Central European pine bogs change along an altitudinal gradient

Změny středoevropských rašelinišť s borovicí blatkou a jejími kříženci podél gradientu nadmořské výšky

Marek Bastl[1], Marek Burian[1], Jan Kučera[1], Karel Prach[1,2], Ladislav Rektoris[3] & Milan Štech[1]

[1]*Department of Botany, Faculty of Science, University of South Bohemia in České Budějovice, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic, e-mail: marek.bastl@prf.jcu.cz, marek.burian@prf.jcu.cz, jan.kucera@prf.jcu.cz, prach@prf.jcu.cz, stech@prf.jcu.cz;* [2]*Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ-379 82 Třeboň, Czech Republic;* [3]*Administration of the Protected Landscape Area Třeboňsko, Valy 121, CZ-379 01 Třeboň, Czech Republic, e-mail ladislav.rektoris@schkocr.cz*

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Vegetation analyses (phytosociological relevés) of 20 peat bogs arranged along an altitudinal gradient in the southern part of the Czech Republic, Central Europe, revealed relationships between vegetation and environmental gradients. Six of the peat bogs were investigated in detail. The bogs were dominated by *Pinus rotundata*, a species endemic to Central Europe, and its hybridogenous populations with *P. mugo* (the hybrid is called *P.* ×*pseudopumilio*), with increasing proportions of the latter at higher altitudes. Data were processed using indirect (DCA) and direct (CCA) gradient analyses. Environmental variables (depth of the water table, mean and minimum temperatures, precipitation, pH, conductivity, NH_4 and PO_4 concentrations, total P, but not total N nor NO_3 concentration), as well as biotic characteristics of the sites, such as species composition, and growth form of the dominant pines, were closely correlated with altitude. Woody species, herbs and bryophytes responded to the altitude similarly. Results also indicated the unique characteristics of each bog.

Keywords: altitude, environmental gradients, growth form, mountain pine, *Pinus mugo*, *Pinus* ×*pseudopumilio*, *Pinus rotundata*, *Pinus uncinata*

Introduction

Central European ombrotrophic bogs and poor fens with bog pines are unique ecosystems, having persisted continuously at the same sites and approximately to the same extent since the early Holocene period (Neuhäusl 1972, Jankovská 1980, Mikkola & Spitzer 1983, Steiner 1992, Svobodová et al. 2002). Continuity and stability over these time scales is unique for Central European ecosystems. Pine bogs are long-term habitat islands (Spitzer 1994), offering opportunities for micro-speciation and occurrence of relic species, yet they are vulnerable to external disturbances. Their extrazonal character in occurring outside the main zone of peatlands in N and NE Europe, makes the Central European peat bogs of interest in a wide biogeographical context (Dierssen 1996, Dierssen & Dierssen 2001).

The similarity of the environmental conditions among such bogs, especially with respect to the water regime, low amounts of available nutrients and low pH, facilitates comparison of vegetation at particular localities. The rather harsh environment restricts the number of biota in pine bogs. Consequently, factors responsible for biotic structure are easier to elucidate than in most other ecosystems (Økland 1992). Descriptions of the strong relationship between vegetation and environmental gradients, especially the level of the water table and peat-nutrient concentrations, are available for boreal peatlands (e.g., Malmer 1962, Damman 1986, Økland 1990, Jeglum & He 1995, Nordbakken 1996), bogs in the S Alps (Gerdol 1995, Bragazza & Gerdol 1999) and some Central European bogs and peat fens (Neuhäusl 1972, Dierssen & Dierssen 1984, Navrátilová & Navrátil 2005, Grootjans et al. 2006, Hájek et al. 2006, Navrátilová et al. 2006). However, there is no detailed information for Central European pine bogs on changes in environmental gradients and vegetation with altitude.

In Central European pine bogs there is an endemic species, *Pinus rotundata* Link, and its hybridogenous cline with *P. mugo* Turra. *Pinus rotundata* has a small geographical range, which includes parts of Germany, Austria, Poland and the Czech Republic (Jalas & Suominen 1973), with the centre of distribution in the southwestern part of the Czech Republic (Fig. 1). The typical tree-shaped *P. rotundata* occurs only in submontaneous bogs. At higher altitudes it forms introgressive hybrids with *P. mugo* and the shape changes to shrub-like (Businský 1998, Skalický 1988).

Previous studies on Central European pine bogs have concentrated on one particular locality (Neuhäusl 1975, Münzbergová et al. 1999, Kučerová et al. 2008), a particular taxon, or special topics such as palynology (Jankovská 1980) or vegetation classification (Neuhäusl 1972). Only pine bog *Lepidoptera* (Spitzer 1994, Spitzer et al. 1999) have been studied in a broader geographical context.

The aims of this study were to describe, and as far as possible explain, the gradients in vegetation in relation to environmental factors. The following questions are addressed: (i) How does the vegetation pattern change with altitude? (ii) How are particular community and environmental characteristics related to altitude? (iii) Do particular vegetation layers respond to environmental gradients in the same way?

Material and methods

Taxonomical and phytogeographical remarks on bog pines

There are several rather contradictory taxonomic views on bog pines. One, in our opinion an extreme approach, is to include all taxa in *Pinus mugo* Turra (Zoller 1981, Christensen 1987). Another is to accept *P. uncinata* Ramond, with two taxa: *P. uncinata* s.s. and *P. rotundata* Link at the subspecific level (Gaussen et al. 1993). *Pinus rotundata* is also often considered to be a polymorphous hybridogenous type between *P. mugo* and *P. uncinata* (e.g., Wisskirchen & Haeupler 1998, Fischer et al. 2005). Because of the relatively clear morphological, geographical and ecological differentiation of the taxa, we have chosen to treat them as three separate species, i.e. *P. mugo, P. uncinata*, and *P. rotundata* (Skalický 1988, Businský 1998).

Pinus mugo is a typical shrubby species of the subalpine belt in central and SE Europe, rarely occurring at lower altitudes. *Pinus uncinata* is a tree-shaped species occurring mostly on mineral sites in W European mountains. *Pinus rotundata* is a tree-shaped species endemic to central European submontane peat bogs (Fig. 1). In our area, where *P. rotundata* grows with *P. mugo*, they hybridize forming a hybridogenous cline with a shrubby growth form increasing in proportion with altitude. The hybrids are sometimes

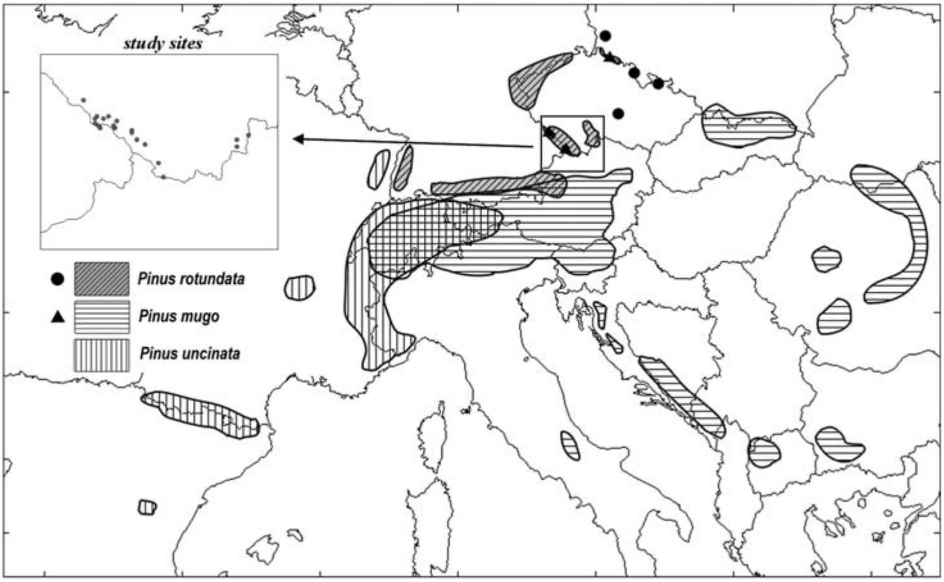

Fig. 1. – Geographical range of *Pinus rotundata*, *P. uncinata* and *P. mugo* with the location of the study sites. Adapted from Jalas and Suominen (1973).

called *P.* ×*pseudopumilio* (Willk.) Beck. Moreover, *P. rotundata* hybridizes with *P. sylvestris* L. (*P.* ×*digenea* Beck), especially at the margins and on disturbed sites in bogs (Skalický 1988).

Study sites

Twenty peat bogs were selected a priori for our study. Our selection was based on the following three criteria: (i) a minimum area of 0.1 km^2, (ii) no evident human disturbance, (iii) satisfies our goal of covering a broad altitudinal range of pine bogs. The low number of peat bogs selected resulted from administrative restrictions, accessibility and undisturbed character of these strictly protected areas.

The locations of the study sites are shown in Fig.1, geographical coordinates, altitude, mean annual temperature and mean annual precipitation are listed in Table 1. We chose S Bohemia as our location because it is the centre of the *P. rotundata* and *P.* ×*pseudopumilio* distribution range, with the largest number of localities spread along an altitudinal gradient. Six out of the twenty peat bogs studied were selected for a more detailed study (repeated sampling was only allowed by the authorities in a limited number of protected areas). This selection included two basic types of pine bogs: (i) pine bogs with the tree-shaped *P. rotundata* – 3 localities (sites 1, 5 and 10); (ii) pine bogs with the prevailing shrubby form of *P. rotundata* introgressively hybridized with *P. mugo* (called *P.* ×*pseudopumilio*) – 3 localities (sites 6, 11, and 15). A final criterion for selection was the accessibility of the site for repeated sampling and monitoring.

Field sampling

One 10 × 10 m plot was established in the centre of each of the 14 bogs studied in 1997. A phytosociological relevé was made of each plot in 2001 using the Braun-Blanquet seven-grade scale (van der Maarel 1979) and the maximum height of the shrub or tree layer (which was identical with the maximum height of bog pines) was measured. Nomenclature follows Kubát et al. (2002) for vascular plants and Kučera & Váňa (2003) for bryophytes.

In the centre of the six bogs studied in detail, one 50 × 50 m permanent research plot was established in 1997. One 10 × 10 m subplot was established in each of the four corners of these plots. A phytosociological relevé was made of each subplot in 2001 using the same methods as above. The level of the groundwater table (measured in bore holes to the nearest 0.5 cm), maximum temperature and minimum temperature (both measured to the nearest 0.1 °C) were measured in the centre of each permanent plot every two weeks during the growth season (May – October) in 1998 and 1999, and average values calculated. The reference level for the groundwater table position was the average ground level in the plot. Maximum and minimum temperatures were recorded from thermometers exposed 15 cm above the surface.

Chemical analyses of ground water samples were performed eight times during the growth season in 1998. Conductivity and pH were measured and NH_4^+, NO_3^-, total N, PO_4^{3-} and total P were analysed using flow injection analysis (FIA) (Tecator Inc; Sweden) and average values calculated. The conductivity data were standardized to 20°C (variable EC), and the conductivity contributed by hydrogen ions (Sjörs 1950) was subtracted in order to eliminate the effect of varying acidity. Because subtraction leads to negative values for the corrected conductivity in some cases, 0.2 was added to pH (Du Rietz 1949 cited by Sjörs 1950) prior to the subtraction and the resulting corrected conductivity (variable ECcorr) used in all analyses.

Mean height, trunk density and mean trunk diameter of the bog pines were measured in each permanent plot and average values calculated. The trunk diameter was measured at DBH for trees and at 10 cm above the soil surface for shrubs.

The altitude of each plot was derived from detailed maps. Mean annual precipitation and mean annual temperatures at each locality were calculated by the Czech Hydrometeorological Institute office in České Budějovice in 2006.

Data analysis

Thirty-eight phytosociological relevés, including 92 species of vascular plants and bryophytes (63 bryophytes, 1 fern, 20 herbs and 8 woody species) were made in 14 localities with one plot and the six localities studied in detail using four subplots. This data plus corresponding environmental data made up the first data set (Electronic Appendix 1, Table 1). The phytosociological relevés of the subplots from bogs studied in detail and corresponding environmental data (Electronic Appendix 1, Table 1, 2) formed the second data set (24 relevés, 76 species). Species cover was expressed as an ordinal transformation (1–7) of the Braun-Blanquet seven-grade cover-abundance scale (van der Maarel 1979). In all the tests the subplots were not treated as independent replicates because the environmental variables were collected for the plots.

Table 1. – Location, altitude, mean annual temperature and mean annual precipitation at the 20 peat bogs arranged according to increasing altitude. Six peat bogs studied in detail are indicated in bold. For details see the text.

Site	Site number	Latitude	Longitude	Altitude (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)
Červené blato	**1**	48°52' N	14°52' E	470	7.4	660
Žofinka	2	48°49' N	14°52' E	474	7.4	675
Široké blato	3	48°54' N	14°59' E	495	7.3	680
Pěkná	4	48°50' N	13°57' E	735	5.5	795
Kyselov	**5**	48°41' N	14°03' E	735	5.5	950
Mrtvý luh	**6**	48°52' N	13°52' E	740	5.2	900
Malá niva	7	48°55' N	13°49' E	751	5.4	840
Velká niva	8	48°56' N	13°49' E	755	5.4	840
Multerberg	9	48°36' N	14°08' E	790	5.7	960
Novohůrecká slať	**10**	49°09' N	13°20' E	865	5.5	1185
Chalupská slať	**11**	49°00' N	13°40' E	910	4.8	890
Ždárek	12	48°57' N	13°39' E	985	4.9	980
Bukovská slať	13	48°58' N	13°38' E	987	5.0	985
Mlýnská slať	14	49°01' N	13°27' E	1050	2.6	1600
Jezerní slať	**15**	49°02' N	13°35' E	1050	2.0	1090
Tříjezerní slať	16	49°02' N	13°28' E	1066	2.7	1500
Tetřeví slať	17	49°01' N	13°32' E	1140	4.0	1200
Březina	18	48°58' N	13°29' E	1150	2.4	1800
Hraniční slať	19	48°57' N	13°30' E	1175	2.3	1720
Novohorský močál	20	48°59' N	13°27' E	1210	2.2	1860

Table 2. – Site characteristics of the six peat bogs studied in detail (see Table 1) arranged according to increasing altitude. See text for details.

Site number	1	5	6	10	11	15
Bog pine characteristics						
Mean height (m)	6.11	5.36	0.78	4.31	1.98	0.76
Trunk density (trunk.m^{-2})	0.27	0.35	2.09	0.63	3.30	1.84
Mean trunk diameter (cm)	19.5	11.3	2.5	10.6	4.3	2.8
Abiotic factors						
Altitude (m a.s.l.)	470	735	740	865	910	1050
Groundwater table level (cm)	–25.8	–24.5	–9.2	–16.6	–9.6	–13.2
Mean maximum temperature (°C)	29.9	31.1	34.3	35.9	33.2	31.9
Mean minimum temperature (°C)	2.0	2.7	–2.9	–1.1	–3.2	–5.0
Chemical analyses						
pH	3.36	3.48	3.65	3.43	3.49	3.73
EC (µS)	164	114	93	120	93	80
ECcorr (µS)	73	46	47	45	27	42
NH_4 (µg·l^{-1})	1803	741	52	311	154	49
NO_3 (µg·l^{-1})	793	873	1524	1466	1052	467
total N (µg·l^{-1})	2183	3159	2528	2399	2347	1526
PO_4 (µg·l^{-1})	143	71	10	36	30	14
total P (µg·l^{-1})	207	98	53	48	57	37

Detrended Correspondence Analysis (DCA) was used to compare species composition among the plots. The axes were interpreted by analysis of correlations between sample scores and environmental variables. The relationships of species composition to environmental variables were evaluated by Canonical Correspondence Analysis (CCA) of the species data set with all species included and with all species from the tree and shrub layer (E_{32}) excluded. Forward selection of environmental variables was performed.

The effect of woody species on ground layer vegetation was tested using CCA, in which the cover of particular woody species and composite variables, i.e. cover of all trees and shrubs (Treeall3), cover of all pines: *P. rotundata*, *P. ×pseudopumilio*, *P. sylvestris* and *P. ×digenea* (Pinuall3) and cover of all bog pines: *P. rotundata*, *P. ×pseudopumilio* and *P. ×digenea* (Pinubog3) were used as environmental variables in the species data set from which all species from the tree and shrub layer (E_{32}) were excluded. Significance was determined using the distribution-free Monte Carlo permutation test. In this test, the distribution of the test statistics under the null hypothesis was generated by restricted random permutations of environmental data (ter Braak & Šmilauer 2002). The DCA and CCA analyses were performed using the software CANOCO for Windows version 4.5 (ter Braak & Šmilauer 1998).

The dependence of *P. rotundata* and *P. ×pseudopumilio* cover and the maximum height of bog pines on altitude was tested and visualized using generalized linear models (GLM, McCullagh & Nelder 1989) implemented in S-plus version 4.5 (Statistical Sciences 1999). The matrix of Pearson correlation coefficients between the recorded variables and that of Spearman correlation coefficients between recorded variables and sample scores on the DCA axes were calculated.

Results

The characteristics considered for all the pine bogs studied generally exhibited a unidirectional trend in relation to altitude (Fig. 2, 3). Many correlations between the site characteristics and altitude were significant (Table 3). The results of the DCA ordinations for 38 plots and all species are shown in Fig. 2 and Table 4. The three inset diagrams in Fig. 2 demonstrate the more or less constant position of the sites if the woody species are excluded from the ordination and only herbs (E_1) or only bryophytes (E_0) are included.

Species are arranged along the first ordination axis in the main DCA diagram in a sequence approximately from a group of forest species (e.g., *Ledum palustre*, *Bazzania trilobata*, *Dicranum polysetum*) through species typical of all peat bogs (e.g., *Vaccinium uliginosum*, *Oxycoccus palustris*, *Sphagnum magellanicum*) and located naturally near the centre of the diagram, to a group of species characteristic of open, mountain peat bogs (*Trichophorum cespitosum*, *Empetrum nigrum*, *Sphagnum fuscum*, *S. russowii*). The complete species list from the phytosociological relevés is given in Electronic Appendix 1.

The sites are clearly arranged along the first ordination axis from low altitude (right side) to high altitude (left side) sites in all DCA diagrams (Fig. 2). But there are some exceptions. For example, site no. 6 (Mrtvý luh) is a bog at the bottom of a valley, which is subject to extreme climatic inversions. This site is more characteristic of those at higher altitudes, including the presence of a shrubby form of the pine.

Results of correlation analysis of the scores on the DCA ordination axes and measured variables for all plots are shown in Table 3. Results of correlation analysis of the scores on the DCA ordination axes and measured variables for the bogs studied in detail (the centroid position for each locality was used) show that the first ordination axis is best correlated with biotic characteristics (Table 3). Correlation analysis indicates that most of the characteristics of the bogs studied in detail exhibit a unidirectional trend with altitude (Table 3).

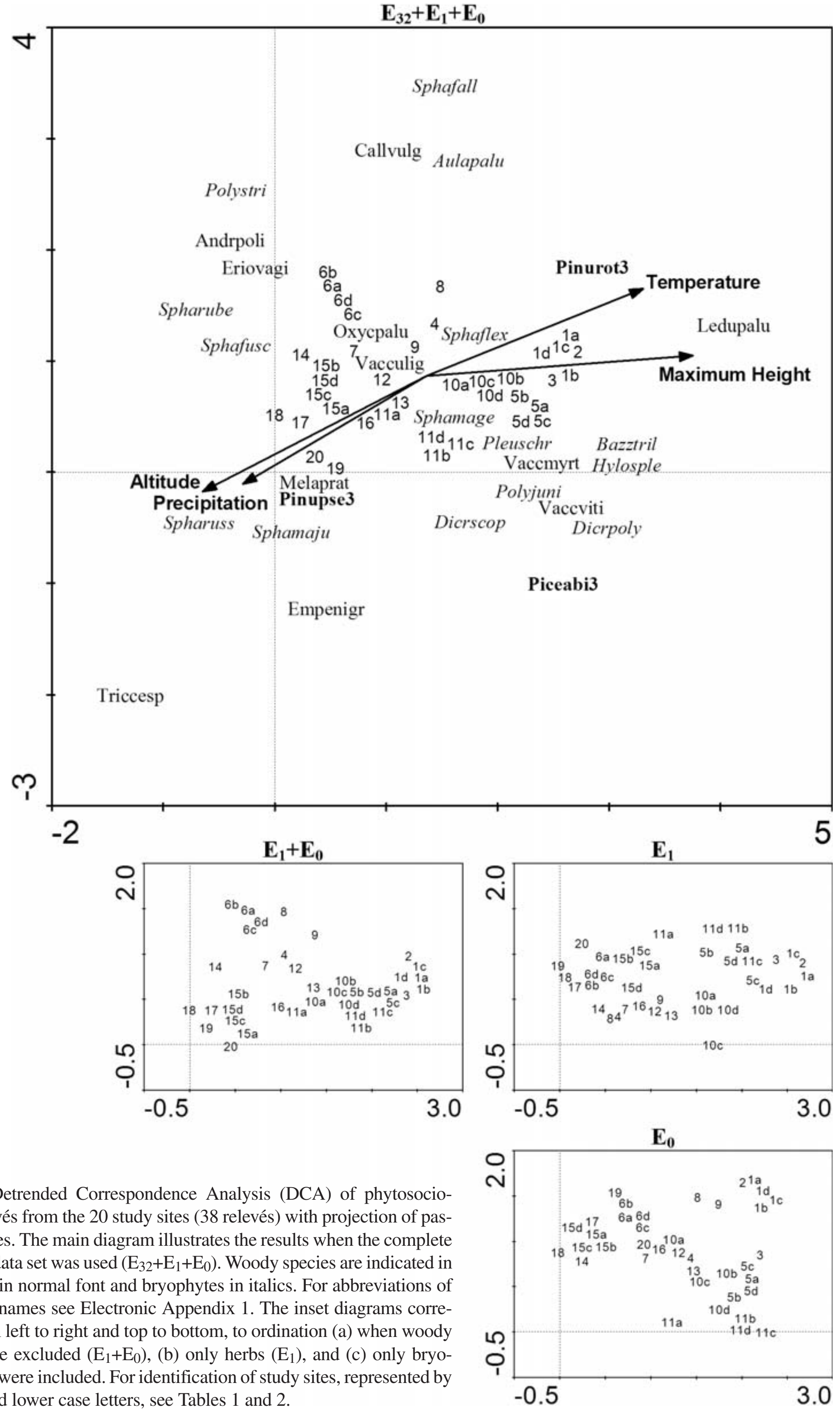

Fig. 2. – Detrended Correspondence Analysis (DCA) of phytosociological relevés from the 20 study sites (38 relevés) with projection of passive variables. The main diagram illustrates the results when the complete vegetation data set was used (E_{32}+E_1+E_0). Woody species are indicated in bold, herbs in normal font and bryophytes in italics. For abbreviations of the species names see Electronic Appendix 1. The inset diagrams correspond, from left to right and top to bottom, to ordination (a) when woody species were excluded (E_1+E_0), (b) only herbs (E_1), and (c) only bryophytes (E_0) were included. For identification of study sites, represented by numbers and lower case letters, see Tables 1 and 2.

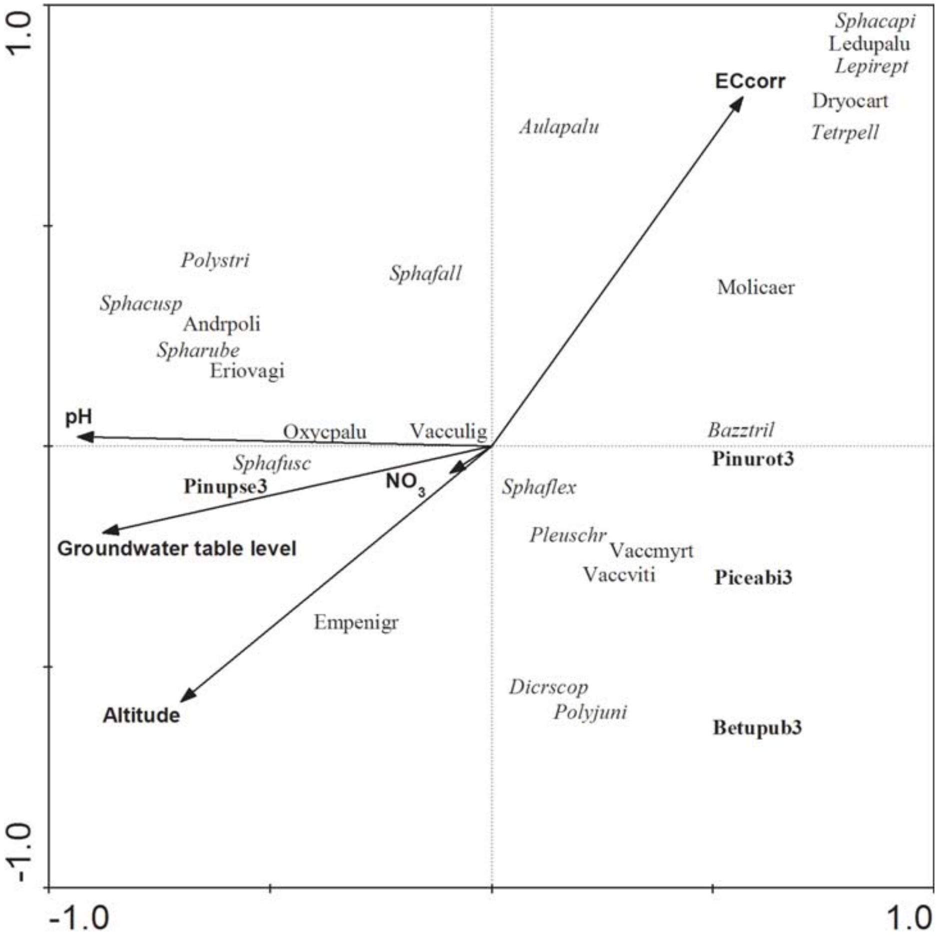

Fig. 3. – Canonical Correspondence Analysis (CCA) of phytosociological relevés from the six sites studied in detail (24 relevés) and abiotic environmental characteristics chosen by forward selection of variables. For abbreviations of the species names see Electronic Appendix 1.

Correlations between pH and PO_4 and pH and NH_4 were found (Table 3). Also the biotic characteristics of the dominant pines were related to altitude as well as to some other environmental factors (Table 3). The physiognomy of the site, which was determined by the growth form of the dominant pine, was correlated with some micro-climatic characteristics such as minimum temperature (Table 3). There were high mutual correlations between the trophic factors, with only total N and NO_3 contents not being well correlated to any other factor (Table 3).

Forward selection in CCA was used (diagram not presented) to select the best explanatory variables for the vegetation composition of the pine bogs studied in detail. Significant explanatory variables, in order of importance, were: mean height, ECcorr, mean trunk density, altitude and maximum height. The first CCA axis ($\lambda_1 = 0.437$) was highly correlated with mean height and explained 31.2% of the variability in the species data. The effect of mean height was highly significant (F = 9.73; P = 0.003; 9999 permutations) when

Table 3. – Selected Spearman correlation coefficients between DCA axis and measured variables, and Pearson correlation coefficients between measured variables for all plots (All) and plots studied in detail (Detail). Correlations in bold are significant ($P < 0.05$).

Plots	Variable 1	Variable 2	r	P
All	DCA axis 1	altitude	**–0.83**	0.0003
All	DCA axis 1	maximum height	**0.92**	0.0001
All	DCA axis 1	precipitation	**–0.79**	0.0005
All	DCA axis 1	mean temperature	**0.87**	0.0002
Detail	DCA axis 1	maximum height	**1.00**	0.0298
Detail	DCA axis 1	minimum temperature	**–0.89**	0.0409
Detail	DCA axis 1	water level	–0.83	0.0553
Detail	DCA axis 1	pH	**–0.94**	0.0298
Detail	DCA axis 1	NH_4	**1.00**	0.0298
Detail	DCA axis 1	PO_4	**0.94**	0.0409
Detail	DCA axis 1	mean height	**1.00**	0.0298
Detail	DCA axis 1	mean trunk diameter	**0.94**	0.0409
Detail	DCA axis 1	mean temperature	**0.93**	0.0444
All	altitude	maximum height	**–0.82**	< 0.0001
All	altitude	precipitation	**0.86**	< 0.0001
All	altitude	mean temperature	**–0.93**	< 0.0001
Detail	altitude	minimum temperature	0.78	0.0652
Detail	altitude	water level	0.66	0.1505
Detail	altitude	pH	0.66	0.1530
Detail	altitude	EC	**–0.86**	0.0265
Detail	altitude	ECcorr	**–0.83**	0.0426
Detail	altitude	NH_4	**–0.86**	0.0263
Detail	altitude	PO_4	**–0.84**	0.0362
Detail	altitude	total P	**–0.90**	0.0155
Detail	altitude	mean height	–0.70	0.1216
Detail	altitude	mean trunk diameter	–0.79	0.0591
Detail	altitude	temperature amplitude	0.75	0.0835
Detail	altitude	precipitation	0.79	0.0602
Detail	altitude	mean temperature	**–0.91**	0.0118
Detail	minimum temperature	mean height	**0.94**	0.0059
Detail	minimum temperature	trunk density	–0.78	0.0647
Detail	minimum temperature	mean trunk diameter	**0.86**	0.0298
Detail	water	mean height	**–0.92**	0.0088
Detail	water	mean trunk diameter	**–0.90**	0.0134
Detail	pH	NH_4	–0.73	0.1023
Detail	pH	PO_4	–0.76	0.0791
Detail	ECcorr	mean trunk diameter	0.79	0.0593
Detail	NH_4	PO_4	**1.00**	< 0.0001
Detail	NH_4	total P	**0.99**	0.0003
Detail	PO_4	total P	**0.98**	0.0007

Table 4. – Results of DCA analyses of phytosociological relevés from the 20 study sites (38 relevés). Four variants are presented: complete vegetation data set ($E_{32}+E_1+E_0$); woody species excluded (E_1+E_0); only herbs (E_1); and only bryophytes (E_0) included.

Species			DCA axis 1		DCA axis 2	
			Explained variability (%)	λ_1	Explained variability (%)	λ_2
E_{32}	E_1	E_0	26.5	0.432	8.4	0.137
–	E_1	E_0	25.1	0.397	7.5	0.118
–	E_1	–	35.5	0.468	7.6	0.100
–	–	E_0	22.3	0.395	9.6	0.172

analysed separately. The second CCA axis ($\lambda_2 = 0.229$) was correlated with ECcorr and altitude and explained 16.3% of the variability in the species data. When we excluded all species from the tree and shrub layer (E_{32}) from our analysis, the most significant explanatory variable was maximum height.

When biotic characteristics were excluded, significant explanatory variables, in order of importance, were: pH, ECcorr, ground water table, NO_3 and altitude. The resulting CCA diagram (Fig. 3) shows practically the same pattern of species position as the previous CCA analysis. The first CCA axis ($\lambda_1 = 0.437$) was correlated with pH and explained 31.2% of the variability in the species data. The effect of pH was significant ($F = 8.59$; $P = 0.01$; 9999 permutations) when analysed separately. The second CCA axis ($\lambda_2 = 0.229$) was correlated with ECcorr and altitude and explained 16.3% of the variability in the species data.

Table 5 shows the effect of the cover of particular woody species and of composite cover variables on vegetation tested in CCA, with all species from tree and shrub layers (E_{32}) excluded from the species data. The strongest effect in this analysis was the cover of *P. rotundata* followed by that of all trees and shrubs. *Pinus ×pseudopumilio* cover also had a strong effect. All other woody species had a much lower explanatory power.

The dependence of *P. rotundata* and *P. ×pseudopumilio* cover and the maximum height of bog pines on altitude is shown in Fig. 4. Linear GLM showed a highly significant dependence of *P. rotundata* cover on altitude ($p < 0.001$) as well as maximum height of bog pines on altitude ($p < 0.001$). A second order polynomial model also showed a highly significant dependence of *P. ×pseudopumilio* cover on altitude ($p < 0.001$). *Pinus rotundata* dominates at altitudes under 700 m a.s.l. In the subsequent transitional zone from 700 to 900 m a.s.l. both *P. rotundata* and *P. ×pseudopumilio* were found. *Pinus ×pseudopumilio* dominates at altitudes over 900 m a.s.l. with maximum cover around 1000 m a.s.l. Maximum height of bog pines decreased continuously with increase in altitude.

Discussion

The results clearly demonstrate the importance of the altitude, to which other environmental gradients are closely linked, in influencing the distinct vegetation pattern (Peet 1978, Ellenberg 1988). Based on the correlations between altitude, climatic, soil and vegetation characteristics it is difficult to identify causality. Thus, some conclusions are only speculative. Some relationships may be certainly indirect, mediated especially through the close association of many variables with altitude.

Despite this, causality was probable in some cases. An interesting aspect of these peat bogs is the close association of altitude and the degree of hybridization with the resulting growth form (reflected in height) of the keystone taxa. This growth form was correlated with other abiotic and biotic characteristics of the site, including species composition. We expect a direct influence of the growth form of the edificator on the species composition of the ground layer (Ewald 2002) and some abiotic characteristics (Stoutjesdijk & Barkman 1992, Chen et al. 1995).

Growth form explained even more of the variability in the vegetation data than altitude. The strong correlation between tree physiognomy and minimum temperature suggests that the physiognomy might directly influence the microclimate. Any such causality should be tested by manipulative experiments which are not, however, allowed at these strictly protected sites.

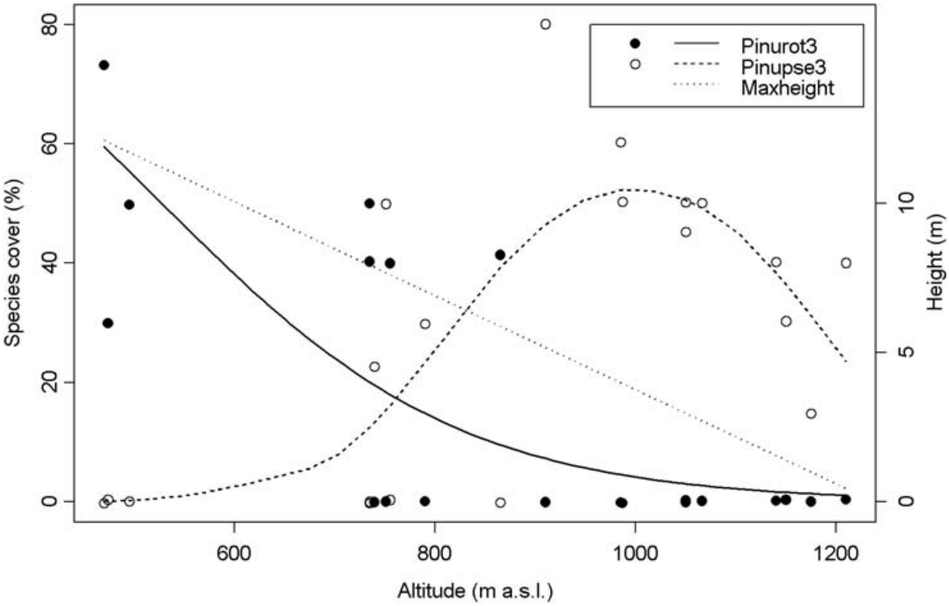

Fig. 4. – The dependence of *P. rotundata* (Pinurot3) and *P. ×pseudopumilio* (Pinupse3) cover and maximum height (Maxheight) of bog pines on altitude visualized using generalized linear models (GLM). Jittering (addition of random noise) was used to separate points with identical values.

Table 5. – Results of Monte Carlo permutation tests (9999 permutations) in CCA analyses used to test the effect of woody species on the herb and moss layers (all trees and shrubs excluded from the data set, only E_1 and E_0 species data included). Composite variables: Treeall3 – cover of all trees and shrubs; Pinuall3 – cover of all pines (*P. rotundata*, *P. ×pseudopumilio*, *P. sylvestris* and *P. ×digenea*); Pinubog3 – cover of all bog pines (*P. rotundata*, *P. ×pseudopumilio* and *P. ×digenea*) are marked in bold. For abbreviations of the other species names see Electronic Appendix 1.

Variable	F	P
Pinurot3	7.132	0.0001
Treeall3	4.848	0.0001
Pinuall3	4.511	0.0001
Pinubog3	4.206	0.0001
Pinupse3	3.297	0.0004
Piceabi3	2.141	0.0214
Betupub3	2.103	0.0246
strightFranaln3	1.698	0.0479
Pinusyl3	1.641	0.0995
Sorbauc3	1.583	0.1073
Pinudig3	0.993	0.5011

In addition to hybridization, the phenotypic plasticity of bog pine may determine the height and growth form changes with altitude. The growth form as well as the other morphological characters (e.g., cone morphology) support the suggestion that there have been past hybridization events between *P. rotundata* and *P. mugo*. The lower limit of the transitional zone may indicate the lower distribution of *P. mugo* during the last cold climate period before the Holocene warming.

We are not aware of any similar example of a relationship between altitude and growth form in a taxonomic complex. Only partly comparable is the cline in growth forms of *Betula pubescens* agg. in the Scandinavian mountains (Dierssen 1996). *Pinus rotundata* and *P.* ×*pseudopumilio* rarely coexist. This is probably because of their different growth forms, which results in the overshadowing of the shrubby hybrids by the tree-shaped *P. rotundata*.

The mutual relationships among the environmental factors are not surprising. Naturally, the sum of annual precipitation and site moisture are positively correlated with altitude, while mean annual temperature and trophic factors are negatively so (Peet 1978).

Our study expands on the work of Kärstner & Flössner (1933) and Neuhäusl (1972), who did not provide detailed data. Temperature amplitude (the difference between minimum and maximum temperatures measured at ground level) increased with altitude. Inside closed forest stands, i.e. those sites with tree-shaped pines in our case, the amplitude is generally lower (Stoutjesdijk & Barkman 1992). The maximum temperatures showed no clear relation with altitude. This was probably because of two opposite trends: the lowering of temperature with increase in altitude and increase in maximum temperatures of the more open stands at higher altitudes.

Peat bog vegetation has been studied in relation to environmental factors in other geographical regions (Jeglum 1971, Pakarinen & Ruuhijärvi 1978, Karlin & Bliss 1984, Damman 1986, Malmer 1986, Økland 1990, Wassen et al. 1990, Gerdol 1995, Jeglum & He 1995, Bragazza & Gerdol 1999, Hájková & Hájek 2003). These studies mostly indicate the ecological importance of moisture and nutrient gradients. Their results generally corresponded with those presented here. The vegetation of the peat bogs studied by us in detail was closely related to trophic factors such as pH and conductivity; level of groundwater table was also an important factor.

The low correlation of total N with vegetation composition obtained in this study, which was expected in the case of the organic sediment, is also reported by Wassen et al. (1990). The trend of increasing pH with altitude in our study and negative correlations of pH with most other trophic factors was rather surprising. However, pH was low at all the sites, with a small range of only 0.4, and the strongest correlations were only marginally significant. Moreover, some long-distance atmospheric deposition, greater at the higher altitudes, could have influenced the trend (Malmer 1986). But more probably this was the effect of higher mineralization of organic matter at sites with lower groundwater tables, typically associated with proton release and acidification (Mitsch & Gosseling 2000). Biotic characteristics of the pines, such as height and trunk diameter, are best correlated with both altitude and species composition of the sites.

The resulting species patterns in the DCA and CCA diagrams are very similar, i.e. in both direct and indirect gradient analyses. This indicates close relationships between the environmental and vegetation gradients and that probably there are no other important environmental factors (see also Jongmann et al. 1987, Jeglum & He 1995). The positions of particular species are mostly ecologically well interpreted, considering their ecological behaviour. Results of the DCA analyses, considering all species together, excluding the woody species, including herbs or moss layer only, show that all vegetation components reflected the environmental gradients in the same way, because the position of the vegetation samples in the ordination diagrams remain more or less the same. The results also indicate the unique character of each peat bog. In the DCA diagram the four samples from each site are notably distinct from those from the other sites, even in the case of closely located sites. This is important information for nature conservation as it indicates that it is necessary to protect all peat bogs.

The peat bogs studied provide a very good example of the close relations between environmental and vegetational gradients, and the taxonomical position of the dominant species. Considering the limited distribution of the dominant species *P. rotundata* (Jalas & Suominen 1973), relictness (Spitzer et al. 1999), sources of paleoecological information (Jankovská 1980), occurrence of rare and endangered species (Neuhäuslová et al. 1998), a continuous micro-evolution and interesting biogeographical relations (Mikola & Spitzer 1983), peat bogs are eminently important and valuable for scientific research, nature conservation and culturally.

Conclusions

The questions posed in the Introduction can be answered in the following way: (i) Species composition of peat bogs and the growth form of dominant pines, i.e. the transition from the tree-shape to the shrubby form resulting from hybridization, is closely associated with altitude. Even closely located bogs are distinct. (ii) Site moisture characteristics and temperature amplitude were positively correlated with altitude, while most trophic factors were negatively correlated. (iii) All components of the vegetation, i.e. woody species, herb and moss layer, respond to the environmental gradients in the same way.

See www.preslia.cz for Electronic Appendix 1.

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Souhrn

Na dvaceti rašeliništích v různé nadmořské výšce v jižní části Čech byly provedeny vegetační analýzy (fytocenologické snímky) se snahou nalézt vztahy mezi vegetací a gradienty prostředí. Podrobně bylo sledováno šest rašelinišť. Studovaná rašeliniště jsou porostlá borovicí blatkou (*Pinus rotundata*), která je endemitem střední Evropy, a jejími hybridogenními populacemi s borovicí klečí (*P. mugo*). Zastoupení křížence *P.* ×*pseudopumilio* vzrůstá směrem k vyšším nadmořským výškám. Data byla zpracována metodami jednorozměrné i mnohorozměrné statistiky. Proměnné prostředí (výška hladiny podzemní vody, průměrná a minimální teplota, srážky, pH, vodivost, koncentrace NH_4 a PO_4 a celkový P) i biotické charakteristiky lokalit (druhové složení, růstová forma dominantních borovic) byly často úzce korelovány s nadmořskou výškou. Tato korelace však neplatila pro koncentrace celkového N a NO_3. Významný byl rovněž vztah mezi růstovou formou dominantních borovic a abiotickými faktory i ostatními vegetačními charakteristikami. Druhové složení všech vegetačních pater (stromového a keřového, bylinného i mechového) se měnilo s nadmořskou výškou a hlavní trendy byly v podstatě stejné pro všechna vegetační patra. Z výsledků je mimo jiné patrná jedinečnost každého ze sledovaných rašelinišť.

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