

Changes in understorey vegetation after Norway spruce colonization of an abandoned grassland

Monika Janišová^{1,*}, Richard Hrivnák¹, Dušan Gömöry², Karol Ujházy²,
Milan Valachovič¹, Erika Gömöryová, Katarína Hegedúšová¹ &
Iveta Škodová¹

¹) Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 14, SK-845 23 Bratislava, Slovakia (*corresponding author's e-mail: monika.janisova@savba.sk)

²) Department of Phytology, Faculty of Forestry, Technical University of Zvolen, Masarykova 24, SK-960 53 Zvolen, Slovakia

³) Department of Natural Environment, Faculty of Forestry, Technical University of Zvolen, Masarykova 24, SK-960 53 Zvolen, Slovakia

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We studied the understorey vegetation (including both herbaceous and moss layers) during the Norway spruce (*Picea abies*) colonization of an abandoned grassland community along a transect established in the direction of spruce dispersal from a linear source (former plantation). We measured a set of climatical, biological, pedological and soil microbiological variables to reveal their effect on the understorey vegetation during the colonization process. Three factors exhibited significant effects — needle and litter accumulation and reduction of light availability. The percentage cover of needles explained 35.8% of the variance in the species data in the RDA and its pure effect (after setting all other significant variables as covariables) exceeded 12%. This factor exhibited the strongest correlation with the first PCA axis representing the colonization progress of spruce. Light conditions (measured as canopy openness by hemispherical canopy photographs or calculated on the basis of tree size and density) explained much lower proportion of the variance (marginal effect about 21.5% and 2.7% pure effect). We discuss the relationship between environmental factors and species abundance (of vascular plants and bryophytes) along the colonization gradient. The results highlight the importance of litter accumulation in controlling the community structure during the successional development of woodland from previous grassland.

Key words: light availability, litter accumulation, *Picea abies*, secondary succession, species-environment relationships, understorey vegetation

Introduction

In the period of intensive land use changes the utilization of remote areas is becoming ineffective and economically unprofitable. In the abandoned grasslands the process of secondary succession is initiated. It has been frequently studied by plant ecologists with the aim of understanding the undergoing successional mechanisms and forecasting the further successional development (e.g. Falińska 1989, Blažková & Březina 2003, Prévosto *et al.* 2003, Pavlů *et al.* 2005).

Succession is a complex process driven by many partial processes acting simultaneously in a given situation (Walker & Chapin 1987). The individual processes and their interaction may affect not only the outcome of succession but also the successional rate. Moreover, the relative importance of successional processes may change through successional time (Connell & Slayter 1977). Starting conditions including the species present at the locality and in the surroundings and the soil seed bank belong to the most important factors influencing the course of secondary succession. Very important is the presence of woody species, which can induce dramatic changes in light availability through their development and so affect significantly the successional rate. Along with stochastic processes, plenty of further factors may influence the successional outcome, life history traits and biological interactions (competitive, facilitative and herbivory processes) being the most important among them (Miles 1979, Walker & Chapin 1987, Glenn-Lewin & van der Maarel 1992). Secondary succession on rich soils starts with high availability of both light and nutrients, thus, successional sequence may be the result of competitive displacement of species with different growth rates and sizes (Tilman 1988). Space and resource competition together with litter accumulation result in site modification, which is considered to be one of leading driving forces of succession (e.g. Grime 1979, Miles 1979, Xiong & Nilsson 1999).

In our contribution, a post-pasture secondary succession was studied at a locality, where spruce stand was introduced by man in the vicinity of abandoned grasslands. In the studied area, the climax community is a beech-dominated mixed forest (Michalko *et al.* 1986). The planted spruce

trees have become a huge source of diaspores which were able to colonize the grassland immediately after being abandoned. During the period of irregular grazing (after mowing cessation) spruce gradually expanded to open grasslands and subsequently overgrew and overshadowed the former vegetation. Even when spruce is a natural component in the local forests, the availability of spruce seeds at the given moment triggered the process of colonization and speeded up the course of main environmental changes.

We measured a set of climatical, biological, pedological and soil microbiological variables to reveal their effect upon the understorey vegetation (including both herbaceous and moss layers) during the colonization process. Two basic questions were addressed: (i) How does the understorey vegetation develop during spruce colonization? (ii) Which are the most significant environmental factors affecting the variability of the understorey vegetation along the colonization gradient?

Material and methods

Study site

The study site is located in central Slovakia at Príslopý (48°38'10"N, 19°25'11"E, 900–920 m a.s.l.). The region has a relatively cold and rainy climate with the mean July temperature of 11.5–13.5 °C and 1000–1400 mm annual precipitation. The bedrock formed by andesite lava flows is covered by deep cambisols. This grassland area of about 100 ha is surrounded by a large forest complex. It was deforested around 1800 and since then it has been utilized as hay meadows. Since 1951 it has been utilized as pasture (cf. Ujházy 2003). Since the late 1990s the studied area has not been utilized any more. Norway spruce (*Picea abies*) was planted along with the former forest margin in the 1890s. This row plantation formed the seed source for the colonization of the grassland, which was gradually overgrown by spruce.

Field sampling and environmental factors

A research transect of 20 × 150 m (perpendicular

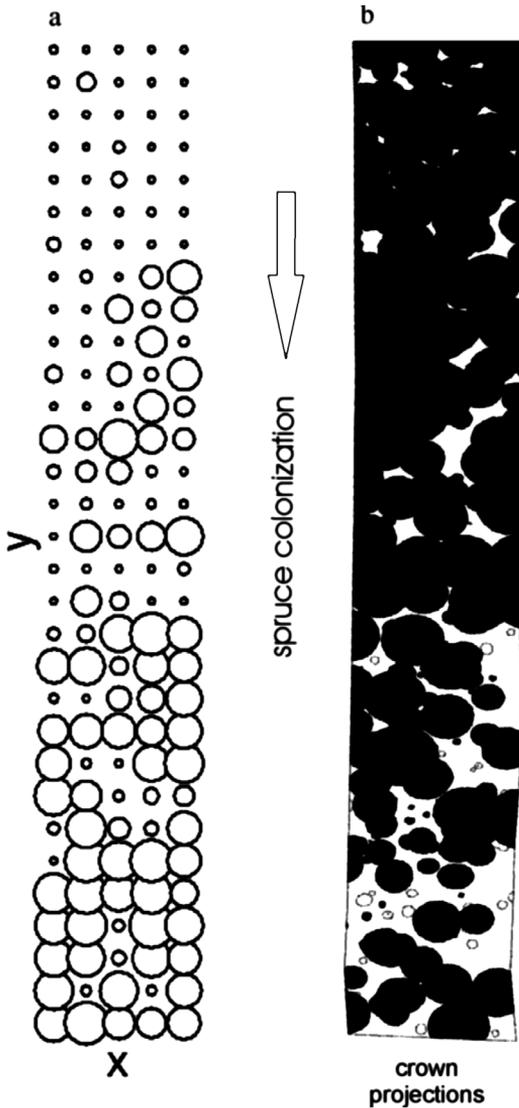


Fig. 1. — **a:** Spatial variation of community composition along the transect. The direction of spruce colonization is shown by an arrow. The position of samples on the first ordination axis of PCA is visualized by the size of sample symbols. — **b:** Crown projections of *Picea abies* (full circles) and *Juniperus communis* (empty circles) along the transect.

to the contour line) was established at the site in 2003 on a regular north-facing slope. The transect crosses all successional stages from the old planted spruce forest margin to a relatively open non-forest grassland area. The transition from a relatively open grassland to a closed forest is, however, rather smooth, and the under-

storey species composition changes accordingly.

On the transect, a grid of 5×5 m was established and geodetically measured (Fig. 1a). The positions (x , y coordinates), breast-height diameters (DBHs), heights and crown projections of all trees were measured (Fig. 1b). In addition, the positions and breast-height diameters of all trees were recorded on two neighboring 10-m belts. Understorey vegetation was recorded on circular plots of 0.5 m^2 . In total, 155 plots were sampled. The following characteristics were estimated for each plot: percentage cover of both vascular plants and bryophyte species, percentage cover of dead plant biomass, percentage cover of fallen needles, depth of dead biomass layer and its variation (see Table 1 for the details).

Soil samples were taken from the uppermost mineral horizon (A horizon; cf. Šály *et al.* 2000) from the depth of 5–10 cm. From fresh samples, gravimetric moisture, basal soil respiration rate, substrate-induced respiration (SIR; Isermeyer in Alef 1991) and catalase activity (Khaziev 1976) were determined. A half of each sample was air-dried and used for measurement of soil acidity (pH), organic matter content (Tyurin 1951), and total N (Kjeldahl's method), P and K (Mehlich 3 extract, K = flame emission spectrometry, P = colorimetry).

To assess the influence of tree layer upon the understorey vegetation we used two methods: (1) calculation of tree influence index, and (2) taking the canopy photographs.

(1) For each sample plot we calculated an index reflecting both density and size of trees in its neighbourhood (Kuuluvainen & Pukkala 1989, Saetre 1999, Kühlmann *et al.* 2001):

$$TI = \sum_i BA_i e^{-r_i} (1 + \cos \alpha_i)$$

where BA_i is basal area of the i th tree within the 5-m neighbourhood of the sampling plot center, r_i is the distance between the plot center and the i th tree and α_i is the angle between the slope line and the plot center \rightarrow tree vector.

(2) Vertical hemispherical canopy photographs were taken in the sample plot center using a digital camera equipped with a fisheye lens. For the evaluation of photographs we used Gap Light Analyser 2.0 (Frazer *et al.* 1999). The canopy openness (CO) was assessed, which is

the percentage of open sky seen from beneath a forest canopy.

Data analysis

Species data were log-transformed. Several samples had no species as they were located underneath the closed canopy with strongly reduced light conditions and a thick needle layer. To keep the valuable information contained in such samples and to keep the empty samples in the analyses, we added a hypothetical species into each plot. The cover value assigned to the hypothetical species was 0.1% for each sample. In a few samples where the plot area interfered with the spruce trunks, environmental variables could not be measured and the missing values were replaced by the mean of the neighbouring plots. This was necessary to perform the Monte Carlo permutation test restricted for a rectangular grid (*see below*).

CANOCO 5 for Windows package (ter Braak

& Šmilauer 2002) was used for running both indirect and direct gradient analyses. Because of the addition of a hypothetical species linear ordination methods were used. This approach was approved by running a detrended correspondence analysis (DCA) in which ordination axes length of < 3 SD were obtained (ter Braak & Šmilauer 2002). Species data were first subjected to principal components analysis (PCA) to find a few major axes of variation with a good fit to the species data. Correlation coefficients were calculated between environmental variables and ordination axes (ter Braak & Prentice 1988). Redundancy analysis (RDA) was performed to investigate which of the measured environmental variables would significantly explain the species composition. The significance of both, environmental variables and RDA axes, was tested by the Monte Carlo permutation test with restricted permutations for a rectangular grid of 31×5 plots (9999 runs). A set of partial RDAs was carried out to quantify the variance partitioning of selected variables. The pure effect of

Table 1. Environmental variables used in the analyses.

Variable	Variable characteristic	Measurement
Biological		
Litter	Percentage cover of grass and forb dead biomass (litter) in the herb layer.	Visual estimate
Needles	Percentage cover of fallen needles on the soil surface consisted mainly of spruce needles with a minor contribution of juniper and fir needles.	Visual estimate
DBL _{av}	Depth of undecomposed litter layer (DBL) over the soil surface measured with a pin with diameter of 2.5 mm. Average of ten measurements.	With a ruler and calculation
DBL _{sd}	Variability of the DBL depth expressed as standard deviation from average of ten measurements of DBL.	Calculation
Pedological		
Moisture	Soil moisture of the fresh sample.	Gravimetrically
pH	Soil acidity (pH-KCl).	*
C	Organic carbon content (%).	*
N	Total nitrogen (mg kg ⁻¹ of dry matter).	*
P	Phosphorus (mg kg ⁻¹ of dry matter).	*
K	Potassium (mg kg ⁻¹ of dry matter).	*
Soil microbial activity		
Resp	Basal respiration.	*
SIR	Substrate-induced respiration.	*
Catalase	Catalase activity.	*
Light conditions and tree influence index		
CO	Canopy openness (percentage of open sky seen from beneath a forest canopy).	Hemispherical photography
TI	Tree Index based on the basal area of trees in the neighbourhood.	Calculation*

* *see* Material and methods for details

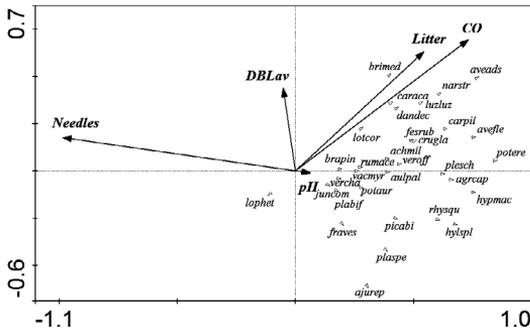


Fig. 2. Redundancy analysis, species position and significant environmental variables which passed the forward selection. The diagram explains 44% of the total variance (the first two eigenvalues: 0.38 and 0.06). The third and fourth eigenvalues are 0.017 and 0.010. Selected species present in more than 5% sample plots are shown by arrow tips. Abbreviations for environmental variables are in Table 1. Bryophytes: aulpal = *Aulacomnium palustre*, hylspl = *Hylocomium splendens*, lophet = *Lophocolea heterophylla*, plaspe = *Plagiomnium* sp. (incl. *P. affine* and *P. cuspidatum*), plesch = *Pleurozium schreberi*, rhysqu = *Rhytidiadelphus squarrosus*. Vascular plants: acepra = *Acetosa pratensis*, achmil = *Achillea millefolium*, agrcap = *Agrostis capillaris*, ajurep = *Ajuga reptans*, aveads = *Avenula adsurgens* subsp. *adsurgens*, avefle = *Avenella flexuosa*, brapin = *Brachypodium pinnatum*, brimed = *Briza media*, caraca = *Carlina acaulis*, carpil = *Carex pilulifera*, crugla = *Cruciata glabra*, dandec = *Danthonia decumbens*, fesrub = *Festuca rubra*, fraves = *Fragaria vesca*, hypmac = *Hypericum maculatum*, juncom = *Juniperus communis*, lotcor = *Lotus corniculatus*, luzluz = *Luzula luzuloides*, narstr = *Nardus stricta*, picabi = *Picea abies*, plabif = *Platanthera bifolia*, potaur = *Potentilla aurea*, potere = *Potentilla erecta*, vacmyr = *Vaccinium myrtillus*, vercha = *Veronica chamaedrys*, veroff = *Veronica officinalis*.

individual variables was set as a percentage variance explained by individual variables after all variables that were significant when alone were factored out by setting as covariables (ter Braak & Prentice 1988).

Nomenclature

Names of bryophytes and vascular plants are according to Marhold and Hindák (1998), the abbreviations are presented in the caption of Fig. 2. Only species present in more than 5% of sample plots are shown in the figures.

Results

PCA showed a strong environmental gradient along the first ordination axis (eigenvalue 0.419). The variation explained by the second, third and fourth axes was much lower (eigenvalues 0.103, 0.099 and 0.055, respectively). The first axis had the strongest positive correlation with Needles (-0.92) and TI (-0.73). The second axis was mostly correlated with DBL_{av} (-0.21) and Litter (-0.20).

The main environmental gradient revealed by PCA was consistent with the colonization progress as indicated by needle accumulation on the ground and reduction of light availability underneath the canopy. Thus the first axis represents the spruce colonization gradient, which is also obvious from Fig. 1. In the figure, the position of sample plots along the first ordination axis is presented by the symbol size while individual plots are displayed on their original grid location. Symbol size obviously increases in the direction of the arrow displaying the progress of spruce invasion from the primary seed source plantation and the spatial distribution pattern reflects also a mosaic character of vegetation in the early to mid-successional stages.

The results of RDA were very similar to those of PCA. The first axis of RDA accounted for 38% of variance in the species data and 77% of the species–environment relationship. The second axis accounted for 6% of variance in the species data and 12% of the species–environment relationship. The variance explained by the third and the fourth axes was very low (eigenvalues 0.02 and 0.01). The significance of all canonical axes was tested (Trace: 0.49, $P = 0.0036$) after including five environmental variables which passed the forward selection as significant (Table 2).

According to the results of forward selection in RDA, understorey vegetation was affected mainly by Needles, the variance explained by this variable was 35.8% of total inertia (Table 2). Other four variables showed a significant effect as well: CO (4.7%), Litter (2.2%), DBL_{av} (1.1%) and pH (0.8%). The impact of DBL_{av} and pH was very low and these variables had no significant marginal effects (Table 2). Only three environmental variables had significant pure effect: Need-

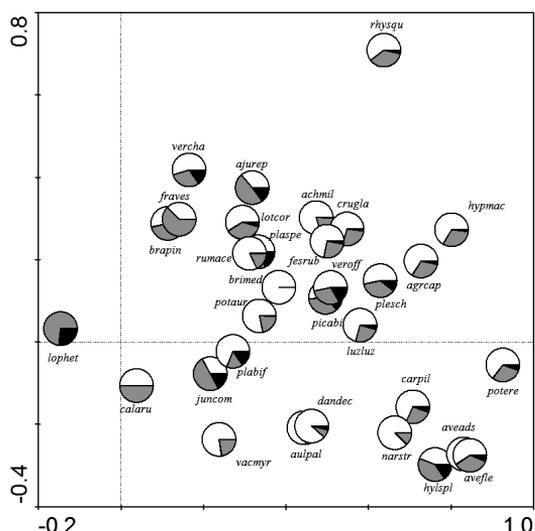


Fig. 3. Principal components analysis, pie symbols plot visualising distribution of species over classes with different % cover of needles (factor Needles). Presence of species in three sample classes of needle cover is shown: white = 0%–3%, grey = 4%–95%, black = over 95%. The first axis explains 42% and the second axis 10% of variance in the species data. Selected species present in more than 5% sample plots are shown, their abbreviations are explained in Fig. 2.

dles (12.2%), CO (2.7%) and Litter (1.7%).

Figure 2 shows the main variation in the understorey vegetation in relation to five environmental variables which passed the forward selection. Among more frequent species, the only one positively correlated with the strongest variable Needles is *Lophocolea heterophylla*. On the other hand, *Hypericum maculatum*, *Agrostis capillaris*, *Hylocomium splendens* and *Rhytidiadelphus squarrosus* are inferred to be negatively correlated with Needles. The relation of species to the Needles is also illustrated in Fig. 3. *Briza media* showed the most sensitive behaviour in relation to litter accumulation. It occurred only in samples with needle cover up to 3%. Other species occurring in stands with the lowest needle cover are *Lotus corniculatus* and *Nardus stricta*. Interestingly, the occurrence of *Picea abies* in the field layer (seedlings and young individuals) is also restricted by needle accumulation and seedlings seldom occur in stands with a higher needle cover. Among the vascular plants, *Ajuga reptans*, *Juniperus communis* and *Fragaria vesca* seem to be most resistant against needle accumula-

tion. *Veronica chamaedrys*, *Veronica officinalis* and *Platanthera bifolia* also frequently occur on plots with high percentage cover of needles. Bryophytes are obviously better adapted to this factor. The order in direction towards the best resistance is as follows: *Aulaacomnium palustre*, *Rhytidiadelphus squarrosus*, *Pleurozium schreberi*, *Hylocomium splendens*, *Plagiomnium* sp. (*P. affine* and *P. cuspidatum*) and *Lophocolea heterophylla*.

The relation of species to light conditions could be indicated from their correlation with the CO arrow (Fig. 2). *Lotus corniculatus*, *Carlina acaulis*, *Danthonia decumbens*, *Briza media*, *Luzula luzuloides*, *Nardus stricta* and *Avenula adsurgens* had the strongest positive correlation with CO. All these species were distrib-

Table 2. Redundancy analysis, results of forward selection. Marginal effect = percentage variance explained by an individual variable while used as the only constraining variable. Conditional effect = additional variance explained by the variable at the time it was included in the stepwise selection. Pure effect = percentage variance explained by the variable after all variables that are significant when alone were used as covariables. Variance explained is shown as percentage of total inertia. Significance was tested by running 9999 restricted Monte Carlo random permutations for rectangular grid.

Variable	Marginal effects	Conditional effects (selection order)	Pure effects
Needles	35.8**	35.8 (1)**	12.2**
TI	23.0**		0.6 ^{ns}
CO	21.5**	4.7 (2)**	2.7**
Litter	12.7**	2.2 (3)**	1.7**
DBL _{sd}	3.4**		0.6 ^{ns}
Catalase	3.5**		0.5 ^{ns}
N	3.2*		0.6 ^{ns}
Moisture	2.3*		0.6 ^{ns}
P	2.0**		0.5 ^{ns}
DBL _{av}	1.4 ^{ns}	1.1 (4)**	
K	1.4 ^{ns}		
SIR	1.1 ^{ns}		
pH	0.8 ^{ns}	0.8 (5)*	
Resp	0.5 ^{ns}		
C	0.3 ^{ns}		
Explained variance by all variables (%)		49.0	
Explained variance by significant variables (%)		44.7	

^{ns} = not significant, * $P < 0.05$, ** $P < 0.01$.

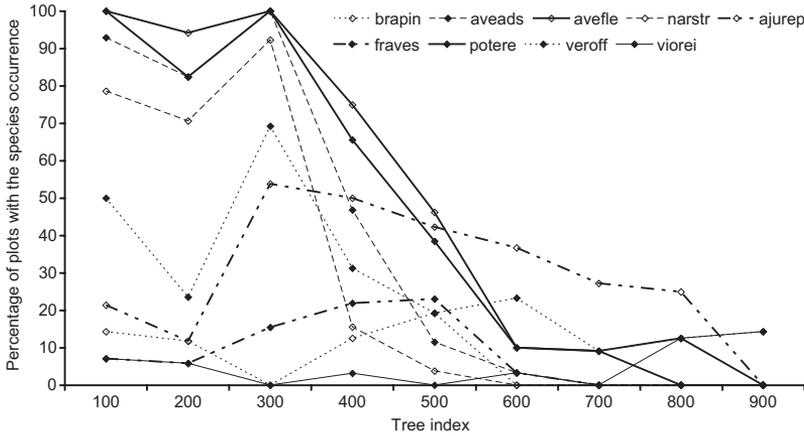


Fig. 4. Performance of vascular plants along the spruce colonization gradient represented by Tree Index (TI) level. Species with different performance types are shown: full bold line (avefle, potere) = gradually decreasing species, dashed line (aveads, narstr) = rapidly decreasing species, dash-dotted line (ajurep, fraves) = species with a peak at intermediate TI levels, dotted line (brapin, veroff) = species with a weak response to the TI level, full line (viorei = *Viola reichenbachiana*) = species with a peak at high TI levels. Abbreviations of species names are explained in Fig. 2.

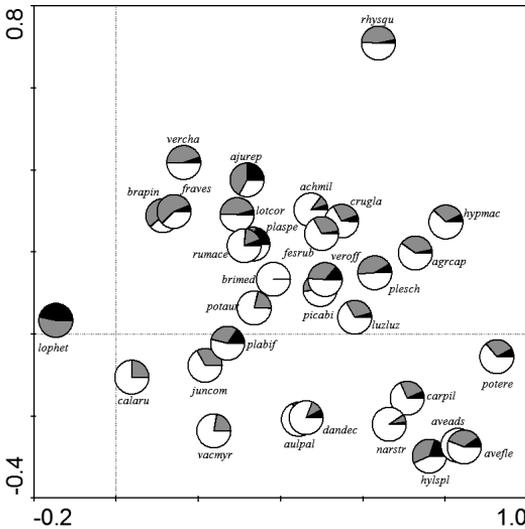


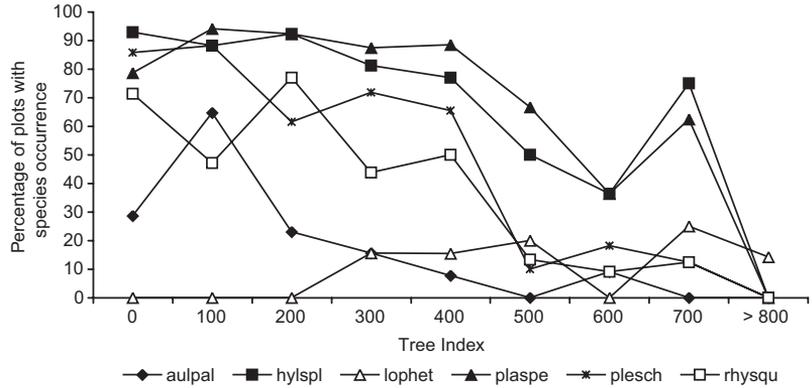
Fig. 5. Principal components analysis, pie symbols plot visualising distribution of species over classes with different light availability (CO). Presence of species in three sample classes is shown according to the CO values: black = 0–9.2, grey = 9.3–13.2, white = 13.2–42.4. The first axis explains 42% and the second axis 10% of variance in the species data. Selected species present in more than 5% sample plots are shown, their abbreviations are explained in Fig. 2.

availability and their abundance decreased rapidly after spruce invasion (Fig. 4). Among vascular plants, *Ajuga reptans* and *Fragaria vesca* were least affected by light conditions (Figs. 2, 4 and 5). In bryophytes, the sensibility to reduced light availability decreases as follows: *Aulacomnium palustre*, *Rhytidiadelphus squarrosus*, *Pleurozium schreberi*, *Hylocomium splendens*, *Plagiomnium* sp. (*P. affine* and *P. cuspidatum*) and *Lophocolea heterophylla* (Fig. 5).

The effect of tree invasion upon vascular plants and bryophytes was estimated based on their response to the increasing tree index (TI) level (Figs. 4 and 6). Besides shading, TI reflects also the other tree effects (needle fall, tree age and thus the duration of tree influence upon the plot). Several types of species performance were observed in relation to the TI level. The group of species rapidly decreasing at a higher TI level included *Nardus stricta*, *Avenula adsurgens* (Fig. 4) as well as the following species not depicted in Fig. 4: *Briza media*, *Carex pilulifera*, *Carlina acaulis*, *Cruciata glabra* and *Acetosa pratensis*. On the other hand, several species declined in abundance only slowly, e.g. *Avenella flexuosa*, *Festuca rubra* agg., *Hypericum maculatum*, *Luzula luzuloides*, *Potentilla erecta* and *Veronica chamaedrys*. Even more persistent were species with the highest abundance at the intermediate levels of TI, such as *Ajuga reptans*, *Fragaria*

uted in the earliest successional stages with the open canopy, and the two last-mentioned species reached the highest cover values. These two species were also very susceptible to a reduced light

Fig. 6. Performance of bryophyte species along the spruce colonization gradient represented by Tree Index (TI) level. Percentage of plots with species occurrence is shown. Abbreviations of species names are explained in Fig. 2.



vesca and *Hieracium murorum*. In the performance of *Brachypodium pinnatum* and to some extent also *Veronica officinalis*, the effect of tree invasion seemed to play the minor role as their abundance peaked at various TI levels. The most shade tolerant species are represented by *Viola reichenbachiana* with the peak at the highest TI level. Among the more frequent bryophyte species, the order from the most retreating to the most persistent species is as follows (Fig. 6): *Aulacomium palustre*, *Rhytidiadelphus squarrosus* \approx *Pleurozium schreberi*, *Hylocomium splendens* \approx *Plagiomnium* sp. (*P. affine* and *P. cuspidatum*) and *Lophocolea heterophylla*.

Discussion

The analyses have confirmed the expectation that in the spruce colonization process, the factors related to light availability and litter accumulation play the most important role. Light as a single factor (measured by canopy openness or tree index) does not sufficiently explain the colonization process. According to our results, litter accumulation affects understorey vegetation much more than a dense canopy limiting the light availability for plants. This is consistent with the hypothesis that litter plays a more profound role in community organization than it does in nutrient cycle (Facelli & Pickett 1991) and supports the idea that litter accumulation belongs to fundamental factors controlling plant community structure.

Three out of five factors passing the forward selection in RDA as significant were related to

litter accumulation (Needles, Litter and DBL_{av}). Two of them (Needles and Litter) had also significant pure effects.

The accumulation and decomposition of plant litter have long since been considered as complex and important factors in controlling both vegetation structure and ecosystem function (Grime 1979, Carson & Peterson 1990, Facelli & Pickett 1991). The effect of litter varies considerably depending on both litter quantity and type (Xiong & Nilsson 1999). Litter may influence vegetation as a result of both physical and chemical effects (Facelli & Pickett 1991) or by its decomposition rate. According to Cornelissen (1996), the decomposition rate of litter follows the sequence forb > deciduous tree leaf > grass > evergreen tree leaf. In our study, needle accumulation (variable Needles) had stronger effect upon the understorey vegetation than the forb and grass litter accumulation (variable Litter). This can be explained by longer residence time of needles (Facelli & Pickett 1991) which multiplies their physical effect upon the herbaceous plants in the field layer. Another reason for a strong needle litter influence is its large quantity, especially in the advanced spruce colonization stages. Not only fallen needles, but also branches, cones and spruce bark contribute substantially to the formation of litter layer.

The significant effect of forb and grass litter found in our analysis was probably mainly a consequence of strong variation of this variable along the transect as it was strongly correlated with cover of herb layer ($r = 0.62$, $P < 0.001$). The direct influence of forb and grass litter accumulation upon the herb layer species

composition was probably low, relevant only in plots with the dominance of tall grasses producing large amounts of dead biomass or *Vaccinium myrtillus* containing phytotoxins in its leaves (Wardle *et al.* 1998). Forb litter is known to exert a strong chemical effect on vegetation because large amounts of phytotoxins and nutrients may be released during a short period (Xiong & Nilsson 1999). Grass litter may influence growing plants indirectly by changed light, temperature and moisture conditions for litter-covered plants especially in dense grass-rich stands (Cornelissen & Thompson 1997). The role of herbaceous litter is obviously more important in open grassland stands than in advanced forest-like stands. According to Muukkonen and Lehtonen (2004), who studied boreal forests, the understorey vegetation produces a notable proportion of the annual yield of litter. In a young spruce forest, litter from understorey vegetation represented about 75% of total litter production, in a forest older than 50 years it was 10%–25% (Muukkonen & Lehtonen 2004).

A negative effect of plant litter on seed germination and seedlings establishment seems to be extremely strong in ecosystems under successional development such as old fields and abandoned grasslands. As they are artificially modified ecosystems the abundance of decomposers increases only slowly after management cessation and litter decomposition is thus very slow (Xiong & Nilsson 1999).

The question “why Needles are more important in explaining the variability of species data than CO?” can be answered as follows. The variable Needles contains important historical information. There is a substantial temporal lag between the production of plant organs and their transformation into litter in coniferous trees (Facelli & Pickett 1991). It not only depends on the growth rate but also on leaf turnover rates. Life span of spruce needles may reach 12 years (Muukkonen & Lehtonen 2004). This time lag is probably correlated with the response rate of vascular plants to changed microhabitat conditions induced by spruce colonization. At the beginning, the vegetation of open grassland communities in the vicinity of fast growing spruce individuals is affected by light reduction. Vascular plant species usually do not react immediately and their

response is expected to be species-specific. Even if the light conditions do not change any more, the litter layer gradually increases in depth as a consequence of litterfall from spruce crowns in the canopy. This co-action of shading and litter accumulation of the invading woody species known from numerous ecosystems (e.g. Wearne & Morgan 2004) seems to be the strongest environmental driving force also in the studied community. Still, the changes in the vegetation composition are proportionate to the changes in the needle-layer percentage cover and not so much to the changes in light conditions, either expressed as CO or TI. The strong ability of Needles to explain the species data variance and its high correlation with the colonization gradient revealed by the 1st PCA axis demonstrate the importance of litter as a historical factor linking interactions across successive generations, and controlling the community structure.

Cummulative effects of successional changes are reflected also by TI to some extent. Along with light availability, it expresses the effects of vertical vegetation profile, potential capacity of litter formation and includes also the secondary effects upon temperature characteristics and both soil pH and microbiological characteristics. The TI belongs to easily measurable variables with a high information value and thus it can be recommended for general use in the studies of successional processes.

Nutrient limitation is in general one of the most important factors affecting the structure of plant communities, biomass production, species composition and diversity (Willems *et al.* 1993, Janssens *et al.* 1998). In large-scale studies the strongest effect of nutrient upon the vegetation was recorded for pH, total nitrogen and organic matter content (e.g. Critchley *et al.* 2002). According to our experience, during the relatively short period of successional changes driven by spruce colonization, most soil parameters changed only slightly. The measured soil pedological and microbiological variables have shown a minor effect upon the understorey vegetation, evident only in the case of pH in the forward selection.

The species turnover during the secondary succession follows the general trends, also detected in our study. According to numerous

authors (e.g. Blažková 1988, Prach & Pyšek 1994, Blažková & Březina 2003, Brockerhoff *et al.* 2003, Pavlí *et al.* 2005), the expansion of woody species is accompanied by a fast decline of heliophilous species and a spread of both tall grasses and shade tolerant species. In later stages the prevailing shade tolerant forbs and grasses retreat and bryophyte species become dominant. Several species of the genera *Brachythecium* and *Plagiomnium* are considered to be most persistent during succession able to survive until the last stages (Blažková & Březina 2003).

The unique position of clonal expansive grasses and dwarf shrubs such as *Brachypodium pinnatum* and *Vaccinium myrtillus* was confirmed also in our study (cf. Hrivnák & Ujházy 2005). The distribution of these species was only slightly related to the main environmental gradient represented by shading and needles accumulation and was more related to their spreading abilities. Both formed large clumps and retained a dominant position even in later successional stages. These may be ascribed to several advantageous attributes such as high potential growth rate, high stature, seasonal storage and remobilization of nitrogen in rhizomes (especially by *Brachypodium*, de Kroon & Bobbink 1997), horizontal space filling by clonal expansion or ability to suppress the seed germination by humus phenolics production (especially by *Vaccinium*, Wardle *et al.* 1998).

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