Secondary succession toward woodland

Changes in the herb layer species composition

Změny bylinného patra v průběhu sekundární sukcese lesa

Alena Dostálová

Plzeň 2010

DOSTÁLOVÁ, A. 2010: Secondary succession toward woodland: Changes in the herb layer species composition [Změny bylinného patra v průběhu sekundární sukcese lesa] – 245p., University of South Bohemia, Faculty of Sciences, České Budějovice, Czech republic

ANNOTATION: This dissertation focus on spontaneously developed forests (SDFs) on mesic stands. The present tree layer was described and the possible changes in the tree layer was estimated. Influence of site- and context-dependent factors on the species composition and general character of the herb layer was studied in detail. An experiment was established to study seed and safe-site limitation of nine forest herb species.

Prohlašuji, že jsem svoji disertační práci vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s §47b zákona 111/1998 Sb., v platném znění, souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách.

V Plzni, 30. dubna 2010

Alena Dostálová

Seznam přiložených publikací:

Dostalova A (2009) Tree seedlings: how they establish in spontaneously developed forests? A study from a mountainous area in the Czech Republic. *Biodiversity and Conservation* 18:1671-1684

Děkuji své rodině a přátelům za trpělivost a všelikou podporu, protože bez té by tato práce nikdy nevznikla.

The research reported in this thesis was supported by grant no. 1159/2004 of the Ministry of Education of the Czech Republic. This support is hereby gratefully acknowledged.

Table of Contents

Obsah

Abbreviations/Zkratky

Abbreviations – Zkratky

1952/1966/1983	vegetation cover in 1952/1966/1983 (field-grassland-scattered trees-closed tree canopy)	vegetační kryt v roce 1952/1966/1983 (pole-louka-roztroušený nálet-zapojený nálet)
A	autochorous species	autochorní druhy
A_a	average age of the tree cover [years]	průměrný věk stromového patra [roky]
A_d	average age of the dominant tree species [years]	průměrný věk druhu dominujícího stromovému patru [roky]
AIC	Akaike Information Criterion	Akaikeho kritérium
A_{max}	maximal age of tree cover [years]	maximální věk stromového patra [roky]
ANOVA	Analysis of Variance	analýza variance
AR	antropochorous and/or ruderal species	antropogenní a/nebo ruderální druhy
A_{SDF}	area of the spontaneously developed forest [m^2]	velikost porostu náletových dřevin [m^2]
BR_s	basal respiration of the microbial community [µg C-CO$_2$.g^{-1}.hod^{-1}]	bazální respirace [µg C-CO$_2$.g^{-1}.hod^{-1}]
C	species typically growing at clearings	druhy pasek
CA	Correspondence Analysis	korespondenční analýza
CCA	Canonical Correspondence Analysis	kanonická korespondenční analýza
centre	nearest distance from the middle of the plot to the SDF border [m]	nejkratší vzdálenost ze středu plochy k okraji porostu náletových dřevin [m]
C_{org}	organic matter content in the soil [%]	obsah organické hmoty v půdě [%]
D	proportion of deciduous trees in the tree layer	podíl opadavých dřevin ve stromovém patře
D_{AB}	removal of above-ground plant biomass	odstranění nadzemní biomasy
D_T	turf disturbance	narušení drnu
D_Fi	distance to the nearest field [m]	vzdálenost k nejbližšímu poli [m]
D_Fst	distance to the nearest forest [m]	vzdálenost k nejbližšímu lesu [m]
D_Grl	distance to the nearest grassland [m]	vzdálenost k nejbližší louce [m]
DBH	diameter in the breast height (120 cm) [cm]	obvod stromu v prsní výšce (120 cm) [cm]
E_1	abundance of the herb layer	pokryvnost bylinného patra
E_3	abundance of the tree layer (logarithmically transformed)	pokryvnost stromového patra (logaritmicky transformovaná)
EIV	Ellenberg indicator value	Ellenbergova indikační hodnota
F	Ellenberg value for humidity	Ellenbergova hodnota pro vlhkost
$Fi_{100/200/300}$	proportion of fields in the 100/200/300 m surroundings	podíl pole v okolí 100/200/300 m
$Fst_{100/200/300}$	proportion of forests in the 100/200/300 m surroundings	podíl lesa v okolí 100/200/300 m
G	grasslandness (index corresponding with the number of grassland species)	lučnatost (index korespondující s počtem lučních druhů)
Gaps	proportion of gaps in the vegetation	otevřenost porostu
GLM	General Linear Model	zobecněný lineární model
GR	graminoids	graminoidy

$Grl_{100/200/300}$	proportion of grassland in the 100/200/300 m surrounding	podíl luk v okolí 100/200/300 m
Gs	grassland species	luční druhy
G_w	weighted grasslandness (index corresponding with abundance of grassland species)	vážená lučnatost (index korespondující s pokryvností lučních druhů)
GW	species growing both in wood and grassland	druhy společné lučním i lesním společenstvům
G_w_A	index corresponding with the abundance of grassland autochorous species	index korespondující s pokryvností lučních autochorních druhů
G_w_M	index corresponding with the abundance of grassland myrmecochorous species	index korespondující s pokryvností lučních myrmekochorních druhů
G_w_Ns	index corresponding with the abundance of grassland species nonspecific to the type of distribution	index korespondující s pokryvností lučních druhů nespecifických ke způsobu rozšiřování
G_w_Wd	index corresponding with the abundance of grassland anemochorous species	index korespondující s pokryvností lučních anemochorních druhů
G_w_Z_{end}	index corresponding with the abundance of grassland endozoochorous species	index korespondující s pokryvností lučních endozoochorních druhů
G_w_Z_{ex}	index corresponding with the abundance of grassland exozoochorous species	index korespondující s pokryvností lučních exozoochorních druhů
$h_1/h_2/h_3/h_4/h_5/h_6$	height categories of the tree-seedlings (0-10 cm, 11-20 cm, 21-40 cm, 41-80 cm, 81-160 cm, <160 cm)	výškové kategorie semenáčků stromů (0-10 cm, 11-20 cm, 21-40 cm, 41-80 cm, 81-160 cm, <160 cm)
HA	annual herbs	jednoletky
HF	forest herbs	lesní byliny
HR	perennial rosettes	druhy s přízemní růžicí listů
HS	perennial small herbs	vytrvalé malé byliny
H_{SSW}	exposition to the south-south-west	sklon k JJZ
H_{SW}	exposition to the south-west	sklon k JZ
HT	perennial tall herbs	vytrvalé vzrostlé byliny
L	Ellenberg value for light	Ellenbergova hodnota pro světlo
M	myrmecochorous species	myrmekochorní druhy
N	Ellenberg value for nitrogen content	Ellenbergova hodnota pro dusík
N_n	normalised number of tree seedlings	normalizovaný počet semenáčků stromů
Ns	species non-specific to the type of distribution	druhy nespecifické ke způsobu rozšiřování
$Ot_{100/200/300}$	proportion of the “other” landscape cover (buildings, water etc.) in the 100/200/300 m surrounding	podíl krajinného pokryvu “ostatní“ v okolí 100/200/300 m
$P_{120}/P_{20}/P_5$	relative irradiance at the 120/20/5 cm above ground	relativní ozářenost ve 120/20/5 cm
PCA	Principal Component Analysis	analýza hlavních komponent
PhAR	photosynthetic active radiation	fotosynteticky aktivní záření
pH_s	soil reaction	půdní reakce
R	Ellenberg value for reaction	Ellenbergova hodnota půdní reakce
RDA	Redundancy Analysis	analýza redundance
R_s	rock fragments content [%]	skeletovitost [%]
RWC	retention water capacity of the soil [%]	retenční vodní kapacita [%]

S_{40}	treatment: shading at the 40% level of incoming radiation	zásah stínění na 40 % dopadajícího záření
S_5	treatment: shading at the 5% level of incoming radiation	zásah stínění na 5 % dopadajícího záření
S_A	treatment: seed addition of typical forest species	výsev lesních druhů
Sc	shrub species	druhy křovin
SDF	spontaneously developed forests	porost náletových dřevin
$SDF_{100/200/300}$	proportion of SDFs in the 100/200/300 m surrounding	podíl porostů náletových dřevin v okolí 100/200/300 m
shape	relative length of the SDF borders to the circle border with the same area	relativní délka hranice porostu náletových dřevin ku délce hranic kruhu o stejné ploše
S_{org}	depth of the organic soil horizon [cm]	hloubka organického půdního horizontu [cm]
T	Ellenberg value for temperature	Ellenbergova hodnota pro teplotu
TL_f	species composition of the estimated tree layer	druhové složení odhadnutého stromového patra
TL_p	species composition of the present tree layer	druhové složení stávajícího stromového patra
TR	trees	stromy
TSD	tree stand density	zakmeněnost
W	woodlandness (index corresponding with the number of woodland species)	lesnatost (index korespondující s počtem lesních druhů)
Wd	anemochourous species	anemochorní druhy
Ws	woodland species	lesní druhy
W_w	weighted woodlandness (index corresponding with the abundance of woodland species)	vážená lesnatost (index korespondující s pokryvností lesních druhů)
W_w_A	index corresponding with the abundance of woodland autochorous species	index korespondující s pokryvností lesních autochorních druhů
W_w_M	index corresponding with the abundance of woodland myrmecochorous species	index korespondující s pokryvností lesních myrmekochorních druhů
W_w_Ns	index corresponding with the abundance of woodland species nonspecific to the type of distribution	index korespondující s pokryvností lesních druhů nespecifických ke způsobu rozšiřování
W_w_Wd	index corresponding with the abundance of woodland anemochorous species	index korespondující s pokryvností lesních anemochorních druhů
W_w_Z_{end}	index corresponding with the abundance of woodland endozoochorous species	index korespondující s pokryvností lesních endozoochorních druhů
W_w_Z_{ex}	index corresponding with the abundance of woodland exozoochorous species	index korespondující s pokryvností lesních exozoochorních druhů
Z_{end}	endozoochorous species	endozoochorní druhy
Z_{ex}	exozoochoroous species	exozoochorní druhy

Nomenclature source: Kubát et al. (2002)

Introduction

Dear readers,

You have just opened a dissertation focusing on spontaneously developed forests (SDFs). Large land areas have been abandoned in recent decades in Europe, and trees have colonised these stands. The areas differ from several dozen square meters to several dozen hectares and SDFs originating on different types of agricultural land (arable land, hay meadows, pastures). The SDFs differ from ancient forests (and potential vegetation cover), from managed forests as well as from former cultivated land. We have insufficient knowledge about their species composition and about factors influencing the course of succession. Their future development is also uncertain.

Species composition could be affected by many factors, and a different course of succession could be assumed for different habitats. I focused on spontaneously developed forests on mesic stands (neither waterlogged nor desiccated, with vegetation neither ruderalised nor typical for poor types of soil). The herb layer (including tree seedlings and seed or safe-site limitation of the forest herb species) was studied in detail.

Most of the chapters are structured in the same way as scientific papers, i.e.: Abstract, Introduction (including questions), Methods, Results and Discussion. References are summarized at the end of the dissertation. This structure was chosen to prevent the need for complicated searching when the reader focuses on a certain part of the study (e.g., to look for methods).

Three chapters focus on woody species. The first of these focuses on the tree layer, which is described and in which the influence of selected factors on the tree species composition was studied. The next two chapters focus on the tree seedlings in SDFs. The species composition and influence of studied factors was studied in the first of these two chapters, while in the second a prediction of future development of tree layer was made for the next generation of the tree layer. The prediction was based on numbers and the height of the tree seedlings. Although approximate numbers were used, it is the first attempt to predict the changes in tree layer species composition for these forests.

The second part of the study is focused on the present herb layer of SDFs and is divided into four chapters. The character of the herb layer and common species in the herb layer were studied separately, along with the influence of site-dependent factors (tree layer, light, climatic and soil conditions) and context-dependent factors (surroundings, SDF characteristics and history).

The seed and safe-site limitation of forest herbs in an early stage of succession (12-year abandoned grassland) was experimentally studied in the third part of the dissertation. The factorial designed experiment was established. The seed limitation of the selected forest herb species was manipulated by sowing. From safe-site limitation the competition of the present herb layer and the influence of light conditions were studied using the above-ground biomass removal, turf disturbance and shading treatments.

Readers who are not willing to go through the long text of the dissertation (caused by the structure and other requirements of a scientific paper) will find the main results summarized and synthesised in the Summary chapter. A particular emphasis has been placed on the herb layer, which was studied in detail in four separate chapters (5, 6, 7 and 8) prioritized as follows: 1) the character of the herb layer and frequent species in the herb layer; 2) the site- and context dependent factors.

The chapters Introduction and Summary, table titles, figure captions, and abstracts are translated into Czech to make the results available for Czech readers (especially from state administration, forest managers and the general public, who usually do not read English well).

28th March 2010, Plzeň, Czech Republic.

Úvod

Vážený čtenáři,

do ruky se Vám dostala disertační práce zabývající se porosty náletových dřevin (Spontaneously developed forests, SDFs). V posledních desetiletích se uchytily na mnoha místech, na nichž bylo upuštěno od klasického zemědělského hospodaření. Jejich rozloha je různá od několika desítek metrů čtverečních po několik desítek hektarů. Porosty náletových dřevin se liší jak od původních lesů (a potenciálně přirozené vegetace), tak od hospodářských lesů i od původních kultur na zemědělské půdě (pole, louky nebo pastviny). O procesech určujících jejich stávající druhové složení víme málo a ještě méně víme o změnách v druhovém složení, ke kterým teprve v budoucnu dojde.

Druhové složení porostů náletových dřevin může být ovlivněné celou řadou faktorů a sukcese může probíhat odlišně na různých stanovištích. Ve své práci jsem se zaměřila pouze na porosty náletových dřevin na mesickém stanovišti (z hlediska půdní vlhkosti a živinových poměrů) a podrobněji jsem se věnovala bylinnému patru (včetně semenáčků stromů a experimentálnímu zjištění limitace lesních bylin semeny nebo stanovištěm), jemuž je věnována rozsahem největší část práce.

Většinu kapitol jsem koncipovala formou vědeckého článku. Tyto kapitoly mají jednotnou strukturu: shrnutí, úvod (včetně otázek), metodiku, výsledky a diskusi. Seznam použité literatury je zařazen na konci práce. Tuto strukturu jsem volila proto, aby čtenář, kterého zajímá jen dílčí část mé práce nemusel složitě přelistovávat (např. aby se dozvěděl o použitých metodách). Najde tak veškeré potřebné informace k dílčí části studie přímo v dané kapitole.

Ve třech kapitolách se věnuji dřevinám. V první z nich naleznete popis současného stromového patra a analýzu vlivu studovaných faktorů na jeho druhové složení. Další kapitola se věnuje semenáčkům stromům. Cílem bylo zjistit, které druhy kolonizují porosty náletových dřevin a které ze studovaných faktorů ovlivňují jednotlivé druhy. Ve třetí kapitole této části jsem se pokusila předpovědět změny druhového složení stromového patra pro druhou generaci stromů. Předpověď je založena na počtu a výšce semenáčků stromů přítomných v současných porostech SDF. Ačkoli je má předpověď založena na odhadnutých hodnotách pro vývoj, jedná se, alespoň pokud je mi známo, o první pokus o takovou extrapolaci do budoucna pro tento typ porostů.

V následujících čtyřech kapitolách se podrobně zabývám bylinným patrem. Jednotlivé kapitoly se věnují celkovému charakteru bylinného patra a druhům hojným v bylinném patře. Zvlášť je také studován vliv na stanovišti závislých faktorů (stromové patro, světelné, klimatické a půdní podmínky) a na kontextu závislých faktorů (okolí, charakteristiky SDF, historie).

Poslední část práce je věnována experimentu, jehož cílem bylo zjistit, zda-li jsou lesní byliny při kolonizaci časně opuštěné zemědělské půdy limitovány nedostatkem diaspor nebo nedostatkem vhodných stanovišť. V rámci faktoriálně uspořádaného pokusu jsem odstranila limitaci semeny vybraných lesních druhů přímým výsevem. Z možných stanovištních limitací jsem studovala vliv přítomného bylinného patra, jehož kompetiční schopnost jsem snižovala disturbancí (odstranění nadzemních částí rostlin, narušení drnu); a vliv osvětlení, kdy dopadající sluneční záření bylo redukováno na 40 % a 5 %.

Čtenář, který nechce procházet dlouhý text celé práce (vyplývající ze struktury a dalších požadavků vědecké práce) nalezne všechny hlavní výsledky práce v kapitole Shrnutí. Zvláštní pozornost byla věnována bylinnému patru, které bylo studováno ve čtyřech kapitolách (5, 6, 7, 8) zaměřených na základě: 1) charakteru porostu a druhů hojných v bylinném patře; 2) vlivu na stanovišti a na kontextu závislých faktorů.

Kapitoly Úvod a Shrnutí, dále popisky k tabulkám a obrázkům a shrnutí jednotlivých kapitol jsem přeložila do češtiny, aby výsledky této práce byly přístupné také českému čtenáři, který angličtinou nevládne.

V Plzni 28. března 2010.

What factors influence the tree layer species composition of spontaneously developed forests on mesic pstands?

Čím je ovlivněno druhové složení stromového patra porostů náletových dřevin na mesickém stanovišti?

Abstract

The influence of site-dependent (soil conditions, Ellenberg indicator values, altitude, exposition, slope, age) and context-dependent factors (area, shape, position within the SDF, surrounding, history) on the first tree generation of spontaneously developed forests (SDFs) in mesic stands was studied.

Tree layer changes during the succession from dense growths to semi-open forests.

Although the pioneer species *Betula pendula* dominated, 11 tree species were able to colonise the tree layer. More species were found in higher altitudes, colder stands and in younger growths. The anemochorous species were the best colonisers, however endozoochorous species (dispersed by birds) were also able to establish in the SDFs. Seed limitation seems to be the most important factor influencing tree layer species composition.

Dominating species were influenced at most by soil conditions, the age of the tree layer, and by surrounding vegetation cover. The character of the tree layer corresponded with the Ellenberg *T* value, and the shape of the SDF. Site- and context-dependent factors also influence the species composition of the SDFs.

Shrnutí

Byl studován vliv na stanovišti závislých proměnných (půdní podmínky, Ellenbergovy indikační hodnoty, nadmořská výška, expozice, sklon, věk) a na kontextu závislých (velikost, tvar, pozice uvnitř porostu, okolí, historie) proměnných na druhové složení první generace stromového patra porostu náletových dřevin (SDF).

Hustota zápoje první generace stromového patra v průběhu sukcese klesá.

Přestože v porostech náletových dřevin dominovala bříza (*Betula pendula*), stromové patro bylo schopno kolonizovat 11 druhů stromů. Více druhů dřevin bylo ve vyšších nadmořských výškách, na chladnějších stanovištích a v mladších porostech. Nejúspěšnější byly anemochorní druhy, druhy endozoochorní (šířené ptáky) se byly také schopny v porostech náletových dřevin uchytit. Zdá se, že limitace semeny je nejvýznamnější faktor ovlivňující druhové složení porostů náletových dřevin.

Dominující druhy byly nejvíce ovlivněny půdními podmínkami, věkem stromového patra a vegetačním krytem v okolí. Celkový charakter stromového patra korespondoval s Ellenbergovou indikační hodnotou T a tvarem porostu náletových dřevin. Stanovištní a na kontextu závislé faktory také ovlivňovaly druhové složení porostů náletových dřevin.

Introduction

A forest is supposed to be natural vegetation in a temperate climate in most locations (Ellenberg 1988). Due to human activities, large natural forests have been cut down and replaced by cultivated land and settlements. However, especially in recent decades, much of the agricultural land has been abandoned, mostly in uninhabitated and less favourable areas for agriculture (e.g., Hamre et al. 2007; Kaligarič et al. 2006; MacDonald et al. 2000). Even where the forests have remained, the composition of tree species has been changed. The most dramatic changes happened during the 19th and 20th centuries in Central Europe. Norway spruce (*Picea abies* (L.) Karsten) and Scots pine (*Pinus sylvestris* L.) have been planted, and agricultural-like management (monocultures, cuts, division of the forests, and building of access to the forests) has been practised in most forests. These species have replaced the European beech (*Fagus sylvatica* L.) and oaks (*Quercus petraea* (Mattuschka) Liebl., *Quercus robur* L.), which had dominated the mesic stands from lowlands to mountains.

After abandonment, the former cultivated land was reforested or left abandoned, and secondary forests spontaneously developed at most of these sites. The increase in forest area was high, especially in the mountains, e.g., Kubeš and Mičková (2003) found a 14% increase of forests during the last 60 years in the Novohradské hory Mountains in the Czech Republic. Many studies do not distinguish between the planted and spontaneously developed forests (SDFs), although the composition of species is not the same. In my study, I focused only on the SDFs.

The rate of succession varies, and areas with rapid overgrowth of trees are mentioned (e.g., Schreiber 1996; Spatz 1980). Prach (1985) predicts that abandoned fields in Finland will have overgrowth of trees within 50 years. Kozak et al. (1999) found from aerial photos, which showed that the spontaneous forest development had taken 30-40 years in the Beskidy Mountains in Poland. Other studies reported a very lengthy duration of tree establishment at abandoned sites (e.g., Blažková 1988; Hadač 1990; Wiegert and Evans 1964). This can be attributed to what can be referred as a "successional window" (Prach 1994), which means that usually only a short period of the first twenty years is suitable for tree establishment. In general, the tree layer develops within 30-40 years and definitely closes after 60-80 years (Flinn and Vellend 2005).

A favourable climate can enhance the tree colonisation process (Dovčiak et al. 2005), and lone trees can facilitate the establishment of tree seedlings (Dzwonko and Loster 1992). The lines (e.g., hedgerows, paths) or disturbed places (e.g., drains, abandoned fields) can be also the sources of trees (Guth 1998). Woody plants can be blocked, especially due to soil conditions or competition – mainly from grasses (e.g., Dickie et al. 2007), or from litter (Facelli and Pickett 1991a).

Pioneer tree species usually dominate the tree layer. The birch (*Betula pendula* Roth) was found to be the most common tree species dominating SDFs in Central Europe (Prach 1994; Prach and Pyšek 1994b), but many other species were reported as well (for review see Prach 1994). However, the tree layer has been insufficiently studied, due to the lengthiness of the process (decades and centuries) and because the SDFs have been neglected by the foresters, who usually do not perceive them as forests, and by ecologists who have focused primarily on the herb layer of the secondary forests (for review see Vellend et al. 2007).

The first tree generation of SDFs in mesic stands on former agricultural land was studied in mountainous areas in the Czech Republic. Tree layer species composition results from the seed availability, which directly limits or enhances the success of the species, and from micro-site conditions, including competition with present vegetation cover, which alters the establishment success of certain species). In the study, the influence of site-dependent factors (such as soil conditions, the site character described by Ellenberg indicator values - *EIV*, altitude, slope and orientation and the age of the tree layer), and context-dependent factors (such as the area and shape of the SDF, the position of the plot within the SDF, surrounding vegetation and historical land-cover) was studied.

The following questions were considered:

1. What tree species are able to establish and dominate the first generation of SDFs in mesic stands?
2. What tree layer character can be found in the first generation of SDFs in mesic stands?
3. Are the site-dependent factors or context-dependent factors important for the species composition of the tree layer of SDFs in mesic stands?

Methods

Study area

The study area was the southern part of the Czech Republic (40°35-38′ N, 14°11-17′ E). Altitude ranged between 665 and 940 m. Climatic conditions moderately oceanic between the warm and cold type (climatic regions MT 3-Ch 7; Quitt, 1971), average year temperature 6.8°C and average year precipitation 718-1003 mm.

Forty-eight plots (10 × 10 m) were fixed in the SDFs which were differed in age, altitude and exposition, but all plots were on mesic stand (neither waterlogged nor desiccated, vegetation neither ruderalised nor typical for poor soils). I fixed the plots in such growths, where significant human influence was not recognisable, which were homogenous and large enough. Different age categories present in the study area were equally presented.

The supposed terminal stage of succession is beech forest (*Dentario enneaphylli-Fagetum* association, or transient to *Luzulo albidae-Quercetum petraeae* association; Neuhäuslová 1998).

All field observations were carried out in 2004 and 2005.

Data collection: tree layer

The number and species composition of trees at the plot were listed. The diameter (*DBH*) and perimeter (average of two measurements taken in a right-angle) of each tree were measured as 120 cm above ground [cm]. The tree stand density (*TSD*) was calculated as the sum of the square basis of the trees at the plot according to the average perimeter.

For age estimation two samples of wood were taken from all the trees, but maximally from ten for each species (randomly searched), using a Pressler's auger. Samples were taken from opposite sides of the trunk 40 cm above ground. After fixation and cutting, tree-rings were counted for estimation of age. The following were counted: average age of trees (A_a) and the maximal age of the trees (A_{max}) for all plots. A_a corresponds with the duration of closed canopy of the tree layer, while A_{max} corresponds rather with the duration of abandonment.

Data collection: site-dependent factors

The altitude of the plot was taken from the map as 1 : 10 000. The altitude corresponds with the climatic conditions (Prach and Řehounková 2006), because the mean temperature and precipitation depends on the altitude. The study area is relatively small, and we can assume that the climatic conditions can be well described by the altitude.

The orientation (using a compass) and slope (using visual estimation) of all plots were determined, and the heat index to the south-south west (H_{ssw}) was calculated as follows:

$$H_{SSW} = \cos(\text{exposition} - 202.5°) \times \text{tg}(\text{slope})$$

A soil sample was taken at each plot (mixture of five point samples). Analyses of the following were done: i) the content of rock fragments >2 mm (R_s) in the dried samples using the 2 mm sieve [%]; ii) the soil reaction in the water solution (pH_s) using 10 g of the fine air-dried soil sample and 20 cm^3 of distilled water (free of CO_2); iii) organic matter content (C_{org}) determined as the loss of the matter content of the dried sample by 450°C [%]; iv) the basal respiration of the microbial community (BR_s) determined as CO_2 production [μg C-CO_2.g^{-1}.hod^{-1}] (Jäggi 1976). The retention water capacity (*RWC*) determined from the undisturbed soil samples (five per plot) taken from the organic soil horizon at each plot. *RWC* was counted from the water content in the soil sample after 24 hours of draining of the water-lodged sample using filter paper. A soil pit was made next to each plot (within the same SDF) to measure the depth of the organic horizon – horizon A, transient A and B horizon (S_{org}) [cm].

The Ellenberg indicator values (*EIVs*) were calculated from the herb layer species composition determined from the phytocenological relevé taken from all the plots. Abundance (visually estimated in percentages of the species) was used as weight in the *EIVs* calculation. The following *EIVs* were calculated: humidity (*F*), temperature (*T*) and nitrogen content (*N*) (Ellenberg 1988). *EIV*s correspond with the character of the habitat, and *N* corresponds more with the productivity of the place (Ertsen et al. 1998).

The mean values of site-dependent factors are summed in the Table 1.

Data collection: Context-dependent factors

Vegetation map 1 : 10 000 (Dostálová unpbl.) redrawn on a slide and digitalized (300dpi colour picture) was used to determine the following context-dependent factors: i) the total area of the SDF (A_{SDF}) [ha]; ii) the shape of the SDF, determined as the multiple of the perimeter of a circle with the same area; iii) the position of the plot within the SDF (*centre*), determined as the nearest distance from the centre of the plot to the border of the SDF [m]; iv) the distance to the nearest forest (*D_Fst*) [m]; v) the vegetation cover of the forest (i.e., managed or natural forest) and the SDF (at least 30% of tree-cover) in 100, 200 and 300 m surrounding (i.e., the round area of a certain semi-diameter with the central point in the centre of the plot) ($Fst_{100/200/300}$, $SDF_{100/200/300}$), determined as the percentage of the vegetation in 100, 200 or 300 m surrounding. Image analysis in the Scion Image for Windows 4.0.3 program was used.

The aerial photos from the Military Geographical and Hydrometeorological Office (Dobruška, Czech Republic) were used to determine the past vegetation cover of the plot. Three sets of photos were available from the vegetation period for the whole study area: 1952 (7th of July, camera RC5-97, focal length 210.0 mm, flying height 5250 m, 1:25000); 1966 (1st of May, MRB, 210.11 mm; 3200 m, 1:12600), 1967 respectively (25th of June, RC 5a, 209.7 mm, 3300 m, 1:13150) and 1983 (8th of June, MRB-9, 88.6 mm, 2900-3200 m, 1:28040). The following vegetation types were distinguished: field (arable land), grassland (meadow, pasture, abandoned grassland), scattered SDF, closed SDF. These types correspond with the supposed successional sere.

The mean values of context-dependent factors are summed in the Table 1.

Table 1. Basic statistics of the site- and context-dependent factors.

	Mean±SD		**Mean±SD**		**Mean±SD**
altitude	788±70.38	F	5.72±0.389	A_{SDF}	74 223±81 223
BR_s	2.73±1.101	SDF_{100}	0.45±0.239	shape	3.09±2.179
C_{org}	11±3.1	SDF_{200}	0.37±0.195	centre	22.04±13.395
R_s	41±23.5	SDF_{300}	0.33±0.171	1952	2.02±0.707
RWC	15.73±3.233	Fst_{100}	0.18±0.209	1966	2.74±1.010
S_{org}	23.43±16.524	Fst_{200}	0.24±0.199	1983	3.43±0.853
T	5.07±0.228	Fst_{300}	0.27±0.186	A_a	30.6±10.82
N	4.01±0.633	D_Fst	110.5±152.53	A_{max}	45.3±18.1

BR_s – basal respiration of the microbial community [µg C-CO_2.g^{-1}.hod^{-1}], C_{org} – organic matter content [%], R_s – rock fragment content in the soil [%], RWC – retention water capacity [%], S_{org} – depth of the organic soil horizon [cm], T/N/F - Ellenberg T/N/F indicator values, $SDF_{100/200/300}$ – proportion of spontaneously developed forests in 100/200/300 m surrounding, $Fst_{100/200/300}$ – proportion of forest in 100/200/300 m surrounding, D_Fst – distance to the nearest forest [m], A_{SDF} – area of SDF [m^2], shape - relative length of the SDF border, centre - nearest distance from the centre of the plot to the border of the SDF, 1952/1966/1983 - vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy), A_a/A_{max} – average/maximal age of the tree cover.

Tabulka 1. Na stanovišti a na kontextu závislé faktory – základní statistika. BR_s - bazální respirace půdy [µg C-CO_2.g^{-1}.hod^{-1}], C_{org} – obsah organické hmoty v půdě [%], R_s - skeletovitost půdy [%], RWC – retenční vodní kapacita [%], S_{org} - hloubka organického půdního horizontu, T/N/F - Ellenbergovi T/N/F indikační hodnoty, $SDF_{100/200/300}$ – podíl náletových dřevin v okolí 100/200/300 m, $Fst_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, D_Fst – vzdálenost k nejbližšímu lesu [m], A_{SDF} - rozloha SDF [m^2], shape – relativní délka hranice SDF ku obvodu kruhu o stejné velikosti, centre – nejkratší vzdálenost středu plochy k okraji SDF, 1952/1966/1983 – vegetační kryt v letech 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-roztroušený nálet, 4-zapojený nálet), A_a/A_{max} – průměrný/maximální věk stromového patra.

Statistical analysis

Ordination methods were used to test the influence of site- and context-dependent factors on tree layer species composition in the CANOCO v. 4.5 program (Lepš and Šmilauer 2003). The “species” data were logarithmically transformed ($y=\log_{10}(y+1)$), and European beech and pear trees were excluded (only one tree was found). Linear analyses were performed (the length of the gradient was 2.6), indirect principal component analysis (*PCA*), and direct redundancy analysis (*RDA*). The independent variables were as follows: altitude, H_{SSW}, BR_s, S_{org}, R_s, pH_s, *RWC*, C_{org}, *EIVs*: *T*, *F* and *N*, vegetation cover in *1952*, *1966* and *1983*,

A_a, A_{max}, $SDF_{100/200/300}$, $Fst_{100/200/300}$, D_Fst, A_{SDF}, *shape, centre*. Manual selection (Forward selection, Monte Carlo permutation test under a full model with 499 permutations) of the factors at the $\propto = 0.05$ level was used. Visualisation of the ordination analysis was performed in the CanoDraw v. 4.0. program (Lepš and Šmilauer 2003).

The relationship between the number of trees per plot (birch, Norway spruce, all trees) or number of tree species per plot or TSD and site- or context-dependent factors (the same as in the ordination analyses) were tested using General Linear Models (*GLM*). Poisson distribution of the data was assumed, because the link function is a “Log” function, which is recommended for counts and frequency data (Lepš and Šmilauer 2003; p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using Akaike Information Criterion (*AIC*) in the CanoDraw v. 4.0 program (Lepš and Šmilauer 2003).

The age prediction formula (dependence of *DBH* on the age of the tree) for birch, Norway spruce and European aspen (*Populus tremula* L.) was determined using a linear regression model in the Statistica v. 5.0 program. Outlayers were removed ($<3\sigma$). The age of trees, which was not determined directly by counting the tree rings, was estimated by the regression model. The difference in age for two species growing together at certain plot was tested using the Analysis of Variance (*ANOVA*) in the Statistica v. 5.0 program.

Results

The number of trees per plot (100 m^2) was found to be 29±39. In total, 11 tree species were found, and the number of species per plot was 2.6±1.07 and ranged between 1 and 5 species. The most common of these were the birch and the Norway spruce, while only one European beech tree and one pear tree (*Pyrus communis* L.) were found (for more detail see Table 2).

Table 2. Basic statistics of the tree species.

	Plots [%]	**Trees [%]**	**Mean±SD per 100 m^2**
Betula pendula	88	60	17.4±27.90
Picea abies	43	15	4.2±9.69
Pinus sylvestris	29	2	0.7±1.80
Salix caprea	29	3	0.8±2.39
Populus tremula	24	14	4.1±11.76
Acer pseudoplatanus	12	4	1.2±5.50
Sorbus aucuparia	12	1	0.3±0.77
Fraxinus excelsior	6	1	0.1±0.66
Prunus avium	6	0.4	0.1±0.54
Fagus sylvatica	2	<0.1	<0.1±0.15
Pyrus communis	2	<0.1	<0.1±0.15

Plots - percentage of occupied plots, Trees - percentage of tree listed, Mean - mean number of trees per 100 m^2, SD – standard deviation.

Tabulka 2. Druhy stromů – základní statistika. Plots – procento obsazených ploch, Trees – podíl na celkovém množství stromů, Mean – průměrný počet stromů na 100 m^2, SD – směrodatná odchylka.

Ordination analysis

Only the Ellenberg *T* value (F = 3.89, p<0.01) and the shape of the SDF (F = 3.30, p = 0.01) significantly influenced the tree layer species composition. The first four ordination axes in the *PCA* explained the large amount of total variability in the data (85.2%), while the *T* and shape did only for 14%. The Norway spruce and Scots pine were more common at plots with lower Ellenberg *T* values, while mountain maple (*Acer pseudoplatanus* L.), wild cherry trees (*Prunus avium* (L.) L.) and common ash (*Fraxinus excelsior* L.) preferred warmer stands. The birch dominated the SDFs with more complicated shapes, while European aspen prevailed among the less complicated shapes. In the growth dominated by European aspen, the endozoochorous cherry tree and mountain ash (*Sorbus aucuparia* L.) trees are more common, while the anemochorous goat willow (*Salix caprea* L.) is more present at plots dominated by birch (Fig. 1).

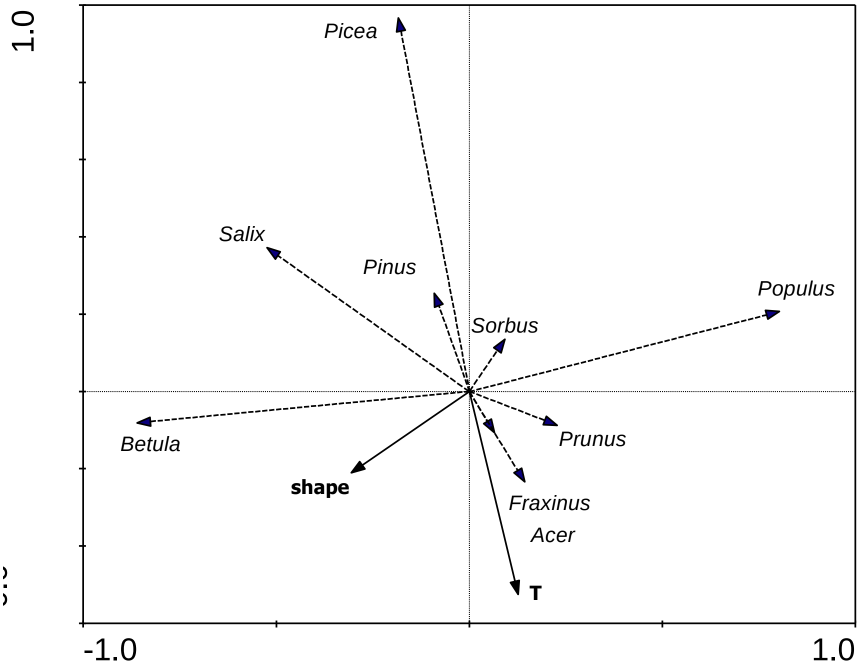


Figure 1. Ordination diagram for PCA of the tree layer (selected environmental factors projected). Acer – *Acer pseudoplatanus*, Betula – *Betula pendula*, Fraxinus – *Fraxinus excelsior*, Picea – *Picea abies*, Pinus – *Pinus sylvestris*, Populus – *Populus tremula*, Prunus - *Prunus avium*, Salix – *Salix caprea*, Sorbus - *Sorbus aucuparia*; T - Ellenberg T value, shape – relative lenght of the SDF border toward the circle with the same area.

Obrázek 1. PCA ordinační diagram stromového patra s promítnutými významnými environmentálními proměnnými. Acer – *Acer pseudoplatanus*, Betula – *Betula pendula*, Fraxinus – *Fraxinus excelsior*, Picea – *Picea abies*, Pinus – *Pinus sylvestris*, Populus – *Populus tremula*, Prunus - *Prunus avium*, Salix – *Salix caprea*, Sorbus – *Sorbus aucuparia*; T - Ellenbergova hodnota T, shape – relativní délka hranice SDF ku obvodu kruhu o stejné velikosti.

GLM

The birch and Norway spruce tree numbers were influenced mostly by soil conditions, history, age characteristics and by the SDF/forests proportion in the 300 m surrounding. The surrounding vegetation in the 100 m, the Ellenberg *F* value and the position within the SDF (centre) did not influence the number of birch, Norway spruce and tree species (Table 3).

The birch was more abundant at plots with lower organic matter content, higher pH_S, low or deep soils (Fig. 2f), at plots which were field in 1966 or grassland/scattered SDF in 1983 (Fig. 2c), in younger growths (Fig. 2a), at plots surrounded by ca 30% by SDFs in 200 and 300 m surrounding (Fig. 2d), less surrounded by forests in the 300 m surrounding (Fig. 2e) and at plots with more complicated shapes (for more detail see Table 3).

The Norway spruce was more common at plots with lower rock fragment content, RWC about 20%, organic horizon depth ca 30 cm (Fig. 2f) and medium *N* values (optimum 4.3). It decreased with the Ellenberg *T* value, was more common at plots, which were grasslands in 1952 (Fig. 2b) in younger growths (Fig. 2a) and plots less surrounded by the SDFs, but more surrounded by forests in the 300 m surrounding (Fig. 2d). For more detail see Table 3.

More species were found in higher altitudes and at colder stands (lower *T*), in younger growths (Fig. 2a) and at plots both with low or high complicated shapes (Table 3).

Table 3. Relation of site- and context-dependent factors and birch, Norway spruce and number of species (N_species) fitted by *GLM* (relevant factors only).

	Betula pendula		***Picea abies***		**N_species**	
	M	**var.**	**M**	**var.**	**M**	**var.**
altitude	×		L↑	9	Q∪	20
H_{SSW}	×		×		L↓	8
BR_S	L↓	6	L↓	6	Q∪	8
C_{org}	L↓	20	L↓	8	×	
R_s	×		L↓	10	Q∩	8
pH_s	L↑	22	×		Q∪	10
RWC	×		Q∩	19	Q∩	9
S_{org}	Q∪	16	Q∩	30	×	
T	×		L↓	29	L↓	13
N	×		Q∩	11	L↓	7
SDF_{200}	Q∩	12	L↓	9	×	
SDF_{300}	Q∩	20	L↓	12	×	
Fst_{200}	L↓	9	×		×	
Fst_{300}	L↓	13	L↑	8	×	
D_Fst	×		×		L↓	5
A_{SDF}	×		×		L↓	6
shape	Q∪	12	×		Q∪	15
1952	L↓	7	Q∩	18	×	
1966	Q∪	36	×		Q∩	9
1983	Q∩	16	L↓	15	×	
A_a	L↓	29	Q∪	35	L↓	13
A_{max}	L↓	20	Q∪	31	L↓	9

M - model: L – linear, Q – square polynom fitted, × - nonsignificant, ↓/↑ - decrease/increase, ∪/∩ - "humped" answer; var. - explained variability [%]. H_{SSW} – Heat to the south-south west, BR_s – basal respiration of the microbial community [µg C-CO$_2$.g^{-1}.hod^{-1}], C_{org} – organic matter content [%], R_s – rock fragment content in the soil [%], pH_s – soil reaction, RWC – retention water capacity [%], S_{org} – depth of the organic soil horizon [cm], T/N – Ellenberg T/N indicator values, $SDF_{200/300}$ – proportion of SDF in the 200/300 m surrounding, $Fst_{200/300}$ – proportion of forests in the 200/300 m surrounding, D_Fst - distance to the nearest forest [m], A_{SDF} – area of SDF [m^2], shape – relative length of the SDF border, 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy), A_a/A_{max} – average/maximal age of the tree cover.

Tabulka 3. Vztah stanovištních a na kontextu závislých faktorů k bříze, smrku a počtu druhů (N_species) zjištěný *GLM* (jen významné faktory). M - model: L – lineární vztah, Q - polynomiální vztah (druhého stupně), × - neprůkazné, ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. – vysvětlená variabilita [%]. H_{SSW} – sklon k JJZ, BR_s – bazální respirace půdy [µg C-CO$_2$.g^{-1}.hod^{-1}], C_{org} – obsah organické hmoty v půdě [%], R_s – skeletovitost [%], pH_s - půdní reakce, RWC - retenční vodní kapacita [%], S_{org} – hloubka organického půdního horizontu [cm], T/N - Ellenbergovi hodnoty T/N, $SDF_{200/300}$ – podíl náletových dřevin v okolí 200/300 m, $Fst_{200/300}$ – podíl lesa v okolí 200/300 m, D_Fst – vzdálenost k nejbližšímu lesu [m], A_{SDF} – velikost SDF [m^2], shape – relativní délka hranice SDF ku obvodu kruhu o stejné velikosti, 1952/1966/1983 – vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet), A_a/A_{max} – průměrný/maximální věk stromového patra.

The orientation of the site and area of the SDF, where the plot was fixed, does not influence the number of trees per plot and tree stand density. The average age of the tree cover was the most important studied factor influencing both the number of trees per plot and *TSD* (50% of total variance explained) – see Table 4.

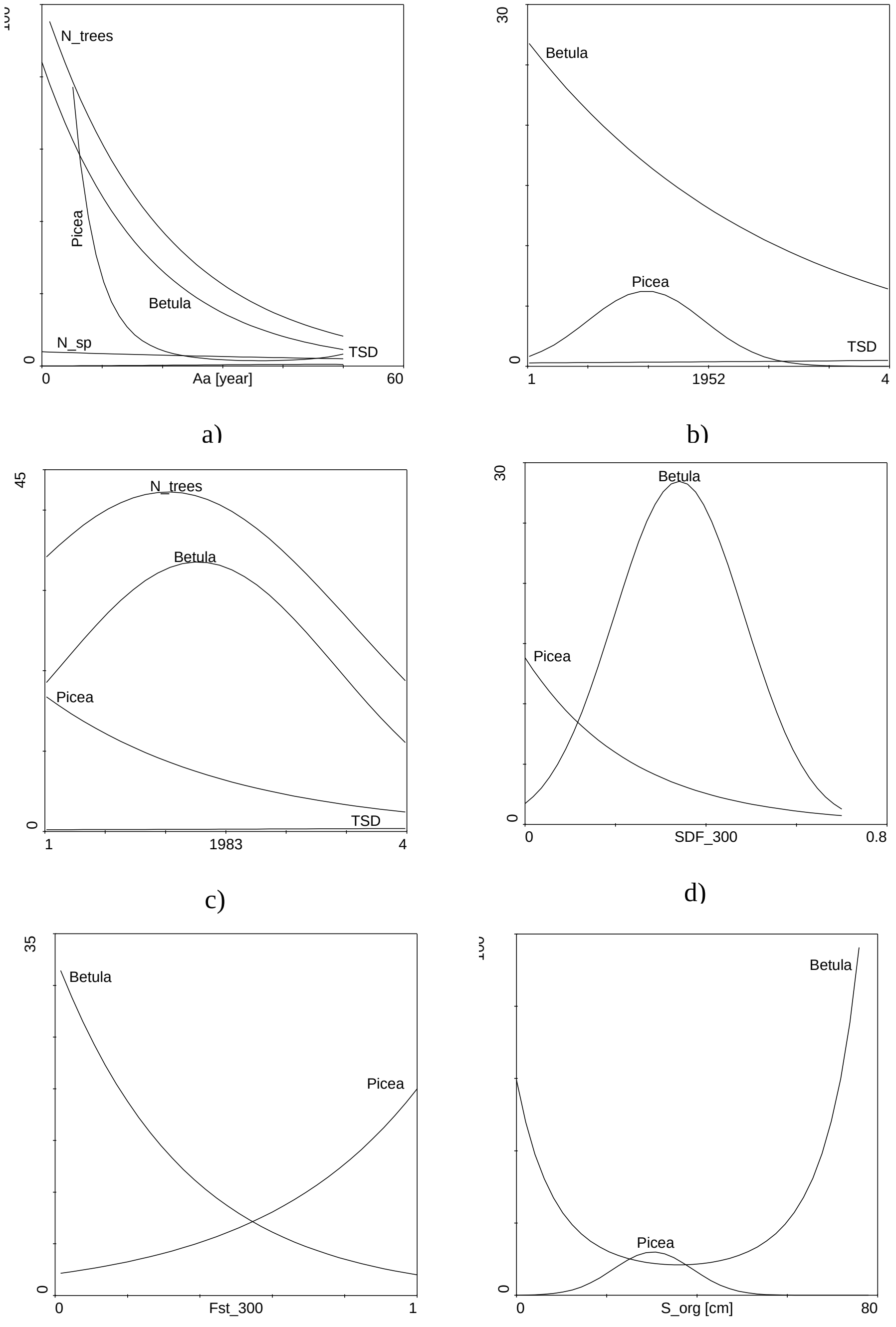
The number of trees per plot was higher in younger growths (A_a, field or grassland in 1966, grasslands in 1983; Figs. 2a, c) and both in lower and higher altitudes, while *TSD* was higher in older growths (A_a, *1952*, *1966*, *1983*, Figs. 2a, b, c) and at medium rich sites (*N* optimum 4.1) – for more detail see Table 4.

Table 4. Relation of site- and context-dependent factors and number of trees (N_trees) and tree stand density (*TSD*) fitted by *GLM* (relevant factors only).

	N_trees [100 m^2]		**TSD [m^2.are^{-1}]**	
	M	**var.**	**M**	**var.**
altitude	Q∪	10	×	
N	×		Q∩	8
1952	×		L↑	7
1966	L↓	15	L↑	26
1983	Q∩	19	L↑	8
A_a	L↓	50	Q∩	50

M - model: L – linear, Q – square polynom fitted, × - nonsignificant, ↓/↑ - decrease/increase, ∪/∩ - “humped” answer, var. - explained variability [%]. N – Ellenberg value for nitrogen, 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy), A_a – average age of the tree cover.

Tabulka 4. Vztah stanovištních a na kontextu závislých faktorů k počtu (N_trees) a zakmenění (*TSD*) zjištěný *GLM* (jen průkazně vztahy). M - model: L – lineární model, Q – polynomiální odpověď (druhého stupně), × - neprůkazné, ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]. N – Ellenbergova hodnota N, 1952/1966/1983 – vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet), A_a - průměrný věk stromového patra.



a) b) c) d) e) f)

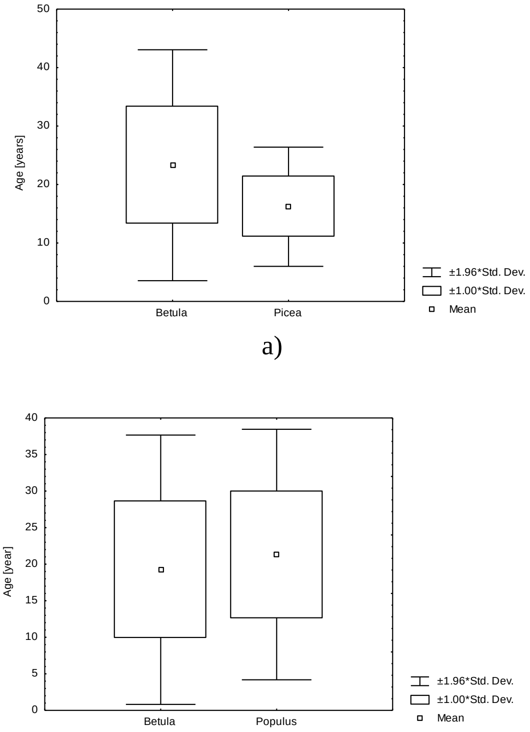
Figure 2. Influence of: a) average age of the tree cover, b) vegetation cover in 1952 and c) in 1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy), d) proportion of SDFs in the 300 m surrounding, e) of forests in the 300 m surrounding, f) depth of the organic soil horizon; on the *Picea abies* and *Betula pendula* [trees per are], number of tree species in the tree cover (N_sp), number of trees in the tree cover (N_trees) [.are^{-1}] and tree stand density (TSD) [m^2.are^{-1}].

Obrázek 2. Vliv: a) průměrného věku stromového patra, b) vegetačního krytu v roce 1952 a c) v roce1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet), d) podíl SDFs v okolí 300 m, e) lesa v okolí 300 m, f) hloubky organického půdního horizontu; na druhy *Picea abies* a *Betula pendula* [stromů.ar^{-1}], počet druhů stromů (N_sp), počet stromů (N_trees) ve stromovém patře [ks.ar^{-1}] a zakmenění (TSD) [m^2.ar^{-1}].

ANOVA

There was strength regression between the age and *DBH* for birch (r = 0.75, p<<0.01; Age = 10.936 + 0.36358×DBH), Norway spruce (r = 0.64, p<<0.01; Age = 11.105 + 0.27531×DBH) and European aspen (r = 0.79, p<<0.01; Age = 10.767 + 0.38184×DBH).

When birch was present at the plot, spruce was on average seven years younger than birch (F = 70.42, p << 0.01; Fig. 3a), while European aspen was on average two years older than the birch (F = 4.41, p = 0.04; Fig. 3b).



a)

b)

Figure 3. The age tree species growing at the same plot: a) birch and Norway spruce, b) birch and European aspen.

Obrázek 3. Věk stromů rostoucích společně na jedné ploše: a) bříza a smrk, b) bříza a osika.

Discussion

The number of tree species was high (11, however only one European beech tree and one pear tree were found). Prach (1994) counted 24 woody species (both trees and shrubs) in 17 different studies focused on succession in Central Europe (from wet to xeric seres), and 10 of them were trees colonising abandoned fields and grassland. The higher species number in higher altitudes, and also by lower *T* values is likely caused by a slower rate of succession in higher altitudes, which was found in several studies (e.g., Blažková 1991; Prach et al. 2007). The slower rate of succession could increase the probability of establishment of seed-limited species. Rare species were less found in older growths, and therefore the number of species decreases with the age of succession. It may result from the self-thinning of the tree layer when rare species have a higher probability of extinction.

The most common species was the birch (88% plots, 60% trees), which is a typical pioneer tree species in a temperate zone of Europe (Blažková 1988; Prach 1994; Prach and Pyšek 1994b). Common species were also the Norway spruce (43% plots, 15% trees), the European aspen (24%, 14%), the goat willow (29%, 3%), the Scots pine (29%, 2%), the mountain maple (12%, 4%) and the mountain ash (12%, 1%). The birch (74%), the European aspen (13%), the Norway spruce (6%), the mountain maple (4%) and the Scots pine (2%) were able to dominate the tree layer. All of the species were reported as common species in the secondary forests in temperate Europe (Dzwonko and Loster 1990; Prach 1994; Prach and Pyšek 1994b; Schreiber 1996; Vojta 2007; Zobel 1989). The anemochory, ability of vegetative reproduction, but also well generative reproduction; anemogamy, deciduous; flowering before leaf appearance; clupping species; low nutrient requirements; low age and low reproductive age were determined as typical attributes of pioneer trees in Europe (Faliński 1980; Prach 1994). The birch fulfils all of them. Other common species fulfil many of the attributes, and all the dominants were anemochorous ones. In general the anemochous species are supposed to be better colonisers (Dzwonko 2001; Prach 1994), and therefore they are supposed to be more successful in the early stages of succession.

The birch as a pioneer tree was more common at sites with lower organic matter content (abandoned agricultural land typically contains lower organic matter content than forest soils, see e.g., Matlack 2009), at plots which were fields in 1966 (the birch seedlings prefer bare soil, see e.g., Atkinson 1992), and grassland or scattered SDF in 1983. The birch is a fast coloniser after abandonment.

The European aspen, similarly to the birch, was able to dominate the tree layer. Both species have similar ecological requirements. Both are anemochorous species, produce large amount of seeds and are bad competitors. Moreover, the European aspen sprouts very well, which facilitates its expansion at sites containing adult aspen trees (e.g., Prach 1985). The SDFs with less complicated shapes were more occupied by European aspen, and regular shapes could be a consequence of the vegetative reproduction, while the birch was more common in the SDFs with irregular shapes. This indicates its preference to the generative reproduction to which it is well adapted with high amount of seeds (ca 4,000-53,000 seeds.m^{-2}, see Atkinson 1992), and it can also benefit from the seed bank (Milberg 1995).

The Norway spruce is the most common tree in the area (due to the forest management), and its relative high presence in the SDFs (43% plots, in average 420 trees.ha^{-1}) even in the first forest generation is an important finding for the forest management. Although the Norway spruce produces a large amount of light seeds well distributed by wind, it can be seed limited – its number increased with the proportion of the forest in the 300 m surrounding (the source of the seeds), while it decreased with the proportion of SDFs in the 300 m surrounding. These changes the number for the in Norway spruce were complemented to the numbers of birch. It seems that seed competition may have occurred during the early colonisation of abandoned agricultural land. D´Orangeville et al. (2008) also found that the percentage of the forest in surroundings was important for the regeneration of tree species valuable for forest management in Canada, and Doubková (2008) found that the Norway spruce was able to colonise abandoned grasslands only near the edges of forest. The delay of the Norway spruce in tree layer colonisation (on average 7 years after the birch) was likely due to the less availability of seeds or due to better conditions for seedling recruitment under the birch tree canopy. The Norway spruce is able to establish itself under low irradiance, but it is a bad competitor with the grassland vegetation (Doubková 2008; Prach et al. 1996), and therefore it may benefit from the lower abundance of grassland in the young shrubs. Timber species benefit more from shrub protection when large herbivores are allowed to graze (Vandenberghe et al. 2009), and therefore the later recruitment of Norway spruce seedlings in young deciduous woods may also be caused by a low number of herbivores. The Norway spruce was more abundant at sites which were grassland in 1952. Favourable years for Norway spruce recruitment at abandoned grasslands were found in the Krkonoše Mountains in the Czech Republic (Doubková 2008), and the result referred to above may be due to correlation with a similar favourable period. Natural disturbances, such as by wild boars, or ant hills (Vlasáková 2009), could also enable the Norway spruce to colonise the grassland vegetation. The Norway spruce was able to establish better in the SDFs in higher altitudes and at colder sites (*T*), which corresponds to assumptions about its ecological behaviour. Good surviving ability and strong competition in similar woods (*Pinus–Betula–Alnus* forests) was reported from the boreal region (Seppä et al. 2009), and therefore due to its good survival ability can be expected to spread.

The scattered mountain ash and wild cherry tree are endozoochorous species usually spread by birds. The bird endozoochory was found to be effective for long-distance distribution (e.g., Corbit et al. 1999; Dzwonko 1993; Pons and Pausas 2007).

The European beech is believed to be dominant in natural forests, but in lower altitudes it has been replaced by pedunculate oak (Neuhäuslová, 1998). However, both species are rare in managed forests in the study area today. The endozoochorous species distributed mostly by mammals (e.g., beech, oak) are assumed to be poor for long-distance dispersal, e.g., Jensen and Nielsen (1986) found the mean distance of 24 m for oak seeds transported by *Apodemus* sp. and *Clethriomys glareoles*. The only one beech listed in the tree layer supports this assumption, but I have found a surprisingly high number of both beech and oak seedlings in the herb layer of the permanent plots (Dostalova 2009) and their absence in the tree layer may be caused by different factors, such as grassland species competition (Provendier and Baladier 2008).

The species composition of the tree layer was influenced from the studied factors by the Ellenberg *T* value and by the shape of the growth. Both variables explained 14% of the total variability, which is a common amount of explained variability in similar studies. For comparison, Vojta (2007) attributed 8.6% to the soil and terrain properties, 6.8% to the ancient environmental variables and 10.3% to historical factors in the *RDA* of the tree layer of secondary forests in former villages (with a wide range of abiotic conditions) in the Czech Republic.

The decrease in the birch and Norway spruce with the A_a is caused by self-thinning, as well the decrease in the total number of trees, while the *TSD* slowly increased. In other words, the SDFs change from the dense canopies of thin young trees into relatively open canopies of adult trees (see also Paquette et al. 2006). This may enable new trees to reach the tree layer. This is supported by a higher age variability in older growths, the relative SD to average age for a 10 to 15-year-old tree layer was found to be on average of 19%, compared to 22% for 15 to 25-year-old and 27% for 25 to 45-year-old growths. However, the self thinning was observed for the tree layer, the density of trees was found to be relatively high. For comparison von Oheimb et al. (2005) found the density of living trees to be on average 263 trees.ha^{-1} in a near natural beech forest in Germany.

The SDFs in my study were relatively highly variable in age structure. For comparison D´Orangeville et al. (2008) found that the SDFs in Canada were on average ±2 years, while in my study ±7 years old. Species establishing themselves later in the tree layer are usually the dominant species, not rare species, and therefore the uniformity of the tree layer increases with the stage of succession.

Dostalova A (2009) Tree seedlings: how they establish in spontaneously developed forests? A study from a mountainous area in the Czech Republic. *Biodiversity and Conservation* 18:1671-1684

Abstract

The aim of this study was to find out which tree species can establish in spontaneously developed forests (SDFs) on mesic stands and how many of tree seedlings are present there. The influence of different factors was examined and an attempt made to find out if there are some general trends true for groups of species typical for different stages of succession or with different type of distribution.

All tree-seedlings present in 48 permanent plots were counted (100 m^2). The following factors were tested: altitude, slope and exposition, distance from the nearest forest, age and species composition of tree layer, species composition of herb layer, light conditions and soil reaction.

The species composition was dependent on altitude and soil reaction. There were surprisingly high numbers of seedlings (in average 145 tree seedlings per 100 m^2) and species (in average 5) present in SDFs. Not only species common in the area were found, but also the uncommon species were present there, although in low numbers. Nonspecific species are the best colonisers of SDFs, and the anemochorous trees are better colonisers than the zoochorous ones. The establishment of different tree species is influenced by different factors. The SDFs most probably shift toward forest with a number of species in the tree layer. The dominant species tend to be spruce and maple, but species typical for early stages of succession will be common in these growths.

Shrnutí

Cílem této studie bylo zjistit, které druhy stromů se mohou uchytit v porostech náletových dřevin (SDFs) na mesickém stanovišti a jaké množství semenáčků stromů se v těchto porostech nalézá. Byl studován vliv různých faktorů na uchycování semenáčků stromů a zjišťovány trendy v uchycování různých skupin druhů typických pro jednotlivé fáze sukcese nebo s rozdílnými strategiemi rozšiřování.

Na 48 trvalých plochách (100 m^2) byly spočítány všechny semenáčky stromů. Byl testován vliv následujících faktorů: nadmořské výšky, sklonu a expozice, vzdálenosti k nejbližšímu lesu, stáří a druhového složení stromového patra, druhového složení bylinného patra, světelných a půdních podmínek.

Druhové složení bylo závislé na nadmořské výšce a půdní reakci. Překvapivě velké množství semenáčků (průměrně 145 ks na 100 m^2) i druhů stromů (průměrně 5) se bylo schopné v porostech náletových dřevin uchytit. Nejen druhy v oblasti hojné, ale také druhy méně běžné zmlazovaly, ačkoli jen v malém množství. Nejlépe se uchycovaly druhy nespecifické ke stádiu sukcese, anemochorní druhy byly lepšími kolonizátory než zoochorní. Různé faktory ovlivňovaly uchycování semenáčků jednotlivých druhů. Zdá se, že dominujícím druhem stromového patra bude v budoucnu smrk a javor klen, ačkoli druhy typické pro časná stádia sukcese budou také hojné.

How will spontaneously developed forests look like? An Estimation of changes in the tree-layer species composition

Jak budou porosty náletových dřevin vypadat? Odhad změn v druhovém složení stromového patra

Abstract

Spontaneously developed forests (SDFs) on the former agricultural land after abandonment are mostly birch-dominated in Central Europe and pioneer trees are the most abundant species in the tree-layer, however, their future development is uncertain.

An estimation of changes in the tree-layer was made for the next generation of SDFs on mesic soils. I based the estimation on the number and height of tree-seedlings for certain species or groups of species according to their stage of succession (43 plots of 100 m^2). I tested the difference between the present and the estimated tree-layer and the influence of factors describing time of succession, climatic, soil and light conditions and character of the herb layer.

The estimated changes in the composition of tree-layer are considerably high. I found different factors to be significant for the estimated species composition at different levels. Some were important for the changes in community, others for different species and others for groups of species typical for different stages of succession.

The estimated tree-layer will be more diverse than the present tree-layer. The species typical for terminal stages of succession are able to colonise these forests but the changes toward potential natural vegetation will take longer than two generations.

Shrnutí

Ve stromovém patře porostů náletových dřevin dominuje ve střední Evropě bříza a další pionýrské dřeviny. Budoucí vývoj stromového patra není znám.

Byla odhadnuta změna druhového složení stromového patra pro následující generaci stromů pro porosty náletových dřevin na mesických stanovištích. Odhad vycházel z počtu a výšky semenáčků stromů, a to pro jednotlivé druhy nebo skupiny druhů typických pro jednotlivé fáze sukcese (43 ploch á 100 m^2). Byl testován vliv faktorů popisujících dobu trvání sukcese, klimatické, půdní, světelné podmínky a charakter bylinného patra na změnu v druhovém složení stávajícího a odhadnutého stromového patra.

Odhadnutá změna v druhovém složení je relativně velká a různé faktory ovlivňovaly odhadnutou druhovou skladbu stromového patra v druhé generaci stromů, a to na různých úrovních. Některé byly významné z hlediska změny společenstva, jiné na druhové úrovni nebo pro skupinu druhů typických pro různé fáze sukcese.

Odhadnuté stromové patro je druhově bohatší než stávající stromové patro. Druhy typické pro pozdní fáze sukcese jsou zastoupeny v odhadnutém stromovém patře, ale pro dosažení druhové skladby typické pro přirozenou vegetaci bude potřeba více než dvou generací stromů.

Introduction

It is supposed that in temperate climates succession changes are towards woodland (Ellenberg 1988). Different rates of succession have been reported; rapid establishment of the tree-layer is mentioned by e.g., Schreiber (1996) or Spatz (1980). Other studies have reported that trees take a very long period of time to establish themselves at abandoned sites (e.g., Blažková 1988; Hadač 1990). There is usually only a short period – about twenty years that are suitable for tree establishment, the so called ‘successional window’ (Prach 1994). Woody plants can be blocked, e.g. due to soil conditions or competition – mainly with grasses (e.g., Dickie et al. 2007) or litter (Facelli and Pickett 1991a). Birch (*Betula pendula* Roth.) is the most common tree dominating spontaneously developed forests (SDFs) in Central Europe (Prach 1994; Prach and Pyšek 1994b).

It is assumed that a long period of time is needed to reach the terminal stage of succession, e.g., Faliński (1988) estimates 350 years for mesic sequence in temperate zone in Europe. However, changes caused by previous agricultural activity could last much longer (e.g., Dupouey et al. 2002).

At present, most abandoned sites are several decades old. Even if we consider only the oldest stages of chronosequence, we usually do not reach 100 years (for 120 year chronosequence see Harmer et al. 2001). We do not know how these SDFs will look in the future, although this knowledge is important for conservation biology, urban and management planning. Decisions about the potential management cannot be made without comparison of vegetation developed without human intervention and spontaneous development should be used as the appropriate “management” in many cases (Pyšek et al. 2001).

The present tree seedlings are the set of individuals which will form the next tree-layer generation. Their species composition results from the seed and microsite availability and from competition between the seedlings and present vegetation cover (Dostalova 2009). However, not every seedling survives. Different species have different survival probability which can change according to the site conditions (e.g., Nilsson et al. 2002) – e.g., light conditions (Szwagrzyk et al. 2001) or competition of the herb layer (e.g., Dickie et al. 2007). The highest mortality is usually in the first year and declines with the age of the seedlings - e.g. 67-94% for one year old spruce seedlings in a natural forest, while for seedlings between one and four year old the average is 27-59% (Šerá et al. 2000). This probability is species dependent (compare e.g., Kerr et al. 2008; Šerá et al. 2000). The growth of the seedlings is also species dependent (Hunziker and Brang 2005) and differs between biotopes (e.g., Agestam et al. 2003). Different factors influence the growth of the seedlings, and therefore published studies report different results: e.g., Madsen and Larsen (1997) found a substantial influence of openness of the tree-layer, organic matter content and humidity of the soil, while Hunziker and Brang (2005) report only a weak influence of the studied factor (e.g., higher radiation income). Unfortunately, I have not found any study focused on the tree seedlings survival and their growth in SDFs. Although models simulating tree-layer development exist they are usually developed for forest management purposes or for mature ecosystems or they deal with other special topics (e.g., global warming) and therefore are not useful for early stages of forest succession on former agricultural land.

I found out from the number of seedlings what tree species are able to colonise SDFs (Dostalova 2009), and I identified some important factors influencing the tree seedling species composition in SDFs on mesic stands in a mountainous area in Central Europe. As the results of former study indicated that the changes in tree-layer species composition would be considerably high, I focused in this study on the estimation of these changes. The estimation was based on number and height of the tree seedlings. The estimated tree-layer species composition was compared with the present tree-layer species composition in this study. Furthermore, I tried to determine the possible source of variability among the SDFs on mesic soils in this study.

Because of the lack of information about the survival and growth of different species in SDFs, I only used simple formula for an extrapolation of the change from the seedling stage to the tree-layer. I transformed the number of the seedlings from different height categories for each species to estimate the percentage of certain species in the tree-layer. In this way I obtained the estimated species composition of the tree-layer which I was able to compare with the present tree-layer species composition and test the influence of different factors describing time of succession, climatic, soil and light conditions and character of the herb layer. Results from only one transformation formula are presented in this study for better comprehensibility of the text and length of the chapter, although the coefficients used and survival probabilities may influence the obtained results. However, I compared results obtained from 11 models based on different height categories and surviving probabilities. This comparison is briefly described in the Discussion.

Based on the knowledge of the present tree-layer species composition and counting the estimated tree-layer species composition from tree seedlings present in the plot I tried to answer the following questions:

1. Is the estimated tree-layer different from the present one?
2. If yes, which species will increase/decrease?

3. Which factors will act to influence these changes? Are the soil, light, climatic conditions, stage of succession or surrounding vegetation cover important?

Methods

Study area

Southern part of the Czech Republic (40°35-38´ N, 14°11-17´ E), altitude 665-940 m. Climatic conditions moderately oceanic between the warm and cold type (climatic regions MT 3 – Ch 7; Quitt 1971), average year temperature 6.8°C and average year precipitation 718-1003 mm.

I fixed 48 plots of 10 × 10 m in the SDFs, which differed in age, altitude and exposition, but all plots were on mesic stand (neither waterlogged nor desiccated, with vegetation neither ruderalised nor typical for poor soils). I fixed the plots in such growths, where significant human influence was not recognisable, and which were homogenous and large enough. Different age categories present in the study area were equally presented.

The supposed terminal stage of succession is beech forest (association *Dentario enneaphylli-Fagetum*, or transient to *Luzulo albidae-Quercetum petraeae*, Neuhäuslová 1998).

The present growths are mostly dominated by birch (*Betula pendula*), common trees are: Norway spruce (*Picea abies* (L.) Karsten), European aspen (*Populus tremula* L.); in some cases Scots pine (*Pinus sylvestris* L.) or common ash (*Fraxinus excelsior* L.) are more abundant, with incidental cherry tree (*Prunus avium* (L.) L.) or European mountain ash (*Sorbus aucuparia* L.).

Data collection and determination of environmental factors

For determination of the present tree-layer I recorded the number and species composition of trees at each plot. For age estimation, I took two samples of wood from each tree, but maximally from 10 randomly chosen trees of each species per plot, using Pressler's auger. Samples were taken from opposite sides of the trunk at the height of 40 cm above ground. After fixation and cutting I counted the tree-rings. The average age of the trees (A_a) and the maximal age of the trees (A_{max}) was determined for all plots. A_a corresponds with the duration of closed canopy of the tree-layer, while A_{max} corresponds rather with the duration of abandonment.

I listed the tree-seedlings of each species present in the plot and I measured their height. Tree-seedlings lower than 180 cm were listed, taller ones were also recorded when their diameter at 120 cm above ground was less than 2 cm.

I took phytocenological relevés from all plots. Species abundance was estimated in percents of abundance of all species for each layer. I counted Ellenberg's indicator values (*EIV*) for soil reaction (*R*), humidity (*F*), light availability (*L*), temperature (*T*) and nitrogen content (*N*) from the species composition of the herb layer (Ellenberg 1988). Abundance of each species was used as weight in the *EIV* calculation. *EIV*s correspond with the character of the biotopes, *N* corresponds more with the productivity of the place (Ertsen et al. 1998).

For estimation of light conditions, relative irradiance of photosynthetic active radiation (*PhAR*) was measured for all plots. The irradiance was measured using simultaneously two luxmeters with *PhAR* sensors: one sensor was placed within the growth, while the other was placed in the open. Relative *PhAR* irradiance was calculated as percentage of incoming *PhAR* in the open from 20 random measurements within each plot and for the certain height level (5, 20 and 120 cm above ground level). Measurements were taken between 11 a.m. and 3 p.m. in July or first half of August. The weather conditions were somewhat cloudy or cloudy without rain. The open stand for reference measurements was at least 100 m from the forest-edge (or other high object, e.g., building), on the west side of the forest, the nearest distance was 200 m. Relative irradiance at 120 cm above ground (P_{120}) corresponds with the density of the tree or shrub layer, while at 20 cm above ground (P_{20}) it corresponds with the density of the tree-layer, shrub layer and tallest herbs in the herb layer. The relative irradiance at 5 cm above ground (P_5) corresponds with the light available for seedling recruitment.

I took soil samples from each plot, and I determined content of rock fragments >2 mm (R_s) in the dried samples using a 2 mm sieve [%]. I measured the soil reaction in the water solution (pH_s) using 10 g of fine air-dried soil samples and 20 cm^3 of distilled water (free of CO_2). I determined the organic matter content (C_{org}) as the loss of the matter content of dried sample by 450°C [%]; the basal respiration of the microbial community (BR_s) as CO_2 production [$\mu g\ C\text{-}CO_2.g^{-1}.hod^{-1}$] (Jäggi 1976).

I measured the distance [m] to the nearest forest (edge to edge) from the topographic map 1 : 10 000, the actual forest-edge was verified in the field and adjusted where necessary. The distance was logarithmically transformed: y=log(y+1) (*D_Fst*). This variable corresponds with the nearest potential seed-source.

The altitude of the plot was taken from the map (1 : 10 000). The altitude corresponds with the climatic conditions (Prach and Řehounková 2006), because the mean temperature and precipitation depend on the altitude. The study area is relatively small, and therefore we can assume that the climatic conditions are at most influenced by the altitude of the plot.

I determined the orientation (using compass) and slope (visual estimation) for all plots. I calculated the heat indices to the south-west (H_{sw}) and to south-south west (H_{ssw}):

$$H_{SW} = \cos(\text{exposition} - 225°) \times \text{tg}(\text{slope})$$

$$H_{SSW} = \cos(\text{exposition} - 202.5°) \times \text{tg}(\text{slope})$$

All field observations were carried out in 2004 and 2005.

Data analysis

Only plots, where the tree-layer was older than 20 years (A_a) were used for further analysis, as the younger growths are too young for seedling establishment; in total, 43 plots out of 48 fulfilled this requirement.

Tree-seedling species were grouped according to the affinity to the stage of succession: 1) species typical for early stages of succession are: birch, Scots pine, European aspen, cherry tree, pear (*Pyrus communis L.*), hawthorn (*Crataegus* sp.), mountain ash and goat willow (*Salix caprea L.*); 2) species typical for terminal stages of succession are: European beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus petraea* (Mattuschka) Liebl.) and fir (*Abies alba* Mill.); and 3) nonspecific species are: Norway spruce, sycamore maple (*Acer pseudoplatanus L.*) and common ash.

The following height categories of the tree-seedlings were distinguished: 0 to 10 cm (h_1), 11 to 20 cm (h_2), 21 to 40 cm (h_3), 41 to 80 cm (h_4), 81 to 160 cm (h_5), <160 cm (h_6). For further analysis the number of seedlings of each species or group (i) was normalised (N_n) by formula advantageous the taller seedlings:

$$N_n(\text{i}) = 0.01 \times h_{1i} + 0.1 \times h_{2\,i} + 0.5 \times h_{3i} + h_{4i} + 2 \times h_{5i} + 4 \times h_{6i}$$

N_n of seedlings corresponded with the estimated tree-layer. From the normalised numbers of different species I obtained the estimated tree-layer species composition (TL_f), which is a matrix similar to the phytocenological relevé, where the abundance of the particular species is the proportion of the species in the estimated tree-layer.

The present tree-layer species composition (TL_p) was a matrix similar to the phytocenological relevé, but the abundance of the species was the proportion of particular species in the present tree-layer.

Both present and future species composition of the tree-layer were counted as a proportion of particular species because it makes the normalisation formula more robust to the changes caused by different numbers of tree seedlings (to 1034) and trees (to 182) and by using different coefficients and height categories.

TL_p and TL_f were compared using ordination methods in the CANOCO v. 4.5 (Lepš and Šmilauer 2003). The "species" data were logarithmically transformed ($y=\log_{10}(y+1)$), fir and pear were excluded (only one seedling found). Unimodal analyses were performed (length of the gradient obtained from the Detrended Correspondence Analysis was found to be 3.2), indirect Correspondence Analysis (*CA*) and direct Canonical Correspondence Analysis (*CCA*). Independent variables were the following: time, which describes the direction of the change (1 – for TL_p, 2 – for TL_f), altitude, H_{sw}, H_{ssw}, *D_Fst*, *R*, *L*, *T*, *F*, and *N*, C_{org}, pH_s, BR_s, R_s, A_a, A_{max}, P_{120}, P_{20}, P_5. I used manual selection (Forward selection, Monte Carlo permutation test under full model with 499 permutations) of the factors at the $\propto = 0.05$ level. The visualisation of the ordination analysis was performed in the CanoDraw v. 4.0. (Lepš and Šmilauer 2003).

General Linear Models (*GLM*) in the CanoDraw v. 4.0 were used to test: 1) differences in species abundance for TL_p and TL_f; 2) influence of selected factors on the N_n (for species present at least at 35% of the plots); 3) influence of selected factors on the N_n of groups of species according to the stage of succession. Poisson distribution of the data was used, because the link function of this distribution is "Log" function, which is recommended for the counts and frequency data (Lepš and Šmilauer 2003, p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using Akaike Information Criterion (Lepš and Šmilauer 2003).

Because many factors were involved in the study according to the number of plots, the *GLM* were fitted separately for particular factor. Eight variables (H_{SSW}, H_{SW}, T, L, R and F, BR_s, R_s) were omitted to eliminate the number of factors. Further factors were used: A_a, A_{max}, altitude, N, C_{org}, pH_s, P_{120}, P_{20}, P_5, D_Fst. Factors were chosen to describe the conditions that are supposed to influence the rate and direction of successional changes.

RESULTS

Species composition of the present and estimated tree-layer

I found 11 tree species in the tree-layer of the present plots and 14 species as seedlings. Only two species of adult trees were present at more than 35% of the plots, while the tree-seedlings were more abundant and a total of 7 species exceeded 35% of the plots (Tab. 8).

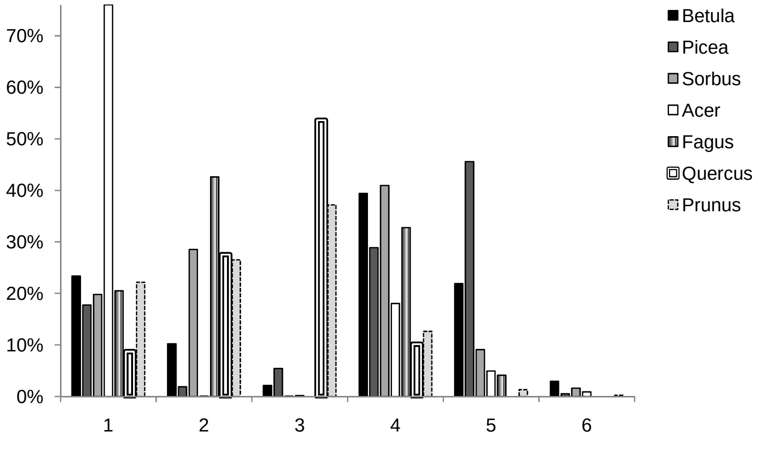


Figure 5. Percentage of tree-seedlings of particular species and different height categories [%]. 1 – 0 to 10 cm, 2 - 11 to 20 cm, 3 – 21 to 40 cm, 4 – 41 to 80 cm, 5 - 81 to 160 cm, 6 – >160 cm.

Obrázek 5. Procento semenáčků stromů jednotlivých druhů ve výškových kategoriích [%].1 - 0 až 10 cm, 2 - 11 až 20 cm, 3 – 21 až 40 cm, 4 – 41 až 80 cm, 5 – 81 až 160 cm, 6 – >160 cm.

Most of the seedlings were 10 to 40 cm tall. There was only a small number of tree-seedlings taller than 80 cm, except for Norway spruce. Sycamore maple had many seedlings in the height category from 0 to 10 cm. For the percentage of the seedlings of the particular species and height category see Fig. 5.

The first ordination axe in the *CA* explained 19.3% of the total variability in the species data; together the first four axes explained 61.8%. Using manual selection for the environmental variables in the *CCA*, the species composition significantly influenced: time ($F = 11.4$, $p < 0.01$), Ellenberg N value ($F = 5.68$, $p < 0.01$), R_S ($F = 3.86$, $p < 0.01$) and Ellenberg F value ($F = 4.03$, $p < 0.02$). All variables explained 25% of the total variability in the data.

The plots with the present species composition of the tree-layer are situated in the left part of the ordination diagram, while the plots with the estimated ones are in the right part (Fig. 6). For the present species composition, birch, Scots pine, mountain ash and goat willow are typical, while sycamore maple, European beech, European aspen and pedunculate oak are typical for the estimated species composition. From the ordination diagram of *CA* with projected selected “environmental” variables we can see that sycamore maple is more common on rather humid and nutrient rich stands, while European aspen dominates on drier, nutrient poor sites and soil with height R_S (Fig. 6).

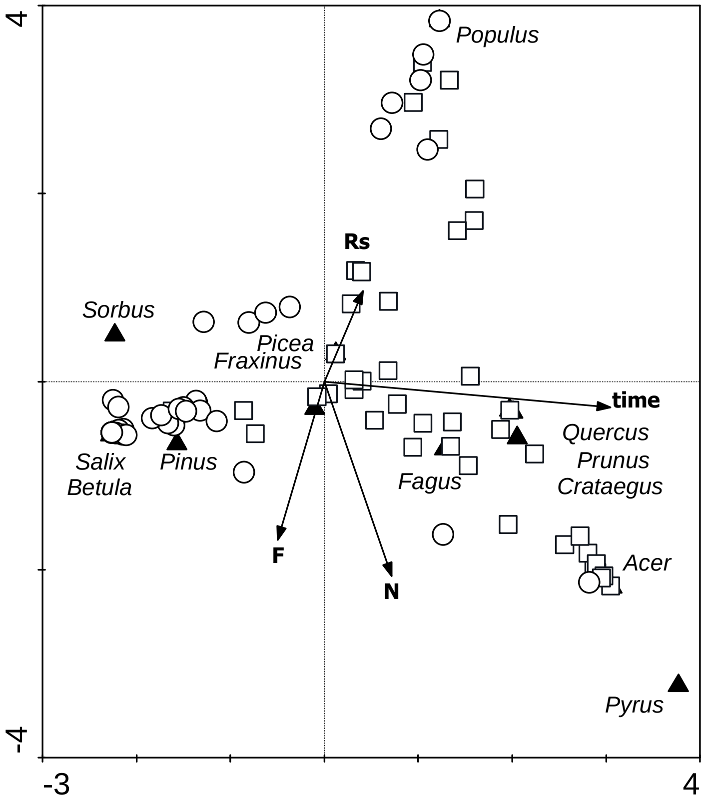


Figure 6. Ordination diagram for *CA* of the present and estimated tree-layer. Squares - estimated plots, circles - present plots, triangles – species: Acer – *Acer pseudoplatanus*, Betula – *Betula pendula*, Crataegus – *Crataegus* sp., Fagus – *Fagus sylvatica*, Fraxinus – *Fraxinus excelsior*, Picea – *Picea abies*, Pinus – *Pinus sylvestris*, Populus – *Populus tremula*, Prunus – *Prunus avium*, Pyrus – *Pyrus communis*, Quercus – *Quercus petraea*, Salix – *Salix caprea*, Sorbus – *Sorbus aucuparia*. Environmental variables: Rs – rock fragments content in the soil, F/N - Ellenberg *F*/*N* values, change - direction of change from present of the tree-layer species composition to the estimated species composition. Environmental variables (selected using manual forward selection) were projected into the *CA* ordination diagram.

Obrázek 6. *CA* ordinační diagram stávajícího a odhadnutého stromového patra. Čtverečky - odhadnuté stromové patro, kolečka – stávající stromové patro, trojúhelníky - druhy: Acer – *Acer pseudoplatanus*, Betula – *Betula pendula*, Crataegus - *Crataegus* sp., Fagus - *Fagus sylvatica*, Fraxinus – *Fraxinus excelsior*, Picea - *Picea abies*, Pinus – *Pinus sylvestris*, Populus – *Populus tremula*, Prunus – *Prunus avium*, Pyrus - *Pyrus communis*, Quercus - *Quercus petraea*, Salix – *Salix caprea*, Sorbus - *Sorbus aucuparia*. Faktory prostředí: Rs – skeletovitost, F/N – Ellenberogovi hodnoty F/N, change – směr změny stávajícího druhového složení k odhadnutému. Faktory prostředí (vybrané pomocí volby “manual forward selection”) byly promítnuty do *CA* ordinačního diagramu.

GLM predicted changes for most of the species tested. Most important changes predicted were decline of birch and increase of Norway spruce and cherry tree (Table 8).

Table 8. Estimated changes in the tree-layer for different species fitted by *GLM*.

	L	**var.**	**Change**	**F_p**	**F_f**
Abies alba	×		0	0.0	2.3
Acer pseudoplatanus	L ↑	14.5	+2	11.6	67.4
Betula pendula	L ↓	48.9	-55	90.7	46.5
Crataegus spp.	L ↑	18.4	+1	0.0	23.3
Fagus sylvatica	L ↑	11.0	+3	2.3	37.2
Fraxinus excelsior	×		+3	7.0	30.2
Picea abies	L ↑	8.5	+18	41.9	81.4
Pinus sylvestris	L ↓	4.9	-4	27.9	7.0
Populus tremula	×		+1	23.3	34.9
Prunus avium	L ↑	24.9	+12	7.0	60.5
Pyrus communis	×		0	2.3	0.0
Quercus petraea	L ↑	19.7	+3	0.0	39.5
Salix caprea	L ↓	13.1	-2	23.3	4.7
Sorbus aucuparia	L ↑	31.7	+19	14.0	81.4

L - linear model: ↑/↓ - representation of the species increases/decreases; var. – explained variability [%], Change - average change in the representation for the present and estimated tree-layer [%]; frequency of the species in present (F_p) and estimated (F_f) tree-layer [%], × - nonsignificant.

Tabulka 8. Odhadované změny v zastoupení jednotlivých druhů pro druhou generaci stromového patra pomocí *GLM*. L – linearní vztah, × - neprůkazné, ↓/↑ - pokles/vzrůst, var. – vysvětlená variabilita [%], Change – průměrná změna zastoupení druhu mezi stávajícím a odhadovaným stromovým patrem [%]; frekvence druhů ve stávajícím (F_p) a odhadnutým (F_f) stromovým patrem [%].

Species responses to the selected factors

Influences of selected factors on the proportion of the species in the TL_f fitted by *GLM* are summarised in Table 9.

Table 9. Response of the species [N_n] to the selected factors fitted by *GLM*.

	Acer		**Betula**		**Fagus**		**Picea**		**Populus**		**Prunus**		**Quercus**		**Sorbus**	
	M	**v.**	**M**	**v.**	**M**	**v.**	**M**	**v.**	**M**	**v.**	**M**	**v.**	**M**	**v.**	**M**	**v.**
A_a	×		×		×		×		×		L↑	13	×		Q∪	16
A_{max}	×		×		×		×		×		L↑	12	×		×	
altitude	Q∩	18	Q∪	24	Q∩	15	L↑	5	Q∪	28	Q∩	29	×		L↑	5
N	L↑	31	×		×		×		Q∩	28	L↓	9	L↓	30	Q∩	13
C_{org}	×		×		L↑	8	×		×		×		L↓	8	Q∩	10
pH_s	×		L↑	12	×		×		×		×		×		×	
P_{120}	×		×		×		×		×		Q∩	21	Q∩	15	Q∩	16
P_{20}	×		L↓	7	×		×		×		L↑	17	×		×	
P_5	×		×		×		×		L↓	11	Q∩	22	Q∩	30	Q∩	10
D_Fst	×		×		×		×		×		Q∪	20	×		×	

M - model: L – linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, v. - explained variability [%]; A_a/A_{max} – average/maximal age of the tree-layer, N – Ellenberg N value, C_{org} - organic matter content, pH_s - soil reaction, P_{120}/P_{20}/P_5 - relative irradiance at the 120/20/5 cm above ground, D_Fst - distance to the nearest forest, × - nonsignificant.

Tabulka 9. Opověď druhů [N_n] na vybrané faktory, testováno GLM. M – model, L – linearní vztah, Q - polynomiální vztah (druhého stupně), × - neprůkazné, ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá”odpověď, v. – vysvětlená variabilita, [%]; A_a/A_{max} – průměrný/maximální věk stromového patra, N – Ellenbergova hodnota N, C_{org} – obsah organické hmoty v půdě, pH_s – půdní reakce, P_{120}/P_{20}/P_5 – relativní ozářenost ve 120/20/5 cm, D_Fst - vzdálenost k nejbližšímu lesu.

All species, except for pedunculate oak, were found to be influenced by altitude. The amount of Norway spruce and mountain ash increased with the altitude, while sycamore maple, European beech and cherry tree were found to be teh most common at medium values and birch was found to be more abundant both at lower and higher altitudes (Fig. 7b).

Ellenberg *N* value was significant for five species: sycamore maple increased with *N*, while pedunculate oak and cherry tree decreased, mountain ash and European aspen were more common at medium values (Fig. 7c).

The abundance of European beech was predicted to increase with organic matter content, while the abundance of pedunculate oak was predicted to decrease, and the abundance of mountain ash was predicted to be highest at medium values (Fig. 7d).

Relative irradiances at 120 cm and 5 cm above ground were important for cherry tree, pedunculate oak and mountain ash. All species preferred medium values (Figs. 7e, f). European aspen was more common by low irradiance at 5 cm level (Fig. 7f).

Only cherry tree and mountain ash were found to be influenced by the age of the trees. Cherry tree was found to be more common in older growths, while mountain ash was found to be less common in growths of medium age (Fig. 7a).

Only cherry tree was found to be influenced by *D_Fst* (Table 9).

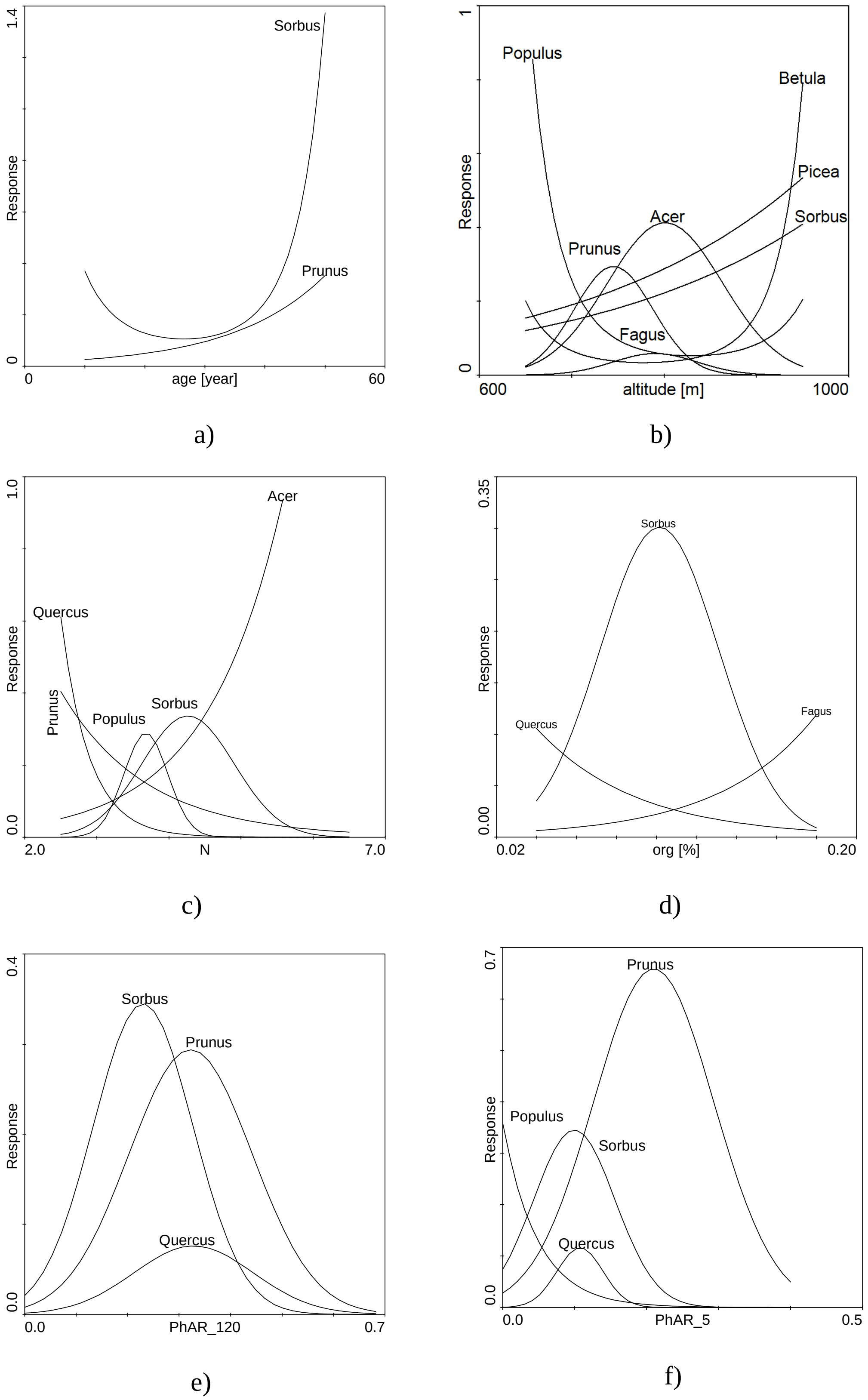


Figure 7. Species response to the factors predicted by *GLM* [N_n]: a) average age of the tree-layer, b) altitude, c) Ellenberg *N* value, d) organic matter content in the soil, e) relative irradiance at the 120 cm above ground, f) relative irradiance at the 5 cm above ground. Acer - *Acer pseudoplatanus*, Betula – *Betula pendula*, Fagus - *Fagus sylvatica*, Picea – *Picea abies*, Populus – *Populus tremula*, Prunus - *Prunus avium*, Quercus – *Quercus petraea*, Sorbus - *Sorbus aucuparia.*

Obrázek 7. Vliv faktorů na pokryvnost stromů [N_n], testováno *GLM*: a) průměrný věk stromového patra, b) nadmořská výška, c) Ellenbergova hodnota *N*, d) obsah organické hmoty v půdě, e) relativní ozářenost ve 120 cm, f) relativní ozářenost v 5 cm. Acer - *Acer pseudoplatanus*, Betula – *Betula pendula*, Fagus - *Fagus sylvatica*, Picea – *Picea abies*, *Populus – Populus tremula*, Prunus - *Prunus avium*, Quercus – *Quercus petraea*, Sorbus - *Sorbus aucuparia.*

Groups of species responses to selected factors

Influences of selected factors on proportion of particular groups of species in the TL_f fitted by *GLM* are summarised in Table 10.

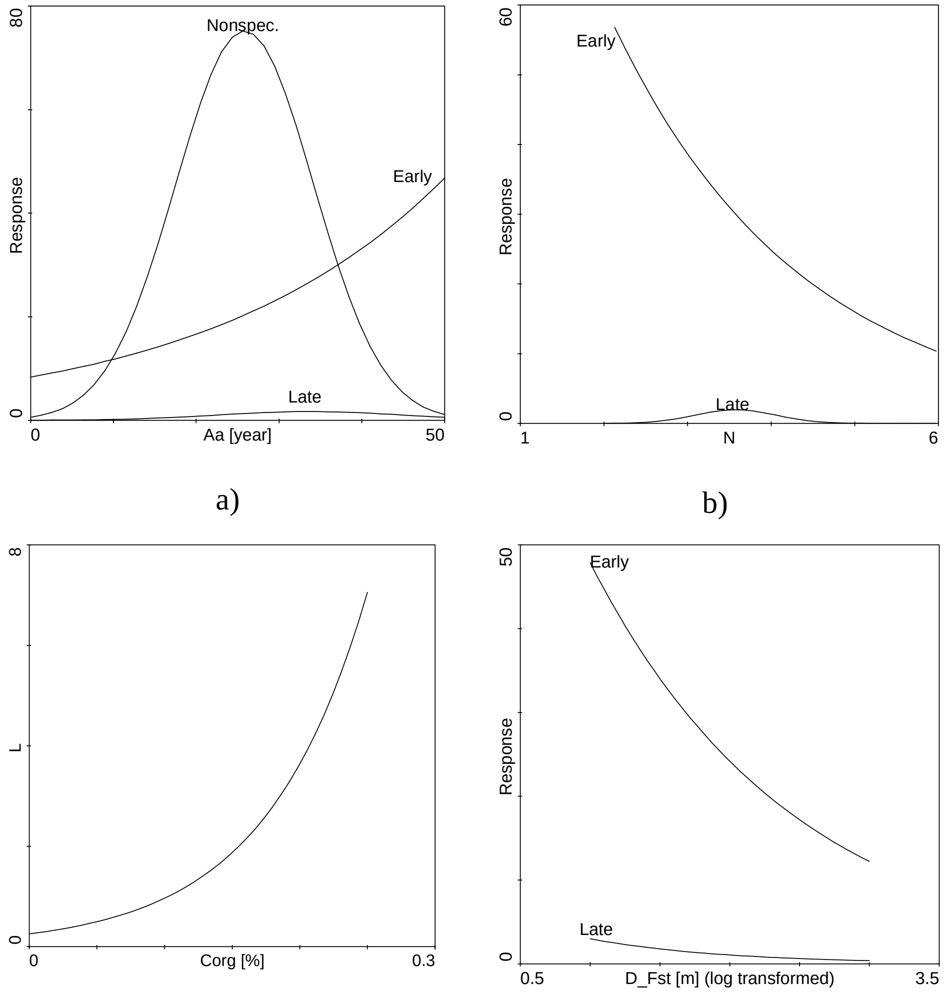
Table 10. Response of the groups [N_n] to the selected factors fitted by *GLM*.

	Early		**Late**		**Nonspecific**	
	Model	**var.**	**Model**	**var.**	**Model**	**var.**
A_a	L ↑	8	Q ∩	13	Q ∩	16
A_{max}	L ↑	7	L ↑	13	×	
altitude	L ↓	5	×		×	
N	L ↓	5	Q ∩	28	×	
C_{org}	×		L ↑	11	×	
pH_s	×		L ↓	5	×	
P_{120}	×		×		L ↓	10
P_{20}	×		×		L ↓	6
P_5	×		×		×	
D_Fst	L ↓	7	L ↓	11	×	

Early/Late/Nonspecific - species typical for early/terminal stages of succession or nonspecific to the stage of succession; Model: L – linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. – explained variability [%]; A_a/A_{max} - average/maximal age of the tree-layer, N – Ellenberg N value, C_{org} – organic matter content, pH_s - soil reaction, P_{120}/P_{20}/P_5 – relative irradiance at the 120/20/5 cm above ground, D_Fst – distance to the nearest forest, × - nonsignificant.

Tabulka 10. Odpověď skupin druhů [N_n] na vybrané faktory, testováno *GLM*. Early/Late/Nonspecific – druhy typické pro časné/pozdní fáze sukcese a druhy nespecifické; Model: L – lineární vztah, Q - polynomiální vztah (druhého stupně), × - neprůkazné, ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. – vysvětlená variabilita [%], A_a/A_{max} - průměrný/maximální věk stromového patra, N – Ellenbergova hodnota N, C_{org} – obsah organické hmoty v půdě, pH_s – půdní reakce, P_{120}/P_{20}/P_5 – relativní ozářenost ve 120/20/5 cm, D_Fst – vzdálenost k nejbližšímu lesu.

Tree-species typical for early stages of succession were more common at lower altitudes, on more oligotrophic stands (Fig. 8b) and in older growths (Fig. 8a). Near to forest, both species typical for early and terminal stages of succession were found to be more frequent (Fig. 8d). Species typical for terminal stages of succession were most common in medium-aged and older growths (Fig. 8a), on soils with medium nutrient content (Fig. 8b), higher organic matter content (Fig. 8c) and lower pH_s (Table 10). Nonspecific species were found to be more common in medium-aged (Fig. 8a) and in more closed growths (Table 10).



a)

b)

c)

d)

Figure 8. Response of the groups of species to the factors predicted by *GLM* [N_n]: a) average age of the tree-layer, b) Ellenberg *N* value, c) organic matter content, d) distance to the nearest forest; Early/Late - species typical for early/terminal stages of succession, Nonspec. – species nonspecific to the stage of succession.

Obrázek 8. Vliv vybraných faktorů na skupiny druhů [N_n], testováno *GLM*. a) průměrný věk stromového patra, b) Ellenbergova hodnota *N*, c) obsah organické hmoty v půdě, d) vzdálenost k nejbližšímu lesu. Early/Late – druhy typické pro časná/pozdní sukcesní stádia, Nonspec. - druhy nespecifické ke stádiu sukcese.

Discussion

Methods

The definition of height categories is derived from the fact that the growth of taller seedlings is faster in absolute numbers than the growth of smaller ones (i.e., the increase in 10 cm is proportionally higher for the seedlings 10 cm in height than for the seedlings 100 cm in height). Larger steps are often used for taller seedlings (e.g., Holgén and Hånnel 2000; Schweiger and Sterba 1997) although equal steps are also sometimes used (e.g., Kuuluvainen and Juntunen 1998).

The younger and/or smaller seedlings usually have higher mortality than the older and/or taller ones (e.g., Lorimer et al. 2001; Tapper 1992). For this reason, taller seedlings were favoured in the normalisation formula. The coefficients were estimated by the author according to the present knowledge (based on 84 studies dealing with seedling regeneration, growth and survival in temperate regions). The coefficients are approximate numbers and they did not differ for particular species, although the survival probability can be species dependent (e.g., Nilsson et al. 2002). This is because the survival probability and growth of seedlings was not studied in the SDFs-stand (e.g., Agestam et al. 2003). Furthermore, many other events can change the direction of the tree-layer development (e.g., herbivory, stochastic events) and high variability both in space and time was observed during the natural regeneration (e.g., Madsen and Larsen 1997; von Oheimb et al. 2005). This study is the first attempt to estimate the course of the succession, other studies may modify the formula for a better description of the tree-layer development. Moreover, they can aid in assuring that the coefficients are accurate and calibrate them for certain species or site conditions (e.g., altitude, type or age). The strength of the estimation can be tested after several years (I suggest after 10-15 years) after the re-measurement of the seedlings. The results can be compared with the present ones in this study however, the coefficients and height categories should be modified.

Eleven models obtained using different coefficients and survival probabilities were compared by the author to see how the changes in the normalisation formula alter the results. TL_f in these models was obtained: 1) from the number of the seedlings: (a) proportion of the species in the TL_f corresponded with the number of the seedlings; (b) proportion of the species in the TL_f corresponded with the number of seedlings taller than 30 cm; 2) from the number of seedlings weighted by their average height; 3) from six height categories – the same as in the paper: (a) coefficients in the normalisation formula progressively increased - the same as in the paper (0.01, 0.1, 0.5, 1, 2, 3, 4); (b) coefficients in the normalisation formula progressively increased but slower than in the paper (0.1, 0.5, 1, 2, 3, 4); (c) coefficients in the normalisation formula progressively increased but more rapidly than in the paper (0.001, 0.01, 0.1, 1, 2, 3); (d) coefficients in the normalisation formula increased linearly; 4) from height categories set each 10 cm (0 - 10 cm, 11 - 20 cm,..., 211 - 220 cm): (a) coefficients in the normalisation formula progressively increased – similar to these used in the paper; (b) coefficients in the normalisation formula progressively increased but at a slower rate than in the paper; (c) coefficients in the normalisation formula progressively increased but more rapidly than in the paper; (d) coefficients in the normalisation formula increased linearly.

The differences between the models were only slight. The explained variability in the *CA* analysis ranged between 61.7 and 65.1%, while in *CCA* between 24.1 and 27.6%. The time change was the most important factor in all the models followed by the Elllenberg *N* value. The rock fragment content and Ellenberg *F* value were important in all the models. In several models A_{max} and *L* were important. Altitude was selected in two models and average age of the tree-layer in one. According to *GLM* the change between the present and estimated tree-layer was the same for the particular species and the explained variability differed only slightly between the simulations (4 to 15% for particular species). The estimated proportion of the species in the tree-layer differed only slightly between the different simulations (2 to 8% for particular species). The reasons for such small differences are caused by using the proportion of the species in TL_p and TL_f.

The results (especially those dealing with the influence of factors on the estimated tree-layer) should also be influenced by the relatively small number of plots. However, the relatively small area (ca 70 km^2) with same the history and plots restricted to mesic stands, were chosen to lower the probability of this type of error. Unfortunately, this makes the results of this study less useful for generalisation (different areas can show different development).

Estimated tree-layer

There was a relatively high number of species present both in the TL_p and TL_f (11 and 14, respectively) in the study (see also Dostalova 2009). Prach (1994) counted 24 woody species in 17 different studies focused on succession in Central Europe (from wet to xeric series), 10 of which were trees colonising abandoned fields and grassland. Bobiec (2007) found 12 tree species regenerating in a natural forest in Poland.

The change in species composition from the present tree-layer to the estimated tree-layer is relatively high. Most of the species will probably change their frequency in the tree-layer and many of them will also change their abundance during the succession. The most important change was found to be the estimated decrease of the pioneer species, i.e., is birch, and the increase of ubiquist species, e.g., Norway spruce and sycamore maple (for comparison see Zobel 1989). It is an important finding that the species typical for terminal stages of succession will be more common in the tree-layer in the next tree generation. European beech and pedunculate oak should be particularly dominant in the terminal stage of succession (Neuhäuslová 1998). Nowadays, however, they are rare in the study area due to the forest management. In this kind of management, coniferous trees are preferred and most of the natural forests in Central Europe have been changed into monocultures of Norway spruce and/or Scots pine (Zerbe 2002). Although beech and oak have heavy seeds, and therefore are usually thought of as poor colonisers (e.g., Battaglia et al. 2008), I found that they are able to colonise the SDFs even when the potential source of the seeds exceeds several hundred meters away (field observation). However, their abundance is low – about 3%.

My results are more optimistic for the forest management than the results from Canada (D´Orangeville et al. 2008). Only 5% of the plots will not be colonised by tree species valuable for forest management (seedlings taller than 30 cm), while D´Orangeville et al. (2008) found 57%. Almost half of the valuable species will be deciduous. In total, 47% of the plots were found to contain more than one species valuable for forest management, while D´Orangeville et al. (2008) found only 11%. In 79% of the plots the number of seedlings species valuable for forest management exceeded 2,000 per hectare which is sufficient for natural regeneration.

These findings indicate that the SDFs will change towards potential natural vegetation but the species composition of the second generation of the tree-layer will still be very different from it. On the other hand, N_n for species typical for early stages of succession increased with the age of the tree-layer, which seems to contradict the former results. The reason is probably in the opening of the canopy in the older growths, while the herb layer is still mostly dominated by grasses (usually *Agrostis capillaris*). Grassland litter was found to be able to slow down the establishment of forest species (Donath and Eckstein 2008). Moreover, species typical for early stages of succession can also regenerate in these growths and can profit from vegetative distribution of adult trees present in the plot, especially the aspen (Faliński 1980; Prach 1994). European aspen was found to be the most common pioneer tree in the estimated tree-layer. These findings indicate that the changes in the tree-layer will be very slow and some retrograde changes could appear, and the development of the tree-layer equal to the potential natural vegetation will take longer than two generations. If we assume generation will take 100 year then succession will take longer than two centuries – the estimation of 350 years by Faliński (1988) seems to be rather optimistic.

Species responses to the selected factors

Several factors seems to influenced the seedling establishment of individual species and a similar finding holds true also for the groups of species (see also Dostalova 2009). This may explain the large differences in species composition for similar stands found in different studies (e.g., Dovčiak et al. 2005; Schreiber 1995).

Time was found to be the most important factor causing changes in the tree-layer. Ellenberg values *N* (which correspond with the productivity of the stand) and *F* and R_s were found to be important for the changes in the tree-layer. In accordance with the findings of most of the studies (for review see Prach and Řehounková 2006; for tree-layer e.g., Vojta 2007), these factors were linked to abiotic conditions.

Although altitude did not significantly influence the overall character of the tree-layer, it influenced most of the species (Fig. 7b). Although the altitude gradient is relatively low (275 m), it covers three different transients in potential natural vegetation in the area (from oak to beech dominated forests and to spruce dominated forests, see Neuhäuslová 1998). The results obtained reflect the ecological requirements of most of the species – Norway spruce and mountain ash prefer higher altitudes, while European beech medium altitudes and cherry tree are more common in lower altitudes. Maple is the most common tree in hedgerows in medium and high altitudes in the area – results obtained in this study probably reflect its distribution.

According to the *GLM* results, the surroundings (*D_Fst*) did not influence the estimated changes, although they were found to be important in other studies (for review see Prach and Řehounková 2006), and only cherry tree species was significantly influenced.

N_n of species typical for early stages of succession was higher at lower altitudes, on less productive sites and near to the forest – which is in accordance with the general assumption that the rate of succession decreases with the altitude and on more extreme stands (Blažková 1991; Prach 1990; Prach et al. 2007), however, the explained variability in the data was low (<10 %). Species typical for terminal stages of succession established better in the older growth, which is not surprising. The medium productivity of the stand, higher C_{org} and low *D_Fst* increased the recruitment of species typical for terminal stages of succession. Low productivity slows down succession changes (Prach 1990), while high productivity increases competition of aboveground vegetation (Prach 1994; Rajaniemi 2003). This may explain the observed preference of the species typical for terminal stages of succession to medium values. Soils with higher C_{org} are closer to forest soils and the value increases during succession towards a natural forest (Strandberg et al. 2005). Moreover, species typical for terminal stages of succession are thought of as being worse colonisers than species typical for early stages of succession (Ehrlén et al. 2006; Vellend et al. 2007).

Although most of results of this study are well interpretable from an ecological point of view, there need not be causality between the observed data patterns and the studied factors. Results of this study should be revised in different studies in more plots, in different areas, with higher factor gradients, and over a longer period of time.

What spontaneously developed forest is woodier? Influence of the site-dependent factors on the character of the herb layer

Který porost náletových dřevin je lesnatější? Vliv stanovištních faktorů na charakter bylinného patra

Abstract

The study focused on the herb layer character of spontaneously developed forests (SDFs) on mesic stands in a mountainous area in the Czech Republic (48 plots, 100 m^2). The changes in the herb layer character during the succession toward forest, and influence of site-dependent factors on the vegetation were studied. The persistence of the grassland character and changes in the herb layer toward the woodland character were studied in detail.

The influence of the tree layer, climatic, and soil conditions on the abundance of species grouped according to the biotope, type of distribution and grassland/woodland character of the herb layer was tested.

Different factors were found to be important for different groups of species. The average age and soil reaction was found to be the most important factor influencing the character of the herb layer described by the groups of species according to the biotope. The abundance of the groups of species according to the biotope was influenced at most by soil conditions and altitude.

The grassland/woodland character of the herb layer was influenced at most by the duration of the tree layer, character of the tree layer and by soil conditions. Soil closer to the forest soils was occupied more by species typical for forests, while the grassland herb layer character was typical for soil closer to the grassland soil. The grassland character is changing very slowly toward the woodland character.

Groups of species according to the type of distribution were influenced by light conditions, by the age of the tree layer and by rock fragment content. The groups typical for woodland tended to be more common in older SDFs, while groups typical for grassland tended to be more abundant in more irradiated SDFs.

Shrnutí

Práce je zaměřena na charakter bylinného patra v porostech náletových dřevin (SDFs) na mesickém stanovišti v horských oblastech v České republice (48 ploch á 100 m^2). Cílem práce bylo zjistit, jak se mění charakter bylinného patra v průběhu sukcese směrem k lesu a které stanovištní faktory ovlivňují vegetaci. Více pozornosti bylo věnování přetrvávání lučního charakteru bylinného patra a změnám v bylinném patře vedoucím směrem k lesnímu charakteru.

Byl testován vliv stromového patra, klimatických a půdních podmínek na skupiny druhů dle jejich biotopu, a způsobu rozšiřování a afinity k lučnímu/lesnímu společenstvu.

Různé faktory ovlivňovaly různé skupiny druhů. Charakter bylinného patra definovaný skupinami druhů vylišených na základě biotopu byl ovlivněn průměrným věkem stromového patra a půdní reakcí. Jednotlivé skupiny ovlivňovaly především půdní podmínky a nadmořská výška.

Lesní/luční charakter bylinného patra byl ovlivněn především dobou trvání stromového patra, charakterem stromového patra a půdními podmínkami. Lesní charakter bylinného patra byl spíše na půdách podobnějších lesním půdám, naopak lučnější charakter byl typický pro půdy více podobné půdám lučních společenstev. Charakter bylinného patra se velmi pomalu měnil směrem od lučního k lesnímu.

Skupiny druhů dle způsobu rozšiřování byly ovlivněny světelnými podmínkami, věkem stromového patra a skeletovitostí půdy. Pokryvnost lesních skupin byla vyšší ve starších porostech, zatímco pokryvnost lučních skupin byla vyšší ve světlejších porostech náletových dřevin.

Introduction

A large area of the cultural landscape has been abandoned mostly due to economic reasons in Europe in recent decades, especially in less favourable areas and in the mountains (e.g., Gellrich and Zimmermann 2007; Hamre et al. 2007; MacDonald et al. 2000). Trees and shrubs establish themselves in abandoned areas due to the spontaneous succession (e.g., Prach and Pyšek 1994b). The rate of tree establishment varies; e.g., Schreiber (1996) or Spatz (1980) found fast overgrowing by trees. Other studies (e.g., Dzwonko 1993; Prach 1987) found that the succession toward woodland was blocked by competition (e.g., by clonal grasses) or by litter (Facelli and Pickett 1991b). Lone trees can facilitate tree establishment (Dzwonko and Loster 1992), trees shading the stands (Dovčiak et al. 2005) or tree litter (Facelli and Pickett 1991b) can lower the competitive ability of grass, and therefore enhance the tree establishment process.

The loss of much semi-natural grassland, which is evaluated for its high biodiversity (e.g., MacDonald et al. 2000; Lindborg 2007) due to the successional changes was observed (e.g., Öster et al. 2007). Reversing of the successional changes was found to be a difficult and long-term process (Dzwonko and Loster 2007; Maccherini et al. 2007). The species composition of recent forests was found to be different from the old-growth forests, and the colonisation of the herb layer of recent forests by typical forest species was found to be very slow (e.g., Bossuyt et al. 1999; Brunet and von Oheimb 1998a; Honnay et al. 1999; Peterken and Game 1984; Whitney and Foster 1988; Wulf 2004). However, a trend toward forest vegetation was observed in several studies (e.g., Vojta 2007). The period needed for terminal stage development is supposedly long. Faliński (1988) estimates 350 years for mesic sequence in the temperate zone in Europe. However, changes caused by previous agriculture could last much longer (e.g., Dupouey et al. 2002), and equilibrium was not even found in natural forests even several centuries after the disturbance (Woods 2000).

In summary, new vegetation type – spontaneously developed forests (SDFs) – have been established in the temperate region. They are not found as high conservation value habitats, and their forest management value is also small. On the other hand, by studying the SDFs, we have an opportunity to observe natural processes, and therefore to understand better the influence of different factors on species colonisation of new habitats.

Many factors can influence the succession: i) the site-dependent factors: succession is under the control of the environment, which determines the direction, rate and limits of changes (Odum 1969); ii) context-dependent factors particularly influence the colonisation of the site (e.g., Řehounková and Prach 2006).

Many site-dependent factors (e.g., climate, water regime, soil conditions) were found to influence the rate and direction of the changes (e.g., Kolb and Dieckmann 2004; Prach and Řehounková 2006; Prach et al. 2007). Dispersion limitation of forest species (e.g., Bossuyt et al. 1999; Brunet and von Oheimb 1998a; Ehrlén et al. 2006), influence of spatiotemporal changes in the environment (e.g., Dovčiak et al. 2005), history (e.g., Vellend et al. 2007) or stochastical events (Brokaw and Busing 2000) are examples of the context-dependent factors.

Of the site-dependent factors, soil conditions (especially humidity, soil reaction, and nutrient content) were found to be important for the species composition of recent forests (e.g., Christensen and Peet 1984; Honnay et al. 1999; Prach and Pyšek 1994b; Verheyen et al. 1999), however no influence of the soil condition was also found (e.g., Ehrlén and Eriksson 2000). Light conditions also influence the species, and therefore the character of the vegetation (e.g., Dzwonko and Loster 1990; Tilman and Wedin 1991).

The aim of this study was to find out how the selected site-dependent factors influence the character of the herb layer. The factors describing the age and character of the tree layer, climate, light and soil conditions were considered. The character of the herb layer was described by the abundance of different functional groups of species according to the biotope, and type of distribution. The grassland and woodland character of the herb layer was determined as indeces counted from the abundances of species grouped according to the biotope, and similar indeces were also derived from abundances of species typical for grassland/woodland grouped according to the type of distribution.

The following questions are considered:

1. What factors influence the character of the vegetation in the SDFs? Are time, climate, light or soil conditions important for different groups of species according to the biotope or type of distribution?
2. Do the time of succession or climatic, soil or light conditions influence the grassland or woodland character of the herb layer of SDFs?

Methods

Study area

The study area was the southern part of the Czech Republic (40°35-38´ N, 14°11-17´ E).

Forty-eight plots (10 × 10 m) were fixed in the growths of SDFs. The growths were different in age, altitude and exposition (see Table 12), but all the plots were on mesic stands. The supposed terminal stage of succession is beech forest of the association *Dentario enneaphylli-Fagetum*, in the lowest altitudes transient to the association *Luzulo albidae-Quercetum petrae* (Neuhäuslová 1998). Present growths were mostly dominated by *Betula pendula* Roth, common trees are also *Picea abies* (L.) Karsten, *Populus tremula* L.; in some cases *Pinus sylvestris* L. or *Fraxinus excelsior* L. were more abundant. The plots were fixed in such growths, where important man influence was not recognisable.

Data collection

Phytocenological releve was taken from all the permanent plots. The species abundance was estimated in percentages of abundance of the species for each layer.

Species listed in the herb layer were grouped as follows:

1. According to the biotope, where they are usually present: antropochorous or ruderal species (*AR*), species typically growing at clearings (*C*), grassland species (*Gs*), species growing both in wood and grassland (*GW*), shrub species (*Sc*) and woodland species (*Ws*). The sum of abundances of species was used for each group. Number of species and mean abundances of groups are summed in Table 11.
2. According to the type of distribution: anemochorous (*Wd*), autochorous (*A*), myrmecochorous (*M*), non-specific (*Ns*), endozoochorous (Z_{end}), and exozoochorous species (Z_{ex}).

From the phytocenological releves, the next indeces were counted: woodlandness (*W*), grasslandness (*G*), weighted woodlandness (W_w) and weighted grasslandness (G_w):

$$W = \Sigma\,(Ws + 0.5 \times GW + 0.5 \times Sc + 0.5 \times C),$$

$$G = \Sigma\,(Gs + 0.5 \times GW + 0.5 \times AR + 0.5 \times C + 0.2 \times Sc),$$

$$W_w = \Sigma\,(\Sigma\, Ws_i \times \mathrm{a_i} + \Sigma\, 0.5 \times GW_\mathrm{j} \times \mathrm{a_j} + \Sigma\, 0.5 \times Sc_\mathrm{k} \times \mathrm{a_k} + \Sigma\, 0.5 \times C_\mathrm{l} \times \mathrm{a_l}),$$

where $\mathrm{a_i}$, $\mathrm{a_j}$, $\mathrm{a_k}$, $\mathrm{a_l}$ indicates abundance of species i, j, k, l.

$$G_w = \Sigma(\Sigma\, Gs_\mathrm{i} \times \mathrm{a_i} + \Sigma\, 0.5 \times GW_\mathrm{j} \times \mathrm{a_j} + \Sigma\, 0.5 \times AR_\mathrm{k} \times \mathrm{a_k} + \Sigma\, 0.5 \times C_\mathrm{l} \times \mathrm{a_l}$$
$$+ \Sigma\, 0.5 \times Sc_\mathrm{m} \times \mathrm{a_m}),$$

where $\mathrm{a_i}$, $\mathrm{a_j}$, $\mathrm{a_k}$, $\mathrm{a_l}$, $\mathrm{a_m}$ indicates abundance of species i, j, k, l, m.

Woodlandness and grasslandness correspond with the number of species typical for woodland or grassland, while weighted woodlandness and grasslandness correspond with the abundance of species typical for woodland or grassland (for basic statistics see Table 11).

Similarly indeces weighted the grasslandness of autochorous (G_w_A), myrmecochorous (G_w_M), species non-specific to the type of distribution (G_w_Ns), anemochorous (G_w_Wd), endozoochorous ($G_w\_Z_{end}$), and exozoochorous species ($G_w\_Z_{ex}$), and weighted woodlandness of autochorous (W_w_A), myrmecochorous (W_w_M), species non-specific to the type of distribution (W_w_Ns), anemochorous (W_w_Wd), endozoochorous ($W_w\_Z_{end}$), and exozoochorous species ($W_w\_Z_{ex}$) were counted to describe the abundance of the species typical for grassland/woodland according to the type of distribution. The values were obtained as the sum of abundances of species from a certain group of species according to the type of distribution. The abundance of species according to the biotope was weighted by the same values that were used by the weighted grasslandness/woodlandness. For mean values of the indeces see Table 11.

Table 11. Groups of species according to the biotope, indeces describing grassland/woodland character and indeces describing abundance of species grouped according to the type of distribution.

	N_sp	Mean		Mean		Mean		Mean
AR	18	3.1	W	8.69	G_w_A	0.00	W_w_A	0.20
C	4	2.1	W_w	17.97	G_w_M	1.95	W_w_M	1.20
Gs	86	32.7	G	20.54	G_w_Ns	11.45	W_w_Ns	4.80
GW	30	16.8	G_w	45.08	G_w_Wd	6.53	W_w_Wd	6.48
Sc	10	0.8			G_w_Z_{end}	1.47	W_w_Z_{end}	5.55
Ws	26	9.6			G_w_Z_{ex}	22.55	W_w_Z_{ex}	0.72

AR - antropochorous or ruderal species, C - species typically growing at clearings, Gs - grassland species, GW - species growing both in grassland and in wood, Sc – shrub species, Ws – woodland species; W - woodlandness, W_w - weighted woodlandness, G - grasslandness, G_w - weighted grasslandness; G_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – weighted grasslandness of autochorous/myrmecochorous/ non-specific/anemochorous/endozoochorous/exozoochorous species, W_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – weighted woodlandness of autochorous/myrmecochorous/non-specific/ anemochorous/endozoochorous/exozoochorous species; N_sp. – number of species, Mean - mean value,.

Tabulka 11. Skupiny druhů dle biotopu, lesní a luční charakter bylinného patra a indexy korespondující s pokryvností lučních a lesních druhů dle jejich způsobu rozšiřování. AR - antropogenní a nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, GW – druhy společné lučním a lesním stanovištím, Sc – křovinné druhy, Ws – lesní druhy; W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů, G – index korespondující s počtem lučních druhů, G_w – index korespondující s pokryvností lučních druhů; G_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – index koresponudjící s pokryvností lučních autochorních/myrmekochorních/nespecifických/anemochorních/endozoochorních/ exozoochorích druhů, W_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – index koresponudjící s pokryvností lesních autochorních/myrmekochorních/nespecifických/anemochorních/endozoochorních/ exozoochorních druhů. N_sp – počet druhů, Mean – průměrná hodnota.

The Ellenberg´s indicator values (*EIVs*) for soil reaction (*R*), humidity (*F*), light availability (*L*), temperature (*T*) and nitrogen content (*N*) were calculated from the phytocenological relevés (Ellenberg 1988). *EIVs* correspond with the character of the habitat, *N* correspond rather with the productivity of the place (Ertsen et al. 1998; Schaffers and Sykora 2000).

The number and species composition of trees at the plot were listed. The abundance of the tree layer was determined from the phytocenological releve, and it was used after logarithmical transformation (E_3). The proportion of deciduous trees in the tree layer

(D) was calculated. This characteristic corresponds with the character of the tree layer (value 1 have deciduous SDFs, 0 have coniferous SDFs).

Two samples of wood were taken from all the trees, but maximally from ten for each species, using a Pressler auger. Samples were taken from opposite sides of the trunk 40 cm above ground. After fixation and cutting, tree-rings were counted for estimation of tree age. The following were counted: average age of trees (A_a), and maximal age of the trees (A_max) for all the plots. A_{max} corresponds with the duration of abandonment, while A_a corresponds rather with the duration of the closed canopy of the tree layer.

Relative irradiance of photosynthetically active radiation (*PhAR*) was measured for all plots. Relative *PhAR* irradiance was determined in fully developed stands. Two luxmeters equipped with *PhAR* sensors were used. One luxmeter recorded *PhAR* irradiance in the open, while the other recorded it simultaneously at a certain level within the growth. Relative *PhAR* irradiance was then calculated as percentage of incoming *PhAR* in the open. The measurements were taken at 5 cm (P_5) and 120 cm (P_{120}) above ground. Twenty measurements of *PhAR* irradiance were taken within each plot. P_{120} corresponds with the abundance of the tree layer, while P_5 corresponds with the light availability for seedlings and it depends on the tree, shrub and herb layer abundance.

A soil sample was taken at each plot (mixture of five point samples). Following analysis were done: i) the content of rock fragments >2 mm (R_s) in the dried samples using a 2 mm sieve [%]; ii) the soil reaction in the water solution (pH_s) using 10 g of fine air-dried soil samples and 20 cm^3 of distilled water (free of CO_2); iii) organic matter content (C_{org}) determined as the loss of the matter content of dried sample by 450°C [%]; iv) the basal respiration of the microbial community (BR_s) determined as CO_2 production [$\mu g\ C\text{-}CO_2.g^{-1}.hod^{-1}$] (Jäggi 1976).

The retention water capacity (*RWC*) determined from the undisturbed soil samples (five per plot) taken from the organic soil horizon at each plot. *RWC* was counted from the water content in the soil sample after 24hours draining of the watterlodged sample using filter-paper. Soil pit was done next to each plot (within the same SDFs) to measure the depth of organic horizon – horizon A and transient A and B horizon (S_{org}) [cm].

The altitude of the plot was taken from the map (1 : 10 000). The altitude corresponds with the climatic conditions (Prach and Řehounková 2006), because the mean temperature and precipitation depend on the altitude. The study area is relatively small and therefore we can suppose that the climatic conditions are at most influenced by the altitude of the plot.

I determined the orientation (using compass) and slope (visual estimation) for all plots. I calculated the heat index to the south-south west (H_{ssw}):

$$H_{SSW} = \cos(\text{exposition} - 202.5°) \times \text{tg}(\text{slope})$$

Basic statistics of the factors are summed in the Table 12.

All measurements and field observations were carried out in 2004 and 2005.

Table 12. Basic statistic of the factors.

	Mean	SD	Range		Mean	SD	Range
A_a	30.2	11.107	10 – 46	**H_{SSW}**	-0.061	1.184	-1.99 - 1.91
A_{max}	45.7	18.366	12 – 84	**pH_S**	4.28	0.298	3.8 - 5.6
E_3	33.3	15.049	5 – 60	**C_{org}**	10.7	3.205	5 - 21
D	83.6	23.759	0 – 100	**S_{org}**	23.1	16.539	4 - 70
P_{120}	19.6	12.197	3 – 68	**R_s**	41.7	23.309	6 - 86
P_5	5.7	5.344	1 – 36	**RWC**	15.77	3.207	7.1 - 22.9
altitude	785	71.57	665 - 940	**BR_s**	2.738	1.098	0.72 - 5.78

A_a/A_{max} - average and maximal age of the tree layer [year], E_3 - abundance of the tree layer [%], D - percentage of the deciduous trees [%], P_{120}/P_5 - relative irradiance at the 120 or 5 cm above ground [%], H_{SSW} – heat to the SSW, C_{org} - organic matter content [%], S_{org} - depth of the organic horizon [cm], R_s – rock fragment content [%], RWC - retention water capacity [%], BR_s - microbial respiration [μg C-CO_2.g^{-1}.hod^{-1}].

Tabulka 12. Základní statistika faktorů prostředí. A_a/A_{max} – průměrný/maximální věk stromového patra [roky], E_3 – pokryvnost stromového patra [%], D – zastoupení listnatých stromů ve stromovém patře [%], P_{120}/P_5 - relativní ozářenost ve 120 a 5 cm [%], H_{SSW} – sklon k JJZ, C_{org} – obsah organické hmoty v půdě [%], S_{org} – hloubka organického půdního horizontu [cm], R_s - skeletovitost [%], RWC – retenční vodní kapacita [%], BR_s – bazální respirace [μg C-CO_2.g^{-1}.hod^{-1}].

Statistical analysis

The following factors were used in the statistical analysis: (1) factors describing character of the growth: A_a, A_{max}, E_3, D, P_5, P_{120}; (2) factors describing climatic conditions: altitude and H_{SSW}; (3) factors describing soil conditions: pH_s, C_{org}, S_{org}, BR_S, R_s, RWC; (4) Ellenberg indicator values: F, L, N, R, T.

Abundances of groups of species according to the biotope, and indeces describing abundances of groups of species according to the type of distribution were analysed using ordination methods in the CANOCO for Windows program v. 4.5. “Species” data were logarithmically transformed. Linear analyses were performed (the length of the gradient was less than 2.0 in all the cases): indirect principal components analysis (*PCA*), direct redundancy analysis (*RDA*) respectively. Manual selection of the factors at the $\propto = 0.05$ level was used (Lepš and Šmilauer 2003).

General Linear Models (*GLM*) in the Canodraw v. 4.0 program were used to test the influence of factors on the abundance of each group of species according to the biotope (*AR*, *C*, *Gs*, *GW*, *Sc*, *Ws*), on indeces describing the grassland/woodland character of the herb layer (G, G_w, W, W_w) and on indeces describing the abundance of groups of species according to the type of distribution (G_w_M, G_w_Ns, G_w_Wd, $G_w\_Z_{end}$, $G_w\_Z_{ex}$, W_w_A, W_w_M, W_w_Ns, W_w_Wd, $W_w\_Z_{end}$, $W_w\_Z_{ex}$). Poisson distribution of the data was used, because the link function of this distribution is “Log” function, which is recommended for the counts and frequency data (Lepš and Šmilauer 2003; p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using Akaike Information Criterion (Lepš and Šmilauer 2003). Factors from the first, second and third group were used (*EIVs* were omitted).

Results

Groups of species according to the biotope

The first ordination axis in the *PCA* analysis explained 33.6 % of the total variability in the data, while the first four axes explained 90.0 %. The A_a (F = 3.03, p = 0.01) and pH_S (F = 2.48, p = 0.04) significantly influenced the abundance of groups. The first ordination axis in the *RDA* explained 4.2 % of the total variability in the data, while the second one explained 7.1 %. Woodland, shrub and grassland species were more abundant in older SDFs, while *C* species were more common in soil with higher soil reaction. For more detail see Fig. 9.

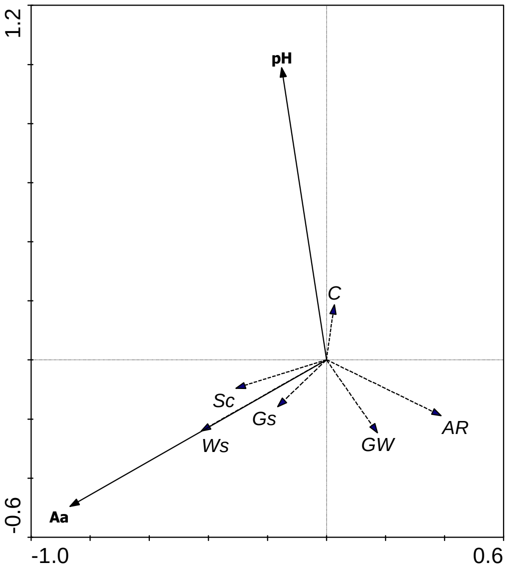


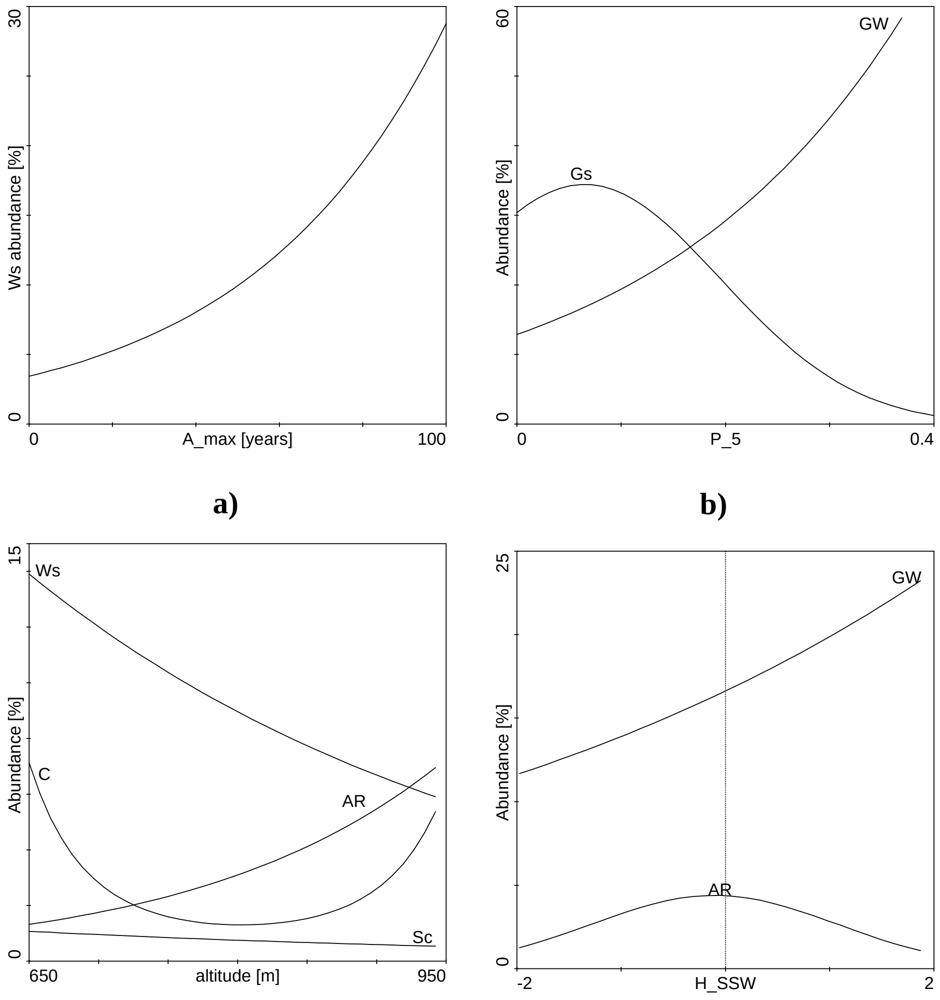
Figure 9. Ordination diagram for *RDA* of groups of species according to the type of biotope. AR - antropochorous or ruderal species, C - species typically growing at clearings, Gs - grassland species, GW - species growing both in grassland and in woodl, Sc - shrub species, Ws - woodland species; Aa - average age of the tree layer.

Obrázek 9. *RDA* ordinační diagram skupin druhů podle typu biotopu. AR – antropogenní a nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, GW – druhy společné lučním a lesním stanovištím, Sc – druhy křovin, Ws – lesní druhy; Aa – průměrný věk stromového patra.

Antropochorous and ruderal species were more abundant at higher altitudes (Fig. 10c), at flat stands (Fig. 10d), and in deeperer soil (Fig. 11b).

Species typically growing at clearings were more abundant in soil with medium rock fragment content (optimum 42%, Fig. 11c), higher pH_s (Fig 11a), and both in lower and higher altitudes (Fig. 10c). More grassland species were found at lower P_5 (Fig. 10b), in soil with lower organic matter content (Table 13), and in both low and deep soil (Fig. 11b), but the explained variability was low (<10%, see Table 13).

Species growing both in grassland and wood were more common at medium irradiated stands at 120 cm above ground (optimum 35%), and at more irradiated stands at 5 cm above ground (Fig. 10b, Table 13). Species typical for shrubs were more abundant in medium deep soil (optimum 30%; Fig. 11b). Species typical for forests were more abundant in older SDFs (Fig. 10a, Table 13), in soil with higher rock fragment content (Fig. 11c), and with higher microbial respiration (Fig. 11d).

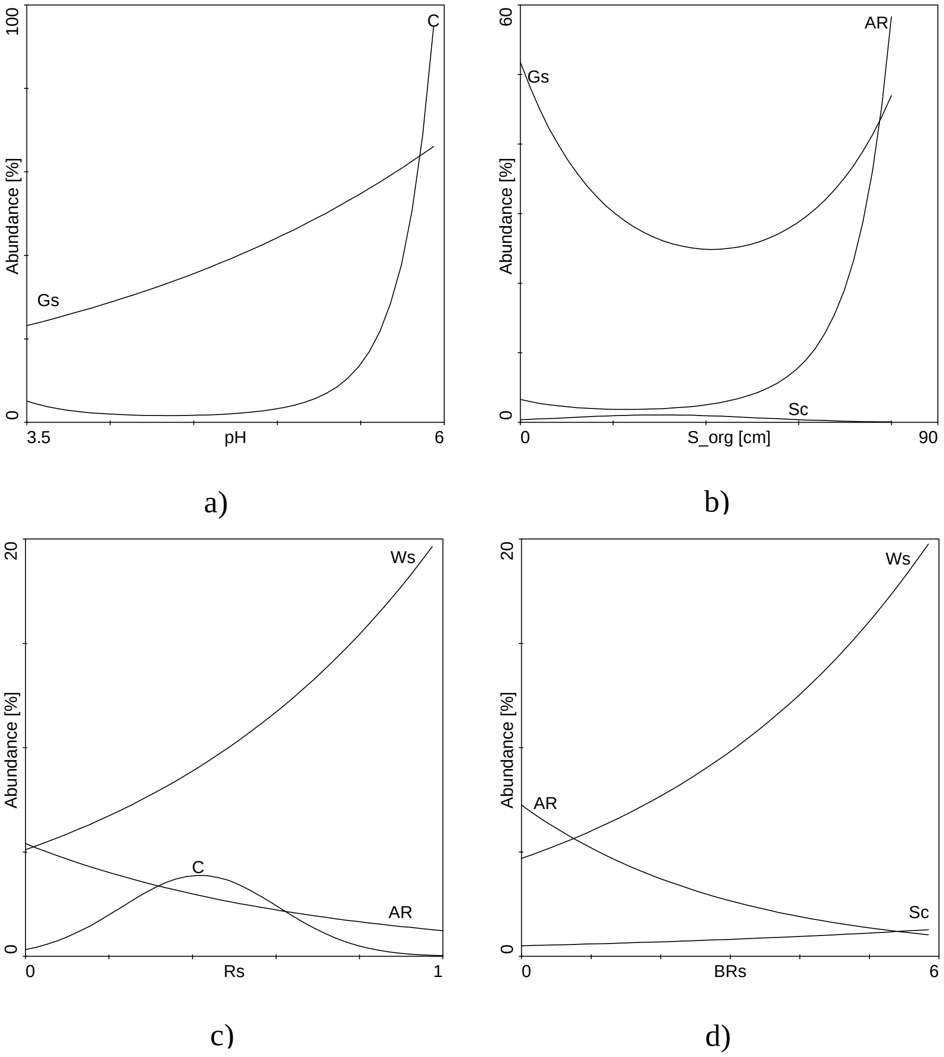


a) **b)**

c) d)

Figure 10. Selected factors influencing abundances of groups of species according to the biotope (*GLM*): a) maximal age of the tree-layer, b) relative irradiance at the 5 cm above ground, c) altitude, d) heat to the SSW. AR - antropochorous or ruderal species, C - species typically growing at clearings, Gs - grassland species, GW - species growing both in grassland and in wood, Sc – shrub species, Ws - woodland species.

Obrázek 10. Vliv vybraných faktorů na pokryvnost skupin druhů dle biotopu (*GLM*): a) maximální věk stromového patra, b) relativní ozářenost v 5 cm, c) nadmořská výška, d) sklon k JJZ. AR – antropogenní a nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, GW - druhy společné lučním a lesním stanovištím, Sc – druhy křovin, Ws – lesní druhy.



a) b)

c) d)

Figure 11. Selected factors influencing abundances of groups of species according to the biotope (*GLM*): a) soil reaction; b) depth of the organic horizon, c) proportion of rock fragment content, d) microbial respiration [µg C-CO_2.g^{-1}.hod^{-1}]. AR - antropochorous or ruderal species, C – species typically growing at clearings, Gs - grassland species, Sc - shrub species, Ws – woodland species.

Obrázek 11. Vliv vybraných faktorů na pokryvnost skupin druhů dle biotopu (*GLM*): a) půdní reakce, b) hloubka organického horizontu, c) skeletovitost [%], d) bazální respirace [µg C-CO_2.g^{-1}.hod^{-1}]. AR – antropogenní a nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, Sc – druhy křovin, Ws – lesní druhy.

Table 13. Factors influencing groups of species according to the biotope (*GLM*).

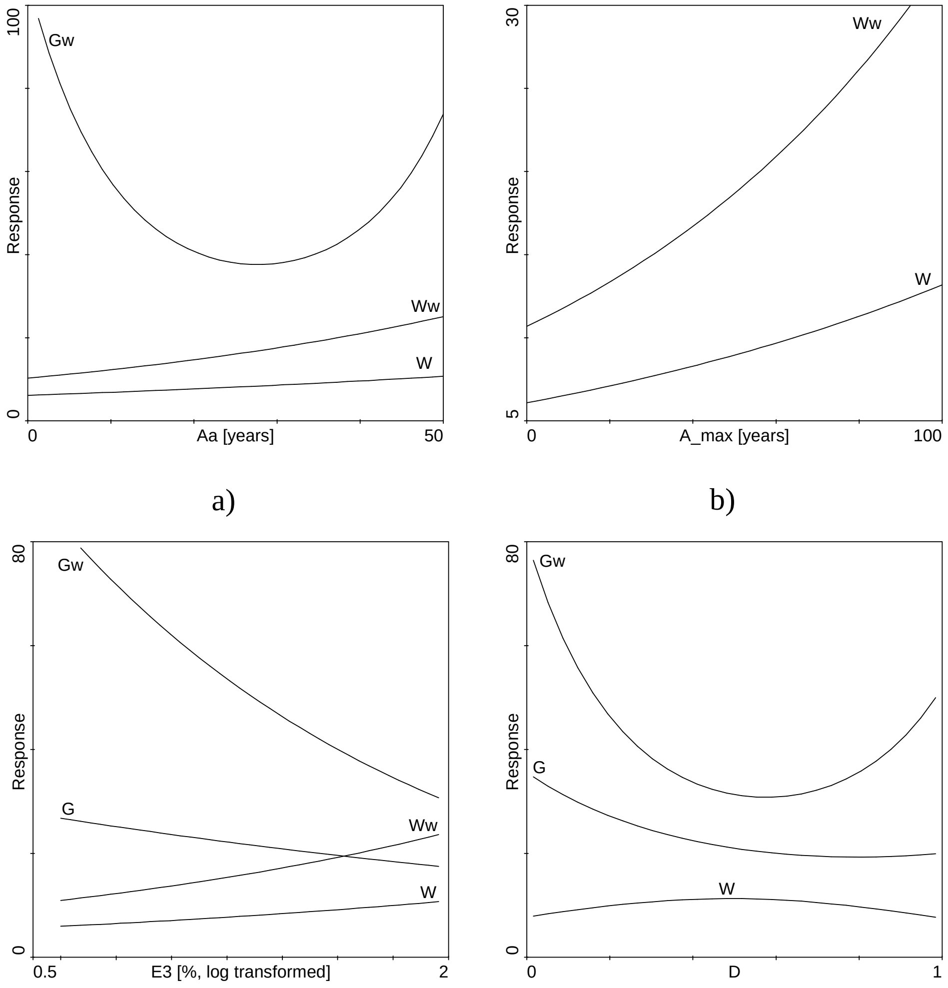
	AR		C		Gs		GW		Sc		Ws	
	M	**var.**	**M**	**var.**	**M**	**var.**	**M**	**var.**	**M**	**var.**	**M**	**var.**
A_a	×		×		×		×		×		L↑	11
A_{max}	×		×		×		×		×		L↑	20
E_3	L↓	8	×		×		×		×		×	
D	×		×		L↑	4	L↑	5	Q∩	7	×	
P_{120}	×		×		×		Q∩	11	×		×	
P_5	×		×		Q∩	8	L↑	12	×		×	
altitude	L↑	10	Q∪	11	×		×		L↓	4	L↓	6
H_{SSW}	Q∩	15	×		×		L↑	6	×		×	
pH_s	×		Q∪	21	L↑	5	×		×		×	
C_{org}	×		L↓	7	L↓	7	×		×		Q∩	8
S_{org}	Q∪	42	×		Q∪	8	×		Q∩	13	×	
R_S	L↓	7	Q∩	12	×		×		×		L↑	14
BR_s	L↓	7	×		×		×		L↑	4	L↑	11

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; AR - antropochorous or ruderal species, C - species typically growing at clearings, Gs - grassland species, GW - species growing both in grassland and in wood, Sc - shrub species, Ws - woodland species; A_a/A_{max} - average and maximal age of the tree layer, E_3 - abundance of the tree layer, D - proportion of deciduous trees in the tree layer, P_{120}/P_5 - relative irradiance at the 120/5 cm above ground, H_{SSW} - Heat to the SSW, C_{org} - organic matter content, S_{org} - depth of the organic soil horizon, R_S – rock fragment content, BR_s - microbial respiration.

Tabulka 13 Vliv studovaných faktorů na pokryvnost skupin druhů vylišených dle typu stanoviště (*GLM*). L – lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. – vysvětlená variabilita [%]; AR - antropogenní a nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, GW – druhy společné lučním a lesním stanovištím, Sc – druhy křovin, Ws – lesní druhy; A_a/A_{max} - průměrný/maximální věk stromového patra, E_3 – pokryvnost stromového patra, D - zastoupení listnatých stromů ve stromovém patře, P_{120}/P_5 – relativní ozářenost ve 120 a 5 cm, altitude - nadmořská výška, H_{SSW} - sklon k JJZ, C_{org} – obsah organické hmoty v půdě, S_{org} – hloubka organického půdního horizontu, R_s - skeletovitost, BR_s - bazální respirace.

Indeces describing grassland and woodland character of the herb layer

Higher indeces for woodland species were found in the older SDFs (Fig. 12a, b), in mixed SDFs (Fig. 12d), at soil reaction between 3.5 and 5 (Fig. 13a), in soil with higher organic matter content (Fig. 13b) and in lower soil (Fig. 13c) with high rock fragment content (Fig. 13d). Higher indeces for (weighted) grasslandness were found for open (Fig. 12c), non-mixed SDFs (Fig. 12d), in medium irradiated SDFs at 5 cm above ground (optimum 9%, Table 14), at soil reaction between 4.0 and 5.5 (Fig. 13a), and in soil with lower organic matter content (Fig. 13b).

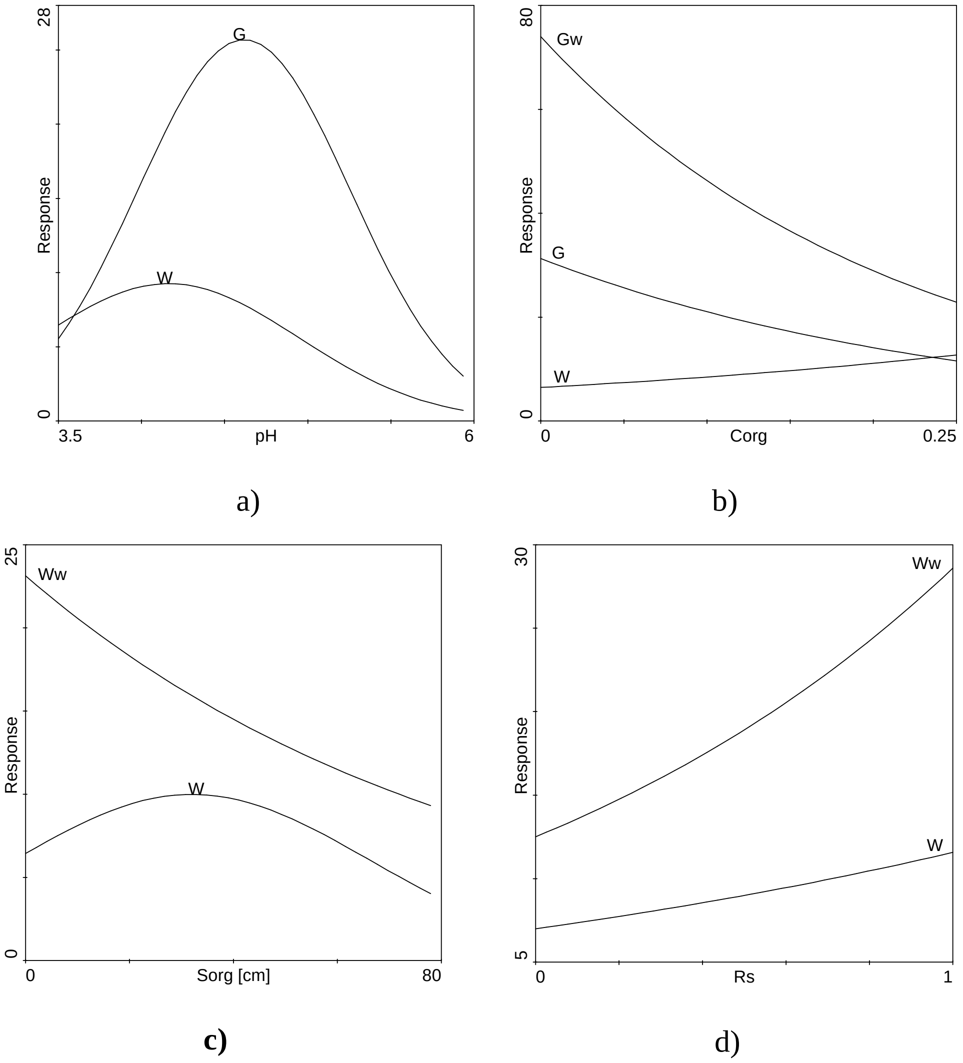


a) b)

c) d)

Figure 12. Selected factors influencing indeces describing grassland and woodland character of the herb layer (*GLM*): a) average, b) maximal age of the tree-layer, c) abundance of the tree-layer, d) percentage of the deciduous trees in the tree-layer, G - grasslandness, W - woodlandness, G_w - weighted grasslandness, W_w - weighted woodlandness.

Obrázek 12. Vliv vybraných faktorů na luční/lesní charakter bylinného patra (*GLM*): a) průměrný, b) maximální věk stromového patra, c) pokryvnost stromového patra, d) podíl opadavých dřevin ve stromovém patře. G – index korespondující s počtem lučních druhů, G_w - index korespondující s pokryvností lučních druhů, W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů.



a)

b)

c)

d)

Figure 13. Selected factors influencing indeces describing grassland and woodland character of the herb layer (*GLM*): a) soil reaction, b) organic matter content, c) depth of the organic soil horizon, d) proportion of rock fragment content. G - grasslandness, W - woodlandness, G_w - weighted grasslandness, W_w - weighted woodlandness.

Obrázek 13. Vliv vybraných faktorů na luční/lesní charakter bylinného patra (*GLM*): a) půdní reakce, b) obsah organické hmoty v půdě, c) hloubka organického půdního horizontu, d) skeletovitost. G – index korespondující s počtem lučních druhů, G_w - index korespondující s pokryvností lučních druhů, W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů.

Table 14. Factors influencing indeces describing grassland and woodland character of the herb layer (*GLM*).

	G		**G_w**		**W**		**W_w**	
	M	var.	M	var.	M	var.	M	var.
A_a	×		Q∪	8	L↑	12	L↑	12
A_{max}	×		×		L↑	17	L↑	13
E_3	L↓	4	L↓	18	L↑	9	L↑	6
D	Q∪	12	Q∪	22	Q∩	19	×	
P_{120}	×		Q∩	9	×		×	
P_5	×		Q∩	10	×		×	
altitude	×		×		×		L↓	2
pH_S	Q∩	29	×		Q∩	21	×	
C_{org}	L↓	10	L↓	9	L↑	7	×	
S_{org}	×		×		Q∩	15	L↓	10
R_S	×		×		L↑	12	L↑	12
RWC	×		L↓	6	×		×	
BR_s	×		L↓	7	L↑	8	×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]. G - grasslandness, G_w - weighted grasslandness, W - woodlandness, W_w - weighted woodlandness; A_a/A_{max} - average and maximal age of the tree layer, E_3 - abundance of the tree layer, D - proportion of deciduous trees in the tree layer, P_{120}/P_5 - relative irradiance at the 120/5 cm above ground, C_{org} - organic matter content, S_{org} - depth of the organic horizon, R_S – rock fragment content, RWC - retention water capacity, BR_s - microbial respiration.

Tabulka 14. Vliv studovaných faktorů na lesní/luční charakter porostu. L – lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. - vysvětlená variabilita [%]; G – index korespondující s počtem lučních druhů, G_w – index korespondující s pokryvností lučních druhů, W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů; A_a/A_{max} – průměrný/maximální věk stromového patra, E_3 – pokryvnost stromového patra, D – zastoupení listnatých stromů ve stromovém patře, P_{120}/P_5 – relativní ozářenost ve 120 a 5 cm, altitude - nadmořská výška, C_{org} - obsah organické hmoty v půdě, S_{org} - hloubka organického půdního horizontu, R_s - skeletovitost, RWC – retenční vodní kapacita, BR_s – bazální respirace.

Indeces describing abundance of groups of species according to the type of distribution

The first ordination axis in the *PCA* analysis explained 33.2% of the total variability in the data, while the first four axes explained 74.2%. The Ellenberg *L* value ($F = 6.06$, $p < 0.01$), rock fragment content ($F = 5.81$, $p < 0.01$) and average age of the tree layer ($F = 2.34$, $p = 0.04$) significantly influenced the indeces describing the abundance of groups of species according to the type of distribution. The first ordination axis in the *RDA* explained 12.2% of the total variability in the data, while the second one explained 11.7%. In general, groups of species according to the type of distribution typical for woodland tended to be more abundant in the older SDFs (left upper quarter of the ordination diagram), while groups typical for grasslands did in more irradiated biotopes (right half of the ordination diagram, Fig. 14).

No autochorous grassland species were found in the SDFs (Table 11). The abundance of woody autochorous species was influenced by many factors, and the explained variability was high in general (see Table 16). The abundance tended to increase with the age of the tree layer (Fig. 15b, Table 16) and with the abundance of the tree layer (Fig. 15c), and they were more abundant in mixed SDFs (optimum 48%, Fig. 15d), at low irradiance at 120 cm above ground (Fig. 16a), in lower altitudes (Fig. 16b), in soil with medium organic matter content (optimum 13%, Table 16), at high rock fragment content (Fig. 16d), and at higher microbial respiration (optimum 4.02, Table 16).

Grassland myrmecochorous species were most abundant in medium aged SDFs (optimum 30.6 year old, Fig. 15a), at lower altitudes (Fig. 16b), at soil reaction close to 4.5 (Table 15), with high rock fragment content (Fig. 16d), while woodland myrmecochorous species were more abundant in older SDFs (Fig. 15b, Table 16), and at soil reaction close to 4.4 (Table 16).

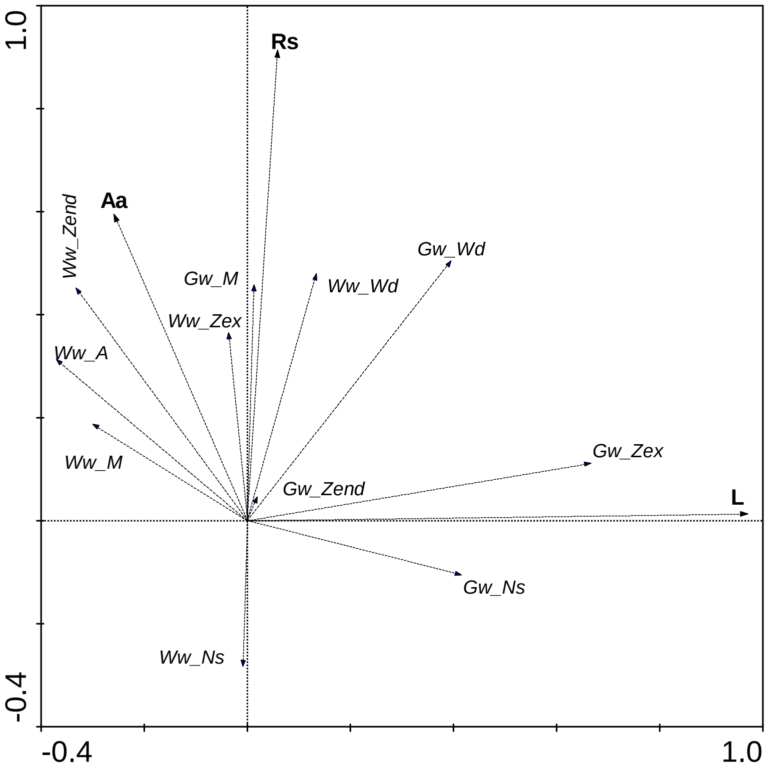


Figure 14. Ordination diagram for *RDA* of indeces corresponding with the abundances of groups of species according to the type of of distribution. G_w_M/Ns/Wd/Zend/Zex - weighted grasslandness of myrmecochorous/ non-specific/anemochorous/endozoochorous/exozoochorous species, W_w_A/M/Ns/Wd/Zend/Zex - weighted woodlandness of autochorous/ myrmecochorous/non-specific/anemochorous/endozoochorous/exozoochorous species; Aa – average age of the tree layer, L - Ellenberg *L* value, Rs – rock fragment content.

Obrázek 14. *RDA* ordinační diagram – indexy korespondující s pokryvností skupin druhů podle způsobu rozšiřování. Gw_M/Ns/Wd/Zend/Zex – index koresponudjící s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů, Ww_A/M/Ns/Wd/Zend/Zex – index koresponudjící s pokryvností lesních autochorních/myrmekochorních/nespecifických/anemochorních/endozoochorních/ exozoochorních druhů; Aa – průměrný věk stromového patra, L – Ellenbergova hodnota *L*, Rs - skeletovitost.

Table 15. Selected factors influencing indeces corresponding with grassland species abundance according to the type of distribution (*GLM*).

	G_w_M		G_w_Ns		G_w_Wd		$G_w\_Z_{end}$		$G_w\_Z_{ex}$	
	M	var.	M	var.	M	var.	M	var.	M	var.
A_a	Q∩	10.3	Q∪	20.2	L↑	5.2	Q∪	30.4	×	
A_{max}	×		Q∪	14.4	L↑	5.8	L↑	12.7	×	
E_3	×		L↓	6.1	×		×		L↓	23.7
D	×		Q∪	15.1	L↓	6.4	×		Q∪	13.2
P_{120}	×		Q∩	9.6	Q∩	11.0	×		L↑	4.2
P_5	×		×		Q∩	18.6	×		Q∩	8.7
altitude	L↓	20.3	×		Q∪	17.6	×		×	
H_{SSW}	×		×		L↑	4.8	×		×	
pH_s	Q∩	19.3	×		×		×		×	
C_{org}	×		Q∩	12.6	×		×		L↓	7.7
S_{org}	×		L↓	5.1	×		×		×	
R_s	L↑	19.0	×		L↑	23.6	×		×	
RWC	×		×		L↓	9.7	×		×	
BR_s	L↑	5.8	×		×		×		L↓	9.2

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]. $G_w\_M/Ns/Wd/Z_{end}/Z_{ex}$ - weighted grasslandness of myrmecochorous/non-specific/anemochorous/endozoochorous/exozoochorous species; A_a/A_{max} - average and maximal age of the tree layer, E_3 - abundance of the tree layer, D - proportion of deciduous trees in the tree layer, P_{120}/P_5 - relative irradiance at the 120/5 cm above ground, H_{SSW} – heat to the SSW, C_{org} - organic matter content, S_{org} - depth of the organic horizon, R_S – rock fragment content, RWC - retention water capacity, BR_s - microbial respiration.

Tabulka 16. Vliv studovaných faktorů na charakter porostu z hlediska pokryvnosti skupin lučních druhů dle různých způsobů rozšiřování. L – lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; $G_w\_M/Ns/Wd/Z_{end}/Z_{ex}$ – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů; A_a/A_{max} – průměrný/maximální věk stromového patra, E_3 - pokryvnost stromového patra, D - zastoupení listnatých stromů ve stromovém patře [%], P_{120}/P_5 – relativní ozářenost ve 120 a 5 cm, altitude - nadmořská výška, C_{org} – obsah organické hmoty v půdě, S_{org} - hloubka organického půdního horizontu, R_s - skeletovitost, RWC – retenční vodní kapacita, BR_s - bazální respirace.

Table 16. Selected factors influencing indeces corresponding with woodland species abundance according to the type of distribution (*GLM*).

	W_w_A		W_w_M		W_w_Ns		W_w_Wd		W_w_Z_{end}		W_w_Z_{ex}	
	M	var.	M	var.	M	var.	M	var.	M	var.	M	var.
A_a	Q∩	16.7	L↑	10.8	×		×		L↑	29.6	Q∪	12.2
A_{max}	L↑	14.3	L↑	21.4	L↓	5.1	×		L↑	26.8	×	
E_3	L↑	10.9	×		×		L↑	7.9	×		Q∩	9.0
D	Q∩	24.5	×		×		×		×		×	
P_{120}	Q∪	25.1	×		×		Q∩	8.0	×		Q∩	14.0
P_5	×		×		×		Q∩	7.7	Q∩	13.6	Q∩	15.1
altit.	Q∪	18.3	×		Q∩	16.9	L↓	4.9	L↓	6.7	Q∪	18.2
H_{SSW}	×		×		L↑	6.6	×		×		×	
pH_s	×		Q∩	10.7	×		×		×		×	
C_{org}	Q∩	17.0	×		×		×		×		×	
S_{org}	×		L↓	8.7	Q∪	19.3	×		×		L↓	6.9
R_s	Q∪	32.3	×		L↓	12.4	L↑	20.5	L↑	18.4	Q∩	28.4
RWC	×		×		×		Q∪	12.1	Q∩	11.3	L↓	7.3
BR_s	Q∩	17.7	×		×		×		Q∪	14.1	×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]. W_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – weighted woodlandness of autochorous/myrmecochorous/ non-specific/anemochorous/endozoochorous/ exozoochorous species; A_a/A_{max} - average and maximal age of the tree layer, E_3 - abundance of the tree layer, D - proportion of deciduous trees in the tree layer, P_{120}/P_5 - relative irradiance at the 120 or 5 cm above ground, altit. – altitude, H_{SSW} – heat to the SSW, C_{org} - organic matter content, S_{org} - depth of the organic horizon, R_S – rock fragment content, RWC - retention water capacity, BR_s - microbial respiration.

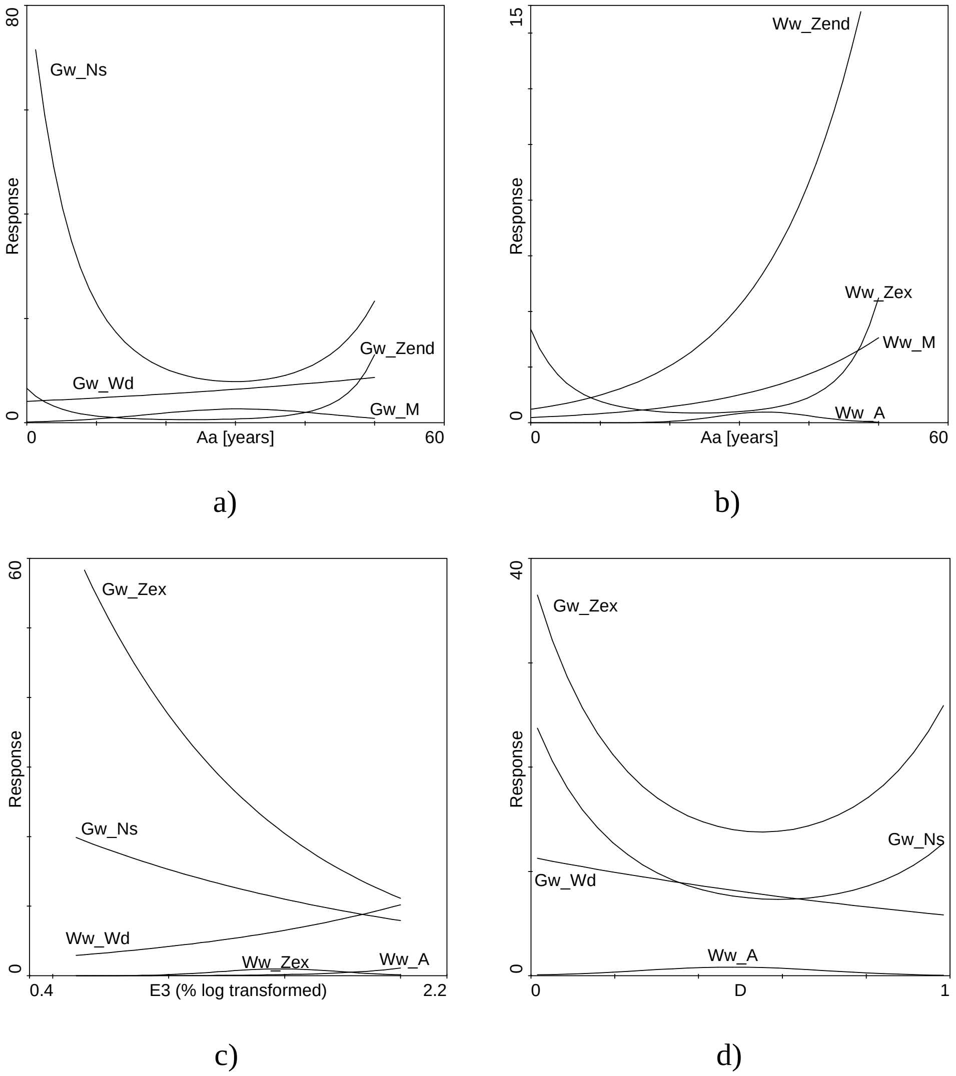
Tabulka 16. Vliv studovaných faktorů na charakter porostu z hlediska pokryvnosti skupin lesních druhů dle různých způsobů rozšiřování. L – lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; W_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – index korespondující s pokryvností lesních autochorních/myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů; A_a/A_{max} – průměrný/maximální věk stromového patra, E_3 – pokryvnost stromového patra, D – zastoupení listnatých stromů ve stromovém patře, P_{120}/P_5 – relativní ozářenost ve 120 a 5 cm, altit. - nadmořská výška, H_{SSW} – sklon plochy k JJZ, C_{org} – obsah organické hmoty v půdě, S_{org} - hloubka organického půdního horizontu, R_s - skeletovitost, RWC – retenční vodní kapacita, BR_s – bazální respirace.

Grassland species non-specific to the type of distribution tended to be more abundant both in young and in old SDFs (ca <15 and >40 year old, Fig. 15a, Table 15), but less abundant in mixed SDFs (Fig. 15d). They preferred soil with about 9% of organic matter content (Table 15). Woodland species non-specific to the type of distribution tended to be more abundant at medium altitudes (Fig. 16b), in both low and deep soils (Fig. 16c), and at low rock fragment content (Fig. 16d).

Grassland anemochorous species were more abundant at medium irradiated sites at 120 cm above ground (optimum 30%, Fig. 16a), and at higher irradiance at 5 cm above ground (optimum 16%, Table 15), at both low and high altitudes (Fig. 16b), and in soil with higher rock fragment content (Fig. 16d). Woodland anemochorous species were more abundant in soil with higher rock fragment content (Fig. 16d), and tended to be more abundant in more dessicated soil (Table 16).

Grassland endozoochorous species tended to be more abundant in older SDFs (Fig. 15a, Table 15). Woodland endozoochorous species were also more abundant in older SDFs (Fig. 15b, Table 16), at higher relative irradiance at 5 cm above ground (optimum 17%, Table 16), in soil with high rock fragment content (Fig. 16d) and is soil with medium *RWC* (optimum 13%, Table 16), and tended to be more abundant at higher microbial respiration (Table 16).

Grassland exozoochorous species were more abundant in the open SDFs (Fig. 15c) and non-mixed SDFs (Fig. 15d). Woodland exozoochorous species were more abundant in older SDFs (Fig. 15b), at medium irradiated sites at 120 cm above ground (optimum 25%, Fig. 16a), and at higher irradiance at 5 cm above ground (optimum 16%, Table 16), and tended to be more abundant at lower altitudes (Fig. 16b), and in soil with relatively high rock fragment content (optimum 58%, Fig. 16d).

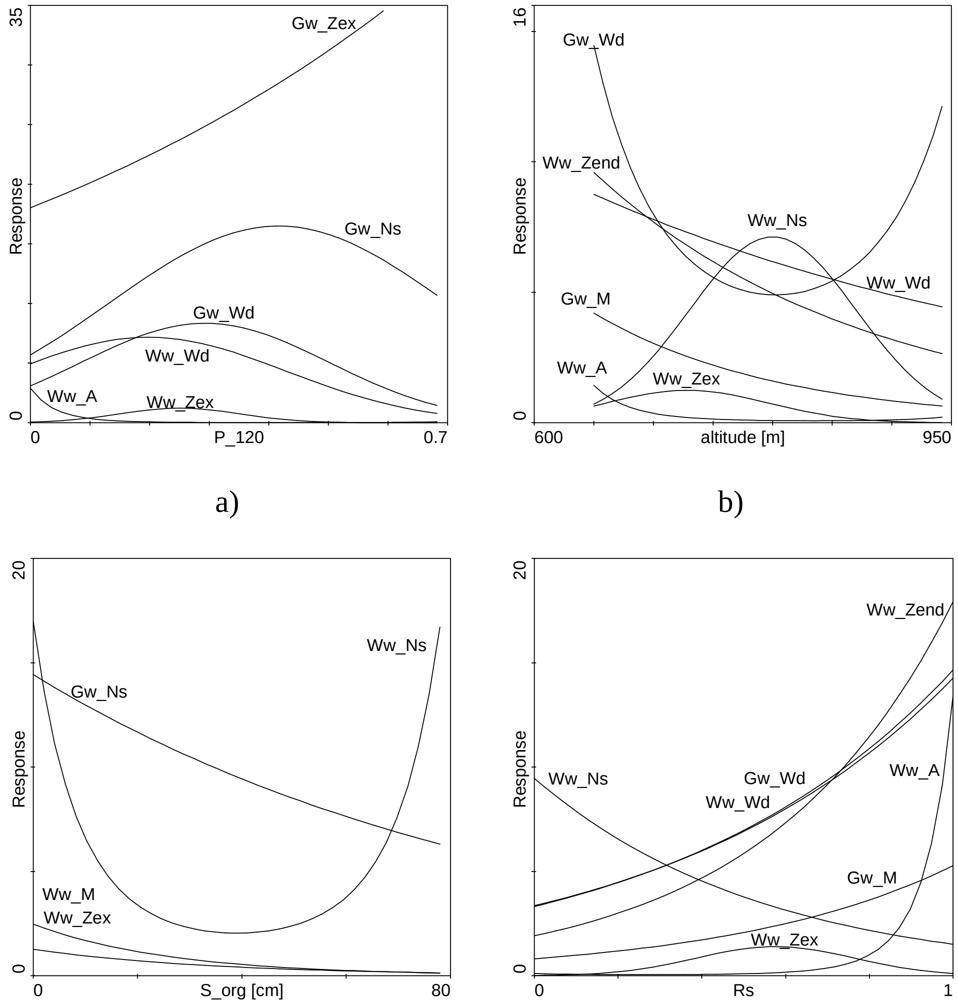


a) b)

c) d)

Figure 15. Selected factors influencing indeces corresponding with grassland and woodland species abundance according to the type of distribution (*GLM*): a) average age of the tree layer (grassland character), b) average age of the tree layer (woodland character), c) abundance of the tree layer, d) percentage of deciduous trees in the tree layer. Gw_M/Ns/Wd/Zend/Zex - weighted grasslandness of myrmecochorous/ non-specific/anemochorous/endozoochorous/exozoochorous species Ww_A/M/Wd/Zend/Zex – weighted woodlandness of autochorous/myrmecochorous/ anemochorous/endozoochorous/ exozoochorous species.

Obrázek 15. Vliv vybraných faktorů na pokryvnosti skupin druhů podle způsobu rozšiřování (*GLM*): a) věk stromového patra (luční charakter), b) věk stromového patra (lesní chrakter), c) pokryvnost stromového patra, d) procento listnatých stromů ve stromovém patře. Gw_M/Ns/Wd/Zend/Zex – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních/ exozoochorních druhů, Ww_A/M/Wd/Zend/Zex – index korespondující s pokryvností lesních autochorních/ myrmekochorních/anemochorních/endozoochorních/exozoochorních druhů.



a) b)

c) d)

Figure 16. Selected factors influencing indeces corresponding with grassland and woodland species abundance according to the type of distribution (*GLM*): a) relative irradiance at 120 cm above ground, b) altitude, c) depth of the organic soil horizon, d) rock fragment content [%]. G_w_M/Ns/Wd/Zex - weighted grasslandness of myrmecochorous/non-specific/anemochorous/exozoochorous species, W_w_A/M/Ns/Wd/Zend/Zex – weighted woodlandness of autochorous/ myrmecochorous/non-specific/anemochorous/endozoochorous/ exozoochorous species.

Obrázek 16. Vliv vybraných faktorů na pokryvnosti skupin druhů podle způsobu rozšiřování (*GLM*): a) relativní ozářenost ve 120 cm, b) nadmořská výška, c) hloubka organického půdního horizontu, d) skeletovitost [%]. Gw_ M/Ns/Wd/Zex – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/exozoochorních druhů, Ww_A/M/Ns/Wd/Zend/Zex – index korespondující s pokryvností lesních autochorních/myrmekochorních/nespecifických/anemochorních/endozoochorních/ exozoochorních druhů.

Discussion

The main subject of the study was to find out whether there are general trends in changes in the herb layer, i.e., from grassland toward woodland character. Groups of species used for the description of the character of the herb layer were determined according to the biotope and type of distribution. Groups according to the biotope respond directly to the objective. However, there are several groups which are transient between the grassland-forest biotopes, i.e., *GW*, *Sc* and *C*. This is why the grassland and woodland character was also described by indeces (weighted) grasslandness, and (weighted) woodlandness. Groups of species according to the type of distribution were used for counting the indeces corresponding with the abundance of woodland and grassland species according to the type of distribution, because seed limitation of forest plant species was found in many studies (for review see Honnay et al. 2002a), and different dispersal ability of forest species was also reported (e.g., Matlack 1994). Typical forest species were also found as species growing at mesic stands (pH, humidity, N content), and they are associated to the order *Fagetalia* (Hermy et al. 1999; Wulf 1997). The focus of this study on the mesic stands results from this evidence.

Low explained variability, however significant, was found for much abundance of groups of species or index values, as well as a low influence of certain factors (e.g., 11.5% of species-environmental relationship for groups of species according to the biotope). Low explained variability is common in the ecological system (e.g., Dzwonko and Loster 1997; Vojta 2007). It may be caused by the high variability both in conditions and species composition, which was reported as typical for early stages of succession (Odum 1969; Prach 1987).

Many factors were found to be significantly related to the abundance of certain groups of species in this study(e.g., *Ws* species: A_a, A_{max}, altitude, R_s, C_{org}, R_s, BR_s). The influence of many factors each contributing by small percentage to the explained variability was found in different studies (see e.g., Prach 1994), and different species have different responses to the abiotic conditions even from the same ecological group (see e.g., Wehling and Diekmann 2009b). In general, factors describing the character of the tree layer (A_a, A_{max}, E_3, D) and soil conditions (pH_s, C_{org}, S_{org}, RWC, R_s, BR_s) were more important, while orientation (H_{SSW}) was only slightly important.

The general character of the herb layer of the SDFs in the first tree generation could be described as follows: grassland character prevails, while woodland character plays a minor role. In general, the abundance of groups of species associated with the forest species was low, e.g., *Ws* on average was one third of the *Gs* (a similar difference holds for W_w and G_w). Grassland species dominate the herb layer, and species typical for forest edges are also abundant. Grassland exozoochorous and grassland non-specific species are most abundant, while no grassland autochorous species was found, and woodland autochorous and exozoochorous species were not very abundant. This is in assumption with other studies focusing on the herb layer of recent forests, which found long term colonisation of forest species. Jacquemyn et al. (2001) estimates that at least 200 years is needed for development of the saturated herb layer of recent forests planted on former agricultural land, and Verheyen et al. (2003) found that the recent forest herb layer was not the same as in the ancient forest even after 200 years. From the *GLM* analyses of the SDFs, it seems that the time needed for the herb layer development that would be saturated by forest species and that would not be occupied by grassland species will be long, and maybe a period of 200 years will be not long enough for this process (see Figs. 10a, 12a, b, 15a, b). The faster colonisation of forest species could be expected at lower altitudes, in soil with higher rock fragment content, shallow soil and in mixed SDFs.

The abundance of forest species (*Ws*, *W*, W_w, and $W_w\_A/M/Ns/Ws/Z_{end}/Z_{ex}$) in general increased with the duration of the tree layer. This is in assumption with the general scheme of succession and in assumption with findings of different studies (e.g., Bossuyt and Hermy 2000; Verheyen et al. 2003). Two reasons may explain this finding: i) the forest species are seed limited, and therefore the probability of establishment increases in time (Jacquemyn et al. 2001); ii) the microsite availability is higher in older SDFs.

Seed limitation and very slow dispersal ability was found for forest species both indirectly (e.g., Brunet and von Oheimb 1998a; Matlack 1994), and directly using seed addition into recent forests (e.g., Ehrlén and Eriksson 2000; Eriksson 1995; Gustafsson et al. 2002; Verheyen and Hermy 2004). In general, endozoochorous, exozoochorous, and anemochorous species were reported as better colonisers in comparison to non-specific, and myrmecochorous species (Matlack 1994). Seed limitation was found to be more important than the microsite limitation in recent forests in many studies (e.g., Verheyen and Hermy 2004). In this study, indirect evidence for seed limitation could be the increase in woodland species with the increasing age of the tree layer, and also the observed slower increase in the abundance of woodland autochorous and myrmecochorous species, which are assumed to be poor colonisers (e.g., Matlack 1994). However, groups of species associated with forests tended to be more abundant in soil with higher rock fragment content, lower microbial respiration, and lower soil reaction (optimum 4.2), while groups of species associated with the grassland tended to be less abundant in more organic soil, in soil with higher microbial respiration, and at higher soil reaction (optimum 4.6). The higher organic matter content, and higher microbial respiration were found to be typical for the forest soil compared to the grassland soil (see Kopáčková 2002). The values found in this study in the SDFs were intermediate. The soil reaction was also found to be intermediate (mean value 4.3) between the values typical for grassland (mean value 5.3, Schusserová 2003), and beech forest soil (mean value 4.0, Kopáček et al. 2002). The decrease in soil reaction during the succession was found in different studies (e.g., Bossuyt and Hermy 2000; Persson et al. 1987; Zobel 1989), but opposite findings were also published (e.g., Gömöryová et al. 2007). High rock fragment content may lower the competitive ability of grassland species, and therefore woodland species may profit at such stands. The higher competitive ability of herb species at more productive sites in successional stages was reported e.g., by Prach (1994). Species typical for ancient forests were also found to be more influenced by soil conditions than the early and mid-term colonisers (Verheyen et al. 2003), which is in assumption with the observed pattern. These findings could serve as indirect evidence of microsite limitation of the forest species in the SDFs.

Surprisingly, a small number of groups of species and indeces, were influenced by the water regime, although the soil water regime was reported as important in many studies (e.g., Kolb and Diekmann 2004). The light condition determined directly as *PhAR* irradiance also was of low importance, but the Ellenberg *L* value was found to be important in the ordination analysis of the groups of species according to the biotope and of indeces describing the abundance of grassland/woodland species according to the type of distribution. The mean irradiance both at 120 cm and 5 cm above ground was intermediate between the forest and grassland (mean value 20% for 120 cm above ground, see Table 12). For comparison, Dzwonko (2001) did not find any differences in the light conditions in recent (both planted and SDFs) and ancient forests (<5%). The high importance of the Ellenberg *L* value found in the ordination analyses may be due to the indirect effect of long-term grassland species persistence in the herb layer, and therefore the high Ellenberg *L* values for the SDFs.

Chapter 6

What spontaneously developed forest is woodier? Influence of the context-dependent factors on the character of the herb layer

Který porost náletových dřevin je lesnatější? Vliv na kontextu závislých faktorů na charakter bylinného patra

Abstract

The influence of the context-dependent factors on the abundance of species grouped according to the biotope and type of distribution in the spontaneously developed forests (SDFs) was studied in a mountainous area (665-940 m) in the Czech Republic.

Forty seven plots (100 m^2) at mesic stands in the SDFs were studied. Abundance of groups of species according to the biotope was found, grassland and woodland character of the herb layer was described using indeces corresponding with the number and abundance of grassland/woodland species, and the abundance of grassland and woodland species according to the type of distribution. The influence of the following context-dependent factors was tested: (1) SDF characteristics: area of the SDF, shape, position of the plot within the SDF; (2) surrounding vegetation (100, 200 and 300 m); (3) vegetation cover in history (1952, 1966, 1983). The ordination methods and General Linear Models were used.

Different groups of species and indeces describing the character of the herb layer were influenced by different context-dependent factors. The vegetation cover in history was the most important context-dependent factor, which influenced most of the groups and indeces. The abundance levels of groups and values of indeces related to the forest species tended to be higher in the SDFs, where the tree layer was long-term developed.

The surrounding vegetation was important for many characteristics related to the grassland and woodland character, especially the proportion of grassland and forest in the surroundings.

Of the SDF characteristics, only the area of the SDF was more important, especially in relation to the characteristics related to the woodland character.

Shrnutí

V porostech náletových dřevin (SDFs) v horských oblastech (665-940 m) České republiky byl studován vliv na kontextu závislých faktorů na pokryvnost skupin druhů vylišených dle biotopu a způsobu rozšiřování.

Ve 47 plochách (100 m^2) byla zjištěna pokryvnost skupin druhů vylišených na základě biotopu a z druhového složení bylinného patra byly spočítány indexy popisující luční a lesní charakter bylinného patra (korespondující s počtem a pokryvností lučních a lesních druhů) a pokryvnost lučních a lesních skupin druhů vylišených dle způsobu rozšiřování. Ordinačními metodami a zobecněnými lineárními modely byl testován vliv na kontextu závislých proměnných: (1) charakter SDF: velikost, tvar a pozice trvalé plochy uvnitř SDF; (2) vegetační kryt v okolí (100, 200 a 300 m); (3) vegetační kryt v minulosti (1952, 1966, 1983).

Různé na kontextu závislé faktory ovlivňovaly různé skupiny druhů nebo indexy popisující charakter bylinného patra. Nejvýznamnějším faktorem byl vegetační kryt v minulosti, který ovlivňoval nejvíce skupin a indexů. Pokryvnost skupin druhů a indexy vztažené k lesnímu charakteru bylinného patra byly vyšší při delším trvání stromového patra na ploše.

Vegetační kryt okolí ovlivňoval celou řadu charakteristik vztažených k lučnímu nebo lesnímu charakteru bylinného patra. Významný byl především podíl luk a lesa v okolí.

Z charakteristik porostu náletových dřevin byla významnější pouze velikost SDF, která ovlivňovala především lesní charakter bylinného patra.

Introduction

Changes in the vegetation cover have happened in Europe in most recent decades. The amount of agricultural land, mostly grassland in less favourable areas, has decreased in particular (e.g., Hamre et al. 2007; Helm et al. 2006), and the number of recent forests has increased. Recent forests can be planted on former agricultural land (e.g., Wulf 2004) or can develop spontaneously due to the successional changes (e.g., Prach and Pyšek 1994b). In this study, they are referred to as spontaneously developed forests (SDFs), while the term recent forests is used for both planted forests and SDFs on former agricultural land (usually <200 years).

The tree layer of SDFs develops usually within 30-40 years and definitely closes after 60-80 years (Flinn and Vellend 2005), but the rate of succession can be faster, e.g., due to the facilitation of trees growing alone (Dzwonko and Loster 1992), hedgerows, disturbances etc. (e.g., Guth 1998), or slower in less favourable conditions, such as in higher altitudes (Blažková 1991; Spatz 1980), or due to competition, e.g., by grass (e.g., Dickie et al. 2007) or litter (e.g., Facelli and Pickett 1991a). The birch (*Betula pendula* ROTH) was found to be the most common tree species dominating SDFs in Central Europe (Prach and Pyšek 1994b).

The herb-layer species composition of recent forests was found to be influenced by many factors, which can be grouped as follows: i) the site-dependent factors, which influence mostly the species establishment process, such as climate, water regime and soil conditions (Prach and Řehounková 2006; Prach et al. 2007); ii) the context-dependent factors, which influence mostly the colonisation potential, such as seed and dispersion limitation (e.g., Butaye et al. 2002; Ehrlén et al. 2006), the area and shape (e.g., Bossuyt et al. 1999; Dzwonko and Loster 1992) and history (e.g., Vellend et al. 2007).

Herb layer colonisation by woodland species was found to be very slow in many studies, and forest species are supposed to be poor colonisers, of which the rate of colonisation usually does not exceed 2 m.year^{-1} (e.g., Bossuyt and Hermy 2000; Peterken and Game 1984; Whitney and Foster 1988; Wulf 2004). Myrmecochorous and species with no adaptation for long-term dispersal were found especially to be seed limited in recent forests (e.g., Brunet and von Oheimb 1998b; Matlack 1994). Seed limitation of forest species was also determined directly by seed addition experiments (see e.g., Ehrlén et al. 2006; Eriksson 1995; Gustafsson et al. 2002). The period needed for development of the herb layer is estimated to be long, e.g., Jacquemyn et al. (2001) estimates that herb layer colonisation of planted forests can take 200 years.

Due to the seed limitation, colonisation of forest herbs depends on the seed availability, and therefore on the surroundings (e.g., Brunet and von Oheimb 1998b; Graae et al. 2004; Matlack 1994) and on connectivity to the ancient forests (e.g., Butaye et al. 2001; Jacquemyn et al. 2003). The hedgerows may be corridors for the forest species, and therefore may enhance the colonisation of recent forests (e.g., Honnay et al. 2002a; Verheyen et al. 2003), but different results were found for different species and in different studies (see Wehling and Diekmann 2009a). The time-span of the colonisation is also important, because with the increasing duration of recent forests, the probability of forest herb species establishment increases (e.g., Jacquemyn et al. 2001).

The area of recent forests has been found to be important in many studies (e.g., Bossuyt et al. 1999; Dzwonko and Loster 1992), but small importance of the area has also been referred (e.g., Matlack 1994). The former agricultural practice may influence the species composition for a relatively long period (see e.g., Dupouey et al. 2002; Hersperger and Forman 2003).

Most of the studies focusing on the influence of context-dependent factors on the herb layer of recent forests were done in planted forests, or the planted forests were not distinguished from the SDFs. This study is focused only on the SDFs. The influence of context-dependent factors on the character of the herb layer of SDFs on mesic stands was studied. Of context-dependent factors, the following were considered: i) the character of the SDF (area, shape, position of the site within the SDF); ii) the surrounding vegetation; iii) historical land use (since 1952). The character of the herb layer was described by the abundance of different functional groups of species according to the biotope and type of distribution. The grassland and woodland character of the herb layer was determined using indeces counted from the abundances of species grouped according to the biotope, and similar indeces were also derived from abundance levels of species typical for grassland/woodland grouped according to the type of distribution.

The following questions are considered:

1. What factors influence the character of the vegetation in the SDFs? Are area, shape, position within the SDF, surrounding vegetation or historical vegetation cover important for different groups of species according to the biotope or type of distribution?
2. Does the area, shape, position within the SDF, surrounding vegetation or historical vegetation cover influence the grassland or woodland character of the herb layer of SDFs?

Methods

Study area

The study area was the southern part of the Czech Republic (40°35-38′ N, 14°11-17′ E).

Forty-seven plots (10 × 10 m) were fixed in the growths of SDFs. The growths were different in altitude and exposition (see Table 12), but all the plots were on mesic stands. The supposed terminal stage of succession is beech forest of the association *Dentario enneaphylli-Fagetum*, in the lowest altitudes transient to the association *Luzulo albidae-Quercetum petrae* (Neuhäuslová 1998). Present growths were mostly dominated by *Betula pendula*, common trees are also *Picea abies* (L.) Karsten, *Populus tremula* L.; in some cases *Pinus sylvestris* L. or *Fraxinus excelsior* L. were more abundant. The plots were fixed in such growths, where important man influence was not recognisable.

Data collection

Phytocenological releve was taken from all the permanent plots. The species abundance was estimated in percentages of abundance of the species for each layer.

Species listed in the herb layer were grouped as follows:

1. According to the biotope, where they are usually present: antropochorous or ruderal species (*AR*), species typically growing at clearings (*C*), grassland species (*Gs*), species growing both in wood and grassland (*GW*), shrub species (*Sc*) and woodland species (*Ws*). The sum of abundances of species was used for each group (Table 11).
2. According to the type of distribution: anemochorous (*Wd*), autochorous (*A*), myrmecochorous (*M*), non-specific (*Ns*), endozoochorous (Z_{end}), and exozoochorous species (Z_{ex}) (Table 11).

From the phytocenological releves, the next indeces were counted: woodlandness (*W*), grasslandness (*G*), weighted woodlandness (W_w) and weighted grasslandness (G_w):

$$W = \Sigma\,(Ws + 0.5 \times GW + 0.5 \times Sc + 0.5 \times C),$$

$$G = \Sigma\,(Gs + 0.5 \times GW + 0.5 \times AR + 0.5 \times C + 0.2 \times Sc),$$

$$W_w = \Sigma\,(\Sigma\, Ws_i \times \mathrm{a_i} + \Sigma\, 0.5 \times GW_\mathrm{j} \times \mathrm{a_j} + \Sigma\, 0.5 \times Sc_\mathrm{k} \times \mathrm{a_k} + \Sigma\, 0.5 \times C_\mathrm{l} \times \mathrm{a_l}),$$

where a_i, a_j, a_k, a_l indicates abundance of species i, j, k, l.

$$G_w = \Sigma(\Sigma\, Gs_\mathrm{i} \times \mathrm{a_i} + \Sigma\, 0.5 \times GW_\mathrm{j} \times \mathrm{a_j} + \Sigma\, 0.5 \times AR_\mathrm{k} \times \mathrm{a_k} + \Sigma\, 0.5 \times C_\mathrm{l} \times \mathrm{a_l} + \Sigma\, 0.5 \times Sc_\mathrm{m} \times \mathrm{a_m}),$$

where a_i, a_j, a_k, a_l, a_m indicates abundance of species i, j, k, l, m.

Woodlandness and grasslandness correspond with the number of species typical for woodland or grassland, while weighted woodlandness and grasslandness correspond with the abundance of species typical for woodland or grassland (for basic statistics see Table 11).

Similarly indeces weighted grasslandness of autochorous (G_w_A), myrmecochorous (G_w_M), species non-specific to the type of distribution (G_w_Ns), anemochorous (G_w_Wd), endozoochorous ($G_w\_Z_{end}$), and exozoochorous species ($G_w\_Z_{ex}$), and weighted woodlandness of autochorous (W_w_A), myrmecochorous (W_w_M), species non-specific to the type of distribution (W_w_Ns), anemochorous (W_w_Wd), endozoochorous ($W_w\_Z_{end}$), and exozoochorous species ($W_w\_Z_{ex}$) were counted to describe the abundance of the species typical for grassland/woodland according to the type of distribution. The values were obtained as the sum of abundances of species from a certain group of species according to the type of distribution. The abundance of species according to the biotope was weighted by the same values that were used in the weighted grasslandness/woodlandness indeces (Table 11).

Context-dependent factors

Vegetation map 1 : 10000 (Dostálová unpbl.) redrawn on a slide and digitalized (300dpi colour picture) was used to determine the following context-dependent factors: i) the total area of the SDF (A_{SDF}) [ha]; ii) the *shape* of the SDF, determined as the multiple of the perimeter of a circle with the same area; iii) the position of the plot within the SDF (*centre*), determined as the nearest distance from the centre of the plot to the border of the SDF [m]; iv) the distance to the nearest field (D_Fi) [m]; v) the distance to the nearest grassland (D_Grl) [m]; vi) the distance to the nearest forest (D_Fst) [m]; vii) the proportion of vegetation cover of the fields in 100, 200 and 300 m surrounding (i.e., the round area of a certain semi-diameter with the central point in the centre of the plot) ($Fi_{100/200/300}$); viii) the proportion of grassland in 100, 200 and 300 m surrounding ($Grl_{100/200/300}$); ix) the proportion of forests in 100, 200 and 300 m surrounding ($Fst_{100/200/300}$); x) the proportion of SDF in 100, 200 and 300 m surrounding ($SDF_{100/200/300}$); xi) the proportion of “other” land cover (e.g., building, water) in 100, 200 and 300 m surrounding ($Ot_{100/200/300}$). Image analysis in the Scion Image for Windows 4.0.3 program was used.

The aerial photos from the Military Geographical and Hydrometeorological Office (Dobruška, Czech Republic) were used to determine the past vegetation cover of the plot. Three sets of photos were available from the vegetation period for the whole study area: 1952 (7th of July, camera RC5-97, focal length 210.0 mm, flying height 5 250 m, 1:25 000); 1966 (1st of May, MRB, 210.11 mm; 3 200 m, 1:12 600), 1967 (25th of June, RC 5a, 209.7 mm, 3 300 m, 1:13 150) and 1983 (8th of June, MRB-9, 88.6 mm, 2 900-3 200 m, 1:28 040). The following vegetation types were distinguished: field (arable land), grassland (meadow, pasture, abandoned grassland), scattered SDF, closed SDF (these types correspond with the supposed successional sere) for the three dates: *1952, 1966, 1983*.

For the basic statistics of context-dependent factors see Table 17.

Table 17. Basic statistics of the context-dependent factors.

	Mean± SD		Mean± SD		Mean± SD
Fi_{100}	0.05±0.120	SDF_{100}	0.45±0.239	A_{SDF}	74 223±81 223
Fi_{200}	0.06±0.119	SDF_{200}	0.37±0.195	shape	3.09±2.179
Fi_{300}	0.06±0.107	SDF_{300}	0.33±0.171	centre	22.04±13.395
Grl_{100}	0.31±0.234	Ot_{100}	0.02±0.032	1952	2.02±0.707
Grl_{200}	0.31±0.204	Ot_{200}	0.02±0.036	1966	2.74±1.010
Grl_{300}	0.31±0.183	Ot_{300}	0.02±0.046	1983	3.43±0.853
Fst_{100}	0.18±0.209	D_Fi	742.9±912.05		
Fst_{200}	0.24±0.199	D_Grl	44.9±60.03		
Fst_{300}	0.27±0.186	D_Fst	110.5±152.53		

$Fi_{100/200/300}$ – proportion of fields in the 100/200/300 m surrounding, $Grl_{100/200/300}$ – proportion of grassland in 100/200/300 m surrounding, $Fst_{100/200/300}$ – proportion of forests in 100/200/300 m surrounding, $SDF_{100/200/300}$ – proportion of spontaneously developed forests in 100/200/300 m surrounding, $Ot_{100/200/300}$ – proportion of "other" land cover in 100/200/300 m surrounding, D_Fi/D_Grl/D_Fst – distance to the nearest field/grassland/forest [m], A_{SDF} – area of SDF [m^2], shape – relative length of the SDF border, centre – nearest distance from the centre of the plot to the border of the SDF [m], 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy).

Tabulka 17. Základní statistka na kontextu závislých faktorů. $Fi_{100/200/300}$ – podíl pole v okolí 100/200/300 m, $Grl_{100/200/300}$ – podíl luk v okolí 100/200/300 m, $Fst_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, $SDF_{100/200/300}$ – podíl porostů náletových dřevin v okolí 100/200/300 m, $Ot_{100/200/300}$ – podíl krajinného pokryvu "ostatní" v okolí 100/200/300 m, D_Fi/D_Grl/D_Fst – vzdálenost k nejbližšímu poli/louce/lesu [m], A_{SDF} – rozloha SDF [m^2], shape – relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), centre – nejkratší vzdálenost k okraji porostu náletových dřevin [m], 1952/1966/1983 – vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).

Statistical analysis

The following factors were used in the statistical analysis: (1) SDF characteristics: A_{SDF}, shape, centre; (2) surrounding vegetation: $Fi_{100/200/300}$, $Grl_{100/200/300}$, $Fst_{100/200/300}$, $SDF_{100/200/300}$, $Ot_{100/200/300}$, *D_Fi, D_Grl, D_Fst*; (3) vegetation cover in *1952, 1966, 1983*.

Abundances of groups of species according to the biotope, and indeces describing abundances of groups of species according to the type of distribution were analysed using ordination methods in the CANOCO for Windows program v. 4.5. “Species” data were logarithmically transformed ($y=\log_{10}(y+1)$). Linear analyses were performed (the length of the gradient was less than 2.0 in all analysis): indirect principal components analysis (*PCA*), direct redundancy analysis (*RDA*) respectively. Manual selection (Forward selection, Monte Carlo permutation test under full model with 499 permutations) of the factors was used at the $\propto = 0.05$ level. The visualisation of the ordination analysis was performed in the CanoDraw v. 4.0. (Lepš and Šmilauer 2003).

General Linear Models (*GLM*) in the Canodraw v. 4.0 program were used to test the influence of factors on the abundance of each group of species according to the biotope (*AR, C, Gs, GW, Sc, Ws*), on indeces describing the grassland/woodland character of the herb layer (G, G_w, W, W_w), and on indeces describing the abundance of groups of species according to the type of distribution (G_w_M, G_w_Ns, G_w_Wd, $G_w\_Z_{end}$, $G_w\_Z_{ex}$, W_w_A, W_w_M, W_w_Ns, W_w_Wd, $W_w\_Z_{end}$, $W_w\_Z_{ex}$). Poisson distribution of the data was used, because the link function of this distribution is “Log” function, which is recommended for the counts and frequency data (Lepš and Šmilauer 2003; p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using Akaike Information Criterion (Lepš and Šmilauer 2003).

Results

Groups of species according to the biotope

The explained variability was high in the indirect *PCA* (first four axis explained 91% of the total variance), while the factors in the *RDA* explained only 17% of the total variability in the data. Vegetation cover in *1952* (F = 4.46, p<0.01), and distance to the nearest grassland (F = 4.31, p<0.01) significantly influenced the abundance of groups.

There was found to be a higher abundance of *GW*, *Sc* and *Ws* (species able to grow in forest or forest species) in the SDFs where the tree layer was established in *1952*, while lower abundance of *AR*, *Gs* and *C* species (species typical for disturbed sites and grassland) was found at such sites. Species typical for disturbed sites (*AR*, *C*) were found to be more abundant in the SDFs remote from grassland (Fig. 17).

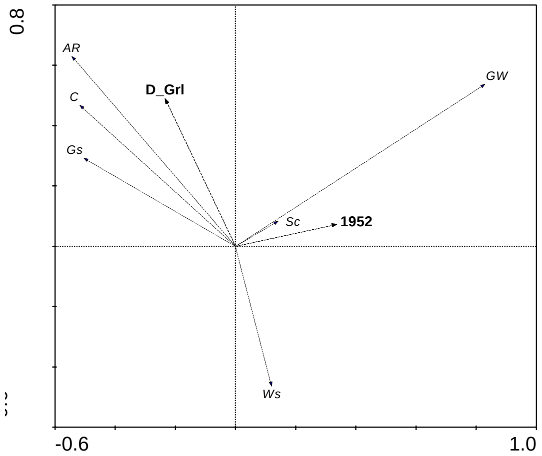


Figure 17. Ordination diagram for *RDA* of groups of species according to biotope. AR - antropochorous or ruderal species, C – species typically growing at clearings, Gs - grassland species, GW – species growing both in grassland and in wood, Sc – shrub species, Ws – woodland species; 1952 - vegetation cover in 1952 (successional sere: field-grassland-scattered trees-closed tree canopy), D_Grl – distance to the nearest

Obrázek 17. *RDA* ordinační diagram skupin druhů podle typu biotopu. AR – antropogenní a nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, GW – druhy společné lučním a lesním stanovištím, Sc – druhy křovin, Ws – lesní druhy; 1952 – vegetační kryt v roce 1952 (sukcesní série: pole-louka-roztroušený nálet-zapojený nálet), D_Grl – vzdálenost k nejbližší louce [m].

Antropochorous and ruderal species were found to be more abundant at sites, which were surrounded by both a low and high proportion of grassland (Grl_{100}, Grl_{200}, Grl_{300}, see Table 18, Fig. 18b), by a relatively high proportion of forest (Fst_{100}, Fst_{200}, Fst_{300}, see Table 18, Fig. 19a), at sites remote from the grassland (Fig. 19b), in the SDFs which were fields or grassland in 1966 (Fig. 19c), or which were overgrown by scattered trees in 1983 (optimum 2.83, Fig. 19d).

Species typically growing at clearings were more abundant in the SDFs surrounded by forests (Table 18, Fig. 19a) or “other” land cover in the 300 m surrounding (Table 18), at sites remote from grassland (Fig. 19b), in the SDFs both small (<5ha) and large (>20 ha, Table 18), and at plots situated deeper in the SDFs (Table 18).

Grassland species surprisingly tended to be less common in the SDFs, where the proportion of grassland in the 300 m surrounding was high (Fig. 18b), while they were more abundant in the SDFs more surrounded by forest in the 300 m (Fig. 19a).

Species growing both in grassland and wood were more abundant in the SDFs with a high proportion of fields in the 300 m surrounding (optimum 14%, Fig. 18a), and at medium distance from the grassland (Fig. 19b).

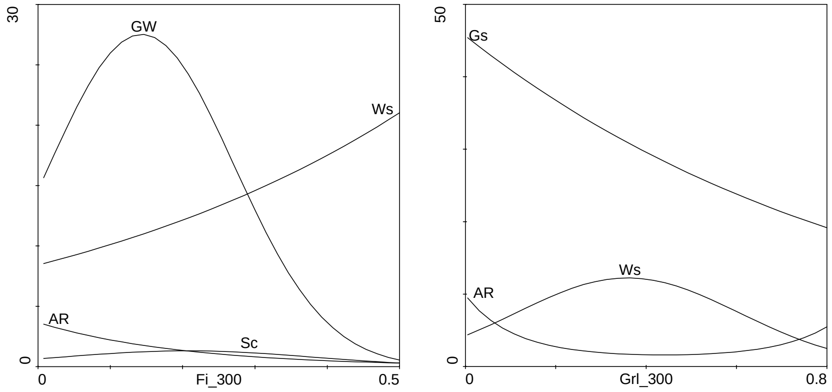
Shrub species were more abundant in the SDFs with a high proportion of fields in the 300 m surrounding (optimum 20%, Fig. 18a), with a high proportion “other” of land cover in the 100 m surrounding (Table 18), and in the SDFs that were fields or closed SDFs in 1983 (Fig. 19d).

Table 18. Factors influencing groups of species according to the biotope (*GLM*).

	AR		C		Gs		GW		Sc		Ws	
	M	var.	M	var.	M	var.	M	var.	M	var.	M	var.
Fi$_{100}$	×		Q∩	16	×		×		×		×	
Fi$_{200}$	L↓	7	×		×		×		Q∩	9	×	
Fi$_{300}$	L↓	9	×		×		Q∩	13	Q∩	10	L↑	7
Grl$_{100}$	Q∪	16	L↓	8	×		×		×		Q∩	9
Grl$_{200}$	Q∪	26	L↓	7	L↓	7	×		×		Q∩	18
Grl$_{300}$	Q∪	23	×		L↓	10	×		×		Q∩	11
Fst$_{100}$	L↑	13	Q∪	38	×		×		×		×	
Fst$_{200}$	Q∪	32	Q∪	32	×		×		×		Q∩	12
Fst$_{300}$	Q∪	47	Q∪	26	Q∪	12	×		×		Q∩	10
Ot$_{100}$	×		×		L↓	7	×		Q∪	13	×	
Ot$_{200}$	×		×		×		×		×		×	
Ot$_{300}$	×		Q∪	19	×		×		×		×	
D_Fi	×		×		L↓	4	×		×		Q∪	11
D_Grl	Q∩	40	L↑	27	L↑	5	Q∩	10	×		L↓	8
A$_{SDF}$	×		Q∪	10	×		×		×		×	
centre	×		L↑	12	×		×		×		×	
shape	×		L↓	6	×		×		×		×	
1952	×		×		×		L↑	8	L↑	9	L↑	24
1966	L↓	13	×		×		×		L↑	4	L↑	23
1983	Q∩	13	×		×		×		Q∪	14	L↑	13

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]. AR - antropochorous or ruderal species, C - species typically growing at clearings, Gs - grassland species, GW - species growing both in grassland and in wood, Sc - shrub species, Ws – woodland species; Fi$_{100/200/300}$ – proportion of fields in the 100/200/300 m surrounding, Grl$_{100/200/300}$ – proportion of grassland in the 100/200/300 m surrounding, Fst$_{100/200/300}$ – proportion of forests in the 100/200/300 m surrounding, Ot$_{100/200/300}$ - proportion of "other" land cover in the 100/200/300 m surrounding, D_Fi/D_Grl – distance to the nearest field/grassland, A$_{SDF}$ – area of the SDF, centre – nearest distance from the centre of the plot to the border of the SDF, shape – relative length of the SDF border, 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy).

Tabulka 18. Vliv studovaných faktorů na pokryvnost skupin druhů vylišených dle stanoviště. L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. – vysvětlená variabilita [%]; AR – antropogenní a/nebo ruderální druhy, C - druhy pasek, Gs - luční druhy, GW – druhy společné lučním a lesním stanovištím, Sc - druhy křovin, Ws - lesní druhy; $Fi_{100/200/300}$ – podíl pole v okolí 100/200/300 m, $Grl_{100/200/300}$ – podíl luk v okolí 100/200/300 m, $Fst_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, $SDF_{100/200/300}$ – podíl porostů náletových dřevin v okolí 100/200/300 m, $Ot_{100/200/300}$ – podíl krajinného pokryvu "ostatní" v okolí 100/200/300 m, D_Fi/D_Grl – vzdálenost k nejbližšímu poli/louce, A_{SDF} - rozloha SDF, centre – nejkratší vzdálenost k okraji porostu náletových dřevin, shape - relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), 1952/1966/1983 - vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).



a) b)

Figure 18. Factors influencing abundance of groups of species according to the biotope (*GLM*): a) proportion of fields in the 300 m surrounding; b) proportion of grassland in the 300 m surrounding. AR - antropochorous or ruderal species, Gs - grassland species, GW – species growing both in grassland and wood, Sc - shrub species, Ws – woodland species.

Obrázek 18. Vliv vybraných faktorů na pokryvnost skupin druhů vylišených dle biotopu (*GLM*): a) podíl pole v okolí 300 m, b) podíl luk v okolí 300 m. AR – antropogenní a/nebo ruderální druhy, Gs – luční druhy, GW - druhy společné lučním a lesním stanovištím, Sc - druhy křovin, Ws - lesní druhy.

Woodland species tended to be more abundant in the SDFs with a medium proportion of grassland in the 200 and 300 m surrounding (optimum 36%, Table 18, Fig. 18b), a lower proportion of forest in the 200 m (optimum 15%) and in the 300 m (optimum 19%) surrounding (Table 18, Fig. 19a), in the SDFs both near and remote from the fields (Table 18), and at sites which were long overgrown by trees, i.e., *1952* (Table 18), *1966* (Fig. 19c), *1983* (Fig. 19d).

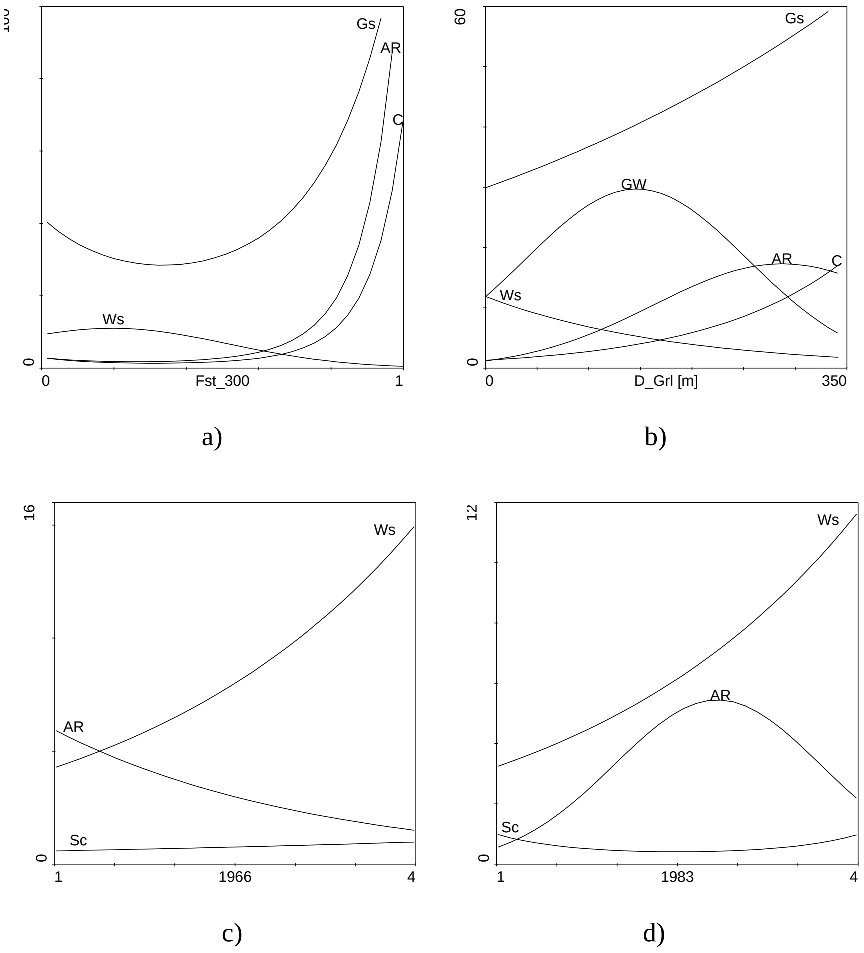


Figure 19. Factors influencing abundance of groups of species according to the biotope (*GLM*): a) proportion of forests in the 300 m surrounding; b) distance to the nearest grassland, c) vegetation cover in 1966, and d) in 1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy). AR - antropochorous or ruderal species, C – species typically growing at clearings, Gs - grassland species, GW - species growing both in grassland and wood, Sc - shrub species, Ws – woodland species.

Obrázek 19. Vliv vybraných faktorů na pokryvnost skupin druhů vylišených dle biotopu (*GLM*): a) podíl lesa v okolí 300 m, b) vzdálenost k nejbližší louce, c) vegetační kryt v roce 1966, d) v roce 1983 (sukcesní série: 1-pole, 2-louka, 3-roztroušený nálet, 4-zapojený nálet). AR - antropogenní a/nebo ruderální druhy, C – druhy pasek, Gs – luční druhy, GW - druhy společné lučním a lesním stanovištím, Sc - druhy křovin, Ws - lesní druhy.

Indeces describing grassland and woodland character of the herb layer

Grasslandness tended to be higher at a higher proportion of SDFs in the 100 m and 300 m surrounding (Fig. 21b, Table 19), and at sites which were fields or grassland in 1983 (Fig. 21d).

Weighted grasslandness was surprisingly higher at a low proportion of grassland in 300 m surrounding (Table 19), at a higher proportion of forests in the 200 m and 300 m surrounding (Fig. 21a, Table 19), and it increased with the distance to the nearest grassland (Table 19). “Other” land cover was related to the G_w, which decreased at the higher proportion of “other” land cover in the 100 m surrounding, and was higher both at a low and high proportion in the 200 m surrounding.

Woodlandness was higher at a medium proportion of fields in the 200 m and 300 m surrounding (optimum 23%, Fig. 20a, Table 19), at sites near and remote from the fields (Fig. 20b) and in the SDFs that were overgrown by trees in 1966 (Fig. 21c) or that were fields or overgrown by trees in 1983 (Fig. 21d).

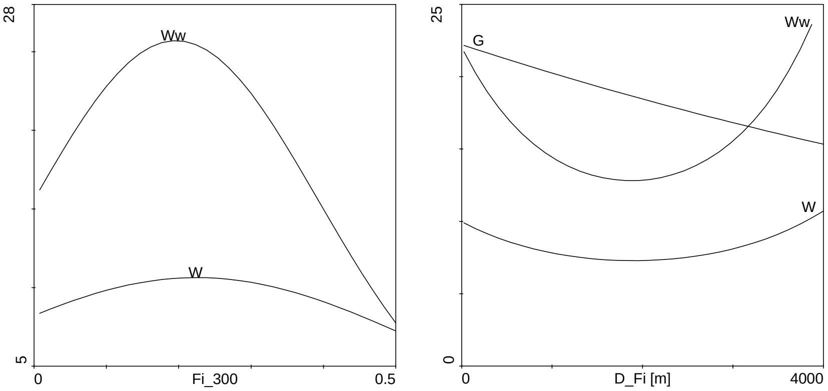
Weighted woodlandness was higher at a medium proportion of fields in the 200 m and 300 m surrounding (optima 21%, 20%, Fig. 20a, Table 19), at sites near and remote from the fields (Fig. 20b) and in the SDFs that were overgrown by trees in 1966 (Fig. 21c) and in 1983 (Fig. 21d).

Table 19. Factors influencing indeces describing grassland and woodland character of the herb layer (*GLM*).

	G		G_w		W		W_w	
	M	var.	M	var.	M	var.	M	var.
Fi_{200}	×		×		Q∩	10	Q∩	10
Fi_{300}	×		×		Q∩	10	Q∩	12
Grl_{200}	×		L↓	9	×		Q∩	8
Grl_{300}	×		L↓	11	×		×	
Fst_{100}	L↑	5	×		L↑	5	×	
Fst_{200}	×		Q∪	10	×		×	
Fst_{300}	L↑	4	Q∪	15	×		×	
SDF_{100}	Q∪	14	×		×		×	
SDF_{200}	L↓	5	×		L↓	4	×	
SDF_{300}	L↓	16	×		L↓	9	×	
Ot_{100}	×		L↓	10	×		×	
Ot_{200}	Q∪	8	Q∪	11	×		×	
Ot_{300}	L↑	5	×		×		×	
D_Fi	L↓	4	×		Q∪	11	Q∪	10
D_Grl	×		L↑	13	×		×	
G_Fst	×		Q∪	8	×		×	
A_{SDF}	L↓	6	×		L↓	6	×	
centre	L↓	4	×		×		×	
shape	×		L↓	5	L↓	4	L↓	6
1952	×		×		L↑	5	L↑	13
1966	Q∪	9	×		L↑	14	L↑	22
1983	Q∪	11	×		Q∪	16	L↑	16

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]. G - grasslandness, G_w - weighted grasslandness, W - woodlandness, W_w - weighted woodlandness; $Fi_{200/300}$ - proportion of fields in the 200/300 m surrounding, $Grl_{200/300}$ - proportion of grassland in 200/300 m surrounding, $Fst_{100/200/300}$ – proportion of forests in 100/200/300 m surrounding, $SDF_{100/200/300}$ - proportion of spontaneously developed forests in 100/200/300 m surrounding, $Ot_{100/200/300}$ – proportion of "other" land cover in the 100/200/300 m surrounding, D_Fi/D_Grl/D_Fst – distance to the nearest field/grassland/forest, A_{SDF} – area of the SDF, centre – nearest distance from the centre of the plot to the border of the SDF, shape - relative length of the SDF border, 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy).

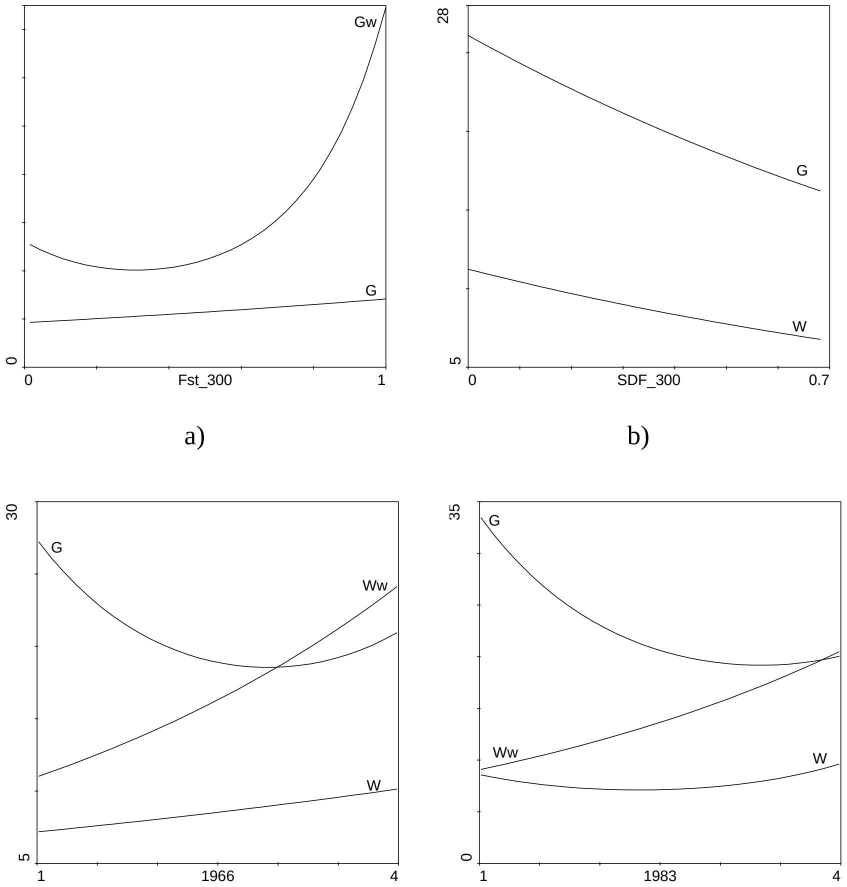
Tabulka 19. Vliv studovaných faktorů na luční/lesní charakter bylinného patra (*GLM*). L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. – vysvětlená variabilita [%]; G – index korespondující s počtem lučních druhů, G_w – index korespondující s pokryvností lučních druhů, W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů; $F_{200/300}$ – podíl pole v okolí 200/300 m, $Grl_{200/300}$ – podíl luk v okolí 200/300 m, $Fst_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, $SDF_{100/200/300}$ – podíl porostů náletových dřevin v okolí 100/200/300 m, $Ot_{100/200/300}$ – podíl krajinného pokryvu “ostatní” v okolí 100/200/300 m, D_Fi/D_Grl/D_Fst - vzdálenost k nejbližšímu poli/louce/lesu, A_{SDF} - rozloha SDF, centre - nejkratší vzdálenost k okraji porostu náletových dřevin, shape – relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), 1952/1966/1983 - vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).



a) b)

Figure 20. Factors influencing indeces describing grassland and woodland character of the herb layer (*GLM*): a) proportion of fields in the 300 m surrounding; b) distance to the nearest field. G - grasslandness,W - woodlandness, W_w - weighted woodlandness.

Obrázek 20. Vliv vybraných faktorů na luční/lesní charakter bylinného patra (*GLM*): a) podíl pole v okolí 300 m, b) vzdálenost k nejbližšímu poli. G – index korespondující s počtem lučních druhů, W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů.



a) b)

c) d)

Figure 21. Factors influencing indeces describing grassland and woodland character of the herb layer (*GLM*): a) proportion of forests in the 300 m surrounding; b) proportion of SDF in the 300 m surrounding, c) vegetation cover in 1966, and d) in 1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy). G - grasslandness, G_w - weighted grasslandness, W - woodlandness, W_w - weighted woodlandness.

Obrázek 21. Vliv vybraných faktorů na luční/lesní charakter bylinného patra (*GLM*): a) podíl lesa v okolí 300 m, b) podíl SDF v okolí 300 m, c) vegetační kryt v roce 1966, d) v roce 1983 (sukcesní série: 1-pole, 2-louka, 3-roztroušený nálet, 4-zapojený nálet). G – index korespondující s počtem lučních druhů, G_w - index korespondující s pokryvností lučních druhů, W - index korespondující s počtem lesních druhů, W_w - index korespondující s pokryvností lesních druhů.

Indeces describing the abundance of groups of species according to the type of distribution

The first ordination axis in the *PCA* explained 33.8% of the total variability in the data, while the first four axes explained 75.6%. The vegetation cover in *1952* (F = 3.51, $p < 0.01$), the proportion of SDFs in the 300 m surrounding (F = 2.57, $p < 0.01$), and vegetation cover in 1983 (F = 2.13, $p < 0.01$) significantly influenced the indeces describing the abundance of groups of species according to the type of distribution. The first ordination axis in the *RDA* explained 12.7% of the total variability in the data, while the first three explained 16.5%. Most of the indeces concerning woodland species were more abundant at higher values of the historical vegetation cover, i.e., with a longer duration of the tree layer (Fig. 22).

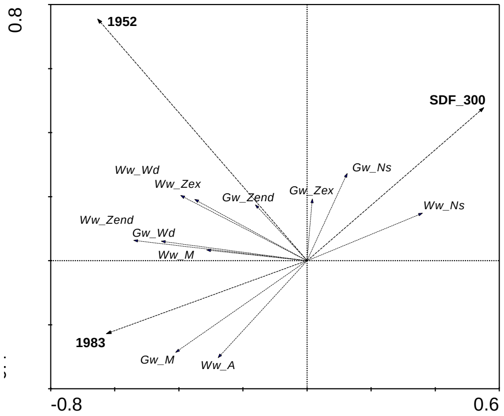


Figure 22. Ordination diagram for *RDA* of the indeces describing the abundance of groups of species according to the type of distribution. G_w_M/Ns/Wd/Zend/Zex - weighted grasslandness of myrmecochorous/ non-specific/anemochorous/endozoochorous/exozoochorous species, W_w_A/M/Ns/Wd/Zend/Zex - weighted woodlandness of autochorous/myrmecochorous/ non-specific/anemochorous/endozoochorous/exozoochorous species; 1952/1983 - vegetation cover in 1952/1983 (successional sere: field-grassland-scattered trees-closed tree canopy), SDF_300 - proportion of SDF in the 300 m surrounding.

Obrázek 22. *RDA* ordinační diagram – indexy korespondující s pokryvností skupin druhů podle způsobu rozšiřování. Gw_M/Ns/Wd/Zend/Zex – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů, Ww_A/M/Ns/Wd/Zend/Zex – index korespondující s pokryvností lesních autochorních/ myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů; 1952/1983 – vegetační kryt v roce 1952/1983 (sukcesní série: pole-louka-roztroušený nálet-zapojený nálet), SDF_300 - podíl SDF v okolí 300 m.

No grassland autochorous species were found.

Grassland myrmecochorous species were more abundant at a higher proportion of fields in the 100 m surrounding (optimum 30%, Table 20), in the 200 m (Fig. 23a), and 300 m (Table 20), at a lower proportion of SDF in the 300 m (Fig. 26b), at sites near and remote from the fields (Fig. 23b) and the forests (Fig. 25c), and at sites which were fields or closed SDFs in 1983 (Fig. 27d).

Grassland species non-specific to the type of distribution were less abundant in the SDFs surrounded by a medium value of grassland in the 200 m (Fig. 24a) and near grassland (Fig. 24b). The G_w_Ns were more abundant at a higher proportion of forests in the 200 m and 300 m surrounding (Fig. 25b, Table 20). Higher G_w_Ns was also found at sites, which were grassland or scattered SDFs in 1983 (Fig. 27d).

Grassland anemochorous species were more abundant at sites relatively highly surrounded by fields in the 300 m (optimum 18%, Table 20), near the fields (Fig. 23b), less surrounded by SDF in the 300 m surrounding (Fig. 26b), in the SDFs which were grassland or overgrown by trees in *1952* (Fig. 27b) and which were fields or closed SDF in 1966 (Fig. 27c) or 1983 (Fig. 27d).

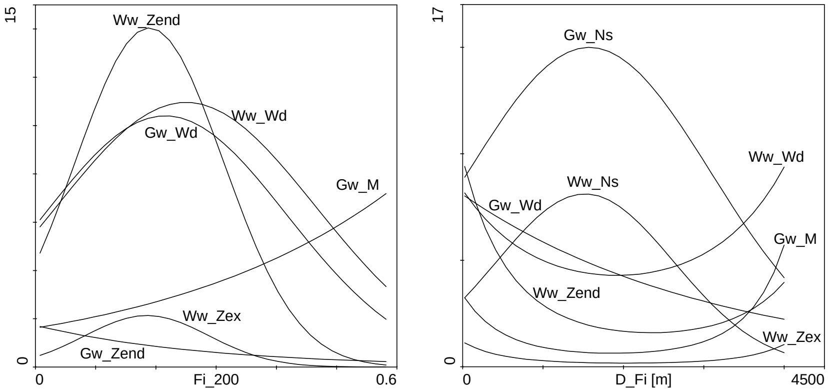
Grassland endozoochorous species were more abundant at sites less surrounded by fields in the 100 m (Table 20), more surrounded by “other” land cover in the 300 m (Fig. 25d), at sites approximately 50 m away from the nearest SDF border (Table 20), and in the SDFs which were overgrown by trees in *1952* (Fig. 27b).

Table 20. Selected factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*).

	G_w_M		G_w_Ns		G_w_Wd		G_w_Z_{end}		G_w_Z_{ex}	
	M	var.	M	var.	M	var.	M	var.	M	var.
Fi_{100}	Q∩	18	L↓	5	×		L↓	10	×	
Fi_{200}	L↑	16	×		Q∩	9	L↓	7	×	
Fi_{300}	L↑	19	×		Q∩	13	×		×	
Grl_{200}	×		Q∪	10	×		×		L↓	6
Grl_{300}	×		L↓	8	×		×		L↓	8
Fst_{100}	Q∩	9	×		L↑	8	×		×	
Fst_{200}	Q∩	8	Q∪	11	L↑	6	×		×	
Fst_{300}	Q∩	9	Q∪	13	×		×		Q∪	12
SDF_{300}	L↓	12	×		Q∪	10	×		×	
Ot_{100}	×		L↓	4	×		×		L↓	14
Ot_{200}	×		×		×		×		Q∪	8
Ot_{300}	×		×		L↑	7	Q∪	15	×	
D_Fi	Q∪	26	Q∪	9	L↓	12	×		×	
D_Grl	Q∩	8	L↑	15	L↑	7	×		×	
G_Fst	Q∪	13	×		Q∪	13	×		×	
A_{SDF}	L↓	4	×		×		×		×	
centre	×		×		×		Q∩	10	×	
shape	×		×		L↓	9	×		×	
1952	×		×		L↑	13	Q∪	22	×	
1966	Q∪	9	×		Q∪	14	×		×	
1983	Q∪	17	Q∩	12	Q∪	12	×		×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]. G_w_M/Ns/Wd/Z_{end}/Z_{ex} - weighted grasslandness of myrmecochorous/non-specific/anemochorous/endozoochorous/exozoochorous species; $Fi_{100/200/300}$ - proportion of fields in the 100/200/300 m surrounding, $Grl_{200/300}$ – proportion of grassland in the 200/300 m surrounding, $Fst_{100/200/300}$ – proportion of forests in the 100/200/300 m surrounding, SDF_{300} - proportion of spontaneously developed forests in the 300 m surrounding, $Ot_{100/200/300}$ - proportion of "other" land cover in the 100/200/300 m surrounding, D_Fi/D_Grl/D_Fst - distance to the nearest field/grassland/forest, A_{SDF} – area of the SDF, centre - nearest distance from the centre of the plot to the border of the SDF, shape – relative length of the SDF border, 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy).

Tabulka 20. Vliv studovaných faktorů na charakter porostu popsaný pokryvností skupin lučních druhů dle různých způsobů rozšiřování (*GLM*). L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. – vysvětlená variabilita [%]; G_{w}_M/Ns/Wd/Z_{end}/Z_{ex} – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů; $Fi_{100/200/300}$ – podíl pole v okolí 100/200/300 m, $Grl_{200/300}$ – podíl luk v okolí 200/300 m, $Fst_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, SDF_{300} – podíl porostů náletových dřevin v okolí 300 m, $Ot_{100/200/300}$ – podíl krajinného pokryvu "ostatní" v okolí 100/200/300 m, D_Fi/D_Grl/D_Fst – vzdálenost k nejbližšímu poli/louce/lesu, A_{SDF} - rozloha SDF, centre - nejkratší vzdálenost k okraji porostu náletových dřevin, shape – relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), 1952/1966/1983 - vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).



a) b)

Figure 23. Factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*): a) proportion of fields in the 200 m surrounding; b) distance to the nearest field. Gw_M/Ns/Wd/Zend - weighted grasslandness of myrmecochorous/non-specific/anemochorous/endozoochorous species, Ww_Ns/Wd/Zend/Zex - weighted woodlandness of non-specific/anemochorous/endozoochorous/exozoochorous species.

Obrázek 23. Vliv vybraných faktorů na charakter porostu popsaný pokryvností skupin druhů dle různých způsobů rozšiřování (*GLM*): a) podíl pole v okolí 200 m, b) vzdálenost k nejbližšímu poli. Gw_M/Ns/Wd/Zend – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/ endozoochorních druhů, Ww_Ns/Wd/Zend/Zex – index korespondující s pokryvností lesních nespecifických/ anemochorních/endozoochorních/exozoochorních druhů.

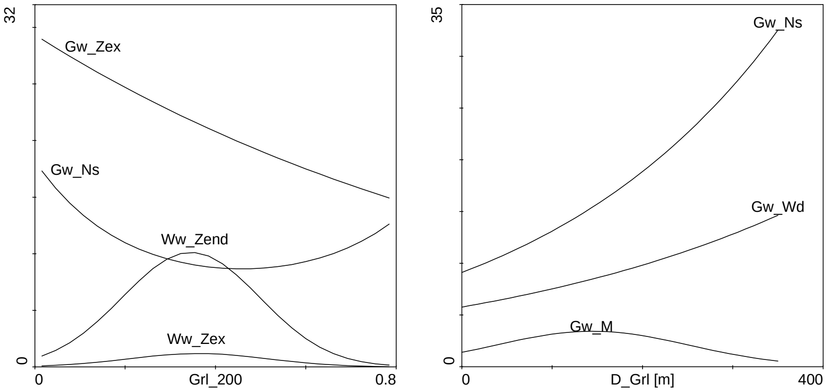
Grassland exozoochorous species were more abundant at sites both at a low proprotion and high proportion of forests in the 300 m surrounding (Fig. 25b), and less surrounded by "other" land cover in the 100 m (Table 20).

Table 21. Selected factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*).

	W_w_A		W_w_M		W_w_Ns		W_w_Wd		W_w_Z_{end}		W_w_Z_{ex}	
	M	var.	M	var.	M	var.	M	var.	M	var.	M	var.
Fi$_{200}$	×		×		×		Q∩	10	Q∩	16	Q∩	20
Fi$_{300}$	×		×		×		Q∩	13	Q∩	13	Q∩	25
Grl$_{100}$	×		×		×		×		Q∩	12	Q∩	14
Grl$_{200}$	×		×		×		×		Q∩	31	Q∩	20
Grl$_{300}$	×		×		×		×		Q∩	21	Q∩	17
Fst$_{100}$	Q∩	29	×		×		×		×		L↓	6
Fst$_{200}$	×		×		×		×		×		L↓	6
Fst$_{300}$	×		×		×		×		×		L↓	6
SDF$_{100}$	Q∪	30	×		Q∩	23	×		×		×	
SDF$_{200}$	L↓	8	×		×		×		×		×	
SDF$_{300}$	Q∪	48	×		×		×		×		×	
Ot$_{100}$	Q∩	58	×		L↓	8	×		×		×	
Ot$_{200}$	L↑	12	×		L↓	7	×		×		×	
Ot$_{300}$	Q∩	21	×		×		×		×		Q∪	12
D_Fi	×		×		Q∩	11	Q∪	8	Q∪	19	Q∪	14
D_Fst	Q∪	16	×		×		×		×		L↑	8
A$_{SDF}$	Q∪	16	Q∩	15	L↑	15	×		×		×	
centre	×		×		×		×		×		L↑	7
shape	L↓	16	×		Q∩	12	×		L↓	8	×	
1952	×		Q∪	36	Q∩	9	L↑	18	L↑	27	Q∩	38
1966	L↑	10	×		×		L↑	8	L↑	33	L↑	18
1983	L↑	19	×		Q∩	13	L↑	11	Q∪	22	Q∪	17

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]. W_w_A/M/Ns/Wd/Z_{end}/Z_{ex} - weighted woodlandness of autochorous/myrmecochorous/non-specific/ anemochorous/endozoochorous/exozoochorous species; Fi$_{200/300}$ – proportion of fields in the 200/300 m surrounding, Grl$_{100/200/300}$ – proportion of grassland in the 100/200/300 m surrounding, Fst$_{100/200/300}$ – proportion of forests in the 100/200/300 m surrounding, SDF$_{100/200/300}$ – proportion of spontaneously developed forests in the 100/200/300 m surrounding, Ot$_{100/200/300}$ – proportion of "other" land cover in the 100/200/300 m surrounding, D_Fi/D_Fst – distance to the nearest field/forest, A$_{SDF}$ – area of the SDF, centre – nearest distance from the centre of the plot to the border of the SDF, shape – relative length of the SDF border, 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy).

Tabulka 21. Vliv studovaných faktorů na charakter porostu popsaný pokryvností skupin lesních druhů dle různých způsobů rozšiřování (*GLM*): L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. – vysvětlená variabilita [%]; W_w_A/M/Ns/Wd/Z_{end}/Z_{ex} – index korespondující s pokryvností lesních autochorních/myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů; $Fi_{200/300}$ – podíl pole v okolí 200/300 m, $Grl_{100/200/300}$ – podíl luk v okolí 100/200/300 m, $Fst_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, $SDF_{100/200/300}$ – podíl porostů náletových dřevin v okolí 100/200/300 m, $Ot_{100/200/300}$ – podíl krajinného pokryvu "ostatní" v okolí 100/200/300 m, D_Fi/ D_Fst – vzdálenost k nejbližšímu poli/lesu, A_{SDF} - rozloha SDF, centre – nejkratší vzdálenost k okraji porostu náletových dřevin, shape – relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), 1952/1966/1983 - vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).



a) b)

Figure 24. Factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*): a) proportion of grassland in the 200 m surrounding, b) distance to the nearest grassland. Gw_M/Ns/Wd/Zex - weighted grasslandness of myrmecochorous/ non-specific/anemochorous/exozoochorous species, Ww_Zend/Zex – weighted woodlandness of endozoochorous/exozoochorous species.

Obrázek 24. Vliv vybraných faktorů na charakter porostu popsaný pokryvností skupin druhů dle různých způsobů rozšiřování (*GLM*): a) podíl louky v okolí 200 m, b) vzdálenost k nejbližší louce. Gw_M/Ns/Wd/Zex – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/exozoochorních druhů, Ww_Zend/Zex - index korespondující s pokryvností lesních endozoochorních/exozoochorních druhů.

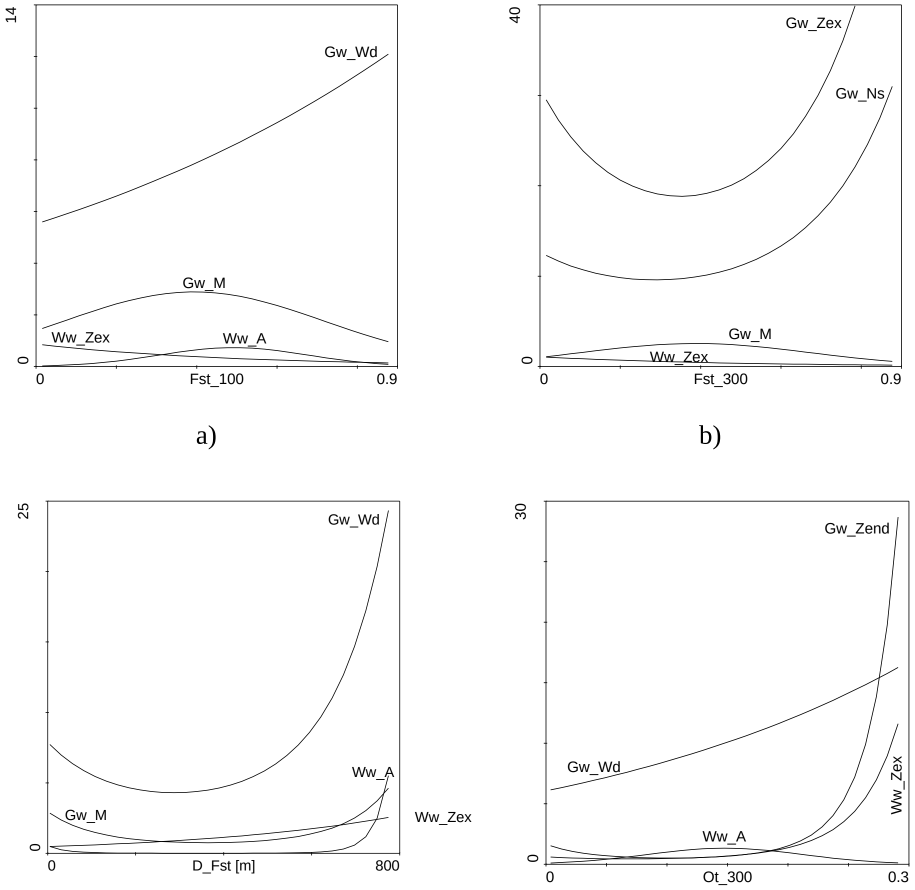
Woodland autochorous species were more abundant at a higher proportion of forests in the 100 m (optimum 49%, Fig. 25a), but also surprisingly at sites remote from the nearest forest (Fig. 25c). Higher abundance was also found at a low proportion of SDFs in the 100 m and 300 m surrounding (Fig. 26a, b), at a medium abundance of “other” land cover in the 100 and 300 m surrounding (optima 6% and 15%; Fig. 25d, Table 21), and at a higher proportion of “other” land cover in the 200 m (Table 21), in both small (<3 ha) and large SDFs (>25 ha; Table 21), in the SDFs with less complicated shapes (Fig. 27a), and at sites which were overgrown by trees in 1966 (Fig. 27c) and 1983 (Fig. 27d).

Woodland myrmecochorous species were more abundant in intermediate large SDFs (Table 21), in larger SDFs (Table 21), and in the SDFs which were overgrown by trees in *1952* (Fig. 27b).

Woodland species non-specific to the type of distribution were more abundant in the SDFs surrounded by a relatively high proportion of SDF in the 100 m (optimum 61%; Fig. 26a), at a medium distance to the nearest field (Fig. 23b), in larger SDFs (Table 21) with relatively complicated shapes (optimum 7.6; Fig. 27a), and in SDFs which were grassland or overgrown by scattered trees in *1952* (Fig. 27b).

Woodland anemochorous species were found to be more abundant in the SDFs surrounded by a relatively high proportion of fields in the 200 m and 300 m (optima 25% and 21%; Fig. 23a, Table 21), in the SDFs which were overgrown by trees in *1952* (Fig. 27b) and 1983 (Fig. 27d).

There was found to be a higher abundance of woodland endozoochorous species in the SDFs surrounded by a relatively high proportion of fields in the 200 m and 300 m (optima 19% and 21%; Fig. 23a, Table 21), at a medium proportion of grassland in the 100, 200 and 300 m (optima 34%, 35% and 34%; Fig 24a, Table 21), at sites both near and remote from the field (Fig. 23b), and in the SDFs which were overgrown by trees in *1952* (Fig. 27b), 1966 (Fig. 27c) and 1983 (Fig. 27d).

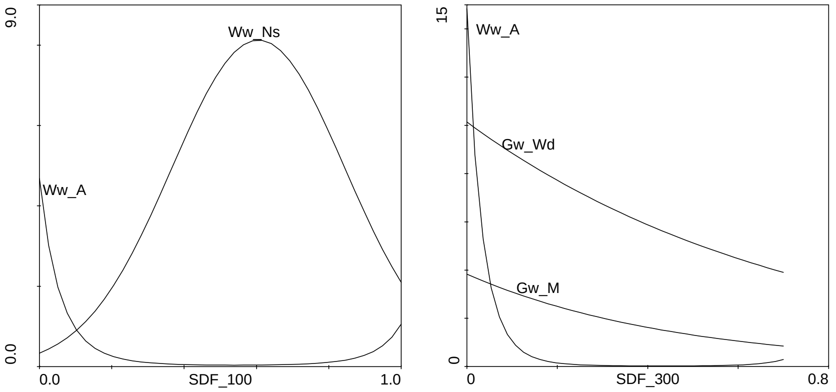


a) b)

c) d)

Figure 25. Factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*): a) proportion of forests in the 100 m surrounding, b) proportion of forests in the 300 m surrounding, c) distance to the nearest forest, d) proportion of “other” land cover in the 300 m surrounding. Gw_M/Ns/Wd/Zend/Zex - weighted grasslandness of myrmecochorous/ non-specific/anemochorous/endozoochorous/exozoochorous species Ww_A/Zex - weighted woodlandness of autochorous/exozoochorous species.

Obrázek 25. Vliv vybraných faktorů na charakter porostu popsaný pokryvností skupin druhů dle různých způsobů rozšiřování (*GLM*): a) podíl lesa v okolí 100 m, b) podíl lesa v okolí 300 m, c) vzdálenost k nejbližšímu lesu, d) podíl krajinného pokryvu „ostatní“ v okolí 300 m. Gw_M/Ns/Wd/Zend/Zex – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů, Ww_A/Zex – index korespondující s pokryvností lesních autochorních/exozoochorních druhů.

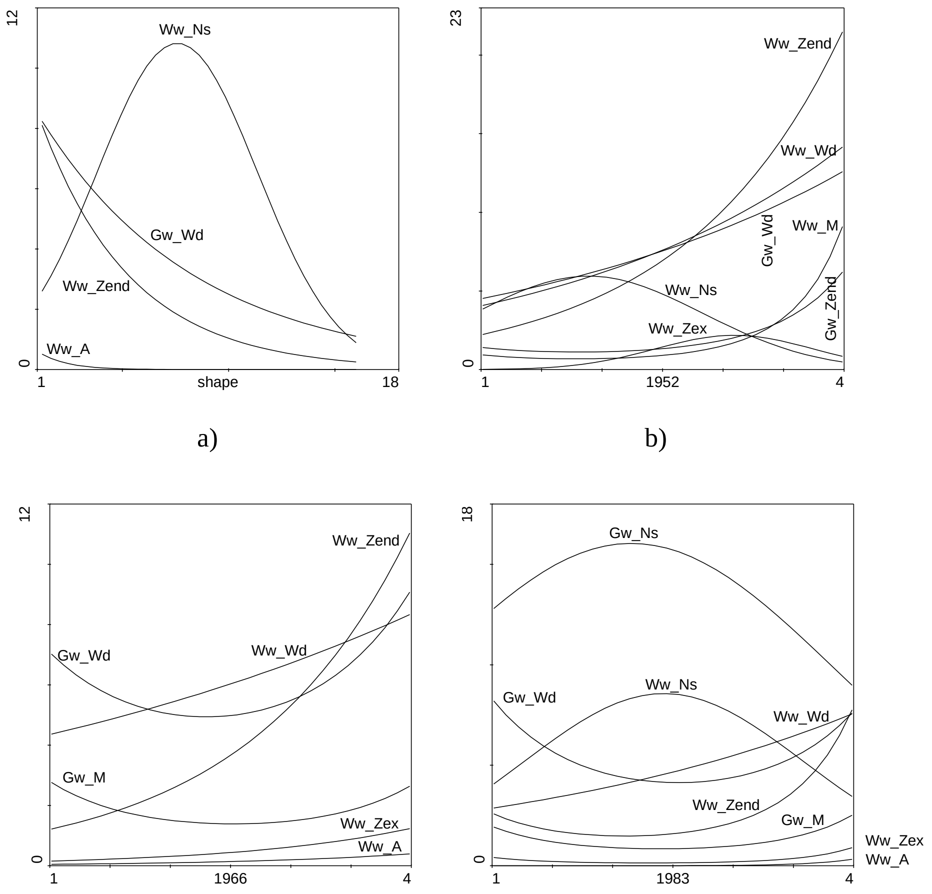


a) b)

Figure 26. Factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*): a) proportion of SDF in the 100 m surrounding, b) in the 300 m surrounding. Gw_M/Wd - weighted grasslandness of myrmecochorous/anemochorous species, Ww_A/Ns – weighted woodlandness of autochorous/non-specific species.

Obrázek 26. Vliv vybraných faktorů na charakter porostu z hlediska pokryvnosti skupin druhů dle různých způsobů rozšiřování (*GLM*): a) podíl porostů náletových dřevin v okolí 100 m, b) 300 m. Gw_M/Wd – index korespondující s pokryvností lučních myrmekochorních/anemochorních druhů, Ww_A/Ns – index korespondující s pokryvností lesních autochorních/nespecifických druhů.

Woodland exozoochorous species were more abundant in the SDFs surrounded by a relatively high proportion of fields in the 200 m and 300 m (optima 19% and 18%; Fig. 23a, Table 21), at a medium proportion of grassland in the 100, 200 and 300 m (optima 36%, 36% and 33%; Fig. 24a, Table 21), at a high proportion of “other” land cover in the 300 m (Fig. 25d), at sites both near and remote from the field (Fig. 23b), and in the SDFs overgrown by trees in *1952* (optimum 3.1; Fig. 27b), 1966 (Fig. 27c) and 1983 (Fig. 27d).



a) b)

c) d)

Figure 27. Factors influencing indeces describing the abundance of groups of species according to the type of distribution (*GLM*): a) shape – relative length of the SDF border, b) vegetation cover in 1952, c) in 1966, d) in 1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy). Gw_M/Ns/Wd/Zend - weighted grasslandness of myrmecochorous/non-specific/ anemochorous/endozoochorous species, Ww_A/M/Ns/Wd/Zend/Zex - weighted woodlandness of autochorous/myrmecochorous/non-specific/anemochorous/ endozoochorous/exozoochorous species.

Obrázek 27. Vliv vybraných faktorů na charakter porostu popsaný pokryvností skupin druhů dle různých způsobů rozšiřování (*GLM*): a) relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), b) vegetační kryt v roce 1952, c) 1966, d) 1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet). Gw_M/Ns/Wd/Zend – index korespondující s pokryvností lučních myrmekochorních/nespecifických/anemochorních/endozoochorních druhů, Ww_A/M/Ns/Wd/Z_{end}/Z_{ex} – index korespondující s pokryvností lesních autochorních/ myrmekochorních/nespecifických/anemochorních/endozoochorních/exozoochorních druhů.

Discussion

Three groups of context-dependent factors were chosen to test their influence on the character of the herb layer. The characteristics of SDF (A_{SDF}, centre, shape) influenced the character of the herb layer only slightly, but the influence of the area (e.g., Kolb and Diekmann 2004) and shape (e.g., Dzwonko and Loster 1992; Honnay et al. 1999) was reported. Only the characteristics related to the forest species were influenced by this group of context-dependent factors. For example, the area significantly influenced species typically growing at clearings, woodland autochorous, myrmecochorous, and woodland species non-specific to the type of distribution. However, no general trend in preference of woodland species was observed. This may be caused by high variability in species composition, which was reported from recent forests (e.g., Honnay et. al. 1999).

The surrounding vegetation cover was important for many groups of species according to the biotope, and for the character of the herb layer described by the indeces. Surrounding vegetation was also found to be very important in different studies, e.g., Řehounková and Prach (2006) explained 44% of the total variability in the data by attributing it to landscape factors studying the disused gravel-sand pits; Kirmer et al. (2008) discovered the influence of the surrounding vegetation cover of 17 km on the species composition of the mined stands.

Species related to the grassland were influenced at most by the proportion of grassland, and by the nearest distance to the grassland, and by the proportion of forest in the surroundings, while “other” land cover was found to be only of small importance. The relationship between grassland species and the grassland and forests seems obvious, but a relationship other than what could have been expected was usually observed (i.e., decrease of grassland character with increasing grassland vegetation cover in surroundings, but its increase with increasing forest in surroundings). This may be caused by the character of grassland in the studied area. The highly diverse areas of grassland are usually small, and they are in less favourable parts of the studied area, while large scale grasslands are usually intensively managed, and/or they were sown as productive grasslands on former arable land. Therefore, the higher proportion of grassland in surroundings is more probably caused by low diversity of productive grassland, which can only slightly increase the abundance of typical grassland species. More forests in surroundings usually means more forest/grassland ecotones, which are of high diversity of grassland species and biotope for the species growing both in grassland and woods (Ihse 1995). Therefore, the higher proportion of forests in the surroundings may, unexpectedly from the first point of view, increase the abundance of species related to the grassland vegetation.

The influence of surrounding vegetation on the abundance of woodland species was not prima facie. However, the forest species were found to be poor colonisers (for review see Honnay et al. 2002a), with a rate of colonisation that hardly ever exceeds 2 m.year^2, but usually is <1 m.year^{-1} (e.g., Bossuyt et al. 1999; Honnay et al. 1999), and of which seed limitation was proved experimentally by seed addition in several studies (e.g., Ehrlén and Eriksson 2000; Ehrlén et al. 2006), the increase of the proportion of forests in surroundings and the distance to the nearest forest was not usually related to the abundance of species connected with forests, or the relationships was not the same as could be expected from the evidence referred to above, and/or the explained variability was low. The evidence could have two causes: i) the species composition of the herb layer of most of the forests in the surroundings is different from the herb layer species composition typical for ancient forests, which is caused by the forest management preferring timber species (especially Norway spruce) in the area, and therefore the regional pool of forest herb species is low; ii) the high variability in early stages of succession (e.g., Odum 1969; Prach 1987) cannot be related to the surrounding vegetation, because the herb layer colonisation is more of a “lottery” than predictable. The relationship of forest species to the duration of the tree layer supports this explanation.

SDF in surroundings did not influence the studied groups and indeces very much. The groups of species according to the biotope were not influenced elsewhere either. This is not in line with the conclusions of other studies, e.g., Hersperger and Forman (2003) found that the number of grassland species decreases with the increase in the proportion of the shrubs of *Populus tremuloides* in the surroundings (Canada) and the increase in number of species typical for shrubs.

The history (i.e., the vegetation cover up to 50 years BP) was the most important factor particularly influencing the groups and indeces related to the woodland species (Sc, Ws, W, W_w, W_w_A, W_w_Ns, $W_w\_Z_{end}$, $W_w\_Z_{ex}$). The influence of the duration of the tree layer was reported in many studies (e.g., Bossuyt and Hermy 2000; Honnay et al. 1999; Jacquemyn et al. 2001). As can be assumed, the abundance of these groups increased in general with the duration of the tree layer, and the explained variability was usually high (up to 38%). Woodland anemochorous, endozoochorous, and exozoochorous were the most influenced groups according to the type of distribution by the duration of the tree layer. This is in line with the finding that species which have a dispersal ability that is not low or high are influenced by the time of succession at most (Jacquemyn et al. 2003).

The relationship of grassland species to the historical vegetation cover was less evident. The decrease was observed only for *AR* species (1966) and grasslandness, while species grouped according to a different type of distribution have responded differently, and the relationships often have not been ecologically well interpretable (e.g., preference of grassland anemochorous species to the field or grassland, see Fig. 23a, 24b). This may indicate the slow change in the grassland character, and therefore the long-term succession toward forest herb layer species composition. Other studies also found very slow changes in the herb layer of recent forests, and the time needed for forest herb layer development assumed to be long, e.g., Jacquemyn et al. (2001) estimated at least 200 years, and Verheyen et al. (2003) did not find the herb layer of recent forest saturated by forest species after 200 years. The influence of former agricultural activity may last much longer, e.g., Dupouey et al. (2002) found a difference in species composition caused by agriculture after more than eleven centuries.

Many of the species occupying the SDFs are species growing both in grassland and woodland (see also Peterken and Game 1984), and therefore their abundance increased the indeces corresponding with the abundance of woodland species (W, W_w, W_w_X), e.g., the percentage of GW in the W_w index was 47% (SD = 32.1). Many of tree seedlings contributed to the abundance of forest species (Ws), and to the indeces corresponding with the abundance of woodland species (e.g., 53% of Ws, SD = 35.5). The tree seedlings are supposed to be better colonisers of the secondary woods (Wulf and Heinken 2008). Of the tree seedlings, maple and Norway spruce were the most abundant (for more detail see Dostalova 2009). The SDFs also correspond with the vegetation typical for hedgerows, which were found to be important corridors for forest herb species (e.g., Bossuyt et al. 1999; Honnay et al. 2002a; Wehling and Diekmann 2009a), which, however, were relatively highly abundant – the forest species without tree seedlings took on average 15.6% of the herb layer (SD = 30.9).

Herb layer species composition of the spontaneously developed forests: Influence of the site-dependent factors on the frequent species abundance

Druhové složení bylinného patra porostů náletových dřevin: vliv na stanovišti závislých faktorů na pokryvnost hojných druhů

Abstract

The herb layer species composition in the spontaneously developed forests (SDFs) was studied in a mountainous area (665-940 m) in the Czech Republic.

Forty-eight permanent plots (100 m^2) were fixed in the SDFs on mesic stands to find out the species composition and species richness. The influence of the character of the tree-layer, climate, light, and soil conditions on the frequent species abundance was tested using General Linear Models (*GLM*).

161 vascular plant species were found (on average 32 species.100 m^{-2}). The mean Shannon-Wiener index of diversity was found to be 2.6.

The herb layer of SDFs is highly variable in the species composition (23% of the species were listed at only one plot, while only 17% were listed at more than 33% of the plots). The average abundance of the species was low for most of the species.

Most of the frequent species and species related to the grassland/woodland vegetation were species related to the grassland vegetation (i.e., *Arrhenatherion elatioris*, *Polygono bistortae-Trisetion flavescentis* and *Violion caninae* alliances). However, several typical forest species were also listed, but their abundance was relatively low (except for *Vaccinium myrtillus*).

All the studied factors influenced the abundance of the frequent species, but different species react differently to the studied factors.

Shrnutí

Bylo studováno druhové složení bylinného patra porostů náletových dřevin (SDFs) v horských oblastech (665-940 m) České republiky.

Na 48 trvalých plochách (100 m^2) bylo zjištěno druhové složení bylinného patra a jeho druhová diverzita. Zobecněnými lineárními modely (*GLM*) byl testován vliv charakteru stromového patra, klimatu, světelných a půdních podmínek na pokryvnost druhů hojných v bylinném patře.

V bylinném patře bylo zaznamenáno celkem 161 druhů cévnatých rostlin (průměrně 32 na 100 m^2). Průměrný Shannon-Wienerův index diverzity byl 2,6.

Druhové složení bylinného patra porostů náletových dřevin je velmi variabilní (23 % druhů bylo nalezeno jen na jediné ploše, zatímco jen 17 % druhů bylo zaznamenáno na více než na třetině ploch) a průměrná pokryvnost druhů je u většiny druhů nízká.

Většina druhů hojných v bylinném patře a druhů typických pro luční nebo lesní vegetaci byly luční druhy (svazy *Arrhenatherion elatioris, Polygono bistortae-Trisetion flavescentis* a *Violion caninae*). Ačkoli v bylinném patře bylo zaznamenáno také několik typicky lesních druhů, jejich pokryvnost byla nízká (s výjimkou *Vaccinium myrtillus*).

Všechny studované faktory ovlivňovaly pokryvnost hojných druhů, ale odpověď druhů na studované faktory byla různá.

Introduction

The area of forests has been increased in Europe in recent decades. A large area of the agricultural land has been reforested by planted trees or has overgrown by spontaneously developed forests after abandonment of agricultural land. This reforestation took place mainly in less favourable areas, e.g., at higher altitudes (Brandt et al. 1999; Hamre et al. 2007). For example, Zemek and Heřman (1998) found an 18.2% increase of forests in the Český Krumlov district (Czech Republic) between 1840 and 1990 (the studied area is situated in this district). These forests were planted or developed spontaneously on abandoned agricultural land. The most often planted tree species in the Czech Republic was the Norway spruce (*Picea abies* (L.) Karsten). The abandoned areas have overgrown due to the spontaneous succession of trees, because the successional changes in temperate climate tend toward woodland (Ellenberg 1988). I refer to such growths as spontaneously developed forests (SDFs) to distinguish them from the planted forests. Both types are often referred to as recent forests (e.g., Dzwonko 1993).

At abandoned sites the tree-layer in general develops within 30-40 years, and definitely closes after 60-80 years (Flinn and Vellend 2005). However, the rate is dependent on altitude and soil conditions (Prach et al. 2007), and many other factors can influence the tree-layer development, e.g., competition by grasses (Dickie et al. 2007) can slower, while lone trees can enhance the tree establishment process (Dzwonko and Loster 1992), etc. Pioneer tree species dominate the first generation of the tree-layer. The birch (*Betula pendula* Roth) was found to be the most common tree species dominating the SDFs in Central Europe (Prach 1994; Prach and Pyšek 1994b).

The herb layer species composition is dependent on the species composition of the vegetation at the start of the succession, e.g., the succession on former arable land is founder-controlled due to the high disturbance regime, while on grassland it is more dominance-controlled (Lepš and Štursa 1989), and many factors may influence the rate and direction of changes, and therefore the species composition. The following types of factors may influence the successional changes: i) the site-dependent factors, or ii) the context-dependent factors.

Of site-dependent factors, influence of e.g., soil conditions (e.g., Christensen and Peet 1984; Verheyen et al. 1999), light conditions (e.g., Dzwonko and Loster 1990; Tilman and Wedin 1991), and climate (e.g. Prach and Řehounková 2006) was reported. Of context-dependent factors, the following were also found to be important: the area and shape of the recent forest (e.g., Bossuyt et al. 1999; Dzwonko and Loster 1988; Peterken and Game 1984), dispersal limitation, i.e., the distance to the ancient forest (e.g., Brunet and von Oheimb 1998a; Dzwonko 1993), surrounding vegetation (e.g., Hersperger and Forman 2003; Řehounková and Prach 2006) and the stage of succession, i.e., the duration of succession (e.g., Bossuyt and Hermy 2000; Honnay et al. 1999; Verheyen et al. 2003).

The development toward the forest herb layer is assumed, but a long period of time will be needed to reach the terminal stage of succession, e.g., Faliński (1988) estimated 350 years for the mesic sequence in the temperate zone in Europe, and Jacquemyn et al. (2001) estimated 200 years for recent forests (planted on former agricultural land).

Although some general trends are known (see Prach and Řehounková 2006; Prach et al. 2007), our knowledge about the processes is incomplete, and some inconsistencies have been reported, e.g., however the forest herb species were found to be poor colonisers, and their rate of colonisation hardly ever exceeds 2 m.year^{2}, but usually is <1 m.year^{-1} (e.g., Bossuyt et al. 1999; Honnay et al. 1999), and they are able to colonise many recent forests, e.g. Dzwonko and Loster (1992) found 59 out of 153 herb species in the recent forests in Poland, but their frequency and abundance was low.

The SDFs have become a component of the landscape cover in Europe, but land owners usually neither considered them to be of high nature value (unlike the semi-natural grasslands from which they often develop), nor valuable land cover (e.g., Benjamin et al. 2007). Forest managers also do not perceive them as valuable timber species, although their importance in timber production was recognised (e.g., Košulič 2001). Their abundance is relatively high in some areas (e.g., in the southern part of the Czech Republic, where they cover 4.1% of high nature value landscape, Dostálova unpbl.). Our knowledge about the successional processes and their future development is important for conservation biology, urban and management planning and for forest management. The spontaneous development should be the best and cheapest management solution (Pyšek et al. 2001).

This study focused on the SDFs on mesic stands (neither waterlogged nor desiccated, with vegetation neither ruderalised nor typical for poor soil) in a mountainous area in the Czech Republic. The influence of the site-dependent factors (character of the tree-layer, light and soil conditions) on the species composition of the herb layer was studied.

The following questions are considered:

1. How diverse is the herb layer of SDFs? What species typical for grassland and forest vegetation are present in the herb layer of the SDFs?
2. What species are frequent in the herb layer of SDFs?
3. Are the frequent species influenced by the character of the tree-layer, light or soil conditions?

Methods

Study area

Southern part of the Czech Republic (40°35-38′ N, 14°11-17′ E), altitude 665-940 m. Climatic conditions moderately oceanic between the warm and cold type (climatic regions MT 3 – Ch 7; Quitt 1971), average year temperature 6.8°C and average year precipitation 718-1003 mm.

I fixed 48 plots of 10 × 10 m in SDFs, which differed in age, altitude and exposition, but all plots were on mesic stand (neither waterlogged nor desiccated, with vegetation neither ruderalised nor typical for poor soil). I fixed the plots in such growths, where significant human influence was not recognisable, and which were homogenous and large enough. Different age categories present in the study area were equally presented.

The supposed terminal stage of succession is beech forest (*Dentario enneaphylli-Fagetum* association, or transient to *Luzulo albidae-Quercetum petraeae* association, Neuhäuslová 1998).

The present growths are mostly dominated by birch (*Betula pendula*), common trees are: Norway spruce (*Picea abies*), European aspen (*Populus tremula* L.); in some cases Scots pine (*Pinus sylvestris* L.) or common ash (*Fraxinus excelsior* L.) are more abundant.

Data collection

Phytocenological releve was taken from all the permanent plots. The species abundance was estimated in percentages of abundance of the species for each layer.

Species related to common grassland or forest vegetation were determined. Diagnostic and constant species were considered for the following types of grassland vegetation: *Arrhenatherion elatioris*, *Polygono bistortae-Trisetion flavescentis*, and *Violion caninae* alliances (Chytrý 2007); and the following types of forest vegetation: *Dentario enneaphylli-Fagetum* association, *Luzulo-Fagion*, and *Quercion petraea* alliances (Moravec et al. 2000).

The number and species composition of trees at the plot were listed. Abundance of the tree-layer was determined from the phytocenological releve and it was used after logarithmical transformation (E_3). Proportion of deciduous trees in the tree-layer (D) was calculated. This characteristic corresponds with the character of the tree-layer (value 1 have deciduous SDFs, 0 have coniferous SDFs).

For age estimation, I took two samples of wood from each tree, but maximally from 10 randomly chosen trees of each species per plot, using Pressler's auger. Samples were taken from opposite sides of the trunk at the height of 40 cm above ground. After fixation and cutting I counted the tree-rings. The average age of the trees (A_a) and the maximal age of the trees (A_{max}) was determined for all plots. A_a corresponds with the duration of closed canopy of the tree-layer, while A_{max} corresponds rather with the duration of abandonment.

For estimation of light conditions, relative irradiance of photosynthetic active radiation (*PhAR*) was measured for all plots. The irradiance was measured using simultaneously two luxmeters with *PhAR* sensors: one sensor was placed within the growth, while the other was placed in the open. Relative *PhAR* irradiance was calculated as percentage of incoming *PhAR* in the open from 20 random measurements within each plot and for the certain height level (5 cm and 120 cm above ground level). Measurements were taken between 11 a.m. and 3 p.m. in July or first half of August. The weather conditions were somewhat cloudy or cloudy without rain. The open stand for reference measurements was at least 100 m from the forest-edge (or other high object, e.g., building), on the west side of the forest, the nearest distance was 200 m. Relative irradiance at the 120 cm above ground (P_{120}) corresponds with the density of the tree or shrub layer, while the relative irradiance at the 5 cm above ground (P_5) corresponds with the light available for seedling recruitment.

I took soil samples from each plot, and I determined content of rock fragments >2 mm (R_s) in the dried samples using a 2 mm sieve [%]. I measured the soil reaction in the water solution (pH_s) using 10 g of fine air-dried soil samples and 20 cm^3 of distilled water (free of CO_2). I determined the organic matter content (C_{org}) as the loss of the matter content of dried sample by 450°C [%]; the basal respiration of the microbial community (BR_s) as CO_2 production [μg C-CO_2.g^{-1}.hod^{-1}] (Jäggi 1976).

The retention water capacity (*RWC*) was determined from the undisturbed soil samples (five per plot) taken from the organic soil horizon at each plot. *RWC* was counted from the water content in the soil sample after 24hours draining of the waterlogged sample using filter-paper. Soil pit was done next to each plot (within the same SDFs) to measure the depth of organic horizon – horizon A and transient A and B horizon (S_{org}) [cm].

The altitude of the plot was taken from the map (1 : 10000). The altitude corresponds with the climatic conditions (Prach and Řehounková 2006), because the mean temperature and precipitation depend on the altitude. The study area is relatively small and therefore we can suppose that the climatic conditions are at most influenced by the altitude of the plot.

I determined the orientation (using compass) and slope (visual estimation) for all plots. I calculated the heat index to south-south west (H_{ssw}):

$$H_{SSW} = \cos(\text{exposition} - 202.5°) \times \text{tg}(\text{slope})$$

For the basic statistics of the site-dependent factors see Table 12.

All field observations were carried out in 2004 and 2005.

Data analysis

Species found at more than 33% of the plots were used for statistical analyses.

General Linear Models (*GLM*) in the CanoDraw v. 4.0 were used to test the influence of the following factors on the species abundance: 1) character of the SDF: A_a, A_{max}, E_3, D, P_5, P_{120}; 2) climatic characteristics: altitude, H_{SSW}; 3) soil conditions: pH_s, C_{org}, S_{org}, BR_s, R_s, *RWC*.

Poisson distribution of the data was used, because the link function of this distribution is “Log” function, which is recommended for the counts and frequency data (Lepš and Šmilauer 2003, p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using Akaike Information Criterion (Lepš and Šmilauer 2003).

Because many factors were involved in the study according to the number of plots, the *GLM* were fitted separately for particular factor.

Table 22. Species listed in more than 33% plots.

	Frequency **[%]**	**Mean abundance** **[%] ± SD**	**Abundance o.p.** **[%]**	**Maximal abundance** **[%]**
Achillea millefolium	67	0.6±0.79	0.9	5
Aegopodium podagraria	46	1.6±2.86	3.5	10
Agrostis capillaris	92	7.9±7.77	8.7	25
Anthriscus sylvestris	44	0.4±0.86	0.9	5
Arrhenatherum elatius	44	1.6±3.69	3.6	15
Avenella flexuosa	77	5.6±7.06	7.3	25
Campanula patula	38	0.2±0.31	0.5	1
Clinopodium vulgare	44	1.5±2.62	3.4	10
Dactylis glomerata	73	0.6±0.80	0.9	5
Euphorbia cyparissias	46	0.7±1.40	1.6	8
Fragaria vesca	48	1.4±3.36	2.9	20
Galeopsis tetrahit	54	1.3±5.48	2.5	38
Galium mollugo agg.	83	1.3±1.88	1.6	8
Galium uliginosum	44	0.4±0.56	0.9	2
Holcus mollis	85	7.8±7.60	9.1	35
Hypericum maculatum	79	0.8±1.26	1.0	8
Knautia arvensis	44	0.3±0.45	0.8	2
Phleum pratense	44	0.4±0.64	1.0	3
Poa angustifolia	44	0.7±1.57	1.5	10
Potentilla erecta	56	0.7±1.16	1.2	5
Ranunculus acris	48	0.3±0.37	0.6	1
Rubus idaeus	54	1.1±1.99	2.0	8
Rumex acetosa	38	0.1±0.12	0.3	0.25
Stellaria graminea	54	0.5±0.83	0.9	4
Urtica dioica	44	0.6±1.60	1.3	10
Vaccinium myrtillus	42	3.0±6.59	7.3	25
Veronica chamaedrys	90	1.4±1.68	1.6	8
Veronica officinalis	44	0.4±0.52	0.8	2
Viola riviniana	38	0.4±0.67	1.1	3

Abundance o.p. – abundance of the species per occupied plot, SD – standard deviation.

Tabulka 22. Druhy zaznamenané na více než třetině ploch. Frequency – procento obsazených ploch, Mean abundance – průměrná pokryvnost, SD – směrodatná odchylka, Abundance o.p. - průměrná pokryvnost na obsazené ploše, Maximal abundance – maximální pokryvnost.

Results

In total, 161vascular plant species were listed in the herb layer, on average 32±8.6 species (range 8-51) at the plot (100 m^2). The average Shannon-Wiener index of diversity was found to be 2.6±0.60 (range 0.4-3.5). Almost one quarter (23%) of the species were found to be only at one plot, while only 29 species (18%) were present at more than 33% of the plots. The following species were most common: *Agrostis capillaris* L., *Veronica chamaedrys* L., *Holcus mollis* L. and *Gallium mollugo* agg. L. (present at more than 80% of the plots), and the following species were most abundant: *Holcus mollis*, *Agrostis capillaris*, *Avenella flexuosa* (L.) Drejer and *Vaccinium myrtillus* L. (abundance >7% per occupied plot). In general, the abundance of the species was low for most of the species (Table 22).

Most of the diagnostic and constant species were species related to the grassland vegetation (33 out of 161 species), i.e., seven diagnostic and fourteen constant species of the *Arrhenatherion elatioris* alliance, six diagnostic and fourteen constant species of the *Polygono bistortae-Trisetion flavescentis* alliance, and six diagnostic and fourteen constant species of the *Violion caninae* alliance were found. Only ten (out of 161 species) were related to the forest vegetation, i.e., one diagnostic and six constant species of the *Dentario enneaphylli-Fagetum* association and *Luzulo-Fagion* alliance, and three diagnostic species of the *Quercion petreae* alliance. For more detail see Table 23.

The age of the tree-layer significantly influenced one fifth of the species. *Arrhenatherum elatius* (L.) J. Presl and C. Presl surprisingly increased with the duration of the tree-layer (Fig. 28a, b). *Hypericum maculatum* Crantz, *Veronica chamaedrys* (Fig. 28a, b) and *Fragaria vesca* (only A_a, Fig. 28a) were more abundant in both young and old SDFs, while *Vaccinium myrtillus* (species typical for forest vegetation) was related to the older growths (Fig. 28a, b). *Galeopsis tetrahit* L. preferred medium aged SDFs (optimum of A_{max} 36 years; Fig. 28b).

The abundance of the tree-layer decreased the abundance of *Galeopsis tetrahit* and *Gallium uliginosum* L. (species typical for ruderalised stands; Fig. 28c). *Urtica dioica* L. preferred 21% abundance of the tree-layer (Fig. 28c).

The higher proportion of deciduous trees in the tree-layer increased the abundance of *Galeopsis tetrahit* (Fig. 28d) and *Knautia arvensis* (L.) Coulter (optimum 88%; Fig. 28d), while *Veronica officinalis* L. preferred mixed SDFs (Fig. 28d). For more detail see Table 24.

Several species were related to the climatic conditions. *Anthriscus sylvestris* (L.) Hoffm. and *Vaccinium myrtillus* decreased with the altitude, while *Arrhenatherum elatius*, *Clinopodium vulgare* L. and *Euphorbia cyparissias* L. preferred medium altitudes (Fig. 29a). The *Arrhenatherum elatius*, *Avenella flexuosa* and *Galeopsis tetrahit* species preferred the SDFs more oriented toward the SE-S-SW, while *Clinopodium vulgare*, *Galium mollugo* agg. and *Aegopodium podagraria* L. preferred the SDFs more oriented toward NE-N-NW (Fig. 29b).

Table 23. Species related to the grassland or forest vegetation.

	A.e.	P-T	V.c.	F.	Q.p.	Ab. [%]	Ab.op [%]	F [%]
Achillea millefolium	C	C	C			0.63	0.94	66.7
Agrostis capillaris		D	D			7.94	8.66	91.7
Alchemilla sp.	C	D	C			0.06	0.69	8.3
Alopecurus pratensis	C	C				0.05	0.83	6.3
Arrhenatherum elatius	D					1.58	3.61	43.8
Athyrium filix-femina				C		0.04	0.50	8.3
Avenella flexuosa		C				5.63	7.30	77.1
Bistorta major		D				0.03	0.50	6.3
Campanula patula	D					0.20	0.54	37.5
Campanula rotundifolia		D	C		D	0.11	0.58	18.8
Dactylis glomerata	D	C				0.65	0.89	72.9
Deschampsia cespitosa		C				0.04	0.67	6.3
Dryoopteris filix-mas				C		0.02	0.25	8.3
Festuca rubra agg.	C	D	D			0.46	1.57	29.2
Galium mollugo	D					1.24	1.57	79.2
Holcus lanatus	C					0.01	0.25	4.2
Hypericum maculatum		D				0.81	1.02	79.2
Knautia arvensis	D					0.33	0.75	43.8
Lathyrus pratensis	C					0.07	0.44	16.7
Leucanthemum vulgare	D	C	C			0.04	0.50	8.3
Lotus corniculatus	C		C			0.07	0.70	10.4
Luzula campestris			D			0.02	0.25	6.3
Luzula luzuloides					D	0.58	1.98	29.2
Mercurialis perennis				C		0.01	0.25	2.1
Mycelis muralis				C		0.10	1.25	8.3
Nardus stricta		C	D			0.05	0.75	6.3
Oxalis acetosella				C		0.19	1.16	16.7
Pimpinella saxifraga			C			0.13	0.52	25.0
Plantago lanceolata	D		C			0.06	0.69	8.3
Poa pratensis	C	C				0.05	0.45	10.4
Potentilla erecta		C	D			0.69	1.22	56.3
Ranunculus acris	C	C	C			0.29	0.61	47.9
Rumex acetosa	C	C	C			0.09	0.25	37.5
Senecio ovatus				C		0.86	2.75	31.3
Taraxacum officinale agg.	C					0.07	0.39	18.8
Thymus sp.			D			0.02	0.75	2.1
Trifolium pratense	C		C			0.06	0.55	10.4
Trifolium repens	C	C	C			0.05	0.83	6.3
Vaccinium myrtillus				D		3.02	7.25	42.0
Veronica chamaedrys	C	C	C			1.42	1.58	89.6
Veronica officinalis					D	0.36	0.83	43.8
Vicia cracca		C				0.18	0.65	27.1

A.e. - *Arrhenatherion elatioris*, P-T - *Polygono bistortae-Trisetion flavescentis*, V.c. - *Violion caninae*, F. - *Dentario enneaphylli-Fagetum* and *Luzulo-Fagion*, Q.p. - *Quercion petreae*; Ab. – mean abundance, Ab. op – mean abundance per occupied plot, F - Frequency; D – diagnostic species, C – constant species.

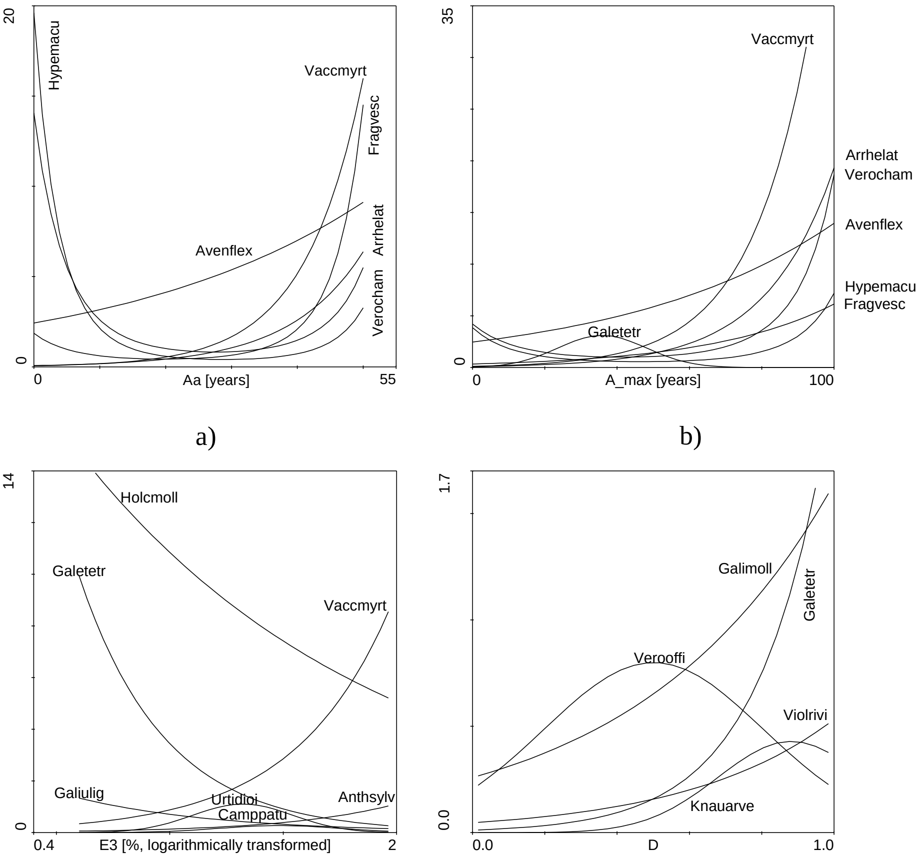
Tabulka 23. Druhy typické pro luční a lesní vegetaci. A.e. - *Arrhenatherion elatioris,* P-T - *Polygolo bistortae-Trisetion flavescentis,* V.c. - *Violion caninae,* F. - *Dentario enneaphylli-Fagetum* a *Luzulo-Fagion,* Q.p. - *Quercion petreae*; Ab. – průměrná pokryvnost, Ab. op - průměrná pokryvnost na obsazené ploše, F - procento obsazených ploch; D - diagnostický druh, C – konstantní druh.

Table 24. Tree-layer characteristics influencing frequent species (*GLM*).

	A_a		**A_{max}**		**E_3**		**D**	
	M	var.	M	var.	M	var.	M	var.
Anthriscus sylvestris	×		×		L↑	7	×	
Arrhenatherum elatius	L↑	19	L↑	24	×		×	
Avenella flexuosa	L↑	5	L↑	6	×		×	
Campanula patula	×		×		Q∩	7	×	
Fragaria vesca	Q∪	23	L↑	9	×		×	
Galeopsis tetrahit	×		Q∩	13	L↓	16	L↑	10
Galium mollugo	×		×		×		L↑	8
Galium uliginosum	×		×		L↓	10	×	
Holcus mollis	×		×		L↓	4	×	
Hypericum maculatum	Q∪	19	Q∪	10	×		×	
Knautia arvensis	×		×		×		Q∩	10
Urtica dioica	×		×		Q∩	11	×	
Vaccinium myrtillus	L↑	25	L↑	30	L↑	8	×	
Veronica chamaedrys	Q∪	15	Q∪	14	×		×	
Veronica officinalis	×		×		×		Q∩	13
Viola riviniana	×		×		×		L↑	7

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; A_a/A_{max} - average and maximal age of the tree-layer, E_3 - abundance of the tree-layer (log. transf.), D - proportion of the deciduous trees in the tree-layer.

Tabulka 24. Vliv charakteru stromového patra na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. – vysvětlená variabilita [%]; A_a/A_{max} – průměrný/maximální věk stromového patra, E_3 – pokryvnost stromového patra, D – zastoupení listnatých stromů ve stromovém patře.



a) b)

c) d)

Figure 28. Characteristics of the tree-layer influencing abundance of frequent species (*GLM*): a) average age, b) maximal age of the tree-layer, c) abundance of the tree-layer, d) proportion of deciduous trees in the tree-layer. Anthsylv - *Anthriscus sylvestris*, Arrhelat – *Arrhenatherum elatius*, Avenflex – *Avenella flexuosa*, Camppatu – *Campanula patula*, Fragvesc - *Fragaria vesca*, Galetetr – *Galeopsis tetrahit*, Galimoll – *Galium mollugo* agg., Galiulig – *Galium uliginosum*, Holcmoll - *Holcus mollis*, Hypemacu - *Hypericum maculatum*, Knauarve – *Knautia arvensis*, Urtidioi – *Urtica dioica*, Vaccmyrt – *Vaccinium myrtillus*, Verocham - *Veronica chamaedrys*, Verooffi – *Veronica officinalis*, Violrivi – *Viola riviniana*.

Obrázek 28. Vliv charakteru stromového patra na pokryvnost hojných druhů (*GLM*): a) průměrný věk stromového patra, b) maximální věk stromového patra, c) pokryvnost stromového patra, d) podíl listnatých stromů ve stromovém patře.

The relative irradiance at the 5 cm above ground influenced more species than the relative irradiance at the 120 cm above ground (Table 25). Most species related to the P_{120} preferred medium irradiated SDFs – *Rubus idaeus* L. optimum 14%, *Fragaria vesca* optimum 18%, *Galium uliginosum* optimum 24%, *Potentilla erecta* L. optimum 29% (Fig. 29c, Table 12, 25). *Aegopodium podagraria* and *Knautia pratensis* preferred approximately 4% of relative irradiance at the 5 cm above ground, *Anthriscus sylvestris* preferred approximately 6%, *Stellaria graminea* L. preferred approximately 9%, *Arrhenatherum elatius*, *Euphorbia cyparissias* and *Vaccinium myrtillus* preferred approximately 12%, and *Fragaria vesca* did approximately 18%. The abundance of *Dactylis glomerata* L. decreased with the P_5 (Fig. 29d).

Rock fragment content significantly influenced more than one third of the species (Table 26). *Euphorbia cyparissias* and *Vaccinium myrtillus* preferred higher rock fragment content, while *Galeopsis tetrahit* preferred lower content (Fig. 30a). Several species preferred medium rock fragment content: *Anthriscus sylvestris* (optimum 48%), *Fragaria vesca* (optimum 48%) and *Poa angustifolia* L. (optimum 39%). For more detail see Fig. 30a and Table 26.

Medium values of RWC preferred *Hypericum maculatum* (optimum 18%) and *Potentilla erecta* (optimum 14%), while *Rubus idaeus* avoided the medium values of RWC (Fig. 30b).

All the species significantly influenced by the basal respiration preferred medium or higher values (Table 26, 12, Fig. 31a), especially the following species: *Achillea millefolium* L., *Avenella flexuosa* and *Vaccinium myrtillus* (optimum 4.53 μg C-CO_2.g^{-1}.hod^{-1}).

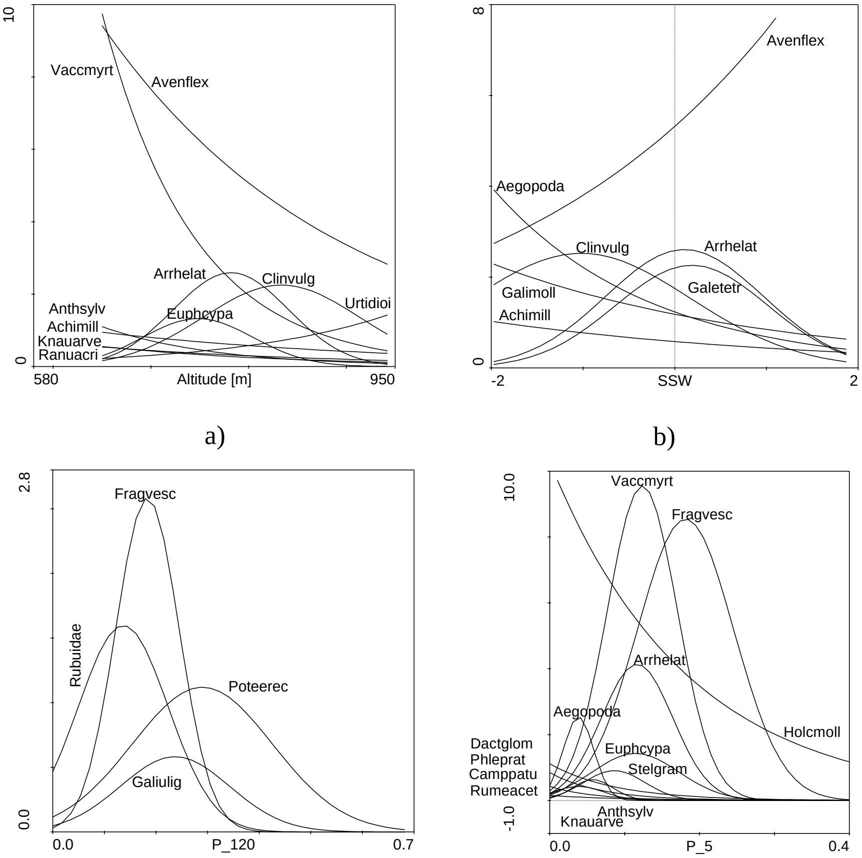
Most of the species that avoided medium or low soil reaction were species typical for grasslands, such as *Dactylis glomerata*, *Hypericum maculatum*, *Poa angustifolia* and *Veronica chamaedrys*. For more detail see Table 26, Fig. 31b.

Table 25. Factors influencing frequent species (*GLM*).

	Altitude		**H_{SSW}**		**P_{120}**		**P_5**	
	M	var.	M	var.	M	var.	M	var.
Aegopodium podagraria	×		L↓	18	×		Q∩	18
Achillea millefolium	L↓	4	L↓	9	×		×	
Anthriscus sylvestris	L↓	14	×		×		Q∩	11
Arrhenatherum elatius	Q∩	10	Q∩	19	×		Q∩	15
Avenella flexuosa	L↓	6	L↑	10	×		×	
Campanula patula	×		×		×		L↓	9
Clinopodium vulgare	Q∩	11	Q∩	13	×		×	
Dactylis glomerata	×		×		×		L↓	11
Euphorbia cyparissias	Q∩	17	×		×		Q∩	10
Fragaria vesca	×		×		Q∩	17	Q∩	31
Galeopsis tetrahit	×		Q∩	15	×		×	
Galium mollugo agg.	×		L↓	10	×		×	
Galium uliginosum	×		×		Q∩	11	×	
Holcus mollis	×		×		×		L↓	5
Knautia arvensis	L↓	4	×		×		Q∩	13
Phleum pratense	×		×		×		L↓	9
Potentilla erecta	×		×		Q∩	10	×	
Ranunculus acris	L↓	8	×		×		×	
Rubus idaeus	×		×		Q∩	15	×	
Rumex acetosa	×		×		×		L↓	6
Stellaria graminea	×		×		×		Q∩	12
Urtica dioica	L↑	6	×		×		×	
Vaccinium myrtillus	L↓	16	×		×		Q∩	21

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]; H_{SSW} - Heat to the SSW, P_{120}/P_5 - relative irradiance at the 120/5 cm above ground.

Tabulka 25. Faktory ovlivňující pokryvnost hojných druhů (*GLM*). M: L – lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. - vysvětlená variabilita [%]; Altitude – nadmořská výška, H_{SSW} – sklon plochy k JJZ, P_{120}/P_5 – relativní ozářenost ve 120/5 cm.



a) b)

c) d)

Figure 29. Factors influencing abundance of frequent species (*GLM*): a) altitude, b) heat to the SSW, c) relative irradiance at the 120 cm above ground, d) at the 5 cm above ground. Achimill – *Achillea millefolium*, Aegopoda – *Aegopodium podagraria*, Anthsylv - *Anthriscus sylvestris*, Arrhelat – *Arrhenatherum elatius*, Avenflex - *Avenella flexuosa*, Camppatu – *Campanula patula*, Clinvulg - *Clinopodium vulgare*, Dactglom – *Dactylis glomerata*, Euphcypa - *Euphorbia cyparissias*, Fragvesc - *Fragaria vesca*, Galetetr – *Galeopsis tetrahit*, Galimoll – *Galium mollugo* agg., Galiulig – *Galium uliginosum*, Holcmoll - *Holcus mollis*, Knauarve – *Knautia arvensis*, Phleprat – *Phleum pratense*, Poteerec – *Potentilla erecta*, Ranuacri – *Ranunculus acris*, Rubuidae – *Rubus idaeus*, Rumeacet – *Rumex acetosa*, Stelgram – *Stellaria graminea*, Urtidioi – *Urtica dioica*, Vaccmyrt – *Vaccinium myrtillus*.

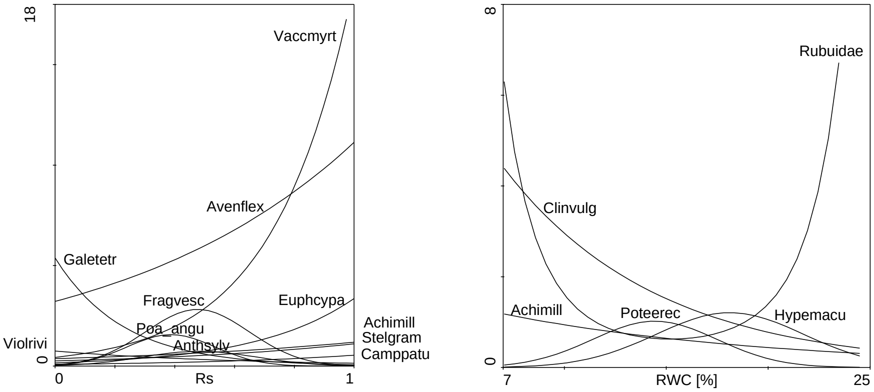
Obrázek 29. Vliv vybraných faktorů na pokryvnosti hojných druhů (*GLM*): a) nadmořská výška, b) sklon k JJZ, c) relativní ozářenost ve 120 cm, d) v 5 cm.

Table 26. Soil characteristics influencing frequent species (*GLM*).

	R_S		RWC		BR_s.		pH_s		C_{org}		S_{org}	
	M	v	M	v	M	v	M	v	M	v	M	v
A. millefolium	L↑	6	L↓	5	Q∪	29	×		×		×	
A. capillaris	×		×		×		L↑	4	×		×	
A. sylvestris	Q∩	12	×		×		×		×		×	
A. elatius	×		×		×		×		×		L↓	8
A. flexuosa	L↑	6	×		L↑	4	×		×		×	
C. patula	L↑	8	×		×		Q∪	8	×		×	
C. vulgare	×		L↓	8	×		×		Q∩	14	×	
D. glomerata	×		×		×		Q∪	11	×		×	
E. cyparissias	L↑	19	×		×		×		L↓	9	×	
F. vesca	Q∩	15	×		×		×		×		Q∩	11
G. tetrahit	L↓	17	×		×		×		Q∩	13	Q∪	61
H. mollis	×		×		Q∩	14	×		L↓	4	Q∪	14
H. maculatum	×		Q∩	16	×		Q∪	46	L↓	7	×	
K. arvensis	×		×		×		L↑	5	×		Q∪	9
P. pratense	×		×		×		×		L↓	6	×	
P. angustifolia	Q∩	18	×		×		Q∪	10	L↑	7	×	
P. erecta	×		Q∩	14	L↑	7	×		Q∩	10	×	
R. idaeus	×		Q∪	23	×		L↑	8	×		×	
R. acetosa	×		×		L↑	7	×		×		×	
S. graminea	L↑	6	×		×		×		×		×	
V. myrtillus	L↑	21	×		Q∩	32	×		×		×	
V. chamaedrys	×		×		×		L↑	24	L↓	16	×	
V. officinalis	×		×		L↑	4	×		×		×	
V. riviniana	L↓	6	×		L↑	5	×		×		×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, v - explained variability [%]; R_S – rock fragment content [%], RWC - retention water capacity [%], BR_s - basal respiration [µg C-CO_2.g^{-1}.hod^{-1}], C_{org} - organic matter content [%], S_{org} - depth of the organic horizon [cm].

Tabulka 26. Půdní podmínky ovlivňující pokryvnost hojných druhů (*GLM*). M: L – lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, v - vysvětlená variabilita [%]; R_s - skeletovitost [%], RWC – retenční vodní kapacita [%], BR_s - bazální respirace [µg C-CO_2.g^{-1}.hod^{-1}], C_{org} – obsah organické hmoty v půdě [%], S_{org} - hloubka organického půdního horizontu [cm].



a) b)

Figure 30. Factors influencing abundance of frequent species (*GLM*): a) proportion of rock fragment content, b) retention water capacity. Achimill – *Achillea millefolium*, Anthsylv - *Anthriscus sylvestris*, Avenflex – *Avenella flexuosa*, Camppatu – *Campanula patula*, Clinvulg - *Clinopodium vulgare*, Euphcypa - *Euphorbia cyparissias*, Fragvesc - *Fragaria vesca*, Galetetr – *Galeopsis tetrahit*, Hypemacu – *Hypericum maculatum*, Poa_angu – *Poa angustifolia*, Poteerec – *Potentilla erecta*, Rubuidae – *Rubus idaeus*, Stelgram – *Stellaria graminea*, Vaccmyrt – *Vaccinium myrtillus*, Violrivi – *Viola riviniana*.

Obrázek 30. Vliv vybraných faktorů na pokryvnosti hojných druhů (*GLM*): a) skeletovitost, b) retenční vodní kapacita.

Species influenced by the organic matter content at most preferred medium values (*Clinopodium vulgare* optimum 9.1%, *Galeopsis tetrahit* optimum 8.7%, *Potentilla erecta* optimum 10.3%), and *Veronica chamaedrys* preferred lower values (Table 26, Fig. 31c).

Some abundance of species was higher in low or deep soils (e.g., *Galeopsis tetrahit*, *Holcus mollis*), and *Fragaria vesca* preferred medium deep soils (optimum 39 cm). For more detail see Table 26, Fig 31d.

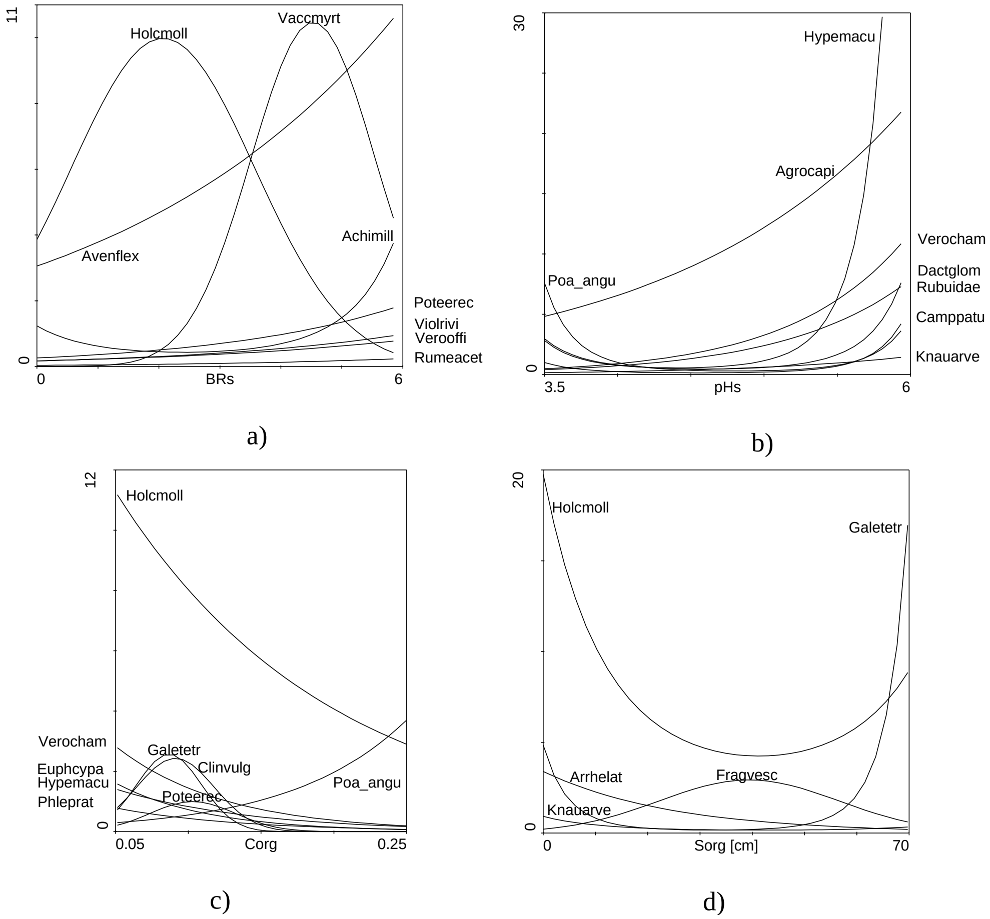


Figure 31. Factors influencing abundance of frequent species (*GLM*): a) basal respiration [µg C-CO$_2$.g^{-1}.hod^{-1}], b) soil reaction, c) organic matter content, d) depth of the organic soil horizon. Achimill – *Achillea millefolium*, Agrocapi – *Agrostis capillaris*, Arrhelat – *Arrhenatherum elatius*, Avenflex – *Avenella flexuosa*, Camppatu – *Campanula patula*, Clinvulg - *Clinopodium vulgare*, Dactglom - *Dactylis glomerata*, Euphcypa - *Euphorbia cyparissias*, Fragvesc - *Fragaria vesca*, Galetetr – *Galeopsis tetrahit*, Holcmoll - *Holcus mollis*, Hypemacu – *Hypericum maculatum*, Knauarve – *Knautia arvensis*, Phleprat - *Phleum pratense*, Poa_angu – *Poa angustifolia*, Poteerec - *Potentilla erecta*, Rubuidae - *Rubus idaeus*, Rumeacet – *Rumex acetosa*, Vaccmyrt – *Vaccinium myrtillus*, Verocham – *Veronica chamaedrys*, Verooffi - *Veronica officinalis*, Violrivi – *Viola riviniana*.

Obrázek 31. Vliv vybraných faktorů na pokryvnosti hojných druhů (*GLM*). a) bazální respirace [µg C-CO$_2$.g^{-1}.hod^{-1}], b) půdní reakce, c) obsah organické hmoty v půdě, d) hloubka organického půdního horizontu.

Discussion

The total number of species (161, 32 per plot) listed in the SDF's herb layer in this study corresponds with findings of other studies dealing with succession, e.g., Dzwonko and Loster (1992) found 153 plant species in 27 recent forests in Poland, Deckers et al. (2004) listed 198 species in 511 hedgerows in Belgium, and Cousins and Aggemyr (2008) found 135 species in twenty grazed ex-fields.

Although a decrease in diversity for abandoned grassland was reported, e.g., Prach et al. (1996) found 14 vascular plant species in long-term abandoned mesic grassland in the Šumava Mountains (100 m^2), it was not observed in this study. The Shannon-Wiener index of diversity corresponds to the mean values typical for grassland in the area, e.g., Zelený et al. (2001) reported values between 1.9 and 2.6 for mowed grassland of the alliance *Polygono–Trisetion*, and Schusserová (2003) found on average value 2.7 for mowed mesic grassland within the studied area. The number of species was also relatively high in comparison to the number of species found in the forests, e.g., Schusserová and Šmahel (2000) found on average 17.5 species per releve in the Medvědí hora Nature Monument within the studied area; Prach et al. (1996) reported only 10 species (100 m^2) in acidophilous beech forest at high altitudes in the Šumava Mountains; and Moravec et al. (2000) reported 28 species as an average number in the herb layer of the *Dentario enneaphylli-Fagetum*, which is the most common type of the potential natural vegetation in the studied area (Neuhäuslová 1998).

Many species were found to be present only at one plot, and only 17% of the species were more common; for a similar finding from recent forests in Germany see Wulf (2004).

All the species present at more than 33% of the plots are common species in the area (for similar finding see also Bernacki 2004).

All the most common (present at more than 80% plots) were species typical for grassland, and most of the species related to the grassland/forest vegetation were diagnostic or constant species of the grassland vegetation (Table 23). Only some typical forest species were able to establish themselves in the SDFs, but they were usually low abundant. Ferns and *Vaccinium myrtillus* were the only more abundant typical forest species. Others relatively frequent included *Oxalis acetosella* L. However, some forest species typical for oak-beech or beech forests were also listed, such as *Asarum europaeum* L., *Geranium robertianum* L., *Mercurialis perennis* L. and *Mycelis muralis* L. This is in line with findings other studies, e.g., Dzwonko (2001) found that even after more than 70 years, the number of forest species was lower in recent forests than it was in the ancient forest. In general, these findings can be attributed to the bad colonising capacity of the forest species (e.g.; Brunet and von Oheimb 1998a; Butaye et al. 2002), which was proved also by seed sowing experiments (e.g., Ehrlén and Eriksson 2000; Ehrlén et al. 2006).

Most of the common species can be classed as follows: 1) clonal grasses (*Agrostis capillaris*, *Arrhenatherum elatius*, *Avenella flexuosa*, *Holcus mollis*, *Dactylis glomerata*, *Phleum pratense* L.) – species typical for grasslands or grassland-forest ecotones, 2) herbs typical for grassland-forest ecotones (*Clinopodium vulgare*, *Euphorbia cyparissias*, *Fragaria vesca*, *Galium uliginosum*, *Potentilla erecta*, *Veronica officinalis*, *Viola riviniana*), 3) herbs typical for grasslands (*Campanula patula* L., *Knautia arvensis*, *Ranunculus acris* L., *Stellaria graminea*, *Veronica chamaedrys*), 4) species typical for sites rich in nutrients (*Aegopodium podagraria*, *Anthriscus sylvestris*, *Galium mollugo* agg., *Urtica dioica*).

The first group contains many good competitors, which can slow down or block the forest succession (e.g., Dzwonko 1993; Prach 1987). Clonal plants were also reported as common dominants in the intermediate stages of succession (e.g., Kahmen and Poschlod 2004; Prach and Pyšek 1994a) and *Arrhenatherum elatius* was reported as the second one most successful species found in the study of Prach and

Pyšek (1999). Moreover, the increase in abundance of clonal grasses with the age of the tree-layer was observed. It may be caused due to the self-thinning effect of the tree-layer, but their abundance was not related to the abundance of the tree-layer. The relatively open canopy of the tree-layer is suitable for the competitive strong species, and it may slow down the rate of the succession. Graminoids dominating the herb layer of recent forest was reported also in other studies (e.g., Dzwonko 2001).

The presence of species typical for forest-grassland ecotones is not surprising, because many SDFs are semi-open mostly deciduous growths, which are similar to the grassland-forest ecotones. However Bruelheide (2000) did not observe the ability of species from the transplanted soil block with the *Violion caninae* vegetation to colonise the present poor vegetation. The results of this study indicate an opposite finding, that in a suitable microsite, the species typical for *Violion caninae* are able to establish. The soil conditions of most of the plots were similar to soil condition of this type of vegetation, and they were intermediate for studied factors between values typical for grassland and forest soil characteristics in the studied area (for comparison see: Kopáček et al. 2002; Kopáčková 2002; Schusserová 2003). This is in line with the findings in other studies. The increase in organic matter content and decrease in soil reaction was also reported for successional stages in other studies (e.g., Matlack 2009; Richter et al. 1994), however opposite finding also was reported (von Oheimb et al. 2008).

Surprisingly many grassland herb species (from unnamed e.g., *Hypochaeris radicata* L., *Leontodon autumnalis* L., L*eucanthemum vulgare* Lamk.*, Lychnis flos-cuculi* L.*, Rhinanthus minor* L.*, Tragopogon pratensis* L.) are able to survive in the SDFs, or they are constantly supplemented from the source populations growing in surrounding grassland. However, their abundance is low. These species were also found to be poor colonisers in many studies (e.g., Stampfli and Zeiter 1999), and these species are often missing in the seed bank (e.g., Bossuyt and Hermy 2001; Kalamees and Zobel 1997; Milberg 1995). Therefore, their survival from the time before the succession seems to be more probable.

All the above-mentioned findings indicate that the changes in the herb layer of SDFs from grassland vegetation toward the forest vegetation are slow and that the time needed for forest herb layer establishment will be long. This was predicted also in other studies, e.g., Jacquemyn et al. (2001) estimated that herb layer colonisation of planted forests can take 200 years.

All the three groups of site-dependent factors influenced the frequent species abundance. There were no big differences between the group of studied factors concerning the relation to the frequent species abundance. The climatic conditions were found to be important for 29% of the tested relations and they explained on average 11% of the variability (for significant relations), while characteristics of the tree-layer were important for 24% relations, and explained on average 13% of the variability, and soil conditions were important for 26% of relations and explained on average 13%. All the studied factors were reported to be important in the succession (for review see Prach and Řehounková 2006).

Each species was influenced by different factors, e.g., *Arrhenatherum elatius* was related especially to the age of the tree-layer (which surprisingly increased its abundance) and to climatic conditions described by altitude and exposure, while *Achillea millefolium* was related especially to the soil conditions. Different responses of the species to environmental factors were found in many studies and also for species with responses which were expected to be similar (e.g., Deckers et al. 2004; Verheyen and Hermy 2004). This finding may cause low predictability of the changes in the vegetation (for a similar assumption see, e.g., Lawton 1999).

Herb layer species composition of the spontaneously developed forests: Influence of the context-dependent factors on the frequent species abundance

Druhové složení bylinného patra porostů náletových dřevin: vliv na kontextu závislých faktorů na pokryvnost hojných druhů

Abstract

The influence of context-dependent factors (surrounding vegetation, history and characteristics of the spontaneously developed forests; SDF) on the frequent herb layer species abundance was studied in the SDFs in a mountainous area in the Czech Republic.

Forty-seven permanent plots (100 m^2) were fixed in the SDFs on mesic stands and the species composition of the herb layer was listed. The following context-dependent factors were considered: (1) SDF characteristics: area, shape, position within the SDF; (2) surrounding vegetation: fields, grassland, forests, SDF, "other" land cover (in the 100, 200 and 300 m surroundings); (3) vegetation cover in 1952, 1966, 1983. The influence of the context-dependent factors on the frequent species abundance was tested using General Linear Models (*GLM*).

Each frequent SDF species was influenced by the context-dependent factors (although different factors were found to be important for different species), and each context-dependent factor significantly influenced the frequent species abundance (although, the amount of explained variability differed). The historical vegetation cover was the most important group of factors influencing the frequent species abundance, followed by the character of the SDF and surrounding vegetation. The latest historical vegetation cover (52 years BP) was found to be more important than the other dates. The explained variability was relatively high, i.e., on average 14% for the historical vegetation cover (for significant relations), 14% for the surrounding vegetation, and 12% for the character of the SDF.

Shrnutí

V horských oblastech České republiky byl studován vliv na kontextu závislých faktorů na pokryvnost druhů hojných v bylinném patře porostů náletových dřevin (SDFs).

Na 47 trvalých plochách (100 m^2) bylo zjištěno druhové složení bylinného patra. Pomocí zobecněných lineárních modelů (*GLM*) byl testován vliv následujících na kontextu závislých faktorů: (1) charakteristik porostu náletových dřevin: velikost, tvar, pozice uvnitř SDF; (2) vegetace v okolí: pole, louka, les, SDF, ostatní (ve vzdálenosti 100, 200 a 300 m); (3) vegetační kryt v roce 1952, 1966, 1983.

Každý druh hojný v bylinném patře porostů náletových dřevin byl ovlivněn některým z na kontextu závislých faktorů (ačkoli různé druhy byly ovlivněny různými faktory) a všechny studované faktory průkazně ovlivňovaly pokryvnost druhů hojných v bylinném patře (procento vysvětlené variability bylo různé pro různé vztahy). Vegetační kryt v minulosti byl nejvýznamnější skupinou ovlivňující pokryvnost hojných druhů, následován charakteristikami SDF a vegetací v okolí. Vegetační kryt v nejdále studované minulosti (52 let) byl významnější než vegetační kryt v termínech blíže současnosti. Procento vysvětlené variability bylo relativně vysoké – průměrně 14 % pro vegetační kryt v minulosti (pro statisticky významné vztahy), 14 % pro okolní vegetaci a 12 % pro charakter SDF.

Introduction

The socio-economic changes in recent decades have also impacted the European vegetation cover. In general, there has been an increase in recent forests and a decrease in agricultural land, especially in less favourable areas (e.g., Hamre et al. 2007; Helm et al. 2006). The recent forests have been planted (e.g., Wulf 2004) or established spontaneously on former agricultural land (e.g., Prach and Pyšek 1994b). The second type I name spontaneously developed forests (SDFs) to distinguish them from the planted forests.

The tree layer of the SDFs develops usually within 30-40 years and definitely closes after 60-80 years (Flinn and Vellend 2005), but many factors may influence the rate of succession (see Prach and Pyšek 1994b). The tree layer of SDFs on mesic stands is mostly dominated by birch (*Betula pendula* Roth) in Central Europe (Prach 1994; Prach and Pyšek 1994b).

The herb-layer colonisation of secondary forests by woodland species was found to be very slow because the forest herb species are poor colonisers (Peterken and Game 1984; Whitney and Foster 1988; Wulf

2004). It is assumed that the time needed to reach the terminal stage of succession is long, e.g., Faliński (1988) estimates 350 years for the mesic sequence in the temperate zone in Europe and Flinn and Vellend (2005) estimates several centuries. However, the changes caused by former agricultural activity can influence the species composition for a much longer time period (e.g., Dupouey et al. 2002).

Many site-dependent factors (e.g., climate, water regime, soil conditions) were reported to influence the rate and direction of the changes (e.g., Prach et al. 2007; Řehounková and Prach 2006). The following context-dependent factors were found to be important: dispersion limitation (e.g., Bossuyt et al. 1999; Brunet and von Oheimb 1998a; Ehrlén et al. 2006), spatiotemporal changes in the environment (e.g., Dovčiak et al. 2005), history (e.g., Vellend et al. 2007), surrounding vegetation (e.g., Hersperger and Forman 2000), area and shape (e.g., Dzwonko and Loster 1992), position of the plot within the patch (e.g., Honnay et al. 2002b), or stochastic events (Brokaw and Busing 2000; Christensen and Peet 1984).

The dispersal limitation of forest herb species was found to be important for recent forests indirectly by studying the herb layer (mostly in planted forests). For example, Bossuyt et al. (1999) found the rate of dispersion of forest herbs between <0.05 and 1.65 m.year^{-1}, Brunet and von Oheimb (1998a) reported a period of 70 years to necessary for forest herb species to spread a distance of 30-35 m from the source population. The seed limitation was also proved by seed addition experiments, e.g., Ehrlén and Eriksson (2000) and Ehrlén et al. (2006) sowed six herb species into planted recent forests and observed their recruitment, and found none of the studied soil factors to be important for seedling establishment. The zoochorous species were found to be the best colonisers, and the anemochorous species were found to be relatively good colonisers, while myrmecochorous species and species not adapted to the type of distribution were found to be poor colonisers (Matlack 1994).

History was found to be a very important factor influencing the species composition of the herb layer in recent forests. The longer the duration of the tree layer was, the more typical forest herbs were found to be able to colonise the herb layer (e.g., Jacquemyn et al. 2001), and the influence of the tree layer on the soil conditions was reported (e.g., Persson et al. 1987). The former agricultural activities may influence the soil conditions for a long period, especially when the agricultural use was long-term (e.g., Honnay et al. 1999).

Surrounding vegetation is related to the seed source of the forest herb layer. The isolation of recent forests was found to be the most important factor influencing the presence of forest species in the herb layer (e.g., Brunet and von Oheimb 1998a; Butaye et al. 2001), and the proportion of shrub vegetation was also found to influence the grassland species in the herb layer (Hersperger and Forman 2003).

The area of the recent forest was found to be an important characteristic influencing the species composition and richness (e.g., Hersperger and Forman 2003). The shape of the recent forest was also important, but biased results were reported regarding the relation of forest species and the shape of the recent forest (for review see Honnay et al. 2002a).

Unfortunately, most of the studies focusing on the influence of context-dependent factors on the herb layer of recent forests in the Europe were carried out in planted forests (e.g., Bossuyt et al. 1999; Jacquemyn et al. 2001; Verheyn and Hermy 2004; for SDFs see e.g., Dzwonko 2001; Schreiber 1995; Vojta 2007).

This study has been focused on the SDFs and the influence of context-dependent factors (surrounding vegetation, history, area, shape and position within the SDF) on the frequent species in the herb-layer. The SDFs were on mesic stands in a mountainous area in the Czech Republic.

The following questions were considered:

1. Are the frequent herb layer species in the SDFs influenced by the following context dependent factors: i) the surrounding vegetation cover; ii) the historical vegetation cover, or by iii) the characteristics of the SDF: area, shape of the SDF or position of the plot within the SDF?
2. How much are the context-dependent factors important for the frequent species abundance?

Methods

Study area

Southern part of the Czech Republic (40°35-38´ N, 14°11-17´ E), altitude between 665 and 940 m. Climatic conditions moderately oceanic between the warm and cold type (climatic regions MT 3-Ch 7; Quitt 1971), average year temperature 6.8°C and average year precipitation 718-1003 mm.

I fixed 47 plots of 10 × 10 m in SDFs, which differed in age, altitude and exposition, but all plots were on mesic stand (neither waterlogged nor desiccated, vegetation neither ruderalised nor typical for poor soils). I fixed the plots in such growths, where significant human influence was not recognisable, which were homogenous and large enough. Different age categories given in the study area were equally presented.

The supposed terminal stage of succession is beech forest (*Dentario enneaphylli-Fagetum* association, or transient to *Luzulo albidae-Quercetum petraeae* association; Neuhäuslová 1998).

Present growths were mostly dominated by *Betula pendula*, common trees are also *Picea abies* (L.) Karsten, *Populus tremula* L.; in some cases *Pinus sylvestris* L. or *Fraxinus excelsior* L. were more abundant.

Data collection

Phytocenological releve was taken from all the permanent plots. The species abundance was estimated in percentages of abundance of the species for each layer.

Vegetation map 1 : 10000 (Dostálová unpbl.) redrawn on a slide and digitalized (300dpi colour picture) was used to determine the following context-dependent factors: i) the total area of the SDF (A_{SDF}) [ha]; ii) the *shape* of the SDF, determined as the multiple of the perimeter of a circle with the same area; iii) the position of the plot within the SDF (*centre*), determined as the nearest distance from the centre of the plot to the border of the SDF [m]; iv) the distance to the nearest field (*D_Fi*) [m]; v) the distance to the nearest grassland (*D_Grl*) [m]; vi) the distance to the nearest forest (*D_Fst*) [m]; vii) the proportion of vegetation cover of fields in the 100, 200 and 300 m surrounding (i.e., the round area of a certain semi-diameter with the central point in the centre of the plot) ($Fi_{100/200/300}$); viii) the proportion of grassland in the 100, 200 and 300 m surrounding ($Grl_{100/200/300}$); ix) the proportion of forests in the 100, 200 and 300 m surrounding ($Fst_{100/200/300}$); x) the proportion of SDF in the 100, 200 and 300 m surrounding ($SDF_{100/200/300}$); xi) the proportion of “other” land cover (e.g., building, water) in the 100, 200 and 300 m surrounding ($Ot_{100/200/300}$). Image analysis in the Scion Image for Windows 4.0.3 program was used.

The aerial photos from the Military Geographical and Hydrometeorological Office (Dobruška, Czech Republic) were used to determine the past vegetation cover of the plot. Three sets of photos were available from the vegetation period for the whole study area: 1952 (7th of July, camera RC5-97, focal length 210.0 mm, flying height 5 250 m, 1:25 000); 1966 (1st of May, MRB, 210.11 mm; 3 200 m, 1:12 600), 1967 (25th of June, RC 5a, 209.7 mm, 3 300 m, 1:13 150) and 1983 (8th of June, MRB-9, 88.6 mm, 2 900-3 200 m, 1:28 040). The following vegetation types were distinguished: field (arable land), grassland (meadow, pasture, abandoned grassland), scattered SDF, closed SDF (these types correspond with the supposed successional sere) for the three dates: *1952, 1966, 1983*.

For the basic statistics of context-dependent factors see Table 17.

Statistical analysis

General Linear Models (*GLM*) in the Canodraw v. 4.0 program were used to test the influence of factors on the abundance of species recorded at more than 33% of the plots. In together, 29 species fulfilled this requirement (see Table 22).

The following factors were used in the statistical analysis: (1) SDF characteristics: A_{SDF}, shape, centre; (2) surrounding vegetation: $Fi_{100/200/300}$, $Grl_{100/200/300}$, $Fst_{100/200/300}$, $SDF_{100/200/300}$, $Ot_{100/200/300}$, *D_Fi, D_Grl, D_Fst*; (3) vegetation cover in *1952, 1966, 1983*.

Poisson distribution of the data was used, because the link function of this distribution is “Log” function, which is recommended for the counts and frequency data (Lepš and Šmilauer 2003; p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using Akaike Information Criterion (Lepš and Šmilauer 2003).

Results

Surrounding vegetation

The proportion of fields in surroundings was related to several frequent species abundances, especially to: *Avenella flexuosa* (L.) Drejer, *Euphorbia cyparissias* L., *Phleum pratense* L., *Rubus idaeus* L., *Stellaria graminea* L., *Urtica dioica* L. and *Vaccinium myrtillus* L. were significantly influenced by the factors related to the field vegetation and the explained variability was relatively high. The *Avenella flexuosa* (optima 17%, 22% and19% for Fi_{100}, Fi_{200}, *and* Fi_{300}), *Euphorbia cyparissias* (optima 39% and 45% for Fi_{100} and Fi_{200}), *Galium* *uliginosum* (optima 12% and 13% for Fi_{200}/Fi_{300}) *Stellaria graminea* (optimum 28% for Fi_{100}) and *Vaccinium myrtillus* (optima 21% and 23% for Fi_{200} and Fi_{300}) preferred SDFs that were surrounded by a relatively high proportion of the fields (mean value in the study 5-6%, see Table 17), while *Rubus idaeus* and *Urtica dioica* L. preferred a low abundance of fields in the surroundings (see Table 27, Fig. 32a). Surprisingly, some species, which were found to be more abundant at a higher proportion of the fields in surroundings, e.g., *Euphorbia cyparissias*, *Galium uliginosum*, *Stellaria graminea*, decreased their abundance with the increasing distance to the nearest field (see Table 27, Fig. 32a, b).

Many species frequent in the herb layer were influenced by the grassland vegetation in the surroundings. In general, the larger surroundings were more related to the species abundance. The following species preferred a medium proportion of the grassland in the surroundings (mean value 31%, see Table 17): *Arrhenatherum elatius* (L.) J. Presl et C. Presl (optima 31% and 27% for Grl_{200} and Grl_{300}), *Clinopodium vulgare* L. (optima 28% and 26% for Grl_{200} and Grl_{300}), *Fragaria vesca* L. (optima 31% and 29% for Grl_{200} and Grl_{300}), *Gallium mollugo* agg. L. (optima 28%, 28% and 19% for Grl_{100}, Grl_{200} and Grl_{300}), *Vaccinium myrtillus* (optima 35%, 36% and 35% for Grl_{100}, Grl_{200} and Grl_{300}). *Stellaria graminea* abundance surprisingly decreased with the increasing proportion of the grassland in the surroundings (species typical for grassland vegetation), while *Hypericum maculatum* Crantz and *Galeopsis tetrahit* L. (both species typical for non-forest vegetation) were more abundant at both a low and high proportion of the grassland in the surroundings (Table 28, Fig. 32c). *Hypericum maculatum*, *Galeopsis tetrahit*, *Rubus idaeus* and *Veronica chamadrys* L. were found to be often present in the SDFs remote from the grassland, while *Campanula patula* L., *Dactylis glomerata* L. and *Phleum pratense* preferred SDFs both near and remote from the grassland (Table. 28, Fig. 32d).

Table 27. Fields surrounding the SDF influencing abundance of the frequent species (*GLM*).

	Fi$_{100}$		**Fi$_{200}$**		**Fi$_{300}$**		**D_Fi**	
	M	var.	M	var.	M	var.	M	var.
Agrostis capillaris	×		L↑	4	L↑	5	L↓	7
Avenella flexuosa	Q∩	12	Q∩	18	Q∩	26	Q∪	28
Campanula patula	L↑	9	×		×		×	
Euphorbia cyparissias	Q∩	34	Q∩	43	L↑	26	L↓	28
Galium uliginosum	×		Q∩	9	Q∩	16	L↓	10
Hypericum maculatum	×		×		×		Q∩	15
Phleum pratense	Q∪	24	Q∪	21	Q∪	16	×	
Potentilla erecta	×		×		Q∩	18	Q∩	13
Ranunculus acris	L↑	8	L↑	7	L↑	7	Q∩	7
Rubus idaeus	L↓	13	L↓	10	L↓	19	Q∩	16
Stellaria graminea	Q∩	16	L↑	17	L↑	14	L↓	9
Urtica dioica	L↓	13	L↓	10	L↓	16	Q∩	18
Vaccinium myrtillus	×		Q∩	19	Q∩	19	Q∪	27
Viola riviniana	×		×		Q∩	10	×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; Fi$_{100/200/300}$ – proportion of fields in the 100/200/300 m surroundings, D_Fi - distance to the nearest field.

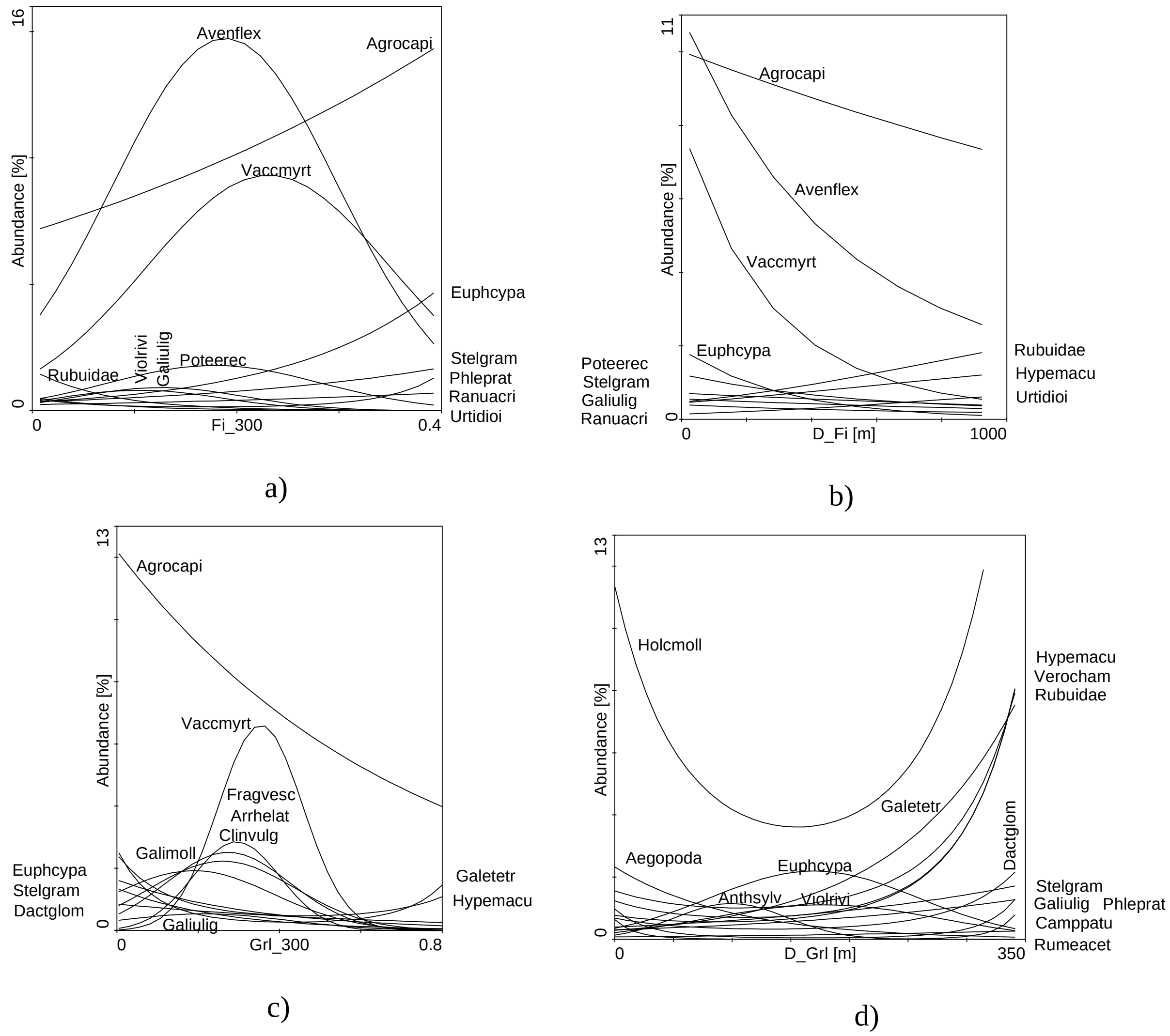
Tabulka 27. Vliv pole v okolí na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; Fi$_{100/200/300}$ – podíl pole v okolí 100/200/300 m, D_Fi - vzdálenost k nejbližšímu poli.

Table 28. Grassland surrounding the SDF influencing abundance of the frequent species (*GLM*).

	Grl$_{100}$		**Grl$_{200}$**		**Grl$_{300}$**		**D_Grl**	
	M	var.	M	var.	M	var.	M	var.
Aegopodium podagraria	×		×		×		L↓	5
Agrostis capillaris	×		L↓	5	L↓	7	×	
Anthriscus sylvestris	×		×		×		Q∩	15
Arrhenatherum elatius	×		Q∩	13	Q∩	10	×	
Campanula patula	×		×		×		Q∪	22
Clinopodium vulgare	×		Q∩	10	Q∩	10	×	
Dactylis glomerata	×		L↓	6	L↓	8	Q∪	14
Euphorbia cyparissias	L↓	6	L↓	9	L↓	11	Q∩	11
Fragaria vesca	×		Q∩	11	Q∩	25	×	
Galeopsis tetrahit	Q∪	14	Q∪	23	Q∪	26	L↑	46
Galium mollugo agg.	Q∩	5	Q∩	5	Q∩	10	×	
Galium uliginosum	L↓	5	L↓	5	Q∩	10	L↑	6
Holcus mollis	×		×		×		Q∪	9
Hypericum maculatum	L↓	11	Q∪	15	Q∪	22	Q∪	45
Phleum pratense	×		×		×		Q∪	14
Poa angustifolia	L↑	5	×		×		×	
Rubus idaeus	×		×		×		Q∪	16
Rumex acetosa	×		×		×		L↑	4
Stellaria graminea	L↓	8	L↓	16	L↓	21	L↑	6
Vaccinium myrtillus	Q∩	16	Q∩	41	Q∩	24	×	
Veronica chamaedrys	×		×		×		Q∪	23
Viola riviniana	×		×		×		Q∪	9

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; Grl$_{100/200/300}$ – proportion of grassland in the 100/200/300 m surroundings, D_Grl - distance to the nearest grassland.

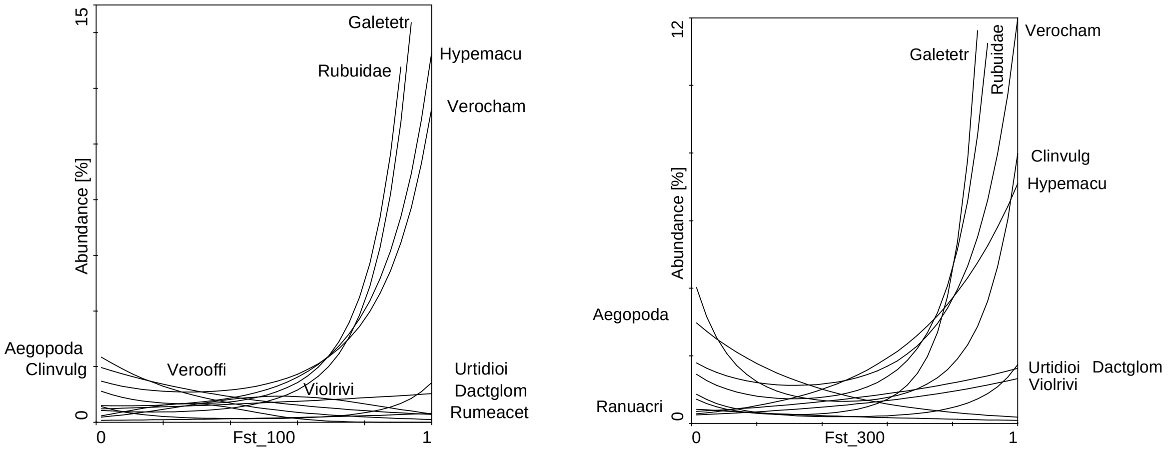
Tabulka 28. Vliv louky v okolí na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; Grl$_{100/200/300}$ – podíl luk v okolí 100/200/300 m, D_Grl - vzdálenost k nejbližší louce.



a) b) c) d)

Figure 32. Surrounding vegetation cover influencing abundance of the frequent species (*GLM*): a) proportion of fields in the 300 m, b) distance to the nearest field, c) proportion of grassland in the 300 m, d) distance to the nearest grassland. Aegopoda - *Aegopodium podagraria*, Agrocapi – *Agrostis capillaris*, Anthsylv - *Anthriscus sylvestris*, Arrhelat – *Arrhenatherum elatius*, Avenflex - *Avenella flexuosa*, Camppatu - *Campanula patula*, Clinvulg - *Clinopodium vulgare*, Dactglom - *Dactylis glomerata*, Euphcypa - *Euphorbia cyparissias*, Fragvesc - *Fragaria vesca*, Galetetr - *Galeopsis tetrahit*, Galimoll – *Galium mollugo* agg., Galiulig – *Galium uliginosum*, Holcmoll - *Holcus mollis*, Hypemacu - *Hypericum maculatum*, Phleprat - *Phleum pratense*, Poteerec – *Potentilla erecta*, Ranuacri – *Ranunculus acris*, Rubuidae - *Rubus idaeus*, Rumeacet – *Rumex acetosa*, Stelgram – *Stellaria graminea*, Urtidioi – *Urtica dioica*, Vaccmyrt – *Vaccinium myrtillus*, Verocham - *Veronica chamaedrys*, Violrivi – *Viola riviniana*.

Obrázek 32. Vliv okolí na pokryvnosti hojných druhů (*GLM*): a) podíl pole v okolí 300 m, b) vzdálenost k nejbližšímu poli, c) podíl luk v okolí 300 m, d) vzdálenost k nejbližší louce.



a) b)

Figure 33. Surrounding vegetation cover influencing abundance of the frequent species (*GLM*): a) proportion of forests in the 100 m, b) in the 300 m. Aegopoda - *Aegopodium podagraria*, Clinvulg - *Clinopodium vulgare*, Dactglom - *Dactylis glomerata*, Galetetr – *Galeopsis tetrahit*, Hypemacu - *Hypericum maculatum*, Ranuacri - *Ranunculus acris*, Rubuidae – *Rubus idaeus*, Rumeacet - *Rumex acetosa*, Urtidioi – *Urtica dioica*, Verocham - *Veronica chamaedrys*, Verooffi – *Veronica officinalis*, Violrivi – *Viola riviniana*.

Obrázek 33. Vliv okolí na pokryvnost hojných druhů (*GLM*): a) podíl lesa v okolí 100 m, b) 300 m.

Galeopsis tetrahit, *Hypericum maculatum*, *Rubus idaeus*, *Veronica chamaedrys* and *Viola riviniana* Rchb. (optimum 55% for Fst_{100}) preferred a higher proportion of the forests in surroundings (Table 17, 29, Fig. 33a, b). *Clinopodium vulgare* and *Urtica dioica* were found to be more abundant in the SDFs remote from the forest, while a higher abundance of *Galium uliginosum*, *Stellaria graminea* and *Viola riviniana* was found to be in the SDFs near the grassland and *Agrostis capillaris* L. preferred both SDFs near and remote from the grassland (Table 29).

Clinopodium vulgare (optima 65% and 59% for SDF_{100} and SDF_{200}), *Galium mollugo* agg. (optimum 56% for SDF_{100}) preferred more SDF in the surroundings of the plot (mean value 45%, 37% and 33% for SDF_{100}, SDF_{200} and SDF_{300}), while *Hypericum maculatum, Rumex acetosa* L., *Viola riviniana* preferred less SDF in the surroundings, and *Veronica officinalis* L. preferred a medium proportion of SDF in the surroundings (optima 32% and 29% for SDF_{200} and SDF_{300}). For more detail see Table 30, Fig. 34a.

The “other” land cover surrounding the SDFs was more important for the 100 m perimeter than the larger distance. *Aegopodium podagraria* L., *Achillea millefolium* L., *Anthriscus sylvestris* (L.) Hoffm. (optimum 5% for Ot_{100}) and *Viola riviniana* (optima 6% and 15% for Ot_{100} and Ot_{300}) preferred a higher proportion of “other” land cover in the surroundings, while *Agrostis capillaris*, *Arrhenatherum elatius* and *Gallium mollugo* agg. preferred lower abundance (Table 17, 31, Fig. 35a).

SDF characteristics

Aegopodium podagraria, Clinopodium vulgare, Galium mollugo agg. and *Urtica dioica* preferred large SDFs, *Galium uliginosum* and *Veronica officinalis* tended also to be more abundant in large SDFs, while *Ranunculus acris* L. and *Rumex acetosa* preferred smaller SDFs, and *Rubus idaeus* preferred both large and small SDFs (Table 32, Fig. 34b).

Aegopodium podagraria (optimum 7.6) and *Campanula patula* (7.3) preferred SDFs with more irregular shapes, while *Galeopsis tetrahit* and *Vaccinium myrtillus* preferred SDFs with circular shapes. *Clinopodium vulgare* (optimum 3.2), *Fragaria vesca* L. (2.8), *Galium mollugo* agg. (3.6) and *Urtica dioica* (3.6) preferred SDF with medium irregular shapes (Table 32, Fig. 34c).

Table 29. Forests surrounding the SDF influencing abundance of the frequent species (*GLM*).

	Fst$_{100}$		**Fst**$_{200}$		**Fst**$_{300}$		**D_Fst**	
	M	var.	M	var.	M	var.	M	var.
Aegopodium podagraria	L↓	10	L↓	6	L↓	8	×	
Agrostis capillaris	×		×		×		Q∪	10
Clinopodium vulgare	L↓	5	L↓	5	Q∪	19	L↑	28
Dactylis glomerata	L↑	3	L↑	8	L↑	11	L↓	4
Galeopsis tetrahit	Q∪	34	Q∪	56	Q∪	56	×	
Galium uliginosum	×		×		×		Q∪	14
Hypericum maculatum	Q∪	31	Q∪	45	L↑	42	L↓	6
Phleum pratense	×		×		×		Q∪	8
Potentilla erecta	×		×		×		L↑	7
Ranunculus acris	×		×		L↓	4	×	
Rubus idaeus	Q∪	17	Q∪	21	Q∪	18	×	
Rumex acetosa	L↑	7	L↑	4	×		×	
Stellaria graminea	×		×		×		Q∪	13
Urtica dioica	Q∪	12	×		Q∪	11	Q∪	13
Vaccinium myrtillus	×		Q∩	10	×		×	
Veronica chamaedrys	Q∪	10	Q∪	14	Q∪	14	×	
Veronica officinalis	Q∩	14	×		×		×	
Viola riviniana	Q∩	17	L↑	5	L↑	5	Q∪	14

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; Fst$_{100/200/300}$ – proportion of forests in the 100/200/300 m surroundings, D_Fst - distance to the nearest forest.

Tabulka 29. Vliv lesa v okolí na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; Fst$_{100/200/300}$ – podíl lesa v okolí 100/200/300 m, D_Fst - vzdálenost k nejbližšímu lesu.

Table 30. SDF in surrounding influencing abundance of the frequent species (*GLM*).

	SDF$_{100}$		**SDF$_{200}$**		**SDF$_{300}$**	
	M	var.	M	var.	M	var.
Aegopodium podagraria	L↑	5	×		Q∩	13
Agrostis capillaris	L↑	6	×		×	
Arrhenatherum elatius	×		Q∩	13	Q∩	11
Clinopodium vulgare	Q∩	17	Q∩	18	L↑	13
Euphorbia cyparissias	×		×		Q∩	36
Fragaria vesca	L↑	8	×		×	
Galeopsis tetrahit	×		×		L↓	6
Galium mollugo agg.	Q∩	14	L↑	11	L↑	18
Hypericum maculatum	×		L↓	13	L↓	10
Knautia arvensis	Q∩	8	×		×	
Phleum pratense	Q∩	9	×		×	
Poa angustifolia	Q∪	13	×		×	
Ranunculus acris	Q∪	13	×		×	
Rumex acetosa	L↓	9	L↓	7	L↓	16
Stellaria graminea	Q∩	9	×		×	
Urtica dioica	×		×		L↑	12
Vaccinium myrtillus	×		×		L↓	6
Veronica officinalis	×		Q∩	12	Q∩	19
Viola riviniana	L↓	9	×		Q∪	27

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; SDF$_{100/200/300}$ – proportion of SDF in the 100/200/300 m surroundings.

Tabulka 30. Vliv porostů náletových dřevin v okolí na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; SDF$_{100/200/300}$ – podíl porostů náletových dřevin v okolí 100/200/300 m.

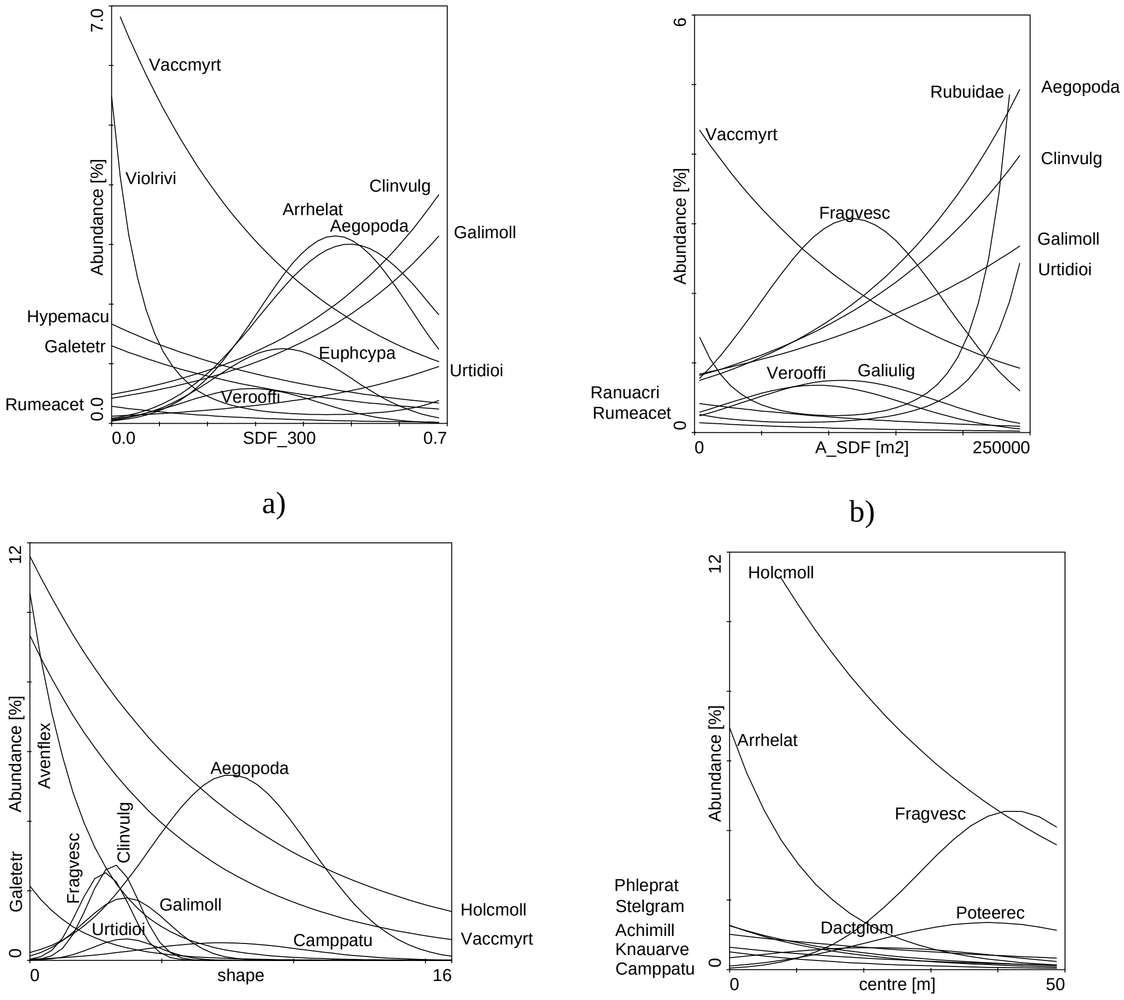
Table 31. “Other” land cover surrounding the SDF influencing abundance of the frequent species (*GLM*).

	Ot_{100}		**Ot_{200}**		**Ot_{300}**	
	M	var.	M	var.	M	var.
Achillea millefolium	L↑	14	×		×	
Aegopodium podagraria	Q∪	10	×		×	
Agrostis capillaris	L↓	10	×		×	
Anthriscus sylvestris	Q∩	11	×		×	
Arrhenatherum elatius	L↓	7	Q∪	14	×	
Clinopodium vulgare	L↓	7	×		L↑	12
Galium mollugo agg.	L↓	11	L↓	5	×	
Galium uliginosum	×		×		L↑	6
Holcus mollis	L↓	9	L↓	7	L↓	6
Phleum pratense	×		Q∪	11	L↓	5
Rubus idaeus	L↓	7	×		Q∪	16
Stellaria graminea	L↓	5	Q∪	10	×	
Viola riviniana	Q∩	25	L↑	8	Q∩	17

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; $Ot_{100/200/300}$ – proportion of “other” land cover in the 100/200/300 m surroundings.

Tabulka 31. Vliv krajinného pokryvu „ostatní“ v okolí na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; $Ot_{100/200/300}$ – podíl krajinného pokryvu “ostatní“ v okolí 100/200/300 m.

Arrhenatherum elatius and *Phleum pratense* were more abundant at plots near the SDFs border, while *Fragaria vesca* tended to be more abundant inside the SDF (optimum 42 m, see Table 32, Fig. 34d).



a)

b)

c)

d)

Figure 34. Factors influencing abundance of the frequent species (*GLM*): a) proportion of SDF in the 300 m, b) area of the SDF, c) relative length of the SDF border, d) nearest distance from the centre of the plot to the border of the SDF. Achimill - *Achillea millefolium*, Aegopoda – *Aegopodium podagraria*, Arrhelat - *Arrhenatherum elatius*, Avenflex - *Avenella flexuosa*, Camppatu - *Campanula patula*, Clinvulg - *Clinopodium vulgare*, Dactglom - *Dactylis glomerata*, Euphcypa - *Euphorbia cyparissias*, Fragvesc - *Fragaria vesca*, Galetetr - *Galeopsis tetrahit*, Galimoll – *Galium mollugo* agg., Galiulig – *Galium uliginosum*, Holcmoll - *Holcus mollis*, Hypemacu - *Hypericum maculatum*, Knauarve – *Knautia arvensis*, Phleprat - *Phleum pratense*, Poteerec – *Potentilla erecta*, Ranuacri - *Ranunculus acris*, Rubuidae – *Rubus idaeus*, Rumeacet – *Rumex acetosa*, Stelgram – *Stellaria graminea*, Urtidioi – *Urtica dioica*, Vaccmyrt - *Vaccinium myrtillus*, Verooffi – *Veronica officinalis*, Violrivi – *Viola riviniana*.

Obrázek 34. Vliv faktorů na pokryvnost hojných druhů (*GLM*): a) podíl SDF v okolí 300 m, b) rozloha SDF, c) relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), d) nejkratší vzdálenost k okraji porostu náletových dřevin.

Historical vegetation cover

Many species were more abundant in the SDFs, which were overgrown by trees in 1952: *Agrostis capillaris*, *Avenella flexuosa*, *Fragaria vesca*, *Galium uliginosum*, *Potentilla erecta* L., *Vaccinium myrtillus* (optimum 3.2), *Veronica officinalis*, while several species were more abundant in the SDFs, which were fields or grassland in 1952: *Campanula patula* (optimum 1.5), *Holcus mollis* L. (1.6), *Rubus idaeus*, *Urtica dioica*. The explained variability by vegetation cover in 1952 was often very high. For more detail see Table 33, Fig. 35b.

Galium uliginosum and *Vaccinium myrtillus* were found to be more abundant in the SDFs, which were covered by trees in 1966, while *Knautia arvensis* (L.) Coulter, *Poa angustifolia* L., *Urtica dioica* (optimum 1.8) and *Phleum pratense* (optimum 2.0) preferred SDFs that were not overgrown by trees in 1966. *Hypericum maculatum* was more abundant in the SDFs, which were covered by scattered trees in 1966 (optimum 2.8), while *Avenella flexuosa*, *Euphorbia cyparissias* and *Potentilla erecta* were more abundant in the SDFs, which were fields or overgrown by trees in 1966. For more detail see Table 33, Fig. 35c.

Avenella flexuosa, *Galeopsis tetrahit* (optimum 2.8), *Vaccinium myrtillus* were more abundant in the SDFs overgrown by trees in 1983, while *Holcus mollis* (optimum 2.3) and *Phleum pratense* (2.1) preferred SDFs, which were grassland in 1983, and *Achillea millefolium* preferred SDFs, which were fields (or grassland) in 1983. For more detail see Table 33, Fig. 35d.

Table 32. Characteristics of the SDF influencing abundance of the frequent species (*GLM*).

	A_{SDF}		shape		centre	
	M	var.	M	var.	M	var.
Achillea millefolium	×		×		L↓	5
Aegopodium podagraria	L↑	20	Q∩	13	×	
Arrhenatherum elatius	×		×		L↓	11
Avenella flexuosa	×		L↓	5	×	
Campanula patula	×		Q∩	11	L↓	8
Clinopodium vulgare	L↑	15	Q∩	16	×	
Dactylis glomerata	×		×		Q∩	9
Fragaria vesca	Q∩	9	Q∩	11	Q∩	23
Galeopsis tetrahit	×		L↓	13	×	
Galium mollugo agg.	L↑	12	Q∩	11	×	
Galium uliginosum	Q∩	10	×		×	
Holcus mollis	×		L↓	5	L↓	9
Knautia arvensis	×		×		L↓	6
Phleum pratense	×		×		L↓	11
Potentilla erecta	×		×		Q∩	9
Ranunculus acris	L↓	11	×		×	
Rubus idaeus	Q∪	19	×		×	
Rumex acetosa	L↓	13	×		×	
Stellaria graminea	×		×		L↓	9
Urtica dioica	Q∪	26	Q∩	13	×	
Vaccinium myrtillus	L↓	6	L↓	10	×	
Veronica officinalis	Q∩	13	×		×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - "humped" answer, var. - explained variability [%]; A_{SDF} – area of the SDF, shape – relative length of the SDF border, centre – nearest distance from the centre of the plot to the border of the SDF.

Tabulka 32. Vliv charakteristik porostu náletových dřevin na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - "hrbatá" odpověď, var. - vysvětlená variabilita [%]; A_{SDF} - rozloha SDF, shape - relativní délka hranic SDF (ku obvodu kruhu o stejné ploše), centre - nejkratší vzdálenost k okraji porostu náletových dřevin.

Table 33. Historical vegetation cover influencing abundance of the frequent species (*GLM*).

	1952		1966		1983	
	M	var.	M	var.	M	var.
Achillea millefolium	×		×		Q∪	24
Aegopodium podagraria	L↓	7	×		×	
Agrostis capillaris	L↑	14	×		L↑	4
Avenella flexuosa	L↑	20	Q∪	24	L↑	20
Campanula patula	Q∩	16	×		×	
Clinopodium vulgare	×		×		L↑	6
Euphorbia cyparissias	×		Q∪	12	L↑	9
Fragaria vesca	L↑	38	×		×	
Galeopsis tetrahit	×		×		Q∩	19
Galium uliginosum	L↑	15	L↑	13	L↑	5
Holcus mollis	Q∩	11	L↓	5	Q∩	10
Hypericum maculatum	×		Q∩	12	×	
Knautia arvensis	×		Q∪	21	×	
Phleum pratense	×		Q∩	13	Q∩	21
Poa angustifolia	×		L↓	11	L↓	12
Potentilla erecta	L↑	12	Q∪	11	×	
Rubus idaeus	L↓	11	×		×	
Rumex acetosa	L↑	4	×		×	
Stellaria graminea	L↑	6	×		×	
Urtica dioica	Q∪	22	Q∩	17	×	
Vaccinium myrtillus	Q∩	33	L↑	41	L↑	21
Veronica officinalis	L↑	10	×		×	

M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%]; 1952/1966/1983 – vegetation cover in 1952/1966/1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy).

Tabulka 33. Vliv vegetačního krytu v minulosti na pokryvnost hojných druhů (*GLM*). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%]; 1952/1966/1983 - vegetační kryt v roce 1952/1966/1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).

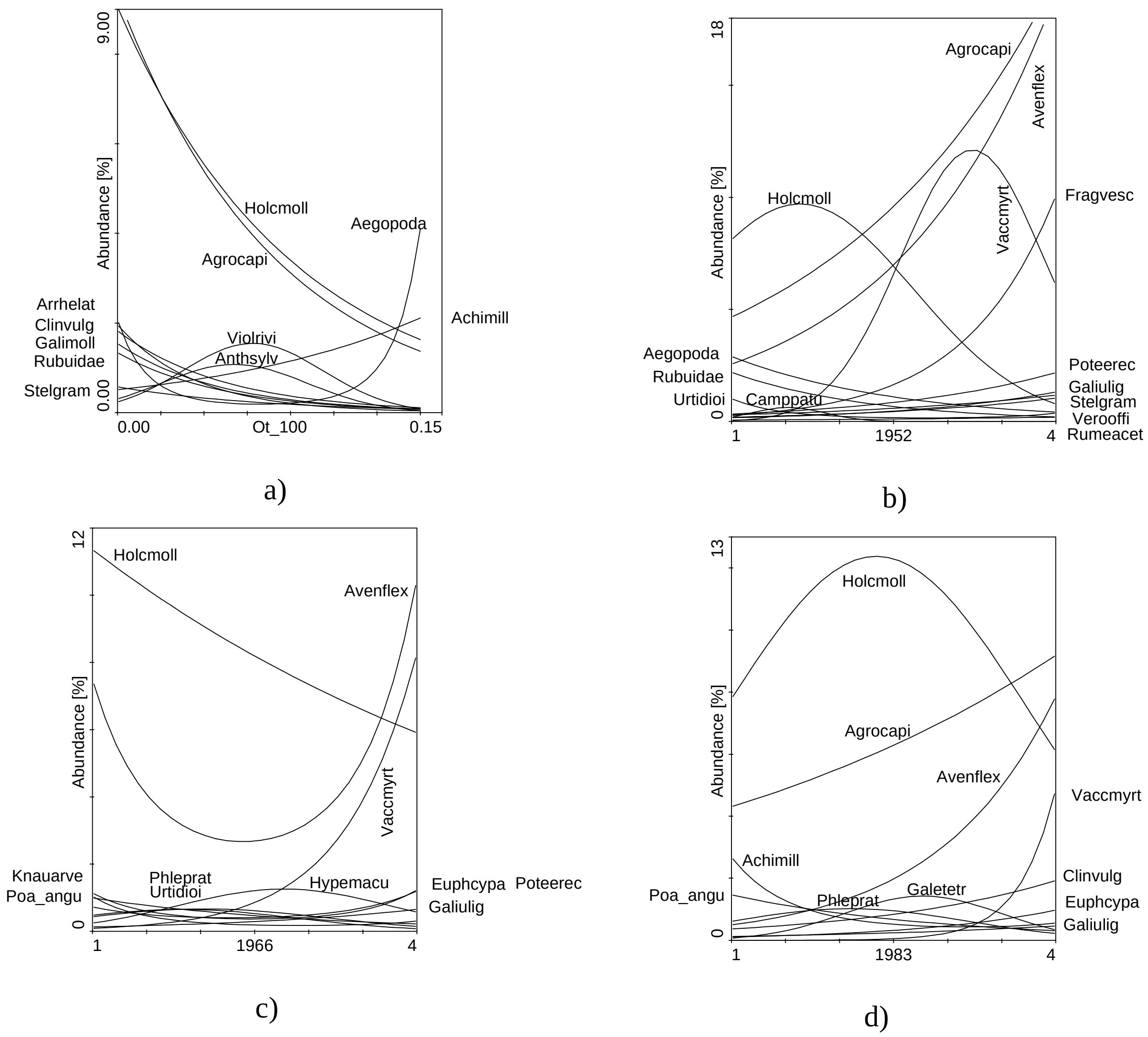


Figure 35. Factors influencing abundance of the frequent species (*GLM*): a) proportion of “other” land cover in the 100 m, b) vegetation cover in 1952, c) in 1966, d) in 1983 (successional sere: 1-field, 2-grassland, 3-scattered trees, 4-closed tree canopy). Achimill – *Achillea millefolium*, Aegopoda – *Aegopodium podagraria*, Agrocapi - *Agrostis capillaris*, Anthsylv - *Anthriscus sylvestris*, Arrhelat - *Arrhenatherum elatius*, Avenflex - *Avenella flexuosa*, Camppatu - *Campanula patula*, Clinvulg - *Clinopodium vulgare*, Euphcypa - *Euphorbia cyparissias*, Fragvesc - *Fragaria vesca*, Galetetr - *Galeopsis tetrahit*, Galimoll – *Galium mollugo* agg., Galiulig – *Galium uliginosum*, Holcmoll - *Holcus mollis*, Hypemacu - *Hypericum maculatum*, Knauarve – *Knautia arvensis*, Phleprat - *Phleum pratense*, Poa_angu – *Poa angustifolia*, Poteerec - *Potentilla erecta*, Rubuidae – *Rubus idaeus*, Rumeacet – *Rumex acetosa*, Stelgram – *Stellaria graminea*, Urtidioi – *Urtica dioica*, Vaccmyrt – *Vaccinium myrtillus*, Verooffi – *Veronica officinalis*, Violrivi – *Viola riviniana*.

Obrázek 35. Vliv faktorů na pokryvnost hojných druhů (*GLM*): a) podíl krajinného pokryvu “ostatní“ v okolí 100 m, b) vegetační kryt v roce 1952, c) 1966, d) 1983 (sukcesní série: 1-pole, 2-louka, 3-rozvolněný nálet, 4-zapojený nálet).

Discussion

All the frequent species in this study (see Table 22) were also common species in the study area and species widespread in Central Europe. This is in assumption with the view of colonisation of recent forests in the context of the theory of island biogeography (Bossuyt et al. 2003), which predicts the colonisation from the close surroundings to be the most probable, and in assumption with findings of other studies (e.g., Hester et al. 1991). Most of the frequent species were related to the grassland vegetation, and many of them were clonal grasses (*Agrostis capillaris*, *Dactylis glomerata*, *Holcus mollis*, *Phleum pratense*), and several other frequent species were also clonal perennial species (e.g., *Galium mollugo* agg., see Table 22). However, clonal species were found to dominate the middle stages of succession, and they were not found to be abundant in an old-field succession in mesic stands after more than 30 years (Prach and Pyšek 1994a). In this study the minimal value of the average age of the tree layer exceeded 10 years, and the average value was 30 years (Table 12). Moreover, we have to assume several more years were needed for the tree establishment on the abandoned agricultural land and to reach the 40 cm above ground (a wood sample was taken from this level to obtain the age estimation from the tree rings).

Each frequent SDF species was influenced by the context-dependent factors (although different factors were found to be important for different species) and each context-dependent factor significantly influenced the frequent species abundance (although the amount of explained variability differed). The history was the most important group of factors influencing the frequent species abundance (41% of the total tested relations), while the characteristics of the SDF influenced 36% and surrounding vegetation influenced 35% of the tested relations. The explained variability was relatively high, i.e., on average 14% for the historical vegetation cover (for significant relations), 14% for the surrounding vegetation, and 12% for the character of the SDF. For comparison, Deckers et al. (2004) found the adjacent land use important for 8-11% of hedgerow species (15-21 out of 198), and the explained variability by all the studied factors (environmental conditions, management, structure, history spatial configuration, in total 27 factors) was on average 29%, the strongest relation of the species was to the environmental conditions.

The time, i.e., successional age was reported as the most important factor influencing the species composition (e.g., Honnay et al. 1999; Prach and Řehounková 2006). However, e.g., Peterken and Game (1984) found, that after several decades there is no significant influence of the time on the forest species in the recent forests, and Kopecký and Vojta (2009) found that the recent forest species composition is determined mostly by the environmental factors, but the type of previous land use was also found to modify the species assemblages. The findings, that the historical vegetation cover significantly influenced most of the species context-dependent relations, and that the highest explained variability was observed, are not surprising, and the fact that the oldest record concerning the vegetation cover tested (52 years BP) influenced most of the frequent species is important.

The *Vaccinium myrtillus*, the only frequent species related to the forest, increased with the duration of the tree layer. This finding is not surprising, because an increase of forest species with the duration of the tree layer was found in several studies (Bossuyt and Hermy 2000; Dzwonko 2001; Dzwonko and Loster 1992; Roy and de Blois 2008). However, this species is often found also in forest edges and at clearings.

Many typical grassland species were not very influenced by the duration of the tree layer, e.g., *Arrhenatherum elatius*, *Dactylis glomerata*, *Ranunculus acris*. However, several species preferred the SDF, which was not overgrown by trees in the past (e.g., *Campanula patula*, *Phleum pratense*). This findings indicates, that the process of transformation from grassland vegetation to forest vegetation is relatively slow, which is in assumption with findings of other studies, e.g., Faliński (1988) estimated 350 years for the succession on mesic grassland of the *Arrhenatherion elatioris* alliance.

The surrounding vegetation cover influenced many frequent species. This is in assumption with the results of many other studies, which reported surroundings as an important factor influencing the succession (e.g., Hersperger and Forman 2003; Prach and Řehounková 2006; Prach et al. 2007). However, the surrounding vegetation cover was correlated for distinguished distances (e.g., $r = 0.81$, $p < 0.05$ for the Grl_{100} and Grl_{200}, and $r = 0.71$, $p < 0.05$ for the Grl_{200} and Grl_{300}), and many of the species influenced by certain factors were more related to the vegetation cover more remote from the plot (e.g., *Galeopsis tetrahit* and *Grl* relation, see Table 28). The influence of long-distance surroundings was found in other studies, e.g., Kirmer et al. (2008) found the influence of surroundings on the species composition of the mined stands up to 17 km.

The surrounding vegetation was found to be important for many species typical for forest-grassland ecotones, which are the most common and most abundant species (Table 22) in the SDFs (Forman and Baudry 1984), and their abundance usually increased with the duration of the tree-layer (e.g., *Euphorbia cyparissias*, *Potentilla erecta*). The higher abundance of these species is in assumption with their ecological behaviour, and the increase in abundance with the duration of the tree layer indicates relatively slow changes of the community toward the forest vegetation.

Although Vojta (2007) found *Hypericum perforatum* to be a species indicating old-fields in the Czech Republic, I have not a found higher abundance of *Hypericum maculatum* on former fields. On the contrary, it was more common in the SDFs, which were scattered SDFs in 1966 (optimum 2.8, 12% explained variability).

A relatively small number of grassland species were influenced by the grassland in surroundings, and some typical grassland species tended to decrease with the proportion of the grassland in the surroundings (e.g., *Stellaria graminea*), while the proportion of forests surprisingly increased the abundance of several grassland species (for similar finding see Cousins and Aggemyr 2008). It may be caused by the general low distance to the nearest grassland (45 m) and by a high proportion of the grassland in the surroundings (31%) in the study area, which allow the effective supply of grassland species. The other reason is assumed to be that most of the large grasslands are species poor, often established on former arable land. A higher proportion of grassland in the surroundings is mostly caused by such vegetation.

The SDFs in surroundings were not very important for the frequent species typical for grassland, but Hersperger and Forman (2003) found that the number of grassland species decreased with the increasing abundance of SDF in the surroundings. Only *Rumex acetosa* decreased the abundance, while *Arrhenatherum elatius* preferred SDF surrounded by nearly 50% of SDF in the 200 and 300 m.

Unfortunately, no species typical for forests, except for the *Vaccinium myrtillus*, was frequent enough for a statistical analysis, although the mean distance to the nearest forest was only 110 m, and the limitable distance for the forest species distribution is supposed to be 200 m (Honnay et al. 2002a). The reason can likely be attributed to the species composition of most of the forests in the study area. Most of them are spruce plantations with poor herb-layers, and “typical forest herbs”, which are mostly species typical for deciduous forests (Hermy et al. 1999), are usually missing in such forests. The other likely reason is that the forest herb species are microsite limited, e.g., Baeten et al. (2009) found that some forest species depended on the vegetation disturbance in the seed sowing experiment. The *Vaccinium myrtillus*, the only one truly forest species, surprisingly preferred the SDFs surrounded by a relatively high proportion of the grassland (ca 35%) and by fields (ca 20%). It was only slightly related to the forests in the surroundings, and the distance to the nearest forest was not important at all.

The area of the SDF influenced one third of the species. The influence of the area of the recent forest on the species composition also was found in other studies (e.g., Dzwonko and Loster 1992).

The position of the plot within the SDF and the shape of the SDF may influence the species especially due to the edge effect, which was proved in other studies (e.g., Honnay et al. 2002b). Many typical grassland species have been more abundant in the edges of the SDF (e.g., *Arrhenatherum elatius*, *Campanula patula*, *Knautia arvensis*, *Phleum pratense*), which is in assumption with the findings of other studies (e.g., Dzwonko and Loster 1992; Honnay et al. 2002b). Preference of the species to the shape of the SDF did not show any ecologically well interpretable evidence, but a relatively high number of species were significantly related to the shape of the SDF. Biased results concerning the influence of the shape on the vegetation of recent forests also were obtained in other studies (for review see Honnay et al. 2002a).

The ruderal species (*Aegopodium podagraria*, *Galium mollugo* agg., *Urtica dioica*, *Rubus idaeus*) tended to be more abundant in large SDFs. More ruderal species were found to be in recent forests compared to the ancient forests in different studies (e.g., Bossuyt et al. 1999; Vojta 2007). A relatively high number of frequent species indicating ruderalization was found in my study (e.g., *Galeopsis tetrahit*, *Galium mollugo*, *Urtica dioica*), but they were usually low abundant (see Table 22). The higher number of ruderal species may be caused by the increase in nutrients in the soil during the tree-layer development (Honnay et al. 2002a), or by their long-distance dispersal ability and persistent seed bank (Bossuyt et al. 1999).

Experimental study on seed and safe-site limitation of forest species in an early successional site in relation to disturbance regime and light conditions

Experimentální zjištění limitace disperzí nebo stanovištěm lesních druhů v ranně sukcesním stádiu ve vztahu k narušení a světelným podmínkám

Abstract

An experiment on seed and safe-site limitation of nine forest herbs was established in a 12-year-old abandoned grassland. Seed limitation was reduced by seed addition treatment, and disturbance and light conditions were manipulated. Factorial design of 16 treatments in 6 randomised blocks was used.

The influence of disturbance and shading on species composition, general characteristics of the vegetation, and on species abundance was studied, and seedling establishment of forest species was monitored.

The resilience of the early stages of succession to the treatment regime was high. Although, the disturbance and shading influenced the species composition, the character of the vegetation and selected species abundance, the between year variability was higher.

Only sown forest species were found during the experiment. Most of the forest species did not germinate, although the seed addition was high (50-600 seeds.m^{-2}). The only species, which established relatively well, was *Dentaria enneaphyllos* (number sufficient for statistical analyses). However, the seedlings were not able to develop leaves except for cotyledons during the experiment.

Although, only shading significantly increased the numbers of *D. enneaphyllos* seedlings, most of the *D. enneaphyllos* seedlings were found in the most manipulated treatment combining both shading and disturbance regime. The results indicate that forest species are in addition to the seed limitation also safe-site limited in the early stages of succession.

Shrnutí

Na ploše dvanáct let ponechané spontánní sukcesi byl založen pokus pro zjištění limitace semeny nebo stanovištěm lesních bylin (9 druhů). Limitace semeny byla odstraněna přidáním semen a manipulací světelných podmínek a disturbanci vegetace byly měněny podmínky prostředí. Pro pokus bylo použito faktoriální uspořádání 16 zásahů v šesti znáhodnělých blocích.

Byl zjišťován vliv zásahů na druhové složení, charakter porostu a na vybrané druhy a uchycování semenáčků lesních druhů.

Vegetace ranně sukcesní louky byla odolná vůči experimentálním zásahům. Ačkoli narušení a stínění ovlivňovalo druhové složení, charakter porostu i pokryvnost sledovaných druhů, meziroční variabilita byla vyšší než změny způsobené zásahy.

Byly nalezeny jen semenáčky druhů, které byly do porostu přisety. Většina přisévaných druhů se nebyla schopna v porostu uchytit vůbec, ačkoli byl počet přidávaných semen vysoký (50-600 ks.m^{-2}). Jediný druh, který se významněji uchycoval (v dostatečném množství pro statistické hodnocení) byla *Dentaria enneaphyllos*. Semenáčky tohoto druhu se však nebyly schopny dále vyvíjet v průběhu pokusu (dosáhly pouze stádia s děložními lístky).

Ačkoli pouze stínění statisticky významně zvyšovalo uchycování *D. enneaphyllos*, nejvíce semenáčků bylo zaznamenáno v zásahu kombinujícím stínění i narušení. Výsledky pokusu naznačují, že lesní druhy jsou v raných stádiích sukcese limitovány kromě nedostatečným množstvím semen také mikrostanovištěm.

Introduction

Colonisation of the recent forest herb layer by the typical forest species is an important topic due to the increase in the recent forest abundance in Europe (e.g., Hamre et al. 2007; Helm et al. 2006). Species typical for ancient forest herb layer were reported to be shade-tolerant species avoiding wet and dry sites (Hermy et al. 1999), growing mostly in forests with intermediate soil reaction and intermediate nitrogen availability (Hermy et al. 1999; Wulf 1997). Their poor dispersal ability is characteristic (Brunet and von Oheimb 1998a; Hermy et al. 1999; Peterken and Game 1984; Wulf 1997), they are poorly represented in the seed bank, and only a limited number establish a persistent seed bank (Bossuyt and Hermy 2001). Most of them are from the class *Fagetalia* (Wulf 1997). A stress-tolerant strategy is typical, and many of them are anemochorous, myrmecochorous or zoochorous species (Hermy et al. 1999; Honnay et al. 2002a).

Slow colonisation of the herb layer of recent forests by typical forest species was reported (e.g., Dzwonko 1993; Bossuyt et al. 1999; Honnay et al. 1999). It is assumed that there are two reasons for this evidence: 1) the forest species are safe-site limited (Christensen and Peet 1984; Hester et al. 1991; Mwangi et al. 2007), or 2) dispersal limited (Brunet and von Oheimb 1998a; Ehrlén and Eriksson 2000; Matlack 1994; Van der Veken et al. 2007a).

Slow changes in environmental conditions, especially soil conditions, during the succession (e.g., Gömöryová et al. 2007; Honnay et al. 1999; Richter et al. 1994; Verheyen et al. 1999), and the influence of competition of the present herb layer (e.g., Dostálek et al. 2007; Prach 1994) are evidence of the safe-site limited hypothesis.

Seed limitation was often studied indirectly from the presence/absence of the forest species and the correlation of the forest species in the herb layer with the distance to the (ancient) forest (e.g., Butaye et al. 2001; Peterken and Game 1984; Sitzia 2007; Vellend et al. 2007). The rate of dispersion of forest species was reported low, i.e., <2 m.year^{-1}, in most cases <1 m.year^{-1} (see Bossuyt et al. 1999; Brunet and von Oheimb 1998a; Honnay et al. 1999).

The direct methods, through which those forms of seed- and safe-site limitation can be distinguished, are seed addition and transplantation (Münzbergová and Herben 2005). There is only a small number of such studies pertaining to the forest species. Kubíková (1994) and Van der Veken et al. (2007b) are examples of transplanting studies. Seed sowing experiments have been more often practiced (see Ehrlén and Eriksson 2000; Ehrlén et al. 2006; Eriksson 1995; Gustafsson et al. 2002; Ohlson and Grønli 2006; Verheyen and Hermy 2004).

The seed sowing experiments proved the seed limitation of forest species in recent forests (most of them planted on former agricultural land), but in several studies the evidence for safe-site limitation also was observed. For example Verheyen and Hermy (2004) found some of the sown species to be influenced by the present herb layer and by the amount of nutrients in soil, although weak influence of the environment and competition was also reported (e.g., Ehrlén et al. 2006; Gustafsson et al. 2002).

The transplanting experiments supported the seed limitation of forest species less than the seed sowing experiments, and the safe-site limitation was found to be more important in these studies. Kubíková (1994) found that most of the species were not able to spread from the transplanted block even after 6 years (some species died on the soil block borders), and those that were able to spread were found near the block (the largest distance was reported to be 10 m for *Pulmonaria obsura*). Van der Veken et al. (2007b) found the transplanted populations of *Hyacinthoides non-scripta* less viable than the source populations and the spread of the species was found to be very slow (0.006-0.06 m.year^{-1}), although 41% of the transplanted populations (out of 27) were able to survive 45 years.

This study is focused on the seed and safe-site limitation of forest species in early successional vegetation (grassland abandoned for twelve years) on mesic stands. Using a factorial designed experiment, the forest species establishment in relation to seed limitation (reduced by seed addition), light conditions (manipulated by shading treatments) and competition of present vegetation cover (manipulated by above-ground vegetation removal treatment and turf disturbance treatment) was studied.

The following questions have been considered:

1. Are the forest species seed or safe-site limited in an early stage of succession?
2. Can the shading or disturbance of the present vegetation cover increase the establishment success of forest species in an early stage of succession?

Methods

Study site and design of the experiment

The experimental site was in the southernmost part of the Czech Republic (48°41.468´ N, 14°17.382´ E, 700 m above sea level). Vegetation cover at the beginning of the experiment was ruderalized abandoned grassland of the *Arrhenatherion elatioris* alliance partly overgrown by birch (*Betula pendula* Roth.). The experiment plots were fixed in the open part of the grassland in April 2004, and all the treatments and measurements ended in May 2006.

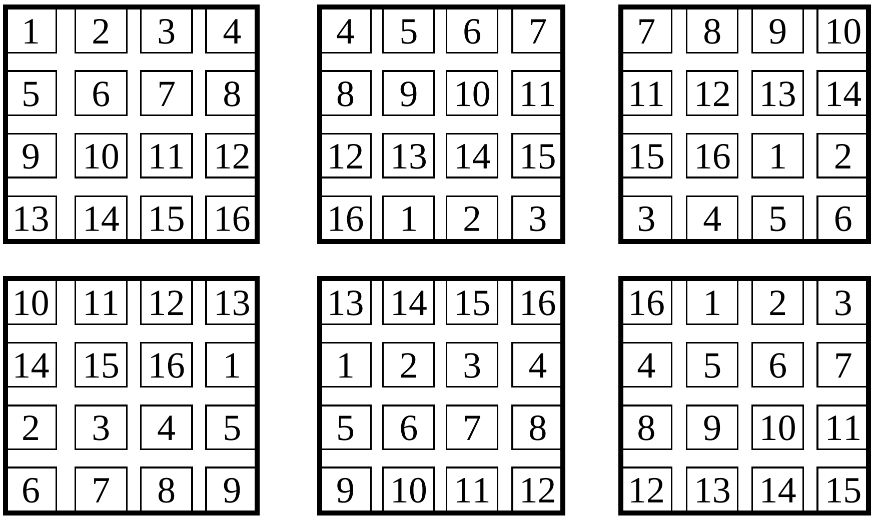
The factorial design of the experiment was used. Plots were organized in six randomized blocks. The following treatments were practiced: i) the shading at a 40% level of incoming photosynthetic active radiation (*PhAR*, S_{40}), ii) the shading at a 5% level of incoming *PhAR* (S_5), iii) the removal of above-ground plant biomass (D_{AB}), iv) the disturbance of the turf (D_T), v) the seed addition of typical forest species (S_A). For the scheme of the experiment see Fig. 36.

The shading at the 40% level of incoming *PhAR* treatment was practiced using one sheet of synthetic net, while three sheets of net were used for shading at the 5% level of incoming *PhAR*. The irradiance decrease was verified using a luxmeter equipped with a *PhAR* sensor. The synthetic net (one or three sheets) was placed above the vegetation, and the net was attached to four woody bars fixed in the corners of the plot. The height of attachment was changed during the vegetation season according to the height of the vegetation to avoid the extra irradiance of the plot in the morning and late afternoon due to the low position of the sun. Shading was practiced only during the vegetation period from the beginning of April to the end of September.

Above-ground plant biomass was cut by scissors twice a year, in May and October, at 3 cm above ground and the above-ground biomass was removed from the plot in the D_{AB} treatment.

To begin with D_T treatment, the above-ground biomass was cut and removed from the plots, the turf disturbance was practiced by a spade, and the soil was turned. This treatment was practiced only in May 2004 and was not repeated.

Seeds of typical forest species were collected in the Uhlířský vrch Nature Monument (ancient beech forest of the *Dentario enneaphylli-Fagetum* alliance) - 4 km from the experimental site in 2004. Species were collected in two dates (according to the seed production) on the 16th of June (*Dentaria enneaphyllos* L., *D. bulbifera* L., *Mercurialis perennis* L.) and on the 23rd of July (*Actaea spicata* L., *Carex sylvatica* Huds., *Galium odoratum* (L.) Scop., *Maianthemum bifolium* (L.) F.W. Schmidt, *Oxalis acetosella* L., *Paris quadrifolia* L.). Only mature seeds with no visible damage were used. Seeds were sown within three days after the collection (stored by 4°C in paper bags), random hand throwing from the height of 1.2 m inside the plot was used for S_A treatment. The following seed numbers were used: 50 seeds of *A. spicata*, 300 seeds of *G. odoratum*, 500 seeds of *C. sylvatica*, 50 pseudobulbs of *D. bulbifera*, 100 siliques (approximately 600 seeds) of *D. enneaphyllos*, 300 seeds of *M. bifolium*, 300 seeds of *M. perennis*, 100 seeds of *O. acetosella* and 50 seeds of *P. quadrifolia*. The seed addition of the following species: *P. quadrifolia*, *A. spicata* and *O. acetosella* was done by adding seeds only into the plots with the treatment numbers 4 and 11 within the blocks 1, 2 and 3 due to the insufficient seed numbers. The germinating capacity of the seeds (fresh, dried, stratified by 4°C for a period of one month) was determined in laboratory conditions after sowing on garden substrate and sand. Due to the seed limitation, some species were sown only in some treatments in the germination capacity determination (see Table 34). The seedlings were removed from the substrate after the development of the cotyledons to reduce the competition between the seedlings and to avoid the duplicates in the counting of the seedlings. The duration of the test of the germination capacity was the same as in the experiment.



1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16

4	5	6	7
8	9	10	11
12	13	14	15
16	1	2	3

7	8	9	10
11	12	13	14
15	16	1	2
3	4	5	6

10	11	12	13
14	15	16	1
2	3	4	5
6	7	8	9

13	14	15	16
1	2	3	4
5	6	7	8
9	10	11	12

16	1	2	3
4	5	6	7
8	9	10	11
12	13	14	15

Figure 36. Experimental design. Bold blocks 5.5 × 5.5 m (1 m apart), small plots 1 × 1 m (0.5 m apart); 1 - control, 2 – shading at the 40% level of incoming PhAR (S_{40}), 3 - shading at the 5% level of incoming PhAR (S_5), 4 - seed addition (S_A), 5 – removal of above-ground biomass (D_{AB}), 6 – turf disturbance (D_T), 7 - D_{AB} + S_{40}, 8 - D_{AB} + S_5, 9 – D_T + S_{40}, 10 - D_T + S_5, 11 – S_A + S_{40}, 12 – S_A + S_5, 13 – D_{AB} + S_A, 14 – D_T + S_A, 15 - D_{AB} + S_{40}+ S_A,
16 D + S + S

Obrázek 36. Schéma pokusu. tučně bloky 5,5 × 5,5 m (1 m od sebe), malé čtverce 1 × 1 m (0,5 m od sebe); 1 - kontrola, 2 – stíněno na 40 % dopadajícího *PhAR* (S_{40}), 3 – stíněno na 5 % dopadajícího *PhAR* (S_5), 4 - výsev (S_A), 5 – odstranění nadzemní biomasy (D_{AB}), 6 – narušení drnu (D_T), 7 - D_{AB} + S_{40}, 8 - D_{AB} + S_5, 9 – D_T + S_{40}, 10 - D_T + S_5, 11 – S_A + S_{40}, 12 – S_A + S_5, 13 - D_{AB} + S_A, 14 – D_T + S_A, 15 - D_{AB} + S_{40}+ S_A, 16 – D_T + S_{40} + S_A.

Data collection

Phytocenological releve was taken in the fully developed vegetation from all the plots in 2004 (before the treatment application), 2005 and 2006. Species abundance was visually estimated in percents of the species.

The Shannon-Wiener index of diversity was calculated from the species composition for all the plots.

The proportion of gaps (*Gaps*) in the vegetation was calculated for all the plots from the abundance of the herb layer (E_1): $Gaps = 1\text{-}E_1$.

To describe the character of the vegetation, the following functional groups of herbs were distinguished: i) graminoids (*GR*), ii) annual herbs (*HA*), iii) perennial rosettes (*HR*), iv) perennial small herbs (*HS*), v) perennial tall herbs (*HT*), vi) forest herbs (*HF*, only *D. enneaphyllos*, *O. acetosella*), vii) trees (*TR*). The abundance of all the groups was obtained as the sum of abundances of all the species included in the group.

Seedlings of typical forest species were listed and signed by color bar every four weeks (from April to October) in all the plots. The plot was carefully viewed by consideration of minimizing the disturbance of the vegetation by the searching activity.

Germinating capacity of the forests species

Only five species germinated in the laboratory conditions (*D. enneaphyllos, G. odoratum, M. bifolium, O. acetosella, P. quadrifolia*).

Only *D. enneaphyllos* germinated well, fresh seeds germinated better than the dried or stratified ones. For more details see Table 34.

Statistical analyses

For the statistical analyses, the following independent variables were used: (1) treatment (nominal variable), (2) disturbance coded as ordinal variables ranging from 0 to 2 (0 – without disturbance, 1 – D_{AB}, 2 - D_T), (3) shading coded as ordinal variables ranging from 0 to 2 (0 – without shading, 1 – S_{40}, 2 - S_5), (4) the number of years of the experiment, (5) seed addition coded as a nominal variable (0 or 1).

From the forest species sown only *D. enneaphyllos* germinated in sufficient number enable statistical analyses.

Phytocenological releves were analysed using ordination methods in the CANOCO for Windows program v. 4.5. Abundances of the species was logarithmically transformed. Unimodal analyses were performed (length of the gradient was higher than 2.0): indirect Correspondence Analysis (*CA*), direct Canonical Correspondence Analysis (*CCA*) respectively. Manual selection of the factors 2, 3, 4, and 5 at the $\propto = 0.05$ level was used. Canodraw v. 4.0 program was used to visualise the results (Lepš and Šmilauer 2003).

General Linear Models (*GLM*) in the Canodraw v. 4.0 program were used to test the influence of disturbance and shading on the species abundances, only species occupying at least 5% of the plots were used for statistical analyses. Poisson distribution of the data was used, because the link function of this distribution is “Log” function, which is recommended for the counts and frequency data (Lepš and Šmilauer 2003; p. 122). Models were fitted by stepwise selection with interaction terms to square polynom using “F” statistics at the $\propto = 0.01$ (Lepš and Šmilauer 2003).

Repeated measure Analysis of Variance (*ANOVA*) in the Statistica v. 5.0 program was used to test the influence of the treatment, disturbance and shading on the *D. enneaphyllos* seedlings (logarithmically transformed numbers).

Repeated measure *ANOVA* in the Statistica v. 5.0 was used to test the influence of disturbance and shading on the abundances of functional groups, *Gaps* and Shannon-Wiener index of diversity. All the dependent variables were logarithmically transformed.

Table 34. Germinating capacity of the forest species [%].

Species	**Fresh**		**Dried**		**Stratified**	
	sand	**substr.**	**sand**	**substr.**	**sand**	**substr.**
Actaea spicata	×	0.00	×	×	×	0.00
Carex sylvatica	0.00	0.00	0.00	0.00	0.00	0.00
Dentaria bulbifera	×	0.00	×	0.00	×	0.00
Dentaria enneaphyllos	70.17	31.17	9.00	2.17	34.17	4.17
Galium odoratum	0.67	1.67	0.00	0.00	0.00	0.00
Maianthemum bifolium	18.00	7.33	0.00	0.00	0.00	0.00
Mercurialis perennis	0.00	0.00	0.00	0.00	0.00	0.00
Oxalis acetosella	1.39	0.00	×	×	×	×
Paris quadrifolia	×	1.07	×	×	×	0.00

Fresh – seeds sown within three days after collection, Dried - seeds sown after drying by 20°C, Stratified- seeds stratified for one month at 4°C; sand – wet sand, substr. – common garden substrate.

Tabulka 34. Klíčivost lesních druhů [%]. Fresh – semena vyseta do tří dnů od sběru, Dried - semena vyseta vysušená při teplotě 20°C, Stratified- semena vyseta po měsíční stratifikaci při 4°C; sand – mokrý písek, substr. – běžný zahradnický substrát.

Results

Species composition

The first ordination axis in the *CA* explained only 4.5% of the total variability in the data, while the first four axes explained 16.0%. The year of the experiment was found to be the most important factor influencing the species composition (F = 7.99, $p < 0.01$), followed by disturbance (F = 5.42, $p < 0.01$), shading (F = 1.93, $p < 0.01$) and seed addition (F = 1.49, $p < 0.01$). The first ordination axis in the *CCA* explained only 2.9% of the total variability in the data, while the first four axes explained 6.3% of the variability.

The between year variability in the species composition was higher than the variability caused by the treatments. The largest change in the species composition was related to the treatment turf disturbance (practiced in 2004) the following year after the treatment practice (i.e., in

2005), but the vegetation was able to close itself after two years (in 2006), and the species composition was able to revert to the species composition similar to the species composition before the disturbance. The ordination diagram (Fig. 37) illustrates the development well: releves taken from the plots with D_T treatment in 2005 are the most different from the others, while the releves taken from those plots in 2006 are close to the other releves in the middle of the ordination diagram.

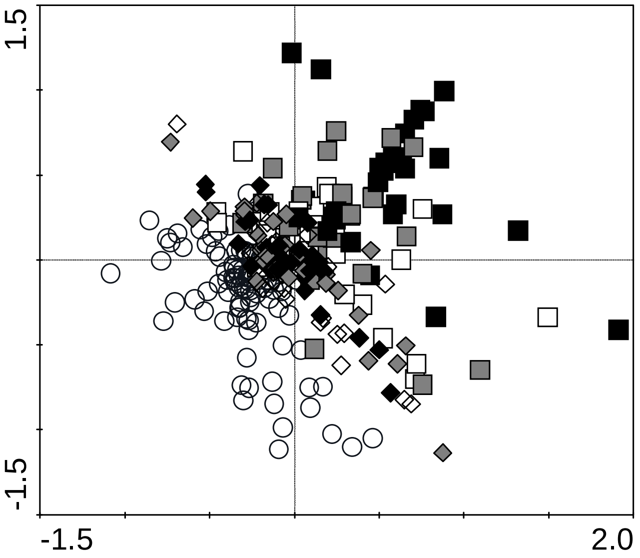


Figure 37. Ordination diagram for *CA* of the phytocenological releves. o - year 2004, - 2005, ◊ - 2006; transparent – no disturbance treatment practiced, grey - above-ground biomass removed, black - disturbance of the turf.

Obrázek 37. *CA* ordinační diagram fytocenologických snímků. o - rok 2004, - 2005, ◊ - 2006; průhledně – plochy bez narušení, šedě – odstranění nadzemní biomasy, černě - narušení drnu.

The influence of the disturbance is visualized in the Fig. 38 (ordination diagram for *CCA*). Releves taken in different years are shifted in the ordination diagram from the left part (2004) to the right part (2005, 2006). The two types of disturbance each change the species composition in a different way – we may distinguish three groups of releves: the non-disturbed treatment (in the upper part of the ordination diagram), the removal of above-ground biomass treatment (in the middle part of the diagram) and the disturbance of the turf treatment (in the lower part of the ordination diagram). The releve from the plots with removal of above-ground biomass treatment are closer to the non-disturbed releves, while the disturbed turf treatment is more distant from the other two groups, which indicates the higher impact of this treatment.

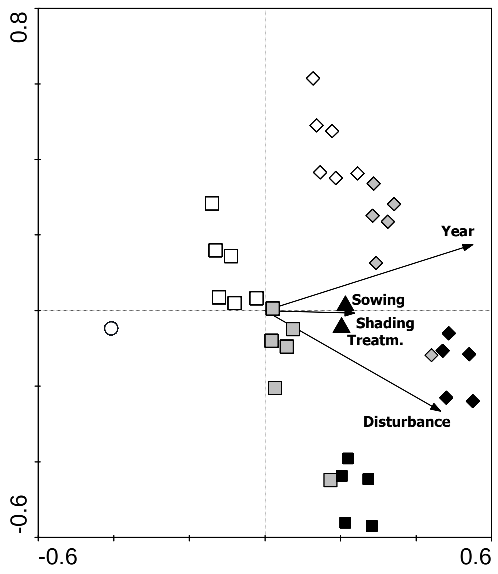


Figure 38. Ordination diagram for *CCA* - disturbance effect. o – year 2004, - 2005, ◊ - 2006; transparent – without disturbance, grey – removal of the above-ground biomass (D_{AB}), black – disturbance of the turf (D_T); Disturbance - disturbance degree (0 – without disturbance, 1 – D_{AB}, 2 - D_T), Sowing - seed addition, Shading – shading degree (0 – without shading, 1 - shaded at the 40% level of incoming radiation, 2 - shaded at the 5% level of incoming radiation), Year – time axis (year of the experiment), Treatm. - treatment.

Obrázek 38. CCA ordinační diagram – vliv narušení. o - rok 2004, - 2005, ◊ - 2006; průhledně – plochy bez narušení, šedivě – odstranění nadzemní biomasy (D_{AB}), černě - narušení drnu (D_T); Disturbance – stupeň narušení (0 – bez narušení, 1 – D_{AB}, 2 - D_T), Sowing – výsev, Shading – stupeň zastínění (0 – bez zastínění, 1 – stíněno na 40 % dopadajícího záření, 2 - stíněno na 5 % dopadajícího záření), Year – časová osa (rok experimentu), Treatm. – zásah.

The influence of the shading treatments is visualised in the Fig. 39. Shaded releves are shifted to the left part of the diagram (unlike the non-shaded releves), which indicates fewer changes in the species composition compared to the changes caused by the influence of the year of the experiment. In other words, shading treatment seems to slow down the changes in the species composition caused by the other environmental factors.

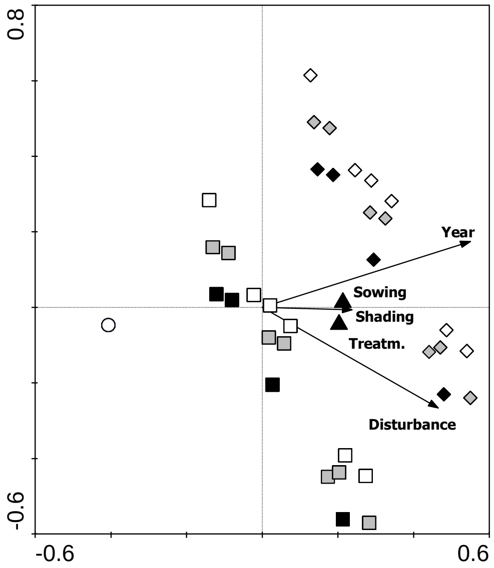


Figure 39. Ordination diagram for *CCA* - shading effect. o – year 2004, - 2005, ◊ - 2006; transparent – without shading, grey - shaded at the 40% level of incoming radiation (S_{40}), black - shaded at the 5% level of incoming radiation (S_5); Disturbance – disturbance degree (0 – without disturbance, 1 - removal of the above-ground biomass, 2 - disturbance of the turf), Sowing – seed addition, Shading – shading degree (0 – without shading, 1 - S_{40}, 2 - S_5), Year – time axis (year of the experiment), Treatm. – treatment.

Obrázek 39. CCA ordinační diagram – vliv zastínění. o - rok 2004, - 2005, ◊ - 2006; průhledně – plochy zastíněné na 40 % dopadajícího záření (S_{40}), černě - plochy zastíněné na 5 % dopadajícího záření (S_5); Disturbance – stupeň narušení (0 – bez narušení, 1 - odstranění nadzemní biomasy, 2 - narušení drnu), Sowing – výsev, Shading – stupeň zastínění (0 – bez zastínění, 1 – S_{40} , 2 - S_5), Year – časová osa (rok experimentu), Treatm. – zásah.

Character of the vegetation

Although, some characteristics were influenced by the shading or disturbance treatment, the time variability was higher. In general, the disturbance treatment influence was higher than the influence of the shading treatment.

Table 35. Disturbance and shading influencing the characteristics of the vegetation.

	Shading			Disturbance		
	Treatm.	**Year**	**Interaction**	**Treatm.**	**Year**	**Interaction**
GR	×	***	*	×	***	**
HA	×	×	×	×	×	×
HR	×	×	×	***	×	**
HS	×	×	***	**	***	***
HT	×	***	×	×	***	***
TR	×	***	×	×	***	×
Gaps	***	×	***	×	×	*
S-W index	×	***	×	***	***	***

Treatm. – influence of the treatment (shading/disturbance), Year – influence of the year of the experiment, Interaction – influence of the year and treatment interatction; GR - graminoids, HA - annual herbs, HR - rosettes, HS – small perennial herbs, HT – tall perennial herbs, TR – tree seedlings, Gaps - proportion of the gaps in the vegetation, S-W index – Shannon-Wiener index of diversity. * - significance 0.01 to 0.05, ** - 0.001 to 0.01, *** - <0.001, × - nonsignificant.

Tabulka 35. Vliv stínění a narušení na charakter vegetace. Shading – stínění, Disturbance - narušení, Treatm. – vliv zásahu (stínění/narušení), Year – vliv roku, Interaction - vliv roku a zásahu; GR - graminoidy, HA - jednoletky, HR – byliny s přízemní růžicí listů, HS - malé vytrvalé byliny, HT – vysoké vytrvalé byliny, TR – semenáčky stromů, Gaps - mezerovitost porostu, S-W index – Shannon-Wienerův index diverzity. * - statistická významnost 0.01 až 0.05, ** - 0.001 až 0.01, *** - <0.001, × - neprůkazné.

Disturbance increased the abundance of annual herbs (nonsignificant, p = 0.06), rosettes and small perennial herbs (for more details see Table 35).

The proportion of the *Gaps* in the vegetation was found to be higher at the plots shaded at the 5% level of incoming radiation, the increase was on average 9% (from 54% to 63%). Shading at the 40% level of incoming radiation did not influence the *Gaps* (Table 35).

The disturbance treatments influenced the diversity of the vegetation. When no disturbance treatment was practiced in the plot, the Shannon-Wiener index of diversity decreased during the experiment (on average from 2.05 in 2004 to 1.78 in 2006). When the above-ground biomass was removed from the plot, the diversity was found to be unchanged. When the turf was disturbed, the diversity was found to increase one year after the disturbance regime (on average in 0.16), and the following year a decrease on the same level as before disturbance was observed. For more detail see Table 35.

Species abundance

Several species were found to be influenced by the disturbance or shading regime.

In general, the disturbance regime influenced more species. The removal of above-ground biomass treatment decreased the abundance of *Hypericum maculatum* Crantz. The disturbance of the turf treatment increased the abundance of the following species: *Matricaria discoidea* DC., *Myosotis arvensis* (L.) Hill, *Stellaria graminea* L., *Trifolium hybridum* L. *Trifolium repens* L., *Tripleurospermum inodorum* (L.) Schultz-Bip., *Veronica hederifolia* L. and *Viola arvensis* Murray, and the abundance of *Trifolium montanum* L. was higher in the non-disturbed plots (see Table 36, Fig. 40 a).

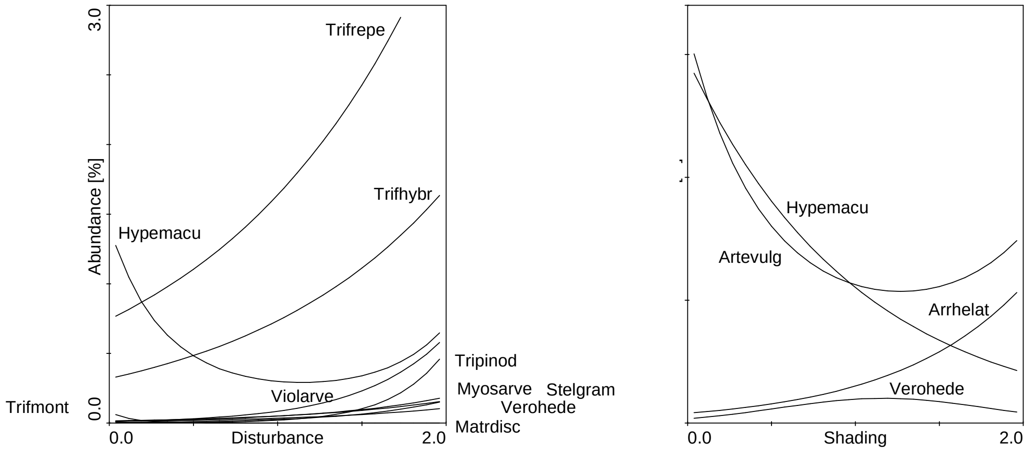
The shading treatment increased the abundance of *Arrhenatherum elatius* (L.) J. Presl et C. Presl, while it decreased the abundance of *Hypericum maculatum*. *Artemisia vulgaris* L. tended to be most abundant in non-shaded plots and less abundant in the plots shaded at the 40% level of the incoming radiation, while *V. hederifolia* was most abundant in the plots shaded at the 40% level of the incoming radiation (optimum 1.17). For more detail see Table 36, Fig. 40b.

Table 36. Disturbance and shading influencing the abundance of species (*GLM*).

Disturbance			Shading		
	M	var.		M	var.
Acer pseudoplatanus	L↓	6	*Arrhenatherum elatius*	L↑	18
Agrostis capillaris	L↑	5	*Artemisia vulgaris*	Q∪	11
Angelica sylvestris	Q∩	5	*Astragalus glycyphyllos*	L↓	8
Artemisia vulgaris	L↓	9	*Dactylis glomerata*	Q∩	4
Cerastium arvense	Q∪	8	*Galeopsis tetrahit*	L↑	9
Epilobium montanum	L↑	5	*Hypericum maculatum*	L↓	19
Galium mollugo agg.	L↓	6	*Veronica hederifolia*	Q∩	10
Hypericum maculatum	Q∪	14	*Vicia tetrasperma*	L↑	7
Matricaria discoidea	L↑	16			
Myosotis arvensis	L↑	21			
Phleum pratense	L↑	7			
Stellaria graminea	L↑	24			
Trifolium hybridum	L↑	12			
Trifolium montanum	L↓	18			
Trifolium pratense	L↓	7			
Trifolium repens	L↑	17			
Tripleurospermum inodorum	L↑	43			
Veronica hederifolia	L↑	33			
Vicia tetrasperma	L↑	5			
Viola arvensis	L↑	52			

only significant relationships; M: L - linear, Q - square polynom fitted, ↓/↑ - decreases/increases, ∪/∩ - “humped” answer, var. - explained variability [%].

Tabulka 36. Vliv stínění a narušení na pokryvnost druhů (*GLM*, jen průkazné vztahy). M: L - lineární vztah, Q - polynomiální vztah (druhého stupně), ↓/↑ - pokles/vzrůst, ∪/∩ - “hrbatá” odpověď, var. - vysvětlená variabilita [%].



a) b)

Figure 40. Disturbance and shading treatment influencing abundance of species (*GLM*): a) disturbance (0 – without disturbance, 1 - removal of the above-ground biomass, 2 - disturbance of the turf), b) shading (0 – without shading, 1 - shaded at the 40% level of incoming radiation, 2 - shaded at the 5% level of incoming radiation). Only the significant relationships with explained variability >10%. Arrhelat – *Arrhenatherum elatius*, Artevulg - *Artemisia vulgaris*, Hypemacu - *Hypericum maculatum*, Matrdisc – *Matricaria discoidea*, Myosarve - *Myosotis arvensis*, Stelgram - *Stellaria graminea*, Trifhybr – *Trifolium hybridum*, Trifmont - *Trifolium montanum*, Trifrepe – *Trifolium repens*, Tripinod - *Tripleurospermum inodorum*, Verohede - *Veronica hederifolia*, Violarve - *Viola arvensis*.

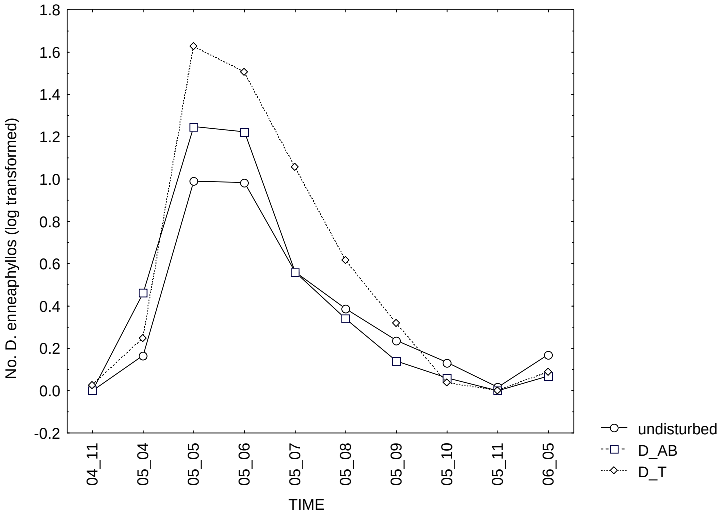
Obrázek 40. Vliv narušení a zastínění na pokryvnost druhů (*GLM*): a) narušení (0 - bez narušení, 1 – odstranění nadzemní biomasy, 2 - narušení drnu), b) zastínění (0 – bez zastínění, 1 – stíněno na 40 % dopadajícího záření , 2 - stíněno na 5 % dopadajícího záření). Jen průkazné vztahy s vysvětlenou variabilitou >10 %.

Seed addition

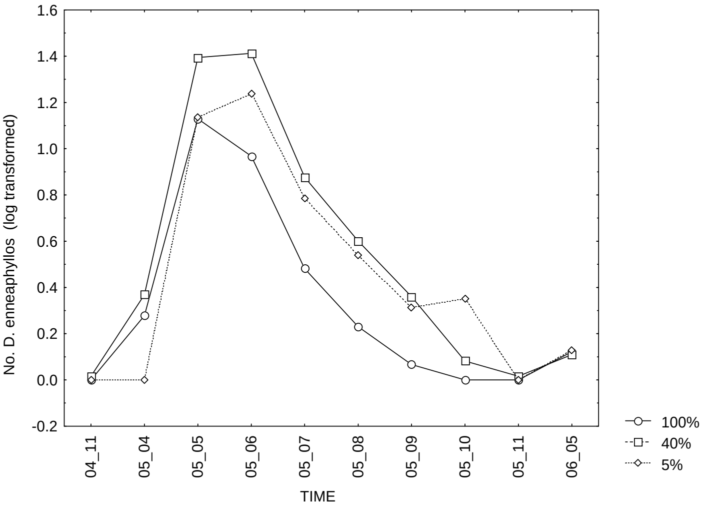
The forest species established poorly in the study site. Only sown forest herb species were found, i.e., *Dentaria bulbifera*, *D. enneaphyllos* and *Oxalis acetosella*. One germinating pseudobulb of *D. bulbifera* was found, while *O. acetosella* seedlings (25 in together) were found in five plots. It was not sown into one of the plots (S_{40} + D_T treatment). A seed was probably transported from the neighboring plot. Most of the seedlings of *Oxalis acetosella* were found to be in the shaded plots, although they were found also in a plot without disturbance or shading. No seedling of *O. acetosella* was able to survive the winter period of 2005-2006.

Seedlings of *D. enneaphyllos* were found from April 2005 (sown in June 2004) until the end of the experiment. They were found to be only in the plots where they were sown. Only a small number survived the winter period of 2005-2006: they were found in only 11 plots in low numbers (ranging from 1 to 4) in May 2006.

The treatment ($F = 246.95$, $p << 0.01$), time ($F = 126.14$, $p << 0.01$) and their interaction ($F = 127.60$, $p << 0.01$) were found to be significant for the numbers of *D. enneaphyllos* seedlings. The most *D. enneaphyllos* seedlings were found to be in the plots shaded at the 40% level of incoming radiation, while less seedlings were in the plots shaded at the 5% level of incoming radiation and in non-shaded plots (Fig. 41b). However, disturbance did not significantly influence the number of seedlings, a trend of increasing the number of seedlings at plots with disturbed turf in 2005 was observed (Fig. 41a).



a)



b)

Figure 41. Disturbance (a) and shading (b) influencing the *Dentaria enneaphyllos* seedling establishment. Time axis: year_month; undisturbed – no disturbance regime, D_AB - removal of the above-ground biomass, D_T – disturbance of the turf, 100% - non-shaded plots, 40% - shaded at the 40% level of incoming radiation, 5% - shaded at the 5% level of incoming radiation. Seedling numbers are logarithmically transformed.

Obrázek 41. Vliv narušení (a) a zastínění (b) na uchycování *Dentaria enneaphyllos*. Time – časová osa (rok_měsíc); undisturbed – bez narušení, D_AB – odstranění nadzemní biomasy, D_T – narušení drnu, 100% - nestíněno, 40% - stíněno na 40 % dopadajícího záření, 5% - stíněno na 5 % dopadajícího záření. No. D. ennneaphyllos (log transformed) - logaritmicky transformovaný počet semenáčků *D. enneaphyllos*.

Discussion

However, the between-year variability in species composition was higher than the changes in vegetation caused by disturbance or shading treatments, and a significant effect of the treatments was found. The high between year variability found in this study is not surprising, because the early stages of succession were reported to be high variable in many studies (see e.g., Christensen and Peet 1984; Collins and Glenn 1991; Symonides and Borowiecka 1985).

Disturbance treatments seem to be able to influence the species composition directly, and the changes in the species composition caused by the disturbance treatments were more quantitative than qualitative (for similar finding see Halada 2000), unlike with the shading treatments. Shading was found to slow changes in the species composition between years, and therefore it was able to stabilize the species composition. More stable species composition was reported to be typical for late stages of succession (Odum 1969), and in this context the shading should be viewed as a force leading the successional changes toward the more stable vegetation.

The turf disturbance treatment practiced in this study is comparable to natural disturbances caused by wild boars. However, the turf disturbance was the most radical treatment causing the biggest changes in the vegetation one year after the treatment practice, and the following year the vegetation was able to close and to decrease the species diversity at the same level as before the disturbance. Gaps created in this way were therefore only short-term (for similar finding see also Goldberg and Gross 1988). Although the proportion of gaps in control plots was relatively high, they were caused mostly by litter, which is unsuitable for most species seedling establishment (e.g., Donath and Eckstein 2008; Facelli and Pickett 1991a). From the shading treatments, the reduction at the 40% level of the incoming radiation treatment was not able to produce new gaps in the vegetation, but the shading at the 5% of the incoming radiation was able to increase the abundance of gaps. These findings could explain the relatively conservative species composition in abandoned sites in the stages of the succession dominated by grass species (e.g., Kučera and Guth 1998; Prach 1987). The fast regeneration of the vegetation toward the vegetation similar to the vegetation in the surroundings in such gaps (for similar finding see also Lanta and Lepš 2009) may also explain the slow changes in the species composition at abandoned sites which were reported in studies focusing on management renewal (Dzwonko and Loster 2007; Maccherini et al. 2007; Sutherland 2006). On the other hand, the synergistic effect with another factor, e.g., abnormal weather conditions, should increase the gap influence, e.g., on tree seedling establishment (De Steven 1991; Ostfeld and Canham 1993), which are poor competitors with the vegetation dominated by grasses (Prach et al. 1996).

The annuals, rosettes and small perennial herbs were more abundant in the plots with the turf disturbance treatment. It seems that these disturbances are able to maintain these species in abandoned vegetation for a relatively long period, although they are less competitive with tall vegetation (e.g., Wiegert and Evans 1964).

Lower irradiance was reported to be able to influence the competitive ability of the species and so indirectly increase the recruitment chance of the species typical for later stages of succession (e.g., Dovčiak et al. 2005), but the shading treatment was able to reduce neither the abundance of *HT* group nor the abundance of dominated grass species in this study. In general, the shading treatments were of lower impact on the species abundance than the disturbance treatment.

The decrease in species diversity in control plots is in assumption with findings of other studies, which also reported a decrease in diversity after the abandonment (e.g., Willems 1983). The diversity found at the beginning of the experiment corresponds to the diversity reported in other studies, e.g., Zelený et al. (2001) found diversity of abandoned grassland of the *Polygono-Trisetion* alliance to be between 2.0 and 2.2. The disturbance was able to increase the diversity, but only for one year.

Only forest species sown directly into the study site were found, which correspond also with findings in other studies dealing with seed sowing experiments of the forest species (e.g., Ehrlén and Eriksson 2000). This finding indicates the seed limitation of the forest species.

Most of the forest species were not able to germinate in this study, although the seed number added were high and also the germination capacity in laboratory conditions was found to be low for most of the species. A similar finding was reported also in other studies (e.g., Ehrlén and Eriksson 2000; Kupferschmid et al. 2000), although such a large proportion of species was not found to be unable to germinate in any of these studies. For comparison, Ehrlén and Eriksson (2000) found the *Denntaria bulbifera* able to establish in 10% and *Paris quadrifolia* in 44% recent woods, where the seeds were sown, and the survival of the seedlings was high, i.e., 15-77%. Gustafsson et al. (2002) was able to find the *D. enneaphylos* in 83% of plots after seven years of the sowing treatment. For comparison, *Dentaria enneaphyllos*, which was the only well establishing species, was not able to germinate in 56% of the plots, and its survival was found to be on average 3% in the plots, where it was able to germinate. None of the seedlings was able to develop into further stages than to the seedling with cotyledons. Shading was able to enhance the seedling recruitment of *D. enneaphyllos*, and there was also a similar trend (however insignificant) for disturbance. The numbers of *Oxalis acetosella* seedlings indicate a similar pattern, but there was found to be an insufficient number of *O. acetosella* for the statistical analysis. These findings indicate the possible safe-site limitation of the forest species in an relatively early stage of succession. The reason for the safe-site limitation of the forest species could be soil conditions (for this opinion see also Pärtel and Helm 2007). The difference in soil conditions was also reported as the reason for the dispersal limitation of species transplanted with soil the block (Bruelheide 2000; Kubíková 1994). Good seedling recruitment was also usually found in the experiments, where the species were sown into habitats similar to those from which they had originated (e.g., Donath et al. 2007; Foster and Tilman 2003; Gustafsson et al. 2002). For example, Ohlson and Grønli (2006) found better recruitment of the transplanted *Actaea spicata* in the forests than in the grassland. However, opposite findings were also published (Ehrlén and Eriksson 2000; Foster et al. 2004; Primack and Miao 1992).

The seed transposition of *Oxalis acetosella*, in the plot where it was not found, is very probable, because the plot was in close surroundings of the plot with seed addition treatment. According to the topography of the surrounding plots, zoochory seems to be the most probable explanation for the transfer of *O. acetosella* seeds. The seed transposition was found in other studies as well (Kupferschmid et al. 2000).

A high germination capacity of *D. enneaphyllos* was observed in laboratory conditions (up to 70%), and the highest germination capacity was observed for the fresh seeds and for the treatment on the sand (see Table 34). The seedling recruitment in the field was much lower than in the laboratory even in the treatments where the highest number of seedlings were listed (about 15%), but a similar finding was reported also in other studies (e.g., Clarke and Davison 2001).

Summary

The study area was situated into the southern part of the Czech Republic (40°35-38´ N, 14°11-17´ E), altitude 665-940 m (Fig. 42). Climatic conditions moderately oceanic between the warm and cold type (climatic regions MT 3 – Ch 7), average year temperature 6.8°C and average year precipitation 718-1 003 mm.

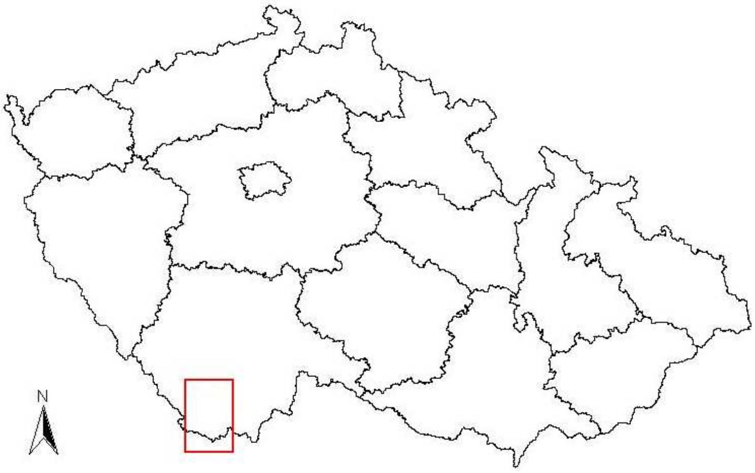


Figure 42. Position of the study area in the Czech Republic.

Obrázek 42. Poloha zájmového území v České republice.

The SDFs on mesic stand (neither waterlogged nor desiccated, with vegetation neither ruderalised nor typical for poor soils) were studied. Forty eight plots (100 m^2) were fixed in SDFs, which differed in age to cover up the chronosequence of successional sere directed toward forests in the study area. The species composition and the influence of the site- and context-dependent factors on the species composition and character of the herb layer were studied, and an estimation of the probable future development of the tree layer was calculated.

The studied SDFs were on average 7.4 ha large (ranging from 0.08 to 22 ha), the shape differed much between the studied SDFs (an average relative length of the SDF border was found to be 3.1, ranging from 1.1 to 15.6), and the nearest distance to the border of the SDF was found to be not long (on average 22 m, ranging from 10 to 80 m).

The SDFs were semi-open growths with an average relative irradiance of 20% of incoming radiation in the 120 cm above ground (ranging from 3 to 68%), with a relatively dense herb layer reducing the incoming radiation on average at 6% in the 5 cm above ground (ranging from 1 to 36%). Most of the SDF were on shallow soils (mean depth of the organic soil horizon was found to be 23 cm, ranging from 4 to 70 cm), with relatively high rock fragment content (mean value 42%, ranging from 6 to 86%). Several soil characteristics were found to be intermediate between the numbers typical for grassland and forest soils: soil reaction (mean value 4.3, ranging from 3.8 to 5.6), organic matter content (mean value 11%, ranging from 5 to 21%), basal respiration of the microbial community (mean value 2.7 μg C-CO_2.g^{-1}.hod^{-1}, ranging from 0.7 to 5.8 μg C-CO_2.g^{-1}.hod^{-1}).

Most of the SDFs were surrounded by SDFs (on average 38%), grassland (31%), and forests (23%), while fields (6%) and “other” land cover (2%) were low abundant. The distance to the nearest grassland was only 45±60 m, while the nearest forest was found to be 111±152 m away and the nearest field 743±912 m.

The average age of the tree layer was found to be 30 years (ranging from 10 to 46 years), but the age structure of the tree layer was not found to be homogeneous, because the maximum age of the tree layer was 46 years (ranging from 12 to 84 years). This finding corresponds with the data from the historical aerial photos: most of the SDFs were not covered by trees in 1952 (65% grasslands, 19% fields; 13% covered by scattered trees, and 4% by closed tree canopies), while half of the SDFs were covered by trees in 1966 (33% grassland, 13% fields, 25% scattered trees, 29% closed tree canopy) and most of the plots were covered by trees in 1983 (4% fields, 13% grassland, 23% scattered tree canopy, 60% closed tree canopy).

The tree layer changes from the dense growth of young thin trees (up to 179 trees.are^{-1}) to open canopies of adult trees (down to 2 trees.are^{-1}). The age structure of the older tree layer is less age uniform than in the young SDFs.

The tree layer was dominated by pioneer tree species. In total, 11 tree species were listed in the tree layer. The anemochorous species dominated the tree layer, but endozoochorous species were also able to colonise these growths. On average 2.6 species were found in a plot, and 83% of the trees were deciduous ones. The birch (*Betula pendula* Roth.) was found to be the most common and most abundant species (occupying 88% of plots, 60% of trees), but the European aspen (*Populus tremula* L.), Norway spruce (*Picea abies* (L.) Karsten), mountain ash (*Sorbus aucuparia* L.), and Scots pine (*Pinus sylvestris* L.) were able to dominate the tree layer as well. Of other species, the goat willow (*Salix caprea* L.) and common ash (*Fraxinus excelsior* L.) were more common incidental trees in these growths.

The species composition of the tree-layer was related from the studied factor to the Ellenberg *T* indicator value and shape of the SDF (14% of the total variability in the data explained). The Norway spruce and Scots pine preferred colder stands, while the sycamore maple, cherry-tree and common ash preferred warmer stands. The birch occupied sites with more irregular shapes, unlike the European aspen which preferred less complicated shapes of the SDF (it may be a result of vegetative reproduction of this species). The growths dominated by the European aspen were found to be more occupied by the endozoochorous cherry tree and mountain ash, while in the SDFs dominated by birch the anemochorous goat willow was more common. More tree species were found to be at higher altitudes and/or at colder stands, in younger growths and in the SDFs with more complicated shapes. The abundance of the two most common species (birch and Norway spruce) were influenced mostly by the soil conditions, history, age and proportion of SDF, and forests in the 300 m surroundings.

In total, fifteen tree-seedling species were listed. Most of the seedlings were 10-40 cm high. An average plot contained 145 seedlings of five species. The best colonisers were species non-specific to the stage of succession (59% of the seedlings, 96% of the plots), and anemochorous species (75% of the seedlings, 98% of the plots). Species typical for terminal stages of succession were able to colonise 65% of the plots, but they took only 4% of the total number of seedlings. Zoochorous species occupied 85% of the plots and took 25% of the seedlings. Species typical for the early stages of succession preferred plots more irradiated at the 20 cm above ground, lower altitudes, less productive sites, and sites near to the forest. Species typical for terminal stages of succession preferred lower altitudes, older growths, medium rich stands with more organic matter content, lower soil reaction, and sites near forests. Species non-specific to the stage of succession gained in medium-aged SDFs and under a dense tree layer. Anemochorous and zoochorous species were not found to be influenced by any studied factor.

The sycamore maple (*Acer pseudoplatanus* L.) was the most common seedling species (60%), while the European aspen (10%), mountain ash (10%), Norway spruce (9%), cherry tree (5%), and common ash (3%) were also abundant. The altitude and soil reaction significantly influenced the tree-seedling species composition. Sycamore maple seedlings were more common in younger SDFs, which grew faster. Norway spruce seedlings were negatively influenced by relative irradiance at the 20 cm above ground. The number of birch seedlings was negatively influenced by the relative irradiance at the 20 cm above ground and/or by the abundance of typical grassland species. More cherry tree seedlings were found at plots in lower altitudes, near forests and in older stands. The mountain ash was more common in the plots where the herb layer was more similar to the herb layer of the forests.

An estimation of the changes for the next generation of the trees was done. It was based on a comparison of the present and estimated species composition. The estimated tree layer species composition was derived from the number of tree seedlings according to their height. The estimation predicts big changes in the tree layer species composition. The estimated tree layer species composition was related to the time of succession, nutrients, and humidity (25% of the total variability explained). The shift was found to be directed toward the species composition typical for terminal stages of succession, but the species composition of the second generation of the tree layer was still estimated to be very different. The succession will probably be long, and several centuries can be expected to be necessary for the successional changes leading to the species composition near the natural species composition.

Most of the species common in the present tree layer are supposed to change their abundance in the estimated tree layer. The most important finding is the estimated decrease of the pioneer species the birch, and the predicted increase of the ubiquitous species the Norway spruce and the sycamore maple and the ability of species typical for terminal stages of succession (beech, pedunculate oak) to establish themselves in the next tree generation. The sycamore maple, European beech, and pedunculate oak (*Quercus petraea* (Mattuschka) Liebl.) were found to be typical species in the estimated tree layer, although present common species (birch, European aspen, Norway spruce) will be more common.

The results are relatively optimistic for the forest managers, because only 5% of the plots probably will not be colonised by species “valuable” for forest management, while 47% of plots will contain more than one of these species. Most of the plots (79%) exceeded 2,000 seedlings of “valuable” species per hectare, which is sufficient for natural regeneration. Almost half of the trees “valuable” for forest management were found to be deciduous.

The general character of the herb layer of the SDFs in the first tree generation could be described as follows: grassland character prevails (average $G = 20.5$, $G_w = 45.1$), while woodland character plays a minor role (average $W = 8.7$, $W_w = 18.0$). Most of the species listed in the herb layer were related to the grassland vegetation (in total, 86 species, mean abundance 33%), followed by a group of species growing both in grassland and wood (30 species, 17%), woodland species (26 species, 10%), antropochorous and/or ruderal species (18 species, 3%), shrub species (10 species, 1%) and species typically growing at clearings (4 species, 2%). Most of the species related to the grassland vegetation were exozoochorous species (average $G_w\_Z_{ex} = 22.6$) and species non-specific to the type of distribution (average $G_w\_Ns = 11.5$), while most of the species related to the forest vegetation were anemochorous (average $W_w\_Wd = 6.5$), endozoochorous species (average $W_w\_Z_{end} = 5.6$) or species non-specific to the type of distribution (average $W_w\_Ns = 4.5$).

Species grouped according to the biotope were in general more influenced by the context-dependent factors, especially by the historical vegetation cover and by the proportion of grassland and forests in the surroundings, while the proportion of “other” land cover and the character of the SDF (area, shape and position within the SDF) were of less importance. Of the site-dependent factors, the soil characteristics were more important for several groups of species, but the relationships were group dependent.

General trend observed was the preference of grassland species to the soil conditions closer to the soil conditions typical for grassland soils (i.e., lower organic matter content, higher soil reaction). The most important finding was that the abundance of the woodland species increased with the age of the tree layer and with the duration of the tree layer. However, a decrease in grassland species was not observed.

The increase in the woodland character of the herb layer with the duration of the tree layer (A_a, A_{max}, historical vegetation cover) was promoted using the (weighted) grasslandness and (weighted) woodlandness indeces. The relationships of the other factors were index dependent, and no general trend was observed, except for the woodlandness related to the soil conditions more similar to the forest soils (i.e., higher organic matter content, lower soil reaction and higher microbial respiration).

Almost all of the groups of species according to the type of distribution related to the woodland were found to be more abundant in the SDFs with the tree layer developed for a longer time period (A_a, A_{max}, historical vegetation cover), but the decrease in groups of species related to grassland vegetation was not observed. Many of the site- and context-dependent factors significantly influenced the abundance of the groups of species, but the relationships were group dependent and no general pattern could be observed.

In total, 161 vascular plant species were listed, on average 32±8.6 species per 100 m^2. The herb layer of SDFs was found to be highly variable (23% of the species were found only at one plot, while only 18% were found at more than 33% of the plots). An average diversity value was found to be 2.6 (ranging from 0.4 to 3.5), measured as a Shannon-Wiener index, which is relatively high.

All the common species in this study were also common species in the study area and species widespread in Central Europe. The most common species were the following: *Agrostis capillaris* L., *Galium mollugo* agg. L., *Holcus mollis* L., *Veronica chamaedrys* L. (present at more than 80% plots), while the most abundant were the following species: *Agrostis capillaris*, *Avenella flexuosa* (L.) Drejer, *Holcus mollis* and *Vaccinium myrtillus* L. (more than 7% abundance per occupied plot). Most of the diagnostic and constant species were species related to the grassland vegetation (33 out of 161 species), especially of the *Arrhenatherion elatioris, Polygono bistortae-Trisetion flavescentis* and *Violion caninae* alliance. Only ten species were related to the forest vegetation, i.e., of the *Dentario enneaphylli-Fagetum* association, *Luzulo-Fagion* and *Quercion petreae* alliance. Only several typical forest species were able to establish in the SDFs, and they were usually low abundant. Ferns and *Vaccinium myrtillus* were the only more abundant typical forest species, and of the *Oxalis acetosella* L. was relatively frequent. However, some forest species typical for oak-beech or beech forests were also listed in the herb layer, e.g., *Asarum europaeum* L., *Geranium robertianum* L., *Mercurialis perennis* L. and *Mycelis muralis* L.

In general, the influence of the studied factors on the frequent species abundance was species specific, and only a few general trends could be observed. Both site- and context-dependent factors influenced the abundance of frequent species, and there was found to be no big difference or general trend true for these two types of factors.

The seed and safe-site limitation of forest herbs was studied in a factorial designed experiment in a 12-year abandoned grassland (48°41.468´ N, 14°17.382´ E, altitude 700 m). The influence of disturbance and shading on species composition, general characteristics of the vegetation, and on species abundances was studied, and seedling establishment of forest species was monitored. In total, 16 treatments in six randomised blocks were fixed and the following manipulations were performed: i) shading at the 40% level of incoming *PhAR*, ii) shading at the 5% level of incoming *PhAR*, iii) removal of above-ground plant biomass, iv) disturbance of the turf, v) seed addition of typical forest species (*Actaea spicata* L., *Carex sylvatica* Huds., *Dentaria enneaphyllos* L., *D. bulbifera* L., *Galium odoratum* (L.) Scop., *Maianthemum bifolium* (L.) F.W. Schmidt*, Mercurialis perennis, Oxalis acetosella, Paris quadrifolia* L.).

However, the between-year variability in species composition was higher than the changes in vegetation caused by disturbance (iii and iv) or shading treatments (i and ii), and the treatments were found to have had a significant effect. Disturbance treatments were found to be able to influence the species composition directly, and the changes in the species composition caused by the disturbance treatments were more quantitative than qualitative, unlike the shading treatments. Shading was found to slow down the changes in the species composition between years, and therefore this treatment was able to stabilise the species composition.

However, the turf disturbance was the most radical treatment causing the biggest changes in the vegetation one year after the treatment practice, and the following year the vegetation was able to close again. The reduction at the 40% level of the incoming radiation treatment was not able to produce new gaps in the vegetation, but the shading at 5% of the incoming radiation was able to increase the abundance of gaps.

The decrease in species diversity in control plots was observed, while the removal of above-ground vegetation was able to stabilise the diversity and the turf disturbance treatment increased the diversity, but only for a one-year period.

The annuals, rosettes and small perennial herbs were more abundant in the plots with the turf disturbance treatment.

Most of the forest species were not able to germinate, although the seed densities were high. The germination capacity in laboratory conditions was also found to be low for most of the species.

Only forest species sown directly into the study site were found. This finding indicates the seed limitation of the forest species. All the recruited species were found the following year after sowing. *Dentaria* *enneaphyllos* was the only well establishing species, but it was not able to germinate in 56% of the plots and its survival was found to be on average 3% in the plots, where it was able to germinate. None of the seedlings was able to develop into a further stage than to the seedling with cotyledons. Shading treatment was able to enhance the seedling recruitment of *D. enneaphyllos*, and there was also a similar trend (however insignificant) for disturbance of the turf treatment. The numbers of *Oxalis acetosella* seedlings indicate a similar pattern, although there was found to be an insufficient number of *O. acetosella* for the statistical analysis. These findings indicate the possible safe-site limitation of the forest species at a relatively early stage of succession.

Shrnutí

Zájmové území se nachází v jižní části České republiky (40°35-38´ N, 14°11-17´ E), v nadmořské výšce 665 – 940 m (Obr. 42). Klima je mírně teplé až chladné (MT 3 až Ch 7) s průměrnou roční teplotou 6,8°C a průměrnými srážkami 718 až 1 003 mm.

Studovány byly porosty náletových dřevin na mesickém stanovišti (ani zamokřená ani vysychavá stanoviště, vegetace nebyla ruderalizovaná ani typická pro chudé půdy). V porostech náletových dřevin bylo vytyčeno 48 trvalých ploch (á 100 m^2), které pokrývaly předpokládanou chronosekvenci sukcesní řady směrem k lesu v zájmovém území. Práce byla zaměřena na vliv na stanovišti závislých faktorů a na kontextu závislých faktorů na druhové složení a charakter bylinného patra. Byla odhadnuta změna v druhovém složení stromového patra pro následující generaci stromů.

Studované porosty náletových dřevin byly v průměru 7,4 ha velké (v rozmezí 0,08 až 22 ha), různých tvarů (průměrná relativní délka obvodu SDF byla 3,1, v rozmezí 1,1 až 15,6) a většina ploch nebyla příliš vzdálena od okraje SDF (průměrně 22 m, v rozsahu 10 až 80 m).

Porosty náletových dřevin jsou poloотevřené hájky s průměrnou relativní ozářeností 20 % ve 120 cm (rozsah 3 až 68%), s relativně hustým bylinným patrem redukujícím relativní ozářenost v 5 cm na 6 % dopadajícího záření (rozsah 1 až 36 %). Většina porostů náletových dřevin byla na relativně mělkých půdách (průměrná hloubka organického horizontu 23 cm, rozsah 4 až 70 cm) s relativně vysokou skeletovitostí (průměrně 42 %, rozsah 6 až 86 %). Některé půdní podmínky v porostech náletových dřevin byly mezi hodnotami typickými pro luční a lesní půdy: půdní reakce (průměrná hodnota 4,3, rozsah 3,8 až 5,6), obsah organické hmoty v půdě (průměrná hodnota 11 %, rozsah 5 až

21 %), bazální respirace (průměrná hodnota 2,7 μg C-CO_2.g^{-1}.hod^{-1}, rozsah 0,7 až 5,8 μg C-CO_2.g^{-1}.hod^{-1}).

Porosty náletových dřevin byly obklopeny především porosty náletových dřevin (průměrně 38 %), loukou (31 %) a lesy (23 %), méně polem (6 %) a krajinným pokryvem "ostatní" (2 %). Vzdálenost k nejbližší louce byla pouze 45±60 m, zatímco k nejbližšímu lesu 111±152 m a k nejbližšímu poli dokonce 743±912 m.

Průměrný věk stromového patra byl 30 roků (rozsah 10 až 46 let), věková struktura stromového nebyla homogenní a průměrný maximální věk stromového patra byl 46 let (rozsah 12 až 84 let). Věk stromového patra koresponduje s daty získanými leteckým snímkováním: v roce 1952 většina ploch nebyla porostlá stromy (65 % louka, 19 % pole, 13 % roztroušený nálet, 4 % zapojený nálet), v roce 1966 byla polovina ploch porostlá stromy (33 % louka, 13 % pole, 25 % roztroušený nálet, 29 % zapojený nálet) a v roce 1983 byla většina ploch porostlá stromy (4 % pole, 13 % louka, 23 % roztroušený nálet, 60 % zapojený nálet).

V průběhu sukcese se stromové patro mění z hustého zápoje mladých stromů (až 179 stromů.ar^{-1}) v relativně otevřený porost (i méně než 2 stromy.ar^{-1}). Věková struktura stromového patra je u starších porostů méně uniformní.

Ve stromovém patře dominovaly pionýrské druhy stromů. Celkem bylo zaznamenáno 11 druhů stromů. Ve stromovém patře dominovaly anemochorní druhy, ale zoochorní druhy byly také schopny kolonizovat tyto porosty. V průměru bylo zaznamenáno 2,6 druhu na jedné ploše, z toho 83 % stromů bylo opadavých. Bříza (*Betula pendula* Roth.) byla nejhojnějším druhem (zaznamenána na 88 % ploch, 60 % všech stromů). Z ostatní druhů osika (*Populus tremula* L.), smrk (*Picea abies* (L.) Karsten), jeřáb (*Sorbus aucuparia* L.) a borovice (*Pinus sylvestris* L.) byly schopny dominovat stromovému patru. Vrba jíva

(*Salix caprea* L.) a jasan (*Fraxinus excelsior* L.) byly nejčastějšími vtroušenými dřevinami.

Ze studovaných faktorů druhové složení stromového patra bylo ovlivněno Ellenbergovou hodnotou *T* a tvarem SDF (tyto faktory vysvětlily 14 % celkové variability v datech). Smrk a borovice byly hojněji zastoupeny na chladnějších stanovištích, zatímco jeřáb, třešeň a jasan preferovaly teplejší stanoviště. Bříza byla častěji v porostech náletových dřevin s nepravidelným tvarem, zatímco osika byla častěji zastoupena v SDFs s pravidelným tvarem (může se jednat o důsledek vegetativního rozmnožování tohoto druhu). V porostech náletových dřevin, v nichž dominovala osika byly více zastoupeny endozoochorní druhy třešeň (*Prunus avium* (L.) L.) a jeřáb, zatímco v porostech, v nichž dominovala bříza byla více zastoupena anemochorní vrba jíva. Více druhů stromů bylo ve vyšších nadmořských výškách a/nebo na chladnějších stanovištích, v mladších porostech a v SDFs s komplikovaným tvarem. Pokryvnost dvou nejčastějších druhů břízy a smrku byla ovlivněna především půdními podmínkami, vegetačním krytem v minulosti, věkem a podílem SDF a lesa v okolí 300 m.

Celkem bylo zaznamenáno 15 druhů semenáčků stromů, většina semenáčků byla 10 až 40 cm vysoká. Průměrná plocha obsahovala 145 semenáčků pěti druhů. Nejlépe se uchycovaly semenáčky druhů nespecifických ke stádiu sukcese (59 % semenáčků, 96 % ploch) a anemochorní druhy (75 % semenáčků, 98 % ploch). Druhy typické pro terminální stádia sukcese byly schopné kolonizovat 65 % ploch, ale na celkovém počtu semenáčků se podílely jen 4 %. Zoochorní druhy obsadily 85 % ploch a tvořily 25 % semenáčků. Druhy typické pro rané fáze sukcese preferovaly plochy s vyšší relativní ozářeností ve 20 cm, nižší nadmořské výšky, méně úživná stanoviště a plochy blízko lesa. Druhy typické pro terminální stádia sukcese preferovaly nižší nadmořské výšky, starší porosty, středně úživná stanoviště s vyšším podílem organické hmoty v půdě, nižší půdní reakci a plochy blíže k lesu. Druhy nespecifické ke stádiu sukcese byly více zastoupeny ve středně starých porostech náletových dřevin a pod hustým zápojem stromového patra. Anemochorní a zoochorní druhy nebyly závislé na žádném studovaném faktoru.

Javor klen (*Acer pseudoplatanus* L.) byl nejčastějším semenáčkem (60 %), hojněji byly zastoupené také druhy: osika (10 %), jeřáb (10 %), smrk (9 %), třešeň (5 %) a jasan (3 %). Nadmořská výška a půdní reakce významně ovlivňovaly druhové složení semenáčků stromů. Semenáčky klenu byly častěji v mladších porostech náletových dřevin, které rostly rychleji. Semenáčky smrku byly negativně ovlivněny relativní ozářeností ve 20 cm. Semenáčky břízy byly negativně ovlivněny relativní ozářeností ve 20 cm a/nebo pokryvem typicky lučních druhů. Více semenáčků třešně bylo na plochách v nižších nadmořských výškách, v blízkosti lesa a ve starších porostech. Jeřáb byl více zastoupen na plochách jejichž bylinné patro bylo více podobné lesnímu bylinnému patru.

Byla odhadnuta změna v druhovém složení stromového patra pro následující generaci stromů. Odhad byl založen na porovnání současného složení stromového patra a odhadnutého složení, které bylo provedeno na základě druhového složení a výšky semenáčků stromů. Odhadované změny v druhovém složení byly velké a byly vztaženy k času sukcese, živinám a půdní vlhkosti (celkem tyto faktory vysvětlily 25 % celkové variability). Změna v druhovém složení byla směřována směrem k druhovému složení typickému pro terminální stádia sukcese, ale druhové složení druhé generace stromů bylo odhadnuto odlišné. Sukcese směrem k terminálnímu stádiu bude pravděpodobně dlouhá a potrvá několik století než sukcesní změny povedou k druhovému složení stromového patra blízkému potenciální přirozené vegetaci.

Většina druhů běžných v první generaci stromového patra pravděpodobně změní zastoupení v následující generaci.

Nejvýznamnějším zjištěním je předpokládaný pokles zastoupení pionýrského druhu břízy, a nárůst zastoupení smrku a klenu, které jsou ke stádiu sukcese nespecifické, a předpokládané uchycení druhů terminálních stádií sukcese (buk, dub). Vyšší zastoupení klenu, buku, osiky a dubu (*Quercus petraea* (Mattuschka) Liebl.) odlišovalo odhadnuté stromové patro od stávajícího, ačkoli druhy typické pro stávající stromové patro (bříza, osika a smrk) budou nadále hojně zastoupené.

Výsledky odhadu změn ve stromovém patře pro následující generaci stromů jsou optimistické z hlediska lesního hospodaření. Jen pro 5 % ploch nebylo předpovězeno, že jejich stromové patro nebude kolonizováno druhy cennými z hlediska lesního hospodářství, zatímco 47 % bude obsahovat více než jeden takovýto druh. Na většině ploch (79 %) počet semenáčků stromů cenných z hlediska lesního hospodářství přesáhl 2 000 ks.ha^{-1}, což je počet dostatečný pro přirozené zmlazení. Téměř polovina semenáčků dřevin cenných pro lesní hospodářství byla opadavou dřevinou.

Celkový charakter bylinného patra porostů náletových dřevin v první generaci je možné popsat následovně: převažuje luční charakter (průměrná $G = 20{,}5$, $G_w = 45{,}1$), zatímco lesní charakter je jen velmi málo vyvinut (průměrná $W = 8{,}7$, $W_w = 18{,}0$). Většina druhů zaznamenaná v bylinném patře byla druhy typickými pro luční společenstva (celkem 86 druhů, průměrná pokryvnost 33 %), hojné byly také druhy společné lučním a lesním stanovištím (30 druhů, 17 %), následovaly lesní druhy (26 druhů, 10 %), druhy vázané na antropogenní a nebo ruderální stanoviště (18 druhů, 3 %), druhy křovin (10 druhů, 1 %) a druhy pasek (4 druhy, 2 %). Většina druhů vázaná na luční společenstva byla exozoochorních (průměrné $G_w\_Z_{ex} = 22{,}6$) a druhy nespecifické ke způsobu rozšiřování (průměrné $G_w\_Ns = 11{,}5$), na rozdíl od druhů typických pro lesní stanoviště, u nichž převažovaly druhy anemochorní (průměrné $W_w\_Wd = 6{,}5$), endozochorní (průměrné

$W_w\_Z_{end}$ = 5,6) nebo druhy nespecifické vzhledem ke způsobu rozšiřování (průměrné W_w_Ns = 4,5).

Skupiny druhů vylišené na základě biotopu byly více ovlivněny na kontextu závislými proměnnými, a to především vegetačním krytem v minulosti a podílem luk a lesa v okolí. Méně důležitými na kontextu závislými faktory byl podíl krajinného pokryvu "ostatní" a faktory spojené s charakterem porostu náletových dřevin (rozloha, tvar a pozice plochy uvnitř SDF). Z na stanovišti závislých faktorů byly významné pro některé skupiny druhů půdní podmínky, ale vztah byl vždy závislý na skupině a výsledky nelze zobecnit. Druhy typické pro luční společenstva dosahovaly vyšší pokryvnosti na půdách s charakterem bližším lučním půdám (nižší obsah organické hmoty a vyšší půdní reakce). Nejvýznamnějším zjištěním bylo, že pokryvnost lesních druhů rostla s věkem stromového patra a s délkou trvání stromového patra. Pokryvnost luční druhů však s věkem průkazně neklesala.

Vliv stáří stromového patra (A_a, A_{max}, vegetační kryt v minulosti) na lesní/luční charakter bylinného patra byl výraznější při použití indexů (vážené) lesnatosti a (vážené) lučnatosti. Ostatní faktory ovlivňovaly jednotlivé indexy, ale nebyl pozorován žádný obecný trend, s výjimkou lesnatosti, která byla vyšší na půdách ve sledovaných charakteristikách bližších lesním půdám (vyšší obsah organické hmoty, nižší půdní reakce a vyšší bazální respirace).

Téměř všechny skupiny druhů vylišených na základě způsobu rozšiřování vztažené k lesním společenstvům byly více zastoupené v porostech náletových dřevin s déle vyvinutým stromovým patrem (A_a, A_{max}, vegetační kryt v minulosti), ačkoli pokles pokryvnosti skupin druhů vztažených k lučním společenstvům s rostoucím věkem stromového patra nebyl pozorován. Celá řada na stanovišti závislých i na kontextu závislých faktorů ovlivňovala pokryvnost skupin druhů vylišených na základě způsobu rozšiřování, ale vztahy byly individuální a nebyl zjištěn žádný obecný trend.

V bylinném patře bylo celkem zaznamenáno 161 druhů cévnatých rostlin, v průměru 32±8,6 druhů na 100 m^2. Druhové složení bylinného patra bylo velmi variabilní (23 % druhů bylo zaznamenáno jen na jediné ploše, jen 18 % druhů bylo přítomno na více než 33 % ploch). Průměrná druhová diverzita, stanovená jako Shannon-Wienerův index diverzity, byla 2,6 (rozsah 0,4 až 3,5), což je relativně vysoká hodnota.

Všechny druhy hojné v bylinném patře byly druhy hojné v zájmovém území a druhy běžné ve střední Evropě. Nejčastěji zaznamenanými druhy (na více než 80 % ploch) byly: *Agrostis capillaris* L., *Galium mollugo* agg. L., *Holcus mollis* L., *Veronica chamaedrys* L.; zatímco nejvíce zastoupenými druhy (více než 7 % na obsazené ploše) byly: *Agrostis capillaris*, *Avenella flexuosa* (L.) Drejer, *Holcus mollis* a *Vaccinium myrtillus* L. Většina diagnostických a/nebo konstantních druhů byly druhy lučních společenstev (33 ze 161 druhů), a to především svazů *Arrhenatherion elatioris*, *Polygono bistortae-Trisetion flavescentis* a *Violion caninae*. Jen deset druhů bylo vztaženo k lesní vegetaci, a to k asociaci *Dentario enneaphylli-Fagetum* a svazům *Luzulo-Fagion* a *Quercion petreae*. V porostech náletových dřevin se bylo schopno uchytit jen relativně málo druhů lesních druhů a tyto měly zpravidla malou pokryvnost. Jen kapradiny a borůvka (*Vaccinium myrtillus* L.) byly více zastoupeny, z ostatních lesních druhů *Oxalis acetosella* L. byl zaznamenán častěji. Z druhů vázaných na bučiny nebo dubo-bukové lesy byly zaznamenány druhy: *Asarum europaeum* L., *Geranium robertianum* L., *Mercurialis perennis* L. a *Mycelis muralis* L.

Odpověď na studované faktory byla druhově specifická a bylo pozorováno jen málo obecných trendů. Hojné druhy byly ovlivňovány jak na stanovišti tak na kontextu závislými faktory a nebyl pozorován výrazný rozdíl mezi těmito dvěma skupinami faktorů.

Limitace semeny a limitace stanovištěm byla zjišťována na dvanáct let opuštěné louce (48°41,468´ N, 14°17,382´ E, 700 m n. m.) pomocí faktoriálně uspořádaného pokusu. Byl sledován vliv narušení a stínění na druhové složení, celkový charakter vegetace a pokryvnost jednotlivých druhů a bylo zjišťováno uchycování semenáčků lesních druhů. Pokus o 16 zásazích byl uspořádán v šesti znáhodnělých blocích s následujícími typy zásahů: i) stínění na 40 % dopadajícího fotosynteticky aktivního zářeni (*PhAR*), ii) stínění na 5 % *PhAR*, iii) odstranění nadzemní biomasy, iv) narušení drnu, v) výsev lesních druhů (*Actaea spicata* L., *Carex sylvatica* Huds., *Dentaria enneaphyllos* L., *D. bulbifera* L., *Galium odoratum* (L.) Scop., *Maianthemum bifolium* (L.) F.W. Schmidt, *Mercurialis perennis*, *Oxalis acetosella*, *Paris quadrifolia* L.).

Ačkoli meziroční variabilita v druhovém složení byla vyšší než změny způsobené narušením (zásahy iii a iv) nebo zastíněním (zásahy i a ii), tyto zásahy významně ovlivňovaly druhové složení vegetace. Zastínění mělo obecně menší vliv na změnu zastoupení jednotlivých druhů než narušení. Narušení ovlivňovalo druhové složení přímo a změna v pokryvnostech byla spíše kvantitativní než kvalitativní, na rozdíl od vlivu zastínění. Zastínění zpomalovalo změnu druhového složení v čase, a proto zastínění stabilizovalo druhové složení vegetace.

Ačkoli narušení drnu jakožto nejvýraznější zásah způsobovalo největší změny ve vegetaci (první rok po zásahu), v druhém roce pokusu se vegetace zapojila. Zastínění na 40 % dopadajícího záření nebylo schopné otevřít zápoj, zatímco stínění na 5 % dopadajícího záření již významně snížilo pokryvnost porostu.

Na kontrolních zásazích došlo k poklesu diverzity, zatímco odstranění nadzemní biomasy bylo schopné stabilizovat úroveň diverzity a narušení drnu vedlo ke zvýšení diverzity jeden rok po zásahu.

Jednoleté rostliny, rostliny s přízemní růžicí listů a malé vytrvalé byliny byly více zastoupeny v zásazích s narušením drnu.

Většina lesních druhů neklíčila a nebyla se schopna v porostu uchytit, ačkoli počet přidaných semen byl vysoký. Většina druhů klíčila málo také v laboratorních podmínkách. Na pokusné ploše byly zaznamenány pouze lesní druhy, které byly přímo vysety, což svědčí o limitaci semeny lesních druhů. Všechny semenáčky lesních druhů se objevily následující rok po vysetí. Jen kyčelnice devítilistá (*Dentaria enneaphyllos*) se uchycovala v počtech dostatečných pro statistické hodnocení, přesto se nebyla schopna uchytit v 56 % ploch do kterých byla vyseta a průměrně jen 3 % semenáčků přežilo do konce pokusu. Žádný ze semenáčků kyčelnice nedosáhl pokročilejšího stádia než semenáčku s děložními lístky. Stínění zvyšovalo počet uchycených semenáčků *D. enneaphyllos*. Podobný trend, ačkoli neprůkazný, byl pozorován pro narušení drnu. Podobná odpověď na jednotlivé zásahy byla pozorována pro šťavel kyselý (*Oxalis acetosella*), který však neklíčil v dostatečném počtu pro statistické hodnocení. Výše zmíněné výsledky indikují, že lesní druhy jsou v rané fázi sukcese limitovány stanovištěm.

References

Agestam E, Ekö P-M, Nilsson U, Welander NT (2003) The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. *Forest Ecology and Management* 176:61-73

Anthelme F, Villaret J-C, Brun J-J (2007) Shrub encroachment in the Alps gives rise to the convergence of the sub-alpine communities on a regional scale. *Journal of Vegetation Science* 18:355-362

Atkinson MD (1992) *Betula pendula* Roth (*Betula verrucosa* Ehrh.) and *Betula pubescens* Ehrh. *Journal of Ecology* 80:837-870

Baeten L, Jacquemyn H, Van Calster H, Van Beek E, Devlaeminck R, Verheyen K, Hermy M (2009) Low recruitment across life stages partly accounts for the slow colonization of forest herbs. *Journal of Ecology* 97:109-117

Battaglia LL, Pritchett DW, Minchin PR (2008) Evaluating dispersal limitation in passive bottomland forest restoration. *Restoration Ecology* 16:417-424

Benjamin K, Bouchard A, Domon G (2007) Abandoned farmlands as components of rural landscapes: An analysis of perceptions and representations. *Landscape and Urban Planning* 83:228-244

Bernacki Z (2004) Secondary succession of the vegetation in the young shelterbelt (Turew area, western Poland). *Polish Journal of Ecology* 52:391-404

Blažková D (1988) Sukcese smilkových porostů východního Slovenska při zarůstání dřevinami (Sukzession der Borstgrasbestände in der Ostslowakei durch Überwachsen mit Gehölzen). *Preslia* 60:127-132

Blažková D (1991) Sukcese na nesečených loukách v SPR Stužica (Bukovské vrchy) (Succession in abandoned mountain meadows in the Stužica nature reserve (The Bukovské vrchy Mts., East Slovakia)). *Preslia* 63:177-188

Bobiec A (2007) The influence of gaps on tree regeneration: a case study of the mixed lime-hornbeam (*Tilio-Carpinetum* Tracz. 1962) communities in the BiaĺowieŻa primeval forest. *Polish Journal of Ecology* 55:441-455

Bossuyt B, Hermy M (2000) Restoration of the understory layer of recent forest bordering ancient forest. *Applied Vegetation Science* 3:43-50

Bossuyt B, Hermy M (2001) Influence of land use history on seed banks in European temperate forest ecosystems: a review. *Ecography* 24:225-238

Bossuyt B, Hermy M, Deckers J (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology* 87:628-638

Bossuyt B, Honnay O, Hermy M (2003) An island biogeographical view of the successional pathway in wet dune slacks. *Journal of Vegetation Science* 14:781-788

Brandt J, Primdahl J, Reenberg A (1999) Rural land-use and landscape dynamics – analysis of “driving forces“ in space and time. In Krönert R, Baudry J, Bowler IR, Reenberg A (eds) *Land-use changes and their environmental impact in rural areas in Europe*. Man and the Biosphere Series Vol. 24, UNESCO and The Parthenon Publishing Group, Paris, pp. 81-102

Brokaw N, Busing RT (2000) Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15:183-188

Bruelheide H (2000) Population dynamics of endangered species in a transplanted montane meadow. *Folia Geobotanica* 35:179-189

Brunet J, von Oheimb G (1998a) Colonization of secondary woodlands by *Anemone nemorosa*. *Nordic Journal of Botany* 18:369-377

Brunet J, von Oheimb G (1998b) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* 86:429-438

Bullock JM, Clarke RT (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* 124:506-521

Butaye J, Jacquemyn H, Hermy M (2001) Differential colonization causing non-random forest plat community structure in a fragmented agricultural landscape. *Ecography* 24:369-380

Butaye J, Jacquemyn H, Honnay O, Hermy M (2002) The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. *Journal of Vegetation Science* 13:27-34

Cain ML, Damman H, Muir A (1998) Seed dispersal and the holocene migration of woodland herbs. *Ecological Monographs* 68:325-347

Christensen NL, Peet RK (1984) Convergence during secondary forest succession. *Journal of Ecology* 72:25-36

Chytrý M (ed) (2007) *Vegetace České republiky 1. Travinná a keříčková vegetace (Vegetation of the Czech republic 1. Grassland and Heathland Vegetation)*. Academia, Praha

Clarke PJ, Davison EA (2001) Experiments on the mechanism of tree and shrub establishment in temperate grassy woodlands: Seedling emergence. *Austral Ecology* 26:400–412

Clements FE (1916) *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington D.C., Washington

Closset-Kopp D, Schnitzer A, Aran D (2006) Dynamics in natural mixed-beech forest of the Upper Vosges. *Biodiversity and Conservation* 15:1063-1093

Clotfelter ED, Pedersen AB, Cranford JA, Ram N, Snajdr EA, Nolan V Jr, Ketterson ED (2007) Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* 154:493-503

Collins SL, Glenn SM (1991) Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology* 72:654-664

Corbit M, Marks PL, Gardescu S (1999) Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* 87:220-232

Cousins SAO, Aggemyr E (2008) The influence of field shape, area and surrounding landscape on plant species richness in grazed ex-fields. *Biological Conservation* 141:126-135

Davies ZG, Pullin AS (2007) Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landscape Ecology* 22:333-351

Deckers B, Hermy M, Muys B (2004) Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica* 26:23-37

De Steven D (1991) Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72:1076-1088

Dickie IA, Reich PB (2005) Ectomycorrhizal fungal communities at forest edges. *Journal of Ecology* 93:244-255

Dickie IA, Schnitzer SA, Reich PB, Hobbie SE (2007) Is oak establishment in old-fields and savanna openings context dependent? *Journal of Ecology* 95:309-320

Donath TW, Eckstein RL (2008) Grass and oak litter exert different effects on seedling emergence of herbaceous perennials from grasslands and woodlands. *Journal of Ecology* 96:272-280

Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. *Biological Conservation* 138:224-234

D´Orangeville L, Bouchard A, Cogliastro A (2008) Post-agricultural forests: Landscape patterns add to stand-scale factors in causing insufficient hardwood regeneration. *Forest Ecology and Management* 255:1637-1646

Dostálek J, Weber M, Matula S, Frantík T (2007) Forest stand restoration in the agricultural landscpe: The effect of different methods of planting establishment. *Ecological Engineering* 29:77-86

Dostalova A (2009) Tree seedlings: how do they establish in spontaneously developed forests? A study from a mountainous area in the Czech Republic. *Biodiversity and Conservation* 18:1671-1684

Doubková P (2008) Uchycování smrku v opuštěných travních porostech ve východních Krkonoších (Norway spruce establishment in abandoned grasslands in the Eastern Giant Mts.). *Opera Concortica* 45:69-79

Dovčiak M, Freilich LE, Reich PB (2005) Pathways in old-field succession to white pine: seed rain, shade, and climate effects. *Ecological Monographs* 75:363-378

Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83:2978-2984

Dzwonko Z (1993) Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *Journal of Vegetation Science* 4:693-698

Dzwonko Z (2001) Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *Journal of Applied Ecology* 38:942-951

Dzwonko Z, Loster S (1988) Species richness of small woodlands on the western Carpathian foothills. *Vegetatio* 76:15-27

Dzwonko Z, Loster S (1990) Vegetation differentiation and secondary succession on a limestone hill in southern Poland. *Journal of Vegetation Science* 1:615-622

Dzwonko Z, Loster S (1992) Species richness and seed dispersal to secondary woods in southern Poland. *Journal of Biogeography* 19:195-204

Dzwonko Z, Loster S (1997) Effects of dominant trees and antropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. *Journal of Applied Ecology* 34:861-870

Dzwonko Z, Loster S (2007) A functional analysis of vegetation dynamics in abandoned and restored limestone grasslands. *Journal of Vegetation Science* 18:203-212

Ehrlén J, Eriksson O (2000) Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81:1667-1674

Ehrlén J, Münzbergova Z, Diekmann M, Eriksson O (2006) Long-term assessment of seed limitation in plants: results from an 11-year experiment. *Journal of Ecology* 94:1224-1232

Ellenberg H (1988) *Vegetation ecology of central Europe*. Ed 4. Cambridge University Press, Cambridge

Eriksson O (1995) Seedling recruitment in the perennial herb *Actaea spicata*. *Flora* 189:187-191

Ertsen ACD, Alkemade JRM, Wassen MJ (1998) Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. *Plant Ecology* 135:113-124

Facelli JM, Pickett STA (1991a) Plant litter: light interception and effects on an old-field plant community. *Ecology* 72:1024-1031

Facelli JM, Pickett STA (1991b) Indirect effect of litter on woody seedlings subject to herb competition. *Oikos* 62:129-138

Faliński JB (1980) Vegetation dynamics and sex structure of the populations of pioneer dioecious woody plants. *Vegetatio* 43:23-38

Faliński JB (1988) Succession, regeneration and fluctuation in the Białowieża Forest (NE Poland). *Vegetatio* 77:115-128

Ferrell WK (1953) Effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina. *Ecology* 34:667-688

Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment* 3:243-250

Forman RTT, Baudry J (1984) Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* 8:495-510

Foster BL, Tilman D (2003) Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology* 91:999-1007

Foster BL, Dickson TL, Murphy CA, Karel IS, Smith VH (2004) Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. *Journal of Ecology* 92:435-449

García D, Obeso JR, Martínez I (2005) Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *Journal of Ecology* 93:693-704

Gellrich M, Zimmermann NE (2007) Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: A spatial statistical modelling approach. *Landscape and Urban Planning* 79:65-76

Goldberg DE, Gross KL (1988) Disturbance regimes of midsuccessional old fields. *Ecology* 69:1677-1688

Gómez-Aparicio L, Gómez JM, Zamora R (2007) Spatiotemporal patterns of seed dispersal in a wind-dispersed Mediterranean tree (*Acer opalus* subsp. *granatense*): implications for regeneration. *Ecography* 30:13-22

Gömöryová E, Ujházy K, Hrivnák R, Střelcová K, Gömöry D (2007) Soil properties and microbial activity changes along spruce forest succession in an abandoned grassland. *Polish Journal of Ecology* 55:457-467

Górski T, Górska K, Nowicki J (1977) Germination of seeds of various herbaceous species under leaf canopy. *Flora* 166:249-259

Graae BJ, Økland RH, Petersen PM, Jensen K, Fritzbøger B (2004) Influence of historical, geographical and environmental variables on undrerstorey composition and richness in Danish forests. *Journal of Vegetation Science* 15:465-474

Grime JP, Hodgson JG, Hunt R (1988) *Comparative plant ecology (A functional approach to common British species)*. Unwin Hyman, London

Gross KL, Werner PA (1982) Colonising abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology* 63:921-931

Gustafsson C, Ehrlén J, Eriksson O (2002) Recruitment in *Dentaria bulbifera*; the roles of dispersal, habitat quality and molluscs herbivory. *Journal of Vegetation Science* 13**:**719-724

Guth J (1998) Evaluation of a landscape story along the former "Iron curtain". In Kovář P, Pušová R, Kulíšek P (eds) *Present and historical Nature-culture interactions in landscapes (Experience for the 3rd millenium) – International conference program and abstract book*. Karlova univerzita, Praha, pp190-195

Hadač E. (1990) Secondary vegetation succession in the Belianské Tatry Mts. three decades after grazing. *Folia Geobotanica & Phytotaxonomica* 25:349-356

Halada L. (2000) Grasslands in the UNESCO-MAB Biosphere Reserve East Carpathians (Poland, Slovakia, and Ukraine): Influences of land use and managament changes. In Ehrendorfer F, Palme H, Schammel G (eds) *Changing Agriculture and Landscape: Ecology, management and biodiversity decline in anthropogenous mountain grassland. EUROMAB Symposium, Vienna-Gumpenstein (15. – 19. 9.1999).* Vienna, pp75-78

Hamre LN, Domaas ST, Austad I, Rydgren K (2007) Land-cover and structural changes in a western Norwegian cultural landscape since 1865, based on an old cadastral map and a field survey. *Landscape Ecology* 22:1563-1574

Harmer R, Peterken G, Kerr G, Poulton P (2001) Vegetation changes during 100 years of development of two secondary woodlands on abandoned arable land. *Biological Conservation* 101:291-304

Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* 9:72–77

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91:9-22

Hersperger AM, Forman RTT (2003) Adjacency arrangement effects on plant diversity and composition in woodland patches. *Oikos* 101:279-290

Hester AJ, Gimingham CH, Miles J (1991) Succession from a heather moorland to birch woodland. III. Seed availability, germination and early growth. *Journal of Ecology* 79:329-344

Hils MH, Vankat JL (1982) Species removals from a first-year old-field plant community. *Ecology* 63:705-711

Holgén P, Hånell B (2000) Performance of planted and naturally regenerated seedlings in *Picea abies*-dominanted shelterwood stands and clearcuts in Sweden. *Forest Ecology and Management* 127:129-138

Honnay O, Hermy M, Coppin P (1999) Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* 115:157-170

Honnay O, Bossuyt B, Verheyen K, Butaye J, Jacquemyn H, Hermy M (2002a) Ecological perspectives for the restoration of plant communities in European temperate forests. *Biodiversity and Conservation* 11:213-242

Honnay O, Verheyen K, Hermy M (2002b) Permeability of ancient forest edges for weedy plant species invation. *Forest Ecology and Management* 161:109-122

Hunziker U, Brang P (2005) Microsite patterns of conifer seedling establishment and growth in a mixed stand in the southern Alps. *Forest Ecology and Management* 210:67-79

Ihse M (1995) Swedish agricultural landscapes – patterns and changes during the last 50 years, studied by aerial photos. *Landscape and Urban Planning* 31:21-37

Inouye RS, Huntly NJ, Tilman D, Tester JR, Stillwell M, Zinnel KC (1987) Old-field succession on a Minnesota sand plain. *Ecology* 68:12-26

Jacquemyn H, Butaye J, Hermy M (2001) Forest plant species richness in small, fragmented mixed decidous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography* 28:801-812

Jacquemyn H, Butaye J, Hermy M (2003) Impacts of restored patch density and distance from natrual forests on colonization success. *Restoration Ecology* 11:417-423

Jäggi W (1976) Die Bestimmung der CO_2–Bildung als Mass der bodenbiologischen Aktivität (Determination of CO_2 production corresponds with the biological soil activitiy). *Schweiz Landwirtschaft Forschung* 15:317 380

Jensen K, Gutekunst K (2003) Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic and Applied Ecology* 4:579-587

Jensen TS, Nielsen OF (1986) Rodents as seed dispersers in a heath-oak wood succession. *Oecologia* 70:214-221

Jonášová M (2004) *Zmlazení dřevin v horských smrčinách odumřelých po napadení lýkožroutem smrkovým (Central-European mountain spruce forests: regeneration of tree species after a bark beetle outbreak).* Conference Aktuality Šumavského výzkumu II, Srní (Czech Republic), 4-7 October 2004, Abstract book, pp265-269

Kahmen S, Poschlod P (2004) Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science* 15:21-32

Kalamees R, Zobel M (1997) The seed bank in an Estonian calcareous grassland: Comparison of different successional stages. *Folia Geobotanica* 32:1-14

Kaligarič M, Culiberg M, Kramberger B (2006) Recent vegetation history of the North Adriatic grasslands: expansion and decay of an anthropogenic habitat. *Folia Geobotanica* 41:241-258

Kerner A (1863) *Das Pflanzenleben der Donaulaender* (*The Background of Plant Ecology*). Verlag der Wagner´schen Universitäts – Buchhandlung, Innsbruck

Kerr G, Gosling P, Morgan G, Stokes V, Cunningham V, Parratt M (2008) Seed production and seedling survival in a 50-year-old stand of Corsican pine (*Pinus nigra* subsp. *laricio*) in southern Britain. *Forestry* 81:525-541

Kirmer A, Tischew S, Ozinga WA, von Lampe M, Baasch A, van Groenendael JM (2008) Importance of regional species pools and functional traits in colonization processes: predicting re-colonization after large-scale destruction of ecosystems. *Journal of Applied Ecology* 45:1523-1530

Kobayashi M, Kamitani T (2000) Effects of surface disturbance and light level on seedling emergence in a Japanese secondary deciduous forest. *Journal of Vegetation Science* 11:93-100

Koerner W, Dupouey JL, Dambrine E, Benoît M (1997) Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology* 85:351-358

Kolb A, Diekmann M (2004) Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science* 15:199-208

Kopáček J, Kaňa J, Šantrůčková H, Porcal P, Hejzlar J, Picek T, Veselý J (2002) Physical, chemical, and microbial characteristics of soils in watersheds of the Bohemian Forest lakes: II. Čertovo and Černé Lakes. *Silva Gabreta* 8:67-94

Kopáčková I (2002) *Vybrané mikrobiální charakteristiky lesních a lučních půd Šumavy (Selected microbial characteristics of forest and grassland soils in the Šumava Mts.).* Ms. Thesis, Faculty of Biological Sciences, The University of South Bohemia, České Budějovice

Kopecký M, Vojta J (2009) Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Applied Vegetation Science* 12:251-260

Košulič M Sen (2001) Smrk jako pomocná dřevina. *Lesnická práce* 80:13-15

Kozak J, Troll M, Widacki W (1999) Semi-natural landscapes of the western Beskidy Mts. *Ekológia (Bratislava)* 18:53-62

Kubát K, Hrouda L, Chrtek J Jr, Kaplan Z, Kirschner J, Štěpánek J (eds) (2002) *Klíč ke květeně České republiky* (*Key to the flora of the Czech Republic)*. Academia, Praha

Kubeš J, Mičková K (2003) Development of horizontal landscape structure in the Pohořsko region (the Czech-Austrian frontier) between 1938-2000. *Ekológia (Bratislava)* 22:269-283

Kubíková J (1994) Oak-pine afforestation of agricultural land: an attempt to enrich its understory diversity. *Novitates Botanicae, Universitatis Carolinae* 8:63-73

Kučera T, Guth J (1998) Stabilization of landscape in the Bohemian Forest frontier area abandoned for 40 years (Czech Republic). In Kovář P, Pušová R, Kulíšek P (eds) *Present and historical Nature-culture interactions in landscapes (Experience for the 3rd millenium) – International conference program and abstract book*. Karlova univerzita, Praha, pp6-13

Kupferschmid AD, Stampfli A, Newbery DM (2000) Dispersal and microsite limitation in an abandoned calcareous grassland of the southern prealps. *Folia*

Geobotanica 35:125-141

Kuuluvainen T, Juntunen P (1998) Seedling establishment in relation to microhabitat variation in a windthrow gap in boreal *Pinus sylvestris* forest. *Journal of Vegetation Science* 9:551-562

Lanta V, Lepš J (2009) How does surrounding vegetation affect the course of succession: A five-year container experiment. *Journal of Vegetation Science* 20:686 – 694

Lawton JH (1999) Are there general laws in ecology? *Oikos* 84:177-192

Lepš J, Šmilauer P (2003) *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge

Lepš J, Štursa J (1989) Species-area curve, life history strategies, and succession: a field test of relationships. *Vegetatio* 83:249-257

Lindborg R (2007) Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *Journal of Ecology* 95:555-564

Lorimer CG, Dahir SE, Nordheim EV (2001) Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *Journal of Ecology* 89:960-971

Maccherini S, Marignani M, Castagnini P, van den Brink PJ (2007) Multivariate analysis of the response of overgrown semi-natural calcareous grasslands to restorative shrub cutting. *Basic and Applied Ecology* 8:332-342

MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Lazpita JG, Gibon A (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management* 59:47-69

Madsen P, Larsen JB (1997) Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. *Forest Ecology and Management* 97:95-105

Matlack GR (1994) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75:1491-1502

Matlack GR (2005) Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology* 93:50-59

Matlack GR (2009) Long-term changes in soils of second-growth forest following abandonment from agriculture. *Journal of Biogeography* 36:2066-2075

McClanahan TR, Wolfe RW (1987) Dispersal of ornitochorous seeds from forest edges in central Florida. *Vegetatio* 71:107-112

Milberg P (1995) Soil seed bank after eighteen years of succession from grassland to forest. *Oikos* 72:3-13

Moravec J, Husová M, Chytrý M, Neuhäuslová Z (2000) *Přehled vegetatce České republiky 2 – Hygrofilní, mezofilní a xerofilní opadavé lesy (Vegetation Survey of the Czech Republic 2 – Hygrophilous, mesophilous and xerophilous deciduous forests).* Academia, Praha

Münzbergová Z, Herben T (2005) Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitation. *Oecologia* 145:1-8

Mwangi PN, Schmitz M, Scherber C, Roscher C, Schumacher J, Scherer-Lorenzen M, Weisser WW, Schmid B (2007) Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology* 95:65-78

Neuhäuslová Z (ed) (1998) *Mapa potenciální přirozené vegetace České republiky (Map of Potencial Vegetation of the Czech republic).* Academia, Praha

Nilsson U, Gemmel P, Johansson U, Karlsson M, Welander T (2002) Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. *Forest Ecology and Management* 161:133-145

Odum EP (1969) The strategy of ecosystem development: an understanding of ecological succession provides a basis for resolving man´s conflict with nature. *Science* 164:262-270

Ohlson M, Grønli KE (2006) Recruitment and growth in *Aconitum septentrionale* and *Actaea spicata* in relation to microbial soil communities manipulated by additions of glucose and nutrients. *Flora – Morphology, Distribution, Functional Ecology of Plants* 201:215-226

Orrock JL, Levey JD, Danielson BJ, Damschen EI (2006) Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. *Journal of Ecology* 94:838-845

Öster M, Cousins SAO, Eriksson O (2007) Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. *Journal of Vegetation Science* 18:859-868

Ostfeld RS, Canham CD (1993) Effect of meadow vole population density on tree seedling survival in old fields. *Ecology* 74:1792-1801

Paquette A, Bouchard A, Cogliastro A (2006) Successful under-planting of red oak and black cherry in early-successional deciduous shelterwoods of North America. *Annals of Forest Science* 63:823-831

Pärtel M, Helm A (2007) Invasion of woody species into temperate grasslands: Relationship with abiotic and biotic soil resource heterogeneity. *Journal of Vegetation Science* 18:63-70

Persson S, Malmer N, Wallén B (1987) Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest. *Vegetatio* 73:31-45

Peterken GF, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire.

Journal of Ecology 72:155-182

Phillips JD, Marion DA (2004) Pedological memory in forest soil development. *Forest Ecology and Management* 188:363-380

Pons J, Pausas JG (2007) Acorn dispersal estimated by radio-tracking. *Oecologia* 153:903-911

Prach K (1985) Succession of vegetation in abandoned fields in Finland. *Annales Botanici Fennici* 22:307-314

Prach K (1987) Succession of vegetation on dumps from strip coal mining, N.W. Bohemia, Czechoslovakia. *Folia Geobotanica & Phytotaxonomica* 22:339-354

Prach K (1990) Směna dominant a rychlost sukcese (Dominant species exchange and the rate of succession). *Preslia* 62:199-204

Prach K (1994) Succession of woody species in derelict sites in Central Europe. *Ecological Engineering* 3:49-56

Prach K, Pyšek P (1994a) Clonal plants – What is their role in succession? *Folia Geobotanica & Phytotaxonomica* 29:307-320

Prach K, Pyšek P (1994b) Spontaneous establishment of woody plants in central European derelict sites and their potential for reclamation. *Restoration Ecology* 2:190-197

Prach K, Pyšek P (1999) How do species dominating in succession differ from others? *Journal of Vegetation Science* 10:383-392

Prach K, Řehounková K (2006) Vegetation succession over broad geographical scales: which factors determine the patterns? *Preslia* 78:469-480

Prach K, Lepš J, Michálek J (1996) Establishment of *Picea abies* seedlings in a central European mountain grassland: an experimental study. *Journal of Vegetation Science* 7:681-684

Prach K, Bufková I, Zemek F, Heřman M, Mašková Z (2000) Grassland vegetation in the former military area Dobrá Voda, the Šumava National Park. *Silva Gabreta* 5:103-112

Prach K, Pyšek P, Jarošík V (2007) Climate and pH as determinants of vegetation succession in Central-European human-made habitats. *Journal of Vegetation Science* 18:701-710

Primack RB, Miao SL (1992) Dispersal can limit local plant distribution. *Conservation Biology* 6:513-519

Provendier D, Balandier P (2008) Compared effects of competition by grasses (*Graminoids*) and broom (*Cytisus scoparius*) on growth and functional traits of beech saplings (*Fagus sylvatica*). *Annals of Forest Science* 65:510-518

Pyšek P, Prach K, Müllerová J, Joyce C (2001) The role of vegetation succession in ecosystem restoration: Introduction. *Applied Vegetation Science* 4:1-4

Quitt E (1971) *Klimatické oblasti Československa (Climatic regions in*

Czechoslovakia). Academia, Brno

Rajaniemi TK (2003) Explaining productivity-diversity relationships in plants. *Oikos* 101:449-457

Řehounková K, Prach K (2006) Spontaneous vegetation succession in disused gravel-sand pits: Role of local site and landscape factors. *Journal of Vegetation Science* 17:583-590

Richter DD, Markewitz D, Wells CG, Allen HL, April R, Heine PR, Urrego B (1994) Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. *Ecology* 75:1463-1473

Roy V, de Blois S (2008) Evaluating hedgerow corridors for the conservation of native forest herb diversity. *Biological Conservation* 141:298-307

Schaffers AP, Sýkora KV (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* 11:225-244

Schreiber KF (1995) Renaturierung von Grünland – Erfahrungen aus langjährigen Untersuchungen und Management-massnahmen. *Berichte der Reinhold-Tüxen-Gesellschaft* 7:111-139

Schreiber KF (1996) Wandel von Artenzusammensetzung, Bedeckung und Struktur der Vegetation in Sukzessionsparzellen der Bracheversuche Baden-Württemberg im Laufe der Vegetationsperiode. *Berichte Umweltforschung Baden-Württemberg* 16:391-404

Schusserová A (2003) *Sekundární travní porosty v západní části Přírodního parku Vyšebrodsko (současný stav, vliv vybraných abiotických faktorů, hospodaření a možné scénáře vývoje v budoucnosti) (Secondary grasslands in western part of the Vyšebrodsko Nature Park - present state, influence of selected abiotic factors, management and possible future development).* Ms. Thesis, Faculty of Biological Sciences, The University of South Bohemia, České Budějovice

Schusserová A, Šmahel L (2000) *Přírodní památka Medvědí hora: Zpráva z biologického průzkumu v rámci projektu "Biologický průzkum západní části Přírodního parku Vyšebrodsko" (Medvědí hora Nature Monument. Biological research report from the project "Biological research of the western part of the Vyšebrodsko Nature Park").* o.s. Gabreta NKK, České Budějovice

Schweiger J, Sterba H (1997) A model describing natural regeneration recruitment of Norway spruce (*Picea abies* (L.) Karst.) in Austria. *Forest Ecology and Management* 97:107-118

Seppä H, Alenius T, Bradshaw RHW, Giesecke T, Heikkilä M, Muukkonen P (2009) Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia. *Journal of Ecology* 97:629 – 640

Šerá B, Falta V, Cudlín P, Chmelíková E (2000) Contribution to knowledge of natural growth and development of mountain norway spruce seedlings. *Ekológia (Bratislava)* 19:420-434

Sitzia T (2007) Hedgerows as corridors for woodland plants: a test on the Po Plain, northern Italy. *Plant Ecology* 188:235-252

Šmilauerová M (2001) Plant root response to heterogeneity of soil resources: Effects of nutrient patches, AM symbiosis, and species composition. *Folia Geobotanica* 36:337-351

Spatz G (1980) Succession patterns on mountain pastures. *Vegetatio* 43:39-41

Špringar Z (1995) *Sukcese vegetace na lokalitách bývalých ženijně technických zátarasů (Vegetation succession on the former military wire-obstacles)*. Bc. Thesis, Faculty of Biological Sciences, The University of South Bohemia, České Budějovice

Strandberg B, Kristiansen SM, Tybirk K (2005) Dynamic oak-scrub to forest succession: Effects of management on understorey vegetation, humus forms and soils. *Forest Ecology and Management* 211:318-328

Sutherland WJ (2006) Predicting the ecological consequences of environmental change: a review of the methods. *Journal of Applied Ecology* 43:599-616

Symonides E, Borowiecka M (1985) Plant biomass structure in old-field successional ecosystems. *Ekologia Polska* 33:81-102

Szwagrzyk J, Szewczyk J, Bodziarczyk J (2001) Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. *Forest Ecology and Management* 141:237-250

Tapper P-G (1992) Demography of persistent juveniles in *Fraxinus excelsior*. *Ecography* 15:385-392

Tilman D, Wedin D (1991) Dynamics of nitrogen competition between successional grasses. *Ecology* 72:1038-1049

Vandenberghe C, Smit C, Pohl M, Buttler A, Freléchoux F (2009) Does the strength of facilitation by nurse shrubs depend on grazing resistance of tree saplings? *Basic and Applied Ecology* 10:427-436

Van der Veken S, Bellemare J, Verheyen K, Hermy M (2007a) Life-history traits are correlated with geographical distribution patterns of western European forest herb species. *Journal of Biogeography* 34:1723–1735

Van der Veken S, Rogister J, Verheyen K, Hermy M, Nathan R (2007b) Over the (range) edge: a 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. *Journal of Ecology* 95:343-351

Vellend M, Verheyen K, Flinn KM, Jacquemyn H, Kolbs A, van Calster H, Peterken G, Graae BJ, Bellemare J, Honnay O, Brunet J, Wulf M, Gerhardt F, Hermy M (2007) Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. *Journal of Ecology* 95:565-573

Verheyen K, Hermy M (2004) Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *Journal of Vegetation Science* 15:125-134

Verheyen K, Bossuyt B, Hermy M, Tack G (1999) The land use history (1278-1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography* 26:1115-1128

Verheyen K, Bossuyt B, Honnay O, Hermy M (2003) Herbaceous plant community structure of ancient and recent forests in two contrasting forest types. *Basic and Applied Ecology* 4:537-546

Vlasáková B, Raabová J, Kyncl T, Dostál P, Kovářová M, Kovář P, Herben T (2009) Ants accelerate succession from mountain grassland towards spruce forest. *Journal of Vegetation Science* 20:577–587

Vojta J (2007) Relative importance of historical and natural factors influencing vegetation of secondary forests in abandoned villages. *Preslia* 79:223-244

von Oheimb G, Westphal C, Tempel H, Härdtle W (2005) Structural pattern of a near-natural beech forest (*Fagus sylvatica*) (Serrahn, North-east Germany). *Forest Ecology and Management* 212:253-263

von Oheimb G, Härdtle W, Naumann PS, Westphal C, Assmann T, Meyer H (2008) Long-term effects of historical heathland farming on soil properties of forest ecosystems. *Forest Ecology and Management* 255:1984-1993

Wehling S, Diekmann M (2009a) Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biological Conservation* 142:2522-2530

Wehling S, Diekmann M (2009b) Hedgerows as an environment for forest plants: a comparative case study of five species. *Plant Ecology* 204:11-20

Whitney GG, Foster DR (1988) Overstorey composition and age as determinants of the understorey flora of woods of central New England. *Journal of Ecology* 76:867-876

Wiegert RG, Evans FC (1964) Primary production and the disappearance of dead vegetation on an old field in southeastern Michigan. *Ecology* 45:49-63

Willems JH (1983) Species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52:171-180

Woods KD (2000) Long-term change and spatial pattern in a late-successional hemlock-northern hardwood forest. *Journal of Ecology* 88:267-282

Wulf M (1997) Plant species as indicators of ancient woodland in northwestern Germany. *Journal of Vegetation Science* 8:635-642

Wulf M (2004) Plant species richness of afforestations with different former use and habitat continuity. *Forest Ecology and Management* 195:191-204

Wulf M, Heinken T (2008) Colonization of recent coniferous versus deciduous forest stands by vascular plants at the local scale. *Applied Vegetation Science* 11:307-316

Zelený D, Šraitová D, Mašková Z, Květ J (2001) Management effects on a mountain meadow plant community. *Silva Gabreta* 7:45-54

Zemek F., Heřman M (1998) Landscape pattern changes in the Šumava region – a GIS approach. *Silva Gabreta* 2:395-403

Zerbe S (2002) Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. *Forest Ecology and Management* 167:27-42

Zobel M (1989) Secondary forest succession in Järvselja, southeastern Estonia: changes in field layer vegetation. *Annales Botanici Fennici* 26:171-182