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Vegetation changes in forests of the Krkonoše Mts. over a period of air pollution stress (1980–1995)

Stanislav Vacek[1], Marek Bastl[2] & Jan Lepš[2,3,*]
[1]*Forestry and Game Management Research Institute, Research Station Opočno, Czech Republic;* [2]*Faculty of Biological Sciences, University of South Bohemia, České Budějovice, Czech Republic;* [3]*Institute of Entomology, Czech Academy of Science, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic (*correspondence)*

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Abstract

Species composition of the understory of spruce (*Picea abies* (L.) Karsten) and beech (*Fagus sylvatica* L.) forests subjected to intense air pollution stress in the Krkonoše Mts., Czech Republic, showed directional changes over the last 15 years. The changes were documented with repeated observations of 29 permanent plots, initiated in 1980 and analysed with constrained ordination methods (Canonical Correspondence Analysis). Ground layer changes were mainly associated with the loss of canopy foliage from air pollution stress. The increased amount of the light at ground level resulted in increased herb cover. The initially dominant species (e.g., *Calamagrostis villosa* (Chaix) J. F. Gmelin, *Deschampsia flexuosa* (L.) P. B., *Vaccinium myrtillus* L., *Athyrium distentifolium* Tausch) were those that increased in cover. Moss cover, and moss and herb richness, declined over the course of the study. Thus, the changes in tree canopy are accompanied with changes in the forest understory, which in turn can affect the dynamics of these forests.

Introduction

Species composition of forests in the Krkonoše Mts. (Giant Mountains) has changed tremendously over the last four centuries (Lokvenc 1987). Beech and fir-beech forests were logged, mainly to provide fuels for the mining and glassworks industries, and spruce forests were also logged. Many forests were re-planted but not in the original species composition (beech and fir were replaced by spruce plantations). Age structure and spatial patterns of planted forests differ dramatically from those of old growth forests. Nevertheless, remnants of both beech and natural spruce forest can still be found. Unfortunately, these forests have been heavily impacted by air pollution over the last 30 years.

The floristic composition of a forest stand changes over time. In the Krkonoše Mts., two types of change are important: natural stand dynamics and changes caused by air pollution. The effect of air pollution on trees is well studied (e.g., Schultze 1989; Smith 1990; Cook & Zedaker 1992). Corresponding changes in the ground layer are less frequently studied (e.g., Nygaard 1994). We have assumed that the majority of changes in the ground layer (i.e., both herb and moss layers, E_1 and E_0) are connected with changes in canopy density, and less by direct pollutant effects. Although repeated observations on permanent plots are considered to be the most reliable method for documenting vegetation dynamics, it is difficult to separate natural stand dynamics from the effects of man-induced stress, and direct effects from indirect ones (Loehle 1988). Unfortunately, there are no good ‘control’ stands, i.e., those with comparable environmental conditions but not influenced by air pollution. Consequently, changes in plant communities can be correlated only with indices of air-pollution stress intensity, thereby not proving causal relationships. However, this is the case in many similar studies of environmental impacts (Green 1979).

Methods of multivariate analysis developed in the last decade (CANOCO, ter Braak 1990) are useful for the analysis of repeated observations. These methods enable statistical testing of hypotheses about the dynamics of community composition.

In 29 permanent plots established in natural spruce, spruce-beech and beech stands in 1980, species composition of the ground layer has been recorded at 5-year intervals. The stands represent a wide range of environmental conditions thus enabling the study of environmental responses of particular species. The condition of the tree canopy was regularly recorded in the plots as an indirect measure of air-pollution stress intensity.

The aim of our study is to describe and analyse changes in the ground layer that have occurred over the last 15 years. Our primary focus is on the relationship between increasing defoliation of trees, and the cover and species composition of the herb and moss layers.

Material and methods

Sampling

The Krkonoše Mts. are located on the Czech-Polish border, their highest peaks surpassing 1500 m a.s.l. Plots were established across a wide altitudinal range from 600 to 1200 m a.s.l., i.e., from beech (*Fagus sylvatica*) to spruce (*Picea abies*) forest zones within area of 360 km^2 (latitude 51°15′–51°24′ N and longitude 15°24′–15°53′ E). The parent rock is formed mainly by granite, mica schist and phyllite, and less frequently by gneiss and paragneiss. At the lowest altitudes brown soils are dominant, from 1000 m to 1100 m podzolized brown soils dominate, and above 1100 m podzols prevail. Average annual precipitation varies with altitude and aspect from 857 mm to 1260 mm, and mean annual temperature decreases with altitude from 6.1 °C to 2.6 °C (Czech Hydrometeorological Office data). The entire area has been under air pollution stress since 1970, with mean annual SO_2 concentrations about 20 μg m^{-3} (Schwarz 1984). Short term measurements also suggest increased concentrations of NO_x, ozone and fluorine compounds. Air pollution is considered to be the main cause of a massive forest dieback that peaked in the first half of the 1980s (Schultze 1989; Kubíková 1991; Balcar et al. 1994).

Twenty nine 50 × 50 m permanent research plots were established in 1980 for the study of air pollution impacts on forest health (Vacek et al. 1996). In each plot, one 25 × 25 m phytosociological relevé was surveyed using the Domin eleven-degree scale (Mueller-Dombois & Ellenberg 1974). Relevés were first surveyed in 1980 and at 5-year intervals thereafter for 15 years. For each plot altitude (m a.s.l.), slope (degrees), and aspect were recorded. Aspect was converted to a linear scale of increasing humidity and decreasing insolation and temperature: S = 0; SE or SW= 1, E or W= 2; NE or NW= 3; and N= 4. A similar conversion was used by Whittaker (1975, p. 122) in his vegetation charts.

Observations on tree health were made by an estimate of the relative amount of foliage retained on each tree. This visual estimation uses a standardized scale and is routinely used in forestry; this procedure is relatively reliable when carried out by an experienced forester (Vacek et al. 1996). Values were averaged over all trees in a plot; the resulting mean represents the amount of foliage present on all the trees at the site. This value is used as a biotic measure of air pollution stress and is also an indicator of increased solar radiation reaching the ground layer. Foliage loss was most pronounced in spruce forests, decreasing from about 80% of foliage present in 1980 to as low as 30% of foliage present (3% in one plot) in 1995. Therefore, further analysis of herb and moss layer response to canopy foliage loss was conducted for the spruce forests only.

Nomenclature follows Rothmaler et al. (1988) for vascular plants and Rothmaler et al. (1983) for mosses.

Data analysis

The repeated relevés of the permanent plots with corresponding environmental data form the basis for all subsequent analyses (matrix of 29 × 4 = 116 relevés, 154 species). Species are characterized by an ordinal transformation of the Domin-Krajina eleven-degree cover-abundance scale (Mueller-Dombois & Ellenberg 1974), corresponding to that of van der Maarel (1979) for the Braun-Blanquet scale. The particular degrees are converted into corresponding values (i.e., degree 1 is converted into value 1, degree 2 into value 2, etc.), with + (solitary, with insignificant cover) converted into 0.1. Van der Maarel (1979) has shown that this transformation reasonably weights both species composition and abundance. The relationship of species composition to environmental variables was evaluated by Canonical Correspondence Analysis (CCA) using the program CANOCO for Windows (ter Braak & Šmilauer 1998). This program enables partial analyses, where the influence of particular variables (termed covariables) is eliminated before the influence of the variables of interest (termed environmental variables) is tested. Various combinations of covariables and environmental variables enable the testing of particular effects. Our data are in the form of repeated measurements, and we are mainly concerned with temporal changes and their correlation with defoliation. The tests of within-subject effects are constructed in CANOCO by the use of a plot identifier as a covariable. (In CANOCO, categorial variables are coded as several binary dummy variables, however, this is a technical detail and we will discuss the plot identifier as if it was a single categorial variable.) Note that when plot is used as a covariable, the environmental variables that remain constant (i.e., altitude, aspect, and slope) do not explain any variability and consequently it is meaningless to use them as either covariables or as environmental variables. However, their interaction with time can be tested (e.g., altitude $\times$ year) and corresponds to differences in temporal change with altitude. Significance was tested by the distribution-free Monte Carlo test. In the Monte Carlo test, the distribution of the test statistics under the null hypothesis is generated by random permutations of cases in the environmental data (for details see ter Braak & Šmilauer 1998). The permutation scheme was adjusted for particular tests. Whenever the within-plot trends were tested, the relevés of the same plot are permutated within the plot, using the permutation for time series (technically, the plot is considered to be a block and within block permutation option is used). When between plot differences are tested, relevés originating from the same plot are kept together (entire plots are permutated; the split-plot permutation option according to ter Braak & Šmilauer 1998).

The Coplot (conditioning plot) procedure was used for visualizing the relationship of a variable to more than one explanatory variables, using the S-PLUS package (Statistical Sciences 1995). A coplot shows how a response depends upon a predictor given another predictor. It creates a matrix of conditioning panels; each panel graphs the response against the predictor for those observations whose value of given predictor lie in an interval. The trends in coplots were fitted by loess (locally weighted regression smoothing).

Results

Over the course of the investigation, defoliation in the spruce forests proceeded rapidly (Figure 1). Total herb cover increased with the exception of the plots at the lowest altitudes (Figure 2). This process was accompanied by a decrease in moss cover (Figure 2), and also a decrease in species richness of both mosses and herbs (Figure 3). Mostly, the herb species that were dominant in 1980 increased in response to canopy foliage reduction. *Calamagrostis villosa*, the dominant understory grass of the spruce forest, is an example of a plant species responding positively to canopy foliage reduction (Figure 1). It did not increase in the sparse forests close to timberline where this species already had very high cover at the time of the first survey.

Eight analyses of the dependence of species composition on environmental gradients and changes in species composition over the 15-year period were conducted. These are summarized in Table 1 (note that the species-environment correlation is used exactly as defined in CANOCO and that some caution is necessary in ecological interpretations – see McCune 1997). We first analysed changes in the entire set of permanent plots (Analyses 1 to 3). Because the most pronounced changes were observed in the spruce forests, their dynamics were analysed in more detail (Analyses 4–8). Whenever plot is used as a covariable (a categorial variable assigns each relevé to a particular permanent plot) the effect of between plot differences is first partialed out and then temporal changes only are analysed.

The relationship of species to the four main environmental variables (aspect, altitude, slope, and year) shows that altitude and aspect were the most important (Analysis 1, Figure 4). Differentiation along the first axis is mainly caused by the altitudinal gradient, from beech forest species on the right (e.g., *Milium effusum* L., *Stellaria nemorum* L., *Polygonatum verticillatum* (L.) All., *Prenanthes purpurea* L., *Dentaria enneaphyllos* L.) to typical spruce forest species on the left (e.g., *Trientalis europea* L., *Homogyne alpina* (L.) Cass.). The second axis mainly reflects north-south orientation, with *Athyrium distentifolium* and many bryophytes with higher abundance on north-facing slopes.

Although the effect of year was negligible in comparison with the other variables, it was still highly significant when analysed separately (Analysis 2). In this analysis, the influence of all environmental variability was partialed out and only temporal changes

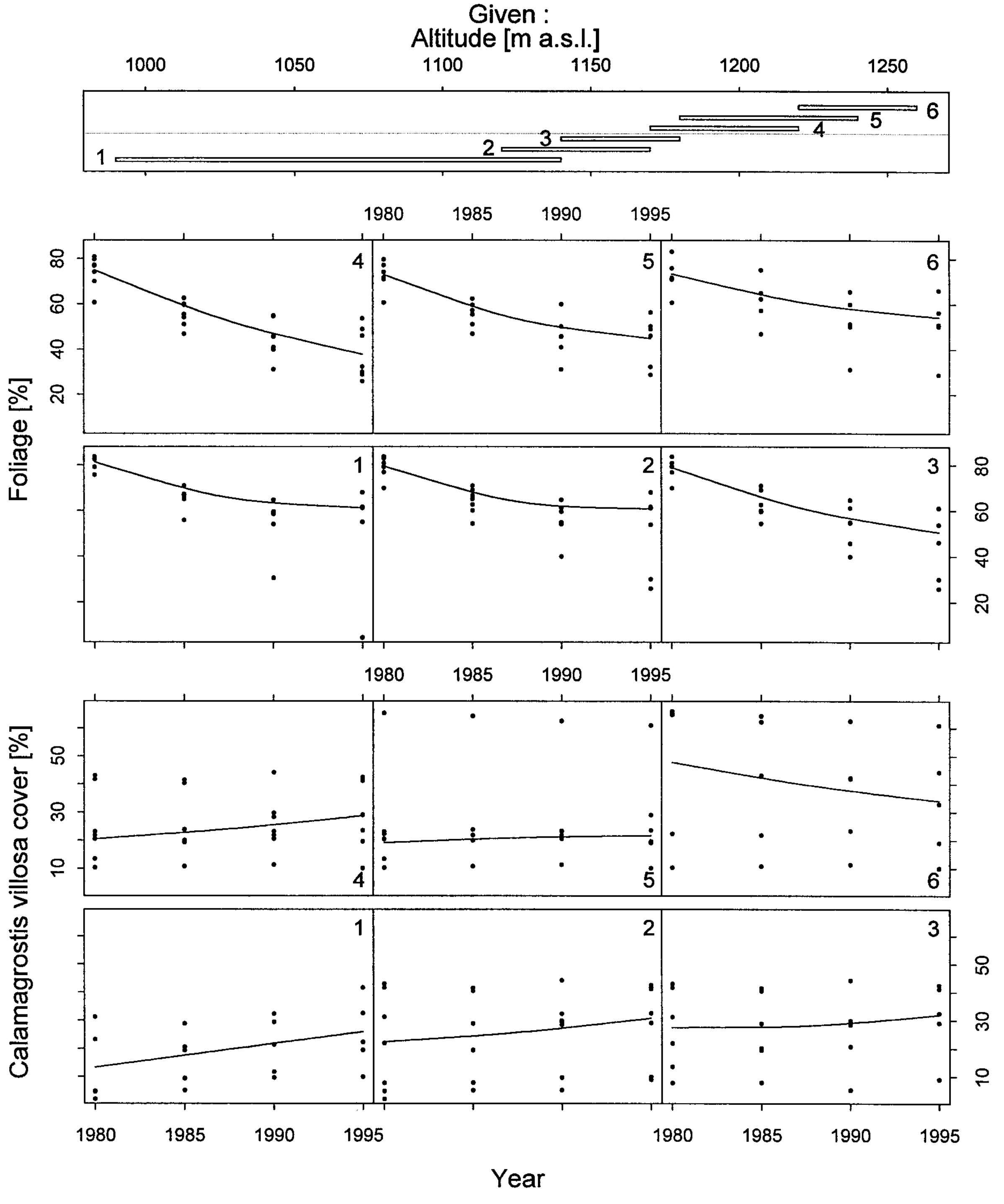

Figure 1. Conditioning plot (Coplot) of changes in amount of foliage present (%) and cover of *Calamagrostis villosa* (%) at various altitudes over time. The bars above the picture indicate the range of altitudes in particular graphs. To read the coplot, read the graphs from left to right, bottom to top.

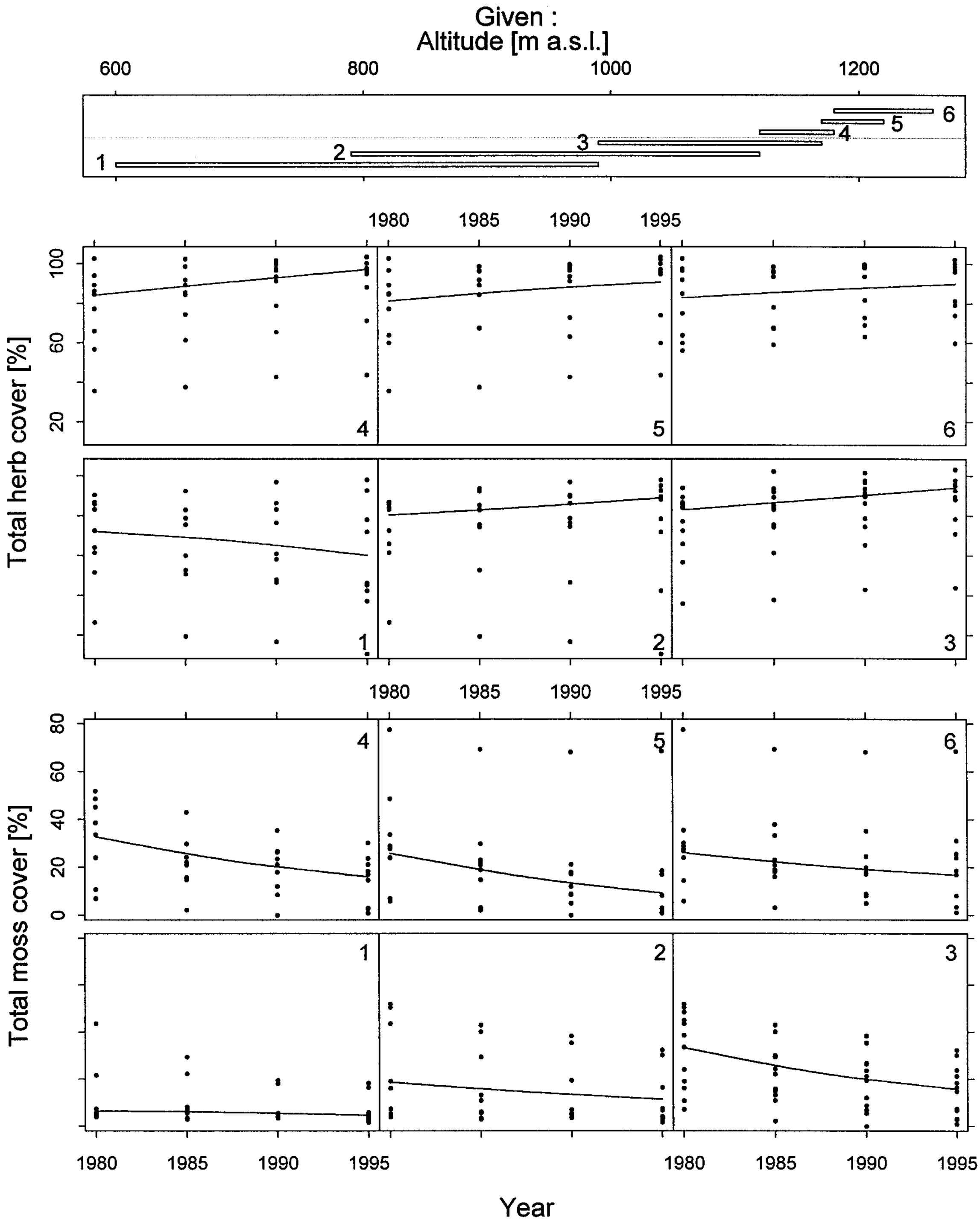

Figure 2. Conditioning plot (Coplot) of changes in cover of moss and herb layers at various altitudes over time. The bars above the picture indicate the range of altitudes in particular graphs. To read the coplot, read the graphs from left to right, bottom to top.

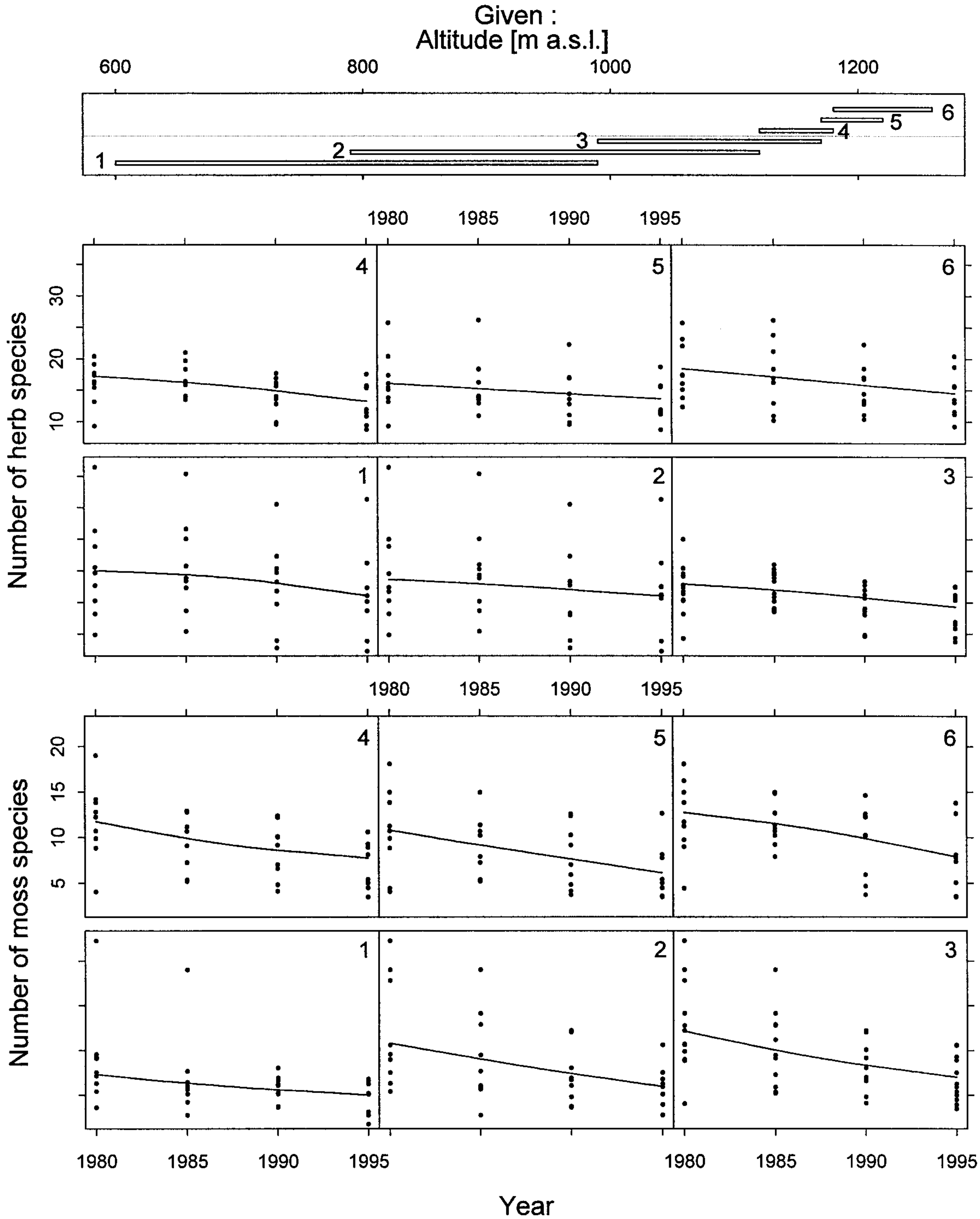

Figure 3. Conditioning plot (Coplot) of changes in moss and herb richness at various altitudes over time. The bars above the picture indicate the range of altitudes in particular graphs. To read the coplot, read the graphs from left to right, bottom to top.

Table 1. Characteristics of CCA analyses (spruce – spruce forests; beech – beech and mixed (beech, spruce) forests; 1st axis variability indicates percentage of variability in species data explained by the first CCA axis; Spec. – env. correl. indicates the species-environment correlations for the first CCA axis; F indicates the F-ratio of the first CCA axis; P indicates significance of the first CCA axis estimated using the Monte Carlo permutation test (1000 permutations).

Analysis	1	2	3	4	5	6	7	8
Species data used	spruce beech	spruce beech	spruce beech	spruce	spruce	spruce	spruce	spruce
Environmental variables	Year Altitude Aspect slope	Year	Year × Altitude	Foliage Year	Year	Foliage	Year	Foliage
Covariables		Plot	Plot Year	Plot	Plot	Plot	Plot Foliage	Plot Year
1-st axis variability	16.6	9.2	4.7	15.7	15.5	13.8	8.0	6.2
Spec.-env. correl.	0.808	0.892	0.813	0.929	0.927	0.882	0.836	0.749
F	22.17	8.69	4.19	6.42	9.21	8.03	4.28	3.22
P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002

were analysed. All of the moss species decreased in cover over time. Most vascular plant species decreased in cover, except for a number of ground layer dominants (e.g., *Calamagrostis villosa* – see also Figure 1, *Deschampsia flexuosa*, *Vaccinium myrtillus*, and *Athyrium distentifolium*), which increased. Analysis 3 shows that the year × altitude interaction is significant. This means that the changes that occurred in species composition varied with altitude.

The spruce forests formed a more homogeneous group, and the defoliation was more pronounced there. Therefore, we tested the relationship between defoliation and herb and moss layer composition using only the spruce forest plots. Species changes can be explained by two variables: year and foliage. These variables are negatively correlated ($r = -0.703$), because defoliation increased with time. Also, the species which increase with time are negatively correlated with the amount of foliage present. The effect of both variables is highly significant (Analysis 4, Figure 5). Also, when each of the variables is taken as the sole explanatory variable (Analyses 5 and 6) the dependence is highly significant. Use of partial analyses, where one of the variables is considered explanatory and the other the covariable, enables partial separation of effects of each variable. Analyses revealed that there is some temporal trend that cannot be explained by the effect of defoliation (Analysis 7), and that there is an effect of defoliation that cannot be explained only temporally (Analysis 8). Both of these effects are highly significant. Species most positively affected by defoliation are *Rubus idaeus* L., *Epilobium angustifolium* L., *Senecio nemorensis* L. and *Adenostyles alliariae* (Gouan) Kerner. The species *Calamagrostis villosa*, *Deschampsia flexuosa*, *Vaccinium myrtillus*, and *Athyrium distentifolium* increased along the year vector (Figure 5).

Discussion

The effect of air pollution stress on forests has been well studied (Wellburn 1988; Smith 1990; Atkinson & Winner 1990; Abrahamsen et al. 1994; Vacek & Lepš 1987, 1996). Montane spruce (*Picea abies*) forests, both indigenous and planted, are among the most heavily damaged ecosystems in Central Europe (Schultze 1989, Kubíková 1991, Balcar et al. 1994). It has been asked, to what degree is forest decline a consequence of air pollution versus natural forest dynamics, and is it possible to separate these two potential effects (Loehle 1988)? It has been inferred, based on temporal and spatial correlations between levels of air pollution and rates of forest decline, that air pollution is a primary cause of forest decline (Kubíková 1991). In our study we have no data on deposition rates or atmospheric pollutant concentrations

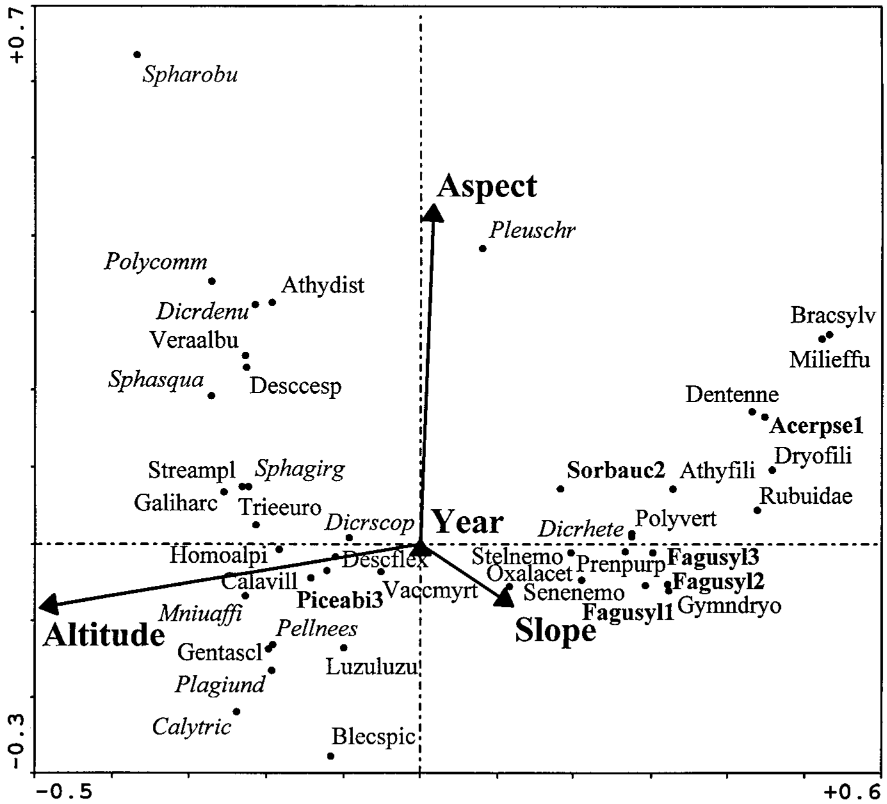

Figure 4. Results of CCA ordination (Analysis 1). Biplot shows the relationship of species and environmental variables. Note that arrow length in the species – environment biplot corresponds to the importance of particular variables for the first two ordination axes and arrow direction reflects their increasing values. Species with low frequency or with no relation to ordination axes are not displayed. Species are labeled with eight-letter abbreviations, composed of four letters of the genus and four letters of the specific name. Full names of species are in Appendix 1. The number at the end of the abbreviations for woody species separates individuals occurring in herb (1), shrub (2) and tree (3) layers. Woody species are in bold and mosses are in italics.

in the permanent plots. Thus, loss of foliage was used as a biotic measure of impact severity. Tree defoliation increased with time in various stands at rates that can not be considered a result of natural stand dynamics. In addition, ground layer species composition showed significant directional changes.

The ground layer can be influenced both directly and indirectly by acid precipitation, but data about ground layer changes are rare. Changes in soil chemistry, particularly soil acidification, could have a direct effect on the growth and survival of both vascular plants and mosses. Nygaard (1994) has shown a decrease of some herbaceous species (e.g., *Melampyrum pratense* L.) and mosses as a direct consequence of an experimental acid rain treatment. Nevertheless, indirect effects may be more pronounced. The loss of tree needles and particularly tree death result in a considerable increase in the amount of light reaching the ground layer changing the conditions for competitive success. This leads to an increase in herb cover and increased dominance by the dominant species. For example, *Calamagrostis villosa* increases in cover and becomes an even stronger dominant (Fiala et al. 1989, Pyšek 1993, 1994, Vosátka et al. 1995). In addition, the increased herb cover might cause the decline in the moss layer.

Our data do not enable us to distinguish between direct and indirect effects. However, in this study the decline in canopy foliage is accompanied by an increase in herb cover. Although we could speculate that acid rain has some positive effect on herb growth, an indirect effect via increased light at the ground layer is a much more plausible explanation. For example, Nygaard (1994) found a decrease in performance of *Vaccinium myrtillus* on plots experimentally influenced by acid rain, whereas in our plots *Vaccinium myrtillus* increased in cover over time. Similarly, the fact that there is a significant effect of canopy cover

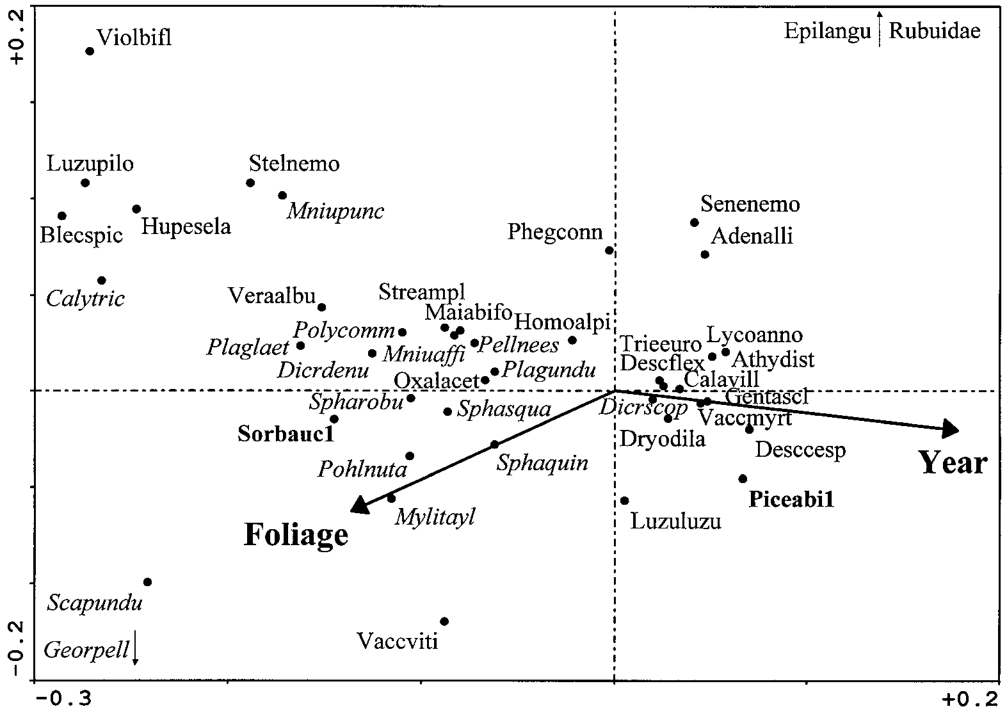

Figure 5. Results of CCA ordination (Analysis 4). Biplot shows the relationship of species and environmental variables. For explanation of symbols see Figure 4 and Appendix 1.

on ground layer species composition, even when year is removed as a covariable, suggests that the ground layer is mainly influenced by indirect effects controlled by decreased shade. For mosses, both the direct effect of acid rain deposition and an indirect effect of increased competition by herbs are plausible explanations for the decreases in cover and richness observed.

We conclude that species composition of the ground layer in Krkonoše Mts. forests has displayed clear directional change over the last 15 years. With the loss of canopy foliage herb cover has increased, and forest understory dominants such as *Athyrium distentifolium*, *Calamagrostis villosa*, *Deschampsia flexuosa* and *Vaccinium myrtillus*, in particular, have increased in cover. Moss cover, and both moss and herb richness have declined. Changes in the forest understory can potentially affect spruce seedling recruitment and thereby alter the internal dynamics of these forests.

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Appendix 1. Abbreviations and full species names used in Figures 4 and 5.

Woody species
Acerpse1 = *Acer pseudo-platanus* E_1, Fagusyl1 = *Fagus sylvatica* E_1, Fagusyl2 = *Fagus sylvatica* E_2, Fagusyl3 = *Fagus sylvatica* E_3, Piceabi1 = *Picea abies* E_1, Piceabi3 = *Picea abies* E_3, Sorbauc1 = *Sorbus aucuparia* E_1, Sorbauc2 = *Sorbus aucuparia* E_2.

Herbs
Adenalli = *Adenostyles alliariae*, Athydist =

Athyrium distentifolium, Athyfili = *Athyrium filix-femina*, Blecspic = *Blechnum spicant*, Bracsylv = *Brachypodium sylvaticum*, Calavill = *Calamagrostis villosa*, Dentenne = *Dentaria enneaphyllos*, Desccesp = *Deschampsia cespitosa*, Descflex = *Deschampsia flexuosa*, Dryodila = *Dryopteris dilatata*, Dryofili = *Dryopteris filix-mas*, Epilangu = *Epilobium angustifolium*, Galiharc = *Galium harcynicum*, Gentascl = *Gentiana asclepiadea*, Gymndryo = *Gymnocarpium dryopteris*, Homoalpi = *Homogyne alpina*, Hupesela = *Huperzia selago*, Luzuluzu = *Luzula luzuloides*, Luzupilo = *Luzula pilosa*, Lycoanno = *Lycopodium annotinum*, Maiabifo = *Maianthemum bifolium*, Milieffu = *Milium effusum*, Oxalacet = *Oxalis acetosella*, Phegconn = *Phegopteris connectilis*, Polyvert = *Polygonatum verticillatum*, Prenpurp = *Prenanthes purpurea*, Rubuidae = *Rubus idaeus*, Senenemo = *Senecio nemorensis*, Stelnemo = *Stellaria nemorum*, Streampl = *Streptopus amplexifolius*, Trieeuro = *Trientalis europaea*, Vaccmyrt = *Vaccinium myrtillus*, Vaccviti = *Vaccinium vitis-idaea*, Veraalbu = *Veratrum album*, Violbifl = *Viola biflora.*

Mosses

Calytric = *Calypogeia trichomanis*, Dicrdenu = *Dicranodontium denudatum*, Dicrhete = *Dicranella heteromalla*, Dicrscop = *Dicranum scoparium*, Georpell = *Georgia pellucida*, Mniuaffi = *Mnium affine*, Mniupunc = *Mnium punctatum*, Mylitayl = *Mylia taylorii*, Pellnees = *Pellia neesiana*, Plaglaet = *Plagiothecium laetum*, Plagundu = *Plagiothecium undulatum*, Pleuschr = *Pleurozium schreberi*, Pohlnuta = *Pohlia nutans*, Polycomm = *Polytrichum commune*, Scapundu = *Scapania undulata*, Sphagirg = *Sphagnum girgensohnii*, Sphaquin = *Sphagnum quinquefarium*, Spharobu = *Sphagnum robustum*, Sphasqua = *Sphagnum squarrosum.*

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