarized in Table 1.

A. Remnants of original spruce forests with tree cover ranging from 50 to 75% and *Calamagrostis villosa* as a dominant understorey species.

B. Forest paths and their margins; apart from *C. villosa*, the species *Senecio nemorensis* subsp. *fuchsii*, *Deschampsia caespitosa*, and *Holcus mollis* were among those typical of this habitat type.

C. Road margins in the open lanscape and associated ditches harbouring rather diverse species set, with *C. villosa* as a dominant.

D. Naturally occurring, moist or wet meadows bound to surface depressions and/or associated with brooks, with *Juncus effusus*, *Deschampsia caespitosa*, and *C. villosa* as dominant species.

E. Sites originated after forest die-back and subsequent timber extraction (further termed as bare spots). These sites have been recently colonized by *C. villosa* and no reclamation practices were carried out here after then. By the time of sampling, the stands were 5–10 years after complete deforestation.

F. Initial stages of succession in sites previously covered by *C. villosa* (i.e. A-type) and reclaimed in order to promote spruce replanting. Top soil layer with rhizomes and diaspores was removed by bulldozing and the sites so created were left without further management, having thus been exposed to spontaneous succession (see Pyšek 1992a for details on reclamation practices). Vegetation was sampled 2 years after soil removal.

G. Old reclaimed bare spots; the characteristic given for F also refers to this habitat type but the plots were sampled 15 years after the reclamation procedure. *Betula pendula* formed tree cover (25–75%) and *C. villosa* and *Deschampsia flexuosa* were dominant species of herb layer.

Sampling and data analysis

Five relevés were made in each habitat type (except of A–6 relevés, and D–4 relevés) using the Braun-Blanquet seven-grade scale (e.g. Westhoff & Van der Maarel 1978). Sampling plots were scattered all over the study area so that they may be considered as true replicates (sensu Hurbert 1984). Species dominance/abundance values

Table 1. Species composition of habitats studied. A–spruce forest, B–forest paths, C–road margins and ditches, D–natural wet meadows, E–non reclaimed bare spot, F–young reclaimed bare spot, G–old reclaimed bare spot. Frequency (%) and range of values in Braun-Blanquet scale are given for each habitat type.

Habitat	A	B	C	D	E	F	G
Calamagrostis villosa	100–15	100–25	100–25	100–14	100–35	100–13	100–25
Cirsium palustre	20–2	75–+2	40–r1				
Senecio nemorensis subsp. *fuchsii*	67–r2	80–24	60–r+	50–r2	40–34	80–r1	60–r1
Epilobium angustifolium	67–r+	20–2	50–r	40–3	20–+		
Deschampsia caespitosa	80–13	20–+	100–24	60–+1			
Juncus effusus	100–24	60–r+	60–12	20–+			
Galeopsis bifida	40–r						
Stellaria media	20–r	20–r					
Picea abies	100–34	20–1					
Circaea intermedia	17–r	40–2					
Dryopteris dilatata	100–r1	20–r	25–r	20–r			
Polytrichum sp.	33–+1	20–+					
Holcus mollis	40–3	20–+	40–13				
Ranunculus repens	80–r1	40–r1	25–3				
Stellaria graminea	20–+	40–r+	25–r	20–r			
Galium saxatile	17–+	80–+1	20–1	40–r+	80–r+		
Deschampsia flexuosa	50–r2	60–+1	40–+	40–12	100–+4		
Dactylis glomerata	20–+	80–r1					
Vaccinium myrtillus	50–r1	20–1					
Alchemila monticola	20–r	60–r					
Rumex acetosa	20–r	20–r	20–+	20–r			
Campanula rotundifolia	20–r	20–r	100–r+				
Carex ovalis	20–r	25–r	20–r	80–r1			
Myosotis nemorosa	20–r	20–r	50–12				
Urtica dioica	20–r	50–+	20–+				
Luzula multiflora	20–r	40–r+	20–1				
Cirsium arvense	20–r	20–r					
Rubus idaeus	40–+2	60–1					
Betula pendula	25–1	40–r	100–24				
Cerastium fontanum subsp. *triviale*	40–r	20–r					
Salix caprea	80–+1	80–r+					
Rumex acetosella	20–r	100–+3					
Trifolium repens	80–r	20–r					
Total number of species	19	25	58	35	24	17	12
Mean spec.no per relevé	8.2	9.0	24.4	12.7	7.6	8.6	5.6
Mean species diversity H′	1.03	2.17	2.48	4.10	1.24	2.27	1.34

Species occurring in only one habitat type: C: *Festuca rubra* 80–r2, *Achillea millefolium* 100–r +, *Vicia sepium* 60–r +, *Tussilago farfara* 40–r, *Veronica chamaedrys* 100– + 3, *Linaria vulgaris* 80– + 1, *Plantago major* 60–r, *Meum athamanticum* 100–r1, *Ranunculus acris* 60–r +, *Poa pratensis* 60–r, *Rhinanthus minor* 60–r +, *Hieracium laevigatum* 60–r +, *Artemisia vulgaris* 60–r +, *Taraxacum officinale* 60–r F: *Agrostis capillaris* 100– + 1.

were transformed to numerical scale 1–7 and in this form used as input data for multivariate analysis. Canonical correspondence analysis (Ter Braak 1987, 1988) was used to treat the data. Age, understood as the time having been available for spontaneous vegetation development in a given habitat type, was considered as an environmental variable (F–2, E–7.5, G–15 years; for other habitats that have not obviously been affected recently by heavy disturbances, the value of 30 was used). Two other nominal variables were included: soil removal (coded 1 for F and G, and 0 for others) and deforestation, showing whether the forest canopy was originally present and removed in recent times (0 for A–D, 1 for E–G). Only those species that occurred in at least 3 relevés (of 35) were included into the multivariate analysis.

Ecological factors were not measured directly. To express main environmental factors, an indirect approach was applied using indicator values (Ellenberg 1991) for light (the tabulated value was available for 94.7% of 115 species totally present in the whole data set), moisture (76.5%), nitrogen (82.6%), and soil reaction (61.7%). Mean values were calculated for each relevé on the basis of species quantities using the values of Braun-Blanquet scale after the transformation to 1–7. To test an effect of these factors on the community composition, mean sample indicator values were correlated a posteriori with sample scores on the first two ordination axes.

Shannon index of species diversity H′ ($\log_e$ base, e.g. Peet 1974) was calculated with cover data to which the original Braun-Branquet scale values were transformed as follows: 5–87.5, 4–62.5, 3–37.5, 2–15, 1–2.5, + –1, r–0.1. Multiple regression (Sokal & Rohlf 1981), using indicator values for light, moisture, soil reaction and nitrogen as predictors, was performed on the data to explain the pattern of species diversity.

Nomenclature follows Flora Europaea (Tutin *et al.* 1964–1980).

Results

Effect of environmental variables on community composition: a multivariate analysis

A CCA run was performed on the complete data set using all environmental variables in order to select those variables that could have been omitted due to their low contribution to the regression equation. High values of variance inflation factor (VIF, see Montgomery & Peck 1982) were found in age (VIF = 76.81) and deforestation (VIF = 49.37) indicating that these two variables were almost perfectly correlated with other variables, in this case with soil removal (r = – 0.72 for

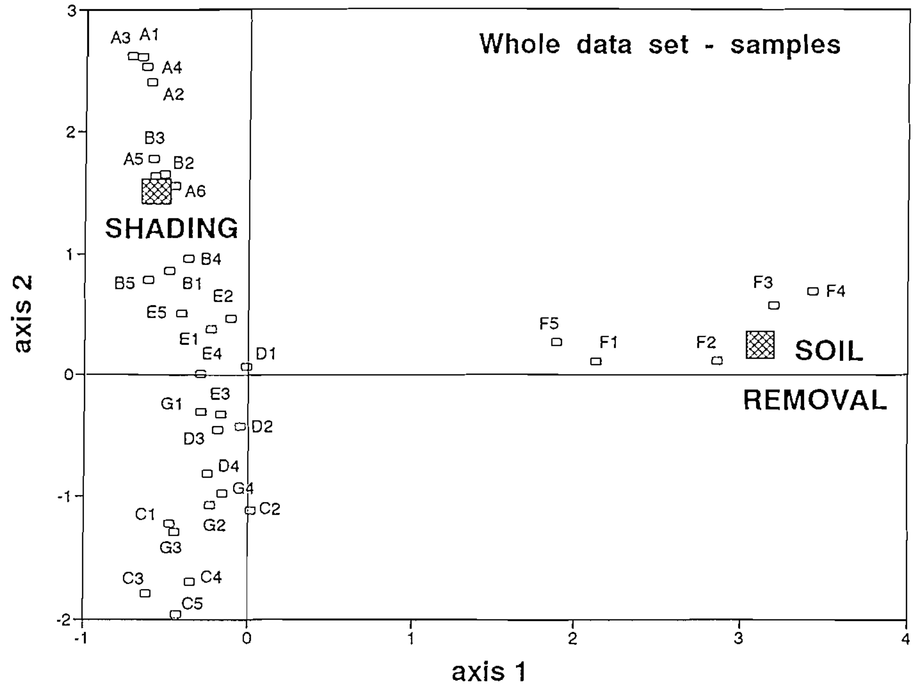

Fig. 1. Ordination diagram referring to analysis of full data set. A–spruce forest, B–forest paths, C–road margins, D–wet meadows, E–non-reclaimed bare spots, F–young reclaimed bare spots, G–old reclaimed bare spots. Centroids are indicated by hatched squares.

age, and r = 0.50 for deforestation) and with each other (r = − 0.95). Consequently, it was suggested that environmental variables selected for further analyses, i.e. shading and soil removal would explain the species data equally well as the full set of variables (Ter Braak 1988).

Fig. 1 displays ordination results for the whole data set, i.e. all habitats included. The first axis ($\lambda_1 = 0.43$) is seen to separate the young reclaimed sites (F) from the others and accounted for 63.6% variance in the data set (Table 2). Monte Carlo test for the first axis was highly significant ($P < 0.01$). The second axis ($\lambda_2 = 0.24$) was best correlated with shading (r = 0.74): the sites are arranged along light gradient from those possessing tree or shrub layer, i.e. spruce forest (A), forest roads (B) to both non-reclaimed (E) and reclaimed bare spots (F,G) and wet meadows (D), and, in particular to road margins (C).

Both ordination axes were highly correlated with mean sample light indicator value which decreased with shading (r = − 0.81) and increased with soil removal (r = 0.44). Soil acidity, moisture and nitrogen showed close correlation with neither of the ordination axes (Table 3).

To obtain a deeper insight into the species/environment pattern in the bare spot originated after forest die-back and subsequent timber extraction, some of the habitats were selected for a separate analysis. This subset included bare spots (E) together with young (F) and old (G) reclaimed sites; in addition, "natural" wet meadows (D) were also included to provide a comparison of graminoid vegetation types differing in site history (particularly in terms of deforestation). In this case, shading was not considered as an environmental variable as all the habitats considered were without tree cover. Furthermore, the value of VIF for age (34.22) lead to the omitting of this variable. Consequently, deforestation and soil removal were included in the ordination procedure.

Table 2. Ordination results provided for two runs of canonical correspondence analysis, using full data set (I) and bare spot vegetation only (II). Inter-set correlations of environmental variables with axes are provided.

Axis	I. Full data		II. Bare spots	
	1	2	1	2
Eigenvalue	0.43	0.24	0.48	0.37
Cummulative % of variance	63.6	–	56.2	–
Variable:				
Soil removal	0.97	0.08	0.98	− 0.02
Shading	− 0.32	0.74	–	–
Deforestation	–	–	0.36	− 0.83

Table 3. Correlations of sample scores with mean sample indicator values for principle ecological factors. Correlation coefficients and F-values for d.f. 1,33 (full data set) and 1,17 (bare spot data) are given. Significance level of the correlation coefficient is not given as both variables represent weighted averages calculated on the basis of the same input values.

	Axis 1		Axis 2	
	F	r	F	r
Full data set:				
Acidity	0.32	0.10	4.13	0.33
Moisture	0.50	− 0.12	0.02	− 0.03
Light	8.03	0.44	64.86	− 0.81
Nitrogen	1.45	− 0.20	0.01	0.01
Bare spots:				
Acidity	0.16	0.10	57.33	− 0.88
Moisture	8.17	− 0.56	7.95	0.56
Light	4.47	0.45	0.91	0.22
Nitrogen	0.02	− 0.03	4.30	0.44

In this analysis (Table 2), the first axis ($\lambda_1 = 0.48$) was best correlated with soil removal (r = 0.97) and clearly separated young reclaimed sites (F) from the remaining samples (Fig. 2a). It is worth of noting that another set of reclaimed plots, aged 15 years (G) cannot not be distinguished, with respect to this variable, from non-reclaimed habitats. Differentiation along the second axis ($\lambda_2 = 0.37$) was mainly due to deforestation (r = − 0.83) with samples from natural wet meadows concentrated in the area of the lowest effect of this factor. Response of particular species to the environmental variables is obvious from Fig. 2b. The first axis accounted for 56.2% of variance in data and was highly significant (Monte Carlo test, $P < 0.01$).

The sample scores on the first ordination axis (i.e. that corresponding to the soil removal)

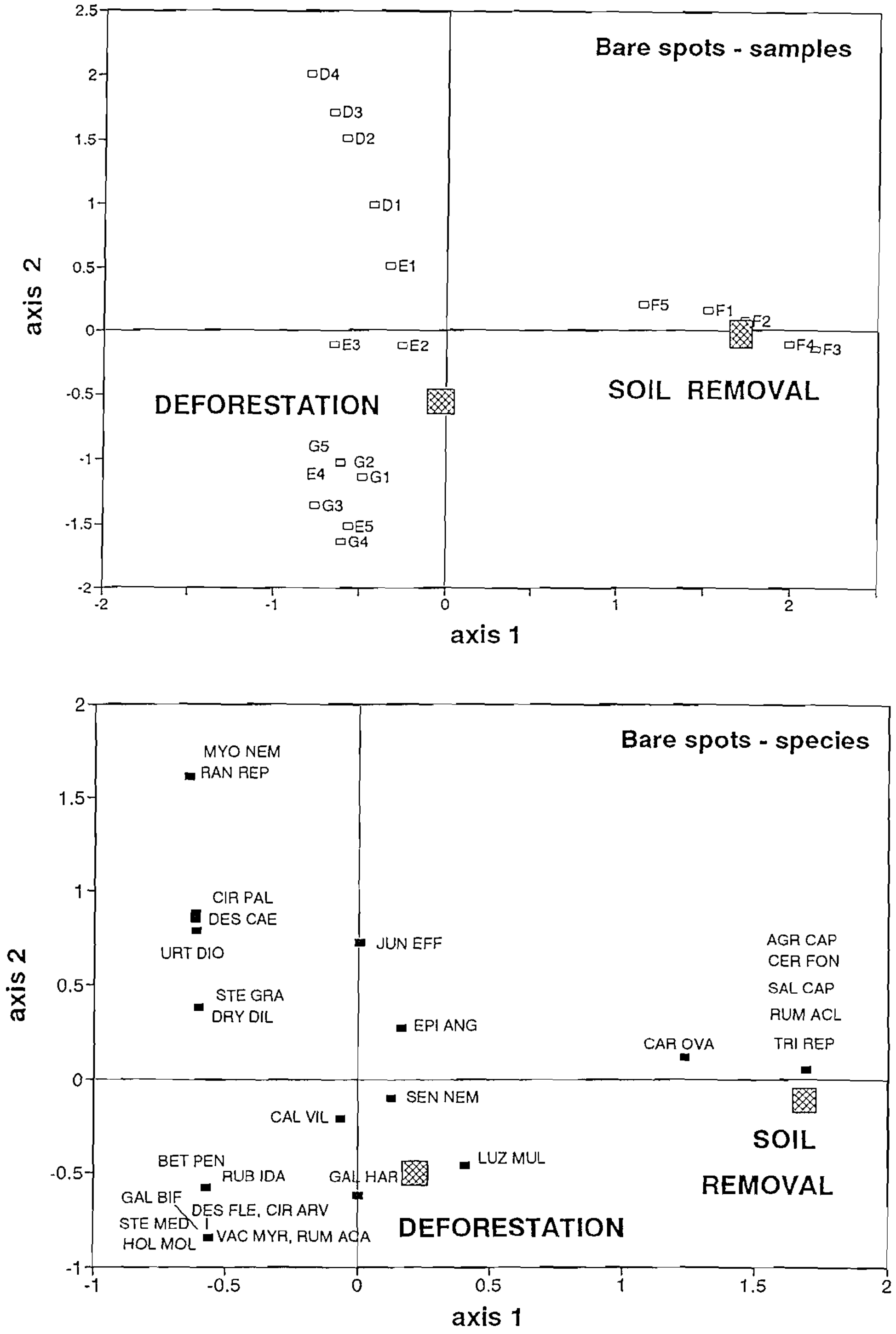

Fig. 2. Ordination diagrams referring to analysis of bare spot data only. Centroids are indicated by hatched squares. a. Ordination of sites (see Fig. 1 for habitat codes). b. Ordination of species. AGR CAP–*Agrostis capillaris*, BET PEN–*Betula pendula*, CAL VIL–*Calamagrostis villosa*, CAR OVA–*Carex ovalis*, CER FON–*Cerastium fontanum*, CIR ARV–*Cirsium arvense*, CIR PAL–*Cirsium palustre*, DES CAE–*Deschampsia caespitosa*, DES FLE–*Deschampsia flexuosa*, DRY DIL–*Dryopteris dilatata*, EPI ANG–*Epilobium angustifolium*, GAL BIF–*Galeopsis bifida*, GAL SAX–*Galium saxatile*, HOL MOL–*Holcus mollis*, JUN EFF–*Juncus effusus*, LUZ MUL–*Luzula multiflora*, MYO NEM–*Myosotis nemorosa*, RAN REP–*Ranunculus repens*, RUB IDA–*Rubus idaeus*, RUM ACA–*Rumex acetosa*, RUM ACL–*Rumex acetosella*, SAL CAP–*Salix caprea*, SEN NEM–*Senecio nemorensis* subsp. *fuchsii*, STE GRA–*Stellaria graminea*, STE MED–*Stellaria media*, TRI REP–*Trifolium repens*, URT DIO–*Urtica dioica*, VAC MYR–*Vaccinium myrtillus*.

were closely negatively correlated with moisture ($r = -0.56$) mean sample indicator value. Furthermore, the high correlations between sample scores on axis 2 and their mean indicator values were found for moisture ($r = 0.56$) and acidity, the latter relationship being very close ($r = -0.88$, Table 3). Considering these results, the second ordination axis of the site/environment biplot (Fig. 2a) may be interpreted as showing a very distinct pattern: "natural" meadows (D) tend to occur in less acid, moist sites whereas especially the old reclaimed bare spots (G) are bound to extremely acid soils. Non-reclaimed bare spots are widely scattered along the acidity/moisture gradient.

Relationship between the species dominance and plant traits in bare spot vegetation

To test the relationships between plant traits and success of dominant species in bare spot vegetation, two-way ANOVA was performed (Table 4) analysing the effects of life form (grasses and grass-like species vs. forbs) and strategy (according to Grime 1979, with C-strategists vs. those exhibiting a combination of S and R strategies) on their scores on the first two ordination axes (see Table 6 for criteria applied for considering a species as dominant). Species scores on axis 1 (Fig. 2b) were taken as a measure of species ability to cope with disturbances (the higher the score, the higher the affinity to sites disturbed by soil removal). In the same vein, considering the high correlation between the second axis and soil acidity (Table 3), species scores on this axis may be assumed to reflect species capability of growing in extremely acid sites.

Species scores on axis 1 were significantly affected by life form (mean score for grasses and grass-like species was -0.66, i.e. significantly lower than 0.36 found for forbs; multiple range analysis, Tukey test, $P < 0.05$). Effect of the life strategy itself was non significant but its interaction with life form provided significant result ($P < 0.05$).

Life strategy had a significant effect on scores of dominant species on the second axis (Table 4): pure C-strategists exhibited significantly higher values (0.44) than species with other strategies in which the mean score -0.46 was found (multiple range analysis, Tukey test, $P < 0.05$). There was no significant effect of life form; however, the

Table 4. Summary of two-way ANOVAs showing the effects of life form and strategy on scores of dominant species of bare spot vegetation (see Table 6 for their characteristics) on the first two ordination axes. Two groups of strategies (according to Grime 1979) were distinguished, i.e. those exhibiting pure C-strategy vs. those whose combined strategy includes S and/or R. Grasses and grass-like species vs. forbs were distinguished among life forms.

	d.f.	M.S.	F	P
Axis 1:				
Main effects	2	1.21	13.43	0.016
Life form	1	2.33	25.92	0.007
Strategy	1	0.46	5.08	0.087
Interaction	1	1.52	12.79	0.023
Residual	4	0.09		
Axis 2:				
Main effects	2	0.83	9.46	0.034
Life form	1	0.02	0.27	0.638
Strategy	1	1.63	18.56	0.012
Interaction	1	0.85	9.66	0.036
Residual	4	0.08		

Table 5. Summary of multiple regressions relating the species diversity to the main environmental factors (expressed as their indicator values). Regression coefficients and their significance levels are given. Data from bare spots (habitats D–G).

Dependent variable	Shannon index H′	P	Species number S	P
Constant	− 11.10	0.118	− 27.11	0.046
Predictors:				
Light	1.77	0.035	4.16	0.010
Moisture	0.06	0.893	−0.11	0.906
Nitrogen	− 0.54	0.286	0.37	0.691
Soil acidity	− 1.06	0.020	− 2.59	0.004
Analysis of variance:				
$F_{4,14}$	5.47		11.25	
P	0.0073		0.0003	
R^2	0.609		0.763	

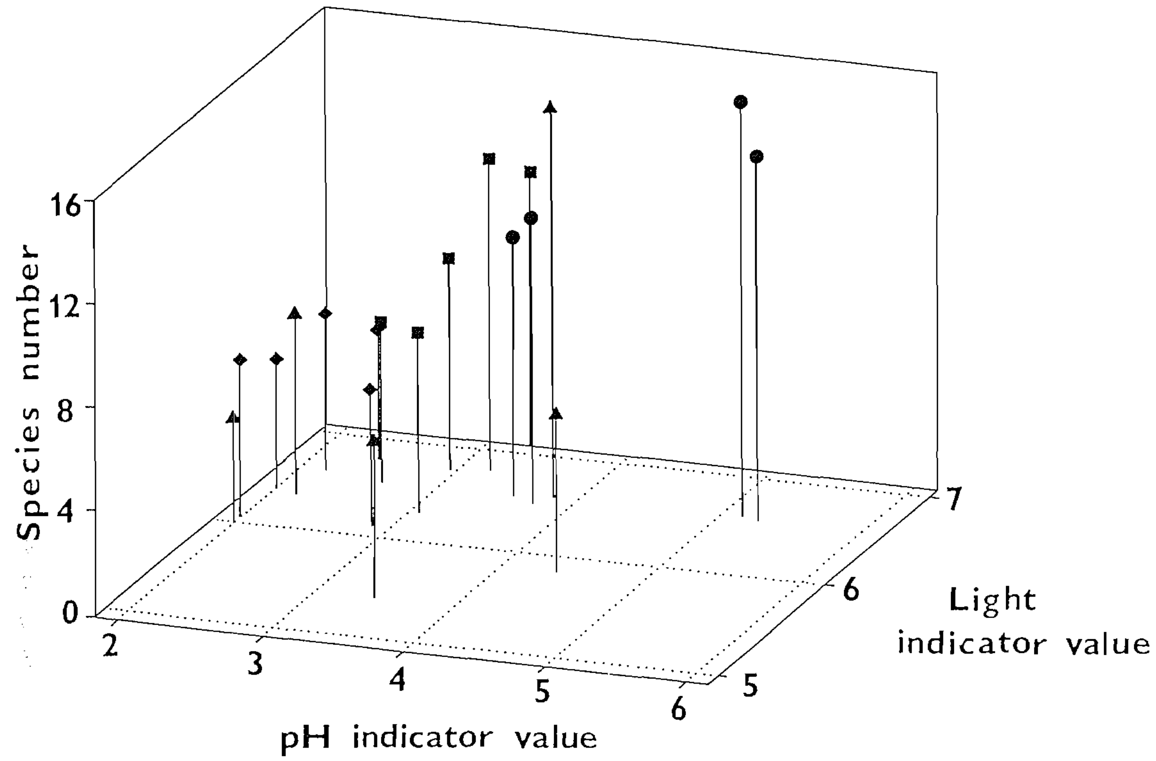

Fig. 3. Effect of light availability and soil acidity (expressed as pH value) on the number of species in a relevé. Habitat types can be distinguished according to symbols used: ● wet meadows (D), ▲ non-reclaimed bare spots (E), ■ young reclaimed sites (F), ◆ old reclaimed bare spots (G). Data from bare spots.

interaction of life form and strategy was significant ($P<0.05$): grasses and grass-like species with pure C-strategy showed the highest scores (0.80) whereas those with other strategies had the lowest scores on the second axis (-0.63).

Pattern of species diversity

The multiple regression relating species diversity to the environmental conditions was highly significant (Table 5) regardless whether the diversity was expressed as a number of species or using Shannon index H′. In the former case, it explained 76.3% of variance in the data set, whereas in the latter one the predictors included accounted for 60.9% of variance. Both the species number and H′ value were negatively correlated with soil acidity and increased with light indicator value; consequently the second axis in the ordination diagram Fig. 2a may be roughly identified with the gradient in species diversity. The relationship between the species number and the both best predictors is shown on Fig. 3.

Discussion

Factors responsible for vegetation differentiation

Areas under the influence of SO_2 deposition undoubtedly represent an extreme ecological situation. Beside the direct SO_2 adverse effect on vegetation (Halbwachs 1983), long-term indirect effects from acidifying precipitation and consequently soil have been reported (Krause 1989; Fuhrer 1990). In the present study, acidity was found to be the main soil factor responsible for structuring community composition in bare spot vegetation (Table 3). The role of nutrient, especially nitrogen, appears to be of minor importance. Generally, under less extreme conditions, nitrogen affects principally the vegetation pattern (Grime 1979; Tilman 1988) and index of soil fertility is often an excellent predictor of community composition (Christensen & Peet 1981). However, vegetation restricted to infertile soils has been reported to show lower response to nutrient addition than do related plants from more-fertile soils (see Chapin *et al.* 1986 for list of references). This is clearly the case in bare spot vegetation in the region studied: Decreased metabolic activity of decomposition microflora, leaching losses of nitrogen and resulting massive efflux of nutrients (Klein & Perkins 1988) and a delay of litter decomposition (Chapin *et al.* 1986) are among the main consequences of acid soil environment and, in turn, contribute to shifting of pH values towards more acidic reaction (Halbwachs 1983).

Two step analysis of the effect of environmental factors performed in this study stresses the importance of hierarchical approach to analyses of vegetation response to environment. Considering the "landscape" level within the region studied, light appears to be the factor best explaining variation in vegetation as it reflects the differences between forest and non-forest communities. When the bare spot vegetation was treated separately the highest variation, with respect to the resource situation, was found along the acidity/moisture gradient. By approaching the even more detailed level, an increasing importance of interspecific relationships and competition processes in determining the community pattern may be found as it has been shown by detailed analysis of *Calamagrostis villosa*-dominated spontaneous bare spot (Pyšek 1990).

The effect of soil removal was only obvious in young reclaimed plots. Convergent development which took place between reclaimed and non-reclaimed bare spots resulted in the fact that 15 years old plots could not have been distinguished from 5–10 years old bare spots having originated spontaneously after the timber extraction. Low species diversity (Table 1) is suggested to contribute to this phenomenon. Generally, most ecosystems under pollution stress show a decrease in the species number by elimination the most sensitive species and promotion of a considerable increase in the resistant species abundances (Halbwachs 1983). A limited pool of species capable of successful performance under the given conditions probable also contributes to the successional development converging between plots of different starting situations.

Pattern of species dominance and diversity

Natural plant communities are normally composed of several species of slightly different characteristics and ecological requirements. Consequently, each species in a community may be limited by a slightly different combination of resources (Chapin *et al.* 1987). Under environmentally stressfull conditions as those in the present study, the pattern of dominance may be even more obvious due to low number of participating species and distinct appearance of a relatively little number of environmental factors.

The species diversity in deforested sites was much lower (mean $H' = 1.24$, 2.27, and 1.34 for non-reclaimed, young reclaimed and old reclaimed bare spots, respectively) in comparison with natural wet meadows ($H' = 4.10$). In a previous paper (Pyšek 1990), the decrease in species diversity in bare spots was shown to be associated with change of the dominance/diversity curve from log-normal to log-series. This trend is suggested to indicate low intensity of species interactions, minor role of interspecific competition and a large influence of a low number of, or even a single, environmental restricting factors (Bobbink *et al.* 1987; see also Magurran 1988 for a review). Although the species diversity is usually an outcome of many contributing factors (Diamond 1988), in the present paper low species diversity was associated with high soil acidity which appeas to be the main controlling factor. Similar trend, i.e. negative correlation between species diversity and soil acidity, has been previously reported from other vegetation types (Vermeer & Berendse 1983; Rey Benayas & Scheiner 1993). In vegetation of deforested sites in the studied region, acidity had an effect on species diversity similar to that of increased nutrient level in chalk grasslands which has been also shown to reduce species diversity (Willems 1985; Bobbink *et al.* 1987; Willems *et al.* 1993; but see Huston 1990; Wilson & Tilman 1991). In both cases, the reduction in species number was due to increased performance of a single strong dominant species.

Generally, using the species number provided better fit to the data (76.3% of variance explained) than considering H′ values (60.9%). *Calamagrostis villosa*, being a strong dominant, reduced H′ values in most samples so that the differences were less profound than if simply the species number was considered. Another possible explanation is that the number of species is a characteristic measurable with higher precision than is the species diversity (see Lepš & Hadincová 1992) so that the bigger estimation error could have biased the results in the latter case.

Some generalizations concerning the pattern of dominance in the bare spot vegetation emerge from the data summarized in Table 6. Since there are no remarkable differences in the way of pollination and mode of dispersal and, according to Grime's classification (Grime 1979; Grime *et al.* 1988) all the species are of at least a combination of C-strategy, it may be suggested that environmental conditions are, to a major extent, responsible for the pattern of species dominance in deforested areas. Among those, soil acidity and moisture form a distinct gradient along which the dominant species are arranged. It appears that rhizomatous grasses producing a large amount of litter which is, in addition, difficult to decompose are successful on very acid soils (pH values in bare spot vegetation in the area under study ranged from 3.59 to 5.25, see Pyšek 1992a). Accumulated litter, moreover, was shown to suppress performances of the majority of other species (Duffey *et al.* 1974; Sydes & Grime 1981; Pyšek 1990) and by producing litter, the species itself may promote the soil acidification (Chapin *et al.* 1986). All species with high acidity-scores are considered stress tolerators according to Grime's classification (Frank & Klotz 1990). The only exception is *Calamagrostis villosa*, being considered a C-strategist; this reflects, however, the fact that presumably rather the natural occurrence was taken in account in classifying this species. Considering its behaviour in secondary habitats, the CSR strategy would fit better to the real situation. Lower disturbance scores are typical of most grasses (*Deschampsia flexuosa, D. caespitosa, Holcus mollis*, except of *C. villosa*) compared to broad-leaved forbs (*Rumex acetosella, Senecio nemorensis* subsp. *fuchsii, Epilobium angustifolium*) which indicates better ability in the latter group to colonize newly created bare ground. The success of *Juncus effusus* and, in particular *Deschampsia caespitosa* is obviously associated with higher moisture level.

Table 6. Characteristics of dominant species of the bare spot vegetation. Species occurring at least in one vegetation type (D–E) with frequency higher than 40% and value 3 in Braun-Blanquet scale were considered as dominant. Habitats: A–spruce forest, B–forest roads, C–road margins and ditches, D–wet meadows, E–non-reclaimed bare spots, F–young reclaimed sites, G–old reclaimed bare spots. Strategies according to the classification of Grime (Grime 1979, Grime *et al.* 1988) and data on pollination (w–wind, i–insect, s–self pollination) and dispersal (w–wind, wa–water, a–by ants, m–man-mediated) were taken from Frank and Klotz (1990).

	Occurrence	Species traits				
	Habitat	Life form	Litter	Pollination	Dispersal	Strategy
Calamagrostis villosa	A–G	Rhizomatous grass	+	w	w	CSR
Deschampsia caespitosa	B, D	Tussock grass		w	w	C
Deschampsia flexuosa	G	Rhizomatous grass	+	w	w	CS
Epilobium angustifolium	E	Perennial herb		i, s	w	C
Holcus mollis	E, B	Rhizomatous grass	+	w	w	CSR
Juncus effusus	D	Tussock graminoid		w	w, wa	C
Rumex acetosella	F	Perennial herb		w, i, s	w, wa	CSR
Senecio nemorensis subsp. *fuchsii*	B, E	Perennial herb		i, s	w, a	C

The present study has shown that the vegetation pattern in areas deforested due to acid air pollution is ruled by the relatively low number of environmental factors. However, correlating vegetation pattern with environment can only suggest possible causes of variation in vegetation which should be then tested experimentally (Olsvig-Whittaker 1988).

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References

Bobbink, R., During, H.J., Schreurs, J., Willems, J. & Zeman, R. 1987. Effects of selective clipping and mowing time on species diversity in chalk grassland. Folia Geobot. Phytotax. 22: 363–376.

Chapin III, F.S., Bloom, A.J., Field, C.B. & Waring, R.H. 1987. Plant responses to multiple environmental factors. Bioscience 37: 49–57.

Chapin III, S.F., Vitousek, P.M. & van Cleve, K. 1986. The nature of nutrient limitation in plant communities. Amer. Natur. 127: 48–58.

Christensen, N.L. & Peet, R.K. 1981. Secondary forest succession on the North Carolina Piedmont. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds) Forest succession: concepts and applications, pp. 230–245. Springer Verlag, New York.

Conert, H.J., 1989. Calamagrostis villosa. In: G.Hegi: Illustrierte Flora von Mitteleuropa. Ed. 3. Paul Parey, Hamburg.

Diamond, J. 1988. Factors controlling species diversity: Overview and synthesis. Ann. Missouri Bot. Gard. 75: 117–129.

Duffey, J. et al. 1974. Grassland ecology and management. Chapman & Hall, London.

Ellenberg, H. et al. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scr. Geobot. 18: 1–248.

Fiala, K. 1989. Underground biomass of three typical grass stands growing on areas deforested by air pollution. Ekológia (CSSR) 8: 105–115.

Fiala, K., Jakrlová, J. & Zelená, V. 1989. Biomass partitioning in two Calamagrostis villosa stands on deforested sites. Folia Geobot. Phytotax. 23: 207–210.

Frank, D. & Klotz, S. 1990. Biologisch-ökologische Daten zur Flora der DDR. Martin-Luther-Univ., Halle.

Fuhrer, E., 1990. Forest decline in Central Europe. Additional aspects of its cause. Forest Ecol.Manage. 37: 249–260.

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

Grime, J.P., Hodgson, J.G. & Hunt, R. 1979. Comparative plant ecology. A functional approach to common British species. Unwin Hyman, London.

Halbwachs, G. 1983. Effects of air pollution on vegetation. In: Holzner, W. & Numata, M. (eds) Man's impact on vegetation, pp. 55–67. Junk, The Hague.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187–211.

Huston, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. J. Biogeogr. 7: 147–157.

Klein, R.M. & Perkins, T.D. 1988. Primary and secondary causes and consequences of contemporary forest decline. Botanical Review 54(1): 1–43.

Krause, G.H.M., 1989. Forest decline in Central Europe: The unravelling of multiple causes. In: Grubb, P.J. & Whittaker, J.B. (ed) Toward a more exact ecology. Blackwell, Oxford.

Lepš, J. & Hadincová, V. 1992. How reliable are our vegetation analyses? J. Veget. Sci. 3: 119–124.

Magrurran, A. 1988. Ecological diversity and its measurement. Croom Helm, London.

Moldan, B. (ed) 1990. Životní prostředí České republiky (Environment of the Czech republic). Academia, Praha.

Montgomery, D.C. & Peck, E.A. 1982. Introduction to linear regression analysis. Wiley, New York.

Olsvig-Whittaker, L. 1988. Relating small-scale vegetation patterns to the environment. In: During, H.J., Werger, M.J.A. & Willems, H.J. (eds) Diversity and pattern in plant communities, pp. 87–94. SPB, The Hague.

Peet, R.K., 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5: 285–307.

Pyšek, P. 1990. The influence of Calamagrostis villosa on the species diversity of deforested sites in the Krušné hory Mts. Preslia 62: 323–335.

Pyšek, P. 1991. Biomass production and size structure of Calamagrostis villosa in different habitats. Preslia 63: 9–20.

Pyšek, P. 1992a. Dominant species exchange during succession in reclaimed habitats: a case study from areas deforested by air pollution. Forest Ecol. Manag. 54: 27–44.

Pyšek, P. 1992b. Seasonal changes in response of Senecio ovatus to grazing by chrysomelid beetle Chrysomela speciosissima. Oecologia 91: 596–602.

Rey Benayas, J.M. & Schenier, S.M. 1993. Diversity patterns of wet meadows along geographical gradients in Spain. J. Veget. Sci. 4: 103–108.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. Freeman, San Francisco.

Sydes, C. & Grime, J. P. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. J. Ecol. 69: 237–248.

Ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69–77.

Ter Braak, C.J.F. 1988. CANOCO–a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis. Wageningen.

Tilman, D., 1988. Plant strategies and processes and the dynamics and structure of plant communities. Princeton Univ. Press, Princeton.

Tutin, T.G. et al. 1964–1980. Flora Europaea. Cambridge Univ. Press.

Vermeer, J.G. & Berendes, F. 1983. The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. Vegetatio 53: 121–126.

Westhof, W. & van der Maarel, E. 1978. Braun-Blanquet approach. In: Whittaker, R.H. (ed) Classification of plant communities, Handbook of Vegetation Science.

Willems, J.H. 1985. Growth form spectra and species diversity in permanent grassland plots with different management. In: Schreiber, K.-F. (ed) Sukzession auf Grünlandbrachen, pp. 35–43. Münster Geogr. Arbeit. 20, Paderborn.

Willems, J.H., Peet, R.K. & Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. J. Veget. Sci. 4: 203–212.

Wilson, S.D. & Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72: 1050–1065.