

Effects of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) on understorey layer species diversity in managed forests

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ABSTRACT: In total, 67 parallel plots were chosen from the database of 153 phytosociological relevés made in the Douglas-fir and parallel Norway spruce, European Beech and oak-dominated stands to find influences of this introduced tree species on the understorey layer in totally 12 localities in the whole Czech Republic territory. Douglas-fir stands influence their habitats, which was indicated by species composition changes in the ground vegetation, as well as by abundance and dominance of particular species. Douglas-fir cultivation increases species diversity of the stands, but decreases their abundance. Described differences in understorey are not so noticeable when European beech and sessile oak stands are substituted by Douglas-fir once. But even the significant phenomenon of striking nitrophilous species such as *Geranium robertianum*, *Urtica dioica* and *Galium aparine* occurs here. This indicates a high content of available nitrates in the humus and top-soil horizons.

Keywords: species community composition; nitrification; ruderalization, species introduction

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is one of the most important commercial tree species worldwide, both in its natural range (North America) and in many other regions including Europe (SCHMID et al. 2014). Its first introduction into European parks dates back to the period between 1826 (ISAAC-RENTON 2013) and 1830 (Anonymous 2003; ANONYMOUS 2012). According to literature sources, there is still one individual being alive in England (Eggesford forest) of the 1820s origin (Anonymous 2003). However, this species was also planted in European commercial forest stands step by step over the next decades (FERRON et DOUGLAS 2010; ISAAC-RENTON 2013). As for the Czech Republic, the oldest Douglas-fir plantation was established in the Mendel University Forest in 1844 (KANTOR et al. 2002). Although the planting

of Douglas-fir has expanded into the whole territory of the Czech Republic, it covers only 0.22 % (5,600 ha) of the total forest area at present. From this point of view, a great potential for its ongoing introduction is obvious (PODRÁZSKÝ, REMEŠ 2010, REMEŠ, al. 2011). This tree species is considered to be a naturalized neophyte in the flora of the Czech Republic (DANIHELKA et al. 2012).

Besides the basic silvicultural treatments, forestry research is focused on the optimization of nutrition and nutrient cycling in the autochthonous managed Douglas-fir forests of particular stand ages (GHOLZ et al. 1985; HORMANN et al. 2001; JUSSY et al. 2004; THIEL, PERAKIS 2009), including different fertilization approaches at young stages (e.g. HENRY 1986; EDMODS, HSIANG 1987; HARRISON et al. 1994; ADAMS et al. 2005a,b). A different

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situation is in European countries where the environmental issues prevail (AUGUSTO et al. 2002, SCHMID et al. 2014), as well as the production in comparison with native species is studied. Also in the Czech Republic, this species was intensively studied from the production point of view, and its production potential was satisfactorily evaluated (KANTOR et al. 2001, MARTINÍK 2003, MARTINÍK, KANTOR 2007, KANTOR 2008, KANTOR, MAREŠ 2009, PODRÁZSKÝ et al. 2009, MAREŠCHAL et al. 2013, COOLS et al. 2014). Also the soil effects of this species were described to some extent, so it is possible to exclude its negative influences on the forest soil (PODRÁZSKÝ, REMEŠ 2008, MENŠÍK et al. 2009, PODRÁZSKÝ et al. 2009), its resistance against droughts was documented as well (URBAN et al. 2009, 2010; EILMANN, RIGLING 2010).

A very important environmental issue is represented also by the effects of introduced tree species on the understory vegetation diversity and status. It is possible to use bioindication of the herb layer for this purpose. PODRÁZSKÝ et al. (2011) and VIEWEGH et al. (2014) presented preliminary studies of changes in the herb layer under introduced Douglas-fir stands in comparison with autochthonous tree species stands in the conditions of the Czech Republic. The aim of this article is the extension of these results evaluating a much broader set of compared plots and concluding the Douglas-fir impact on understory vegetation in comparison with common native tree species.

MATERIAL AND METHODS

Data were collected from different regions of the Czech Republic (Fig. 1) in the period 2010–2013. Stands of dominant native tree species (*Picea abies* [L.] Karst.), (*Fagus sylvatica* L.), (*Quercus petraea* [Matt.] Liebl.) or (*Q. robur* L.) and some others were located in the vicinity of Douglas-fir stands. All stands were at least 60 years old. Both stands of Douglas-fir and the comparative species ones were situated under similar environmental conditions, i.e. altitude, aspect, slope, soil type and site unit according to the Czech forest ecosystem (typological) classification (VIEWEGH 2003).

Phytosociological relevés (vegetation descriptions) were collected using the DBreleve database (MATĚJKA 2009). The database totals 153 phytosociological relevés in our study. Before the numerical analysis, data were transformed in the following way: the original abundance-dominance degrees

(Zlatník's scale) were transformed into average abundance. Then abundances of all species in the layer (storey - ε) were transformed so as their sum for the corresponding layer would equal the total of this layer (C_ε):

$$x'_{ei} = C_\varepsilon x_{ei} / \sum_{i=1}^n x_{ej} \quad (1)$$

where:

x_{ei} – abundance of the i -th species in layer ε .

Layers are marked in a standard way like in phytosociology: E_3 – tree layer, E_2 – shrub layer, E_1 – herb layer and E_0 – moss layer.

Three groups of parallel plots according to dominant tree species were considered: Douglas-fir–Norway spruce, Douglas-fir–European beech, and Douglas-fir–oaks (*Q. petraea* + *Q. robur*).

The difference in frequencies of a species in two sets of relevés (sets of the parallel plots) was evaluated using the statistics

$$t = \frac{f_1 - f_2}{\sqrt{\left(\frac{f_1(1-f_1)}{n_1-1}\right) + \left(\frac{f_2(1-f_2)}{n_2-1}\right)}} \quad (2)$$

where:

f_i – frequency of the species in i^{th} set,

n_i – number of relevés in i^{th} set of relevés.

This variable shows Student's t -distribution and thus it can be tested (with n_1+n_2-2 degrees of freedom; e.g. ŠKRÁČEK, TICHÝ 1990).

Two measures of distance between two communities in the pair of comparable plots were selected. The first measure – the Jaccard distance (equal to 1 –

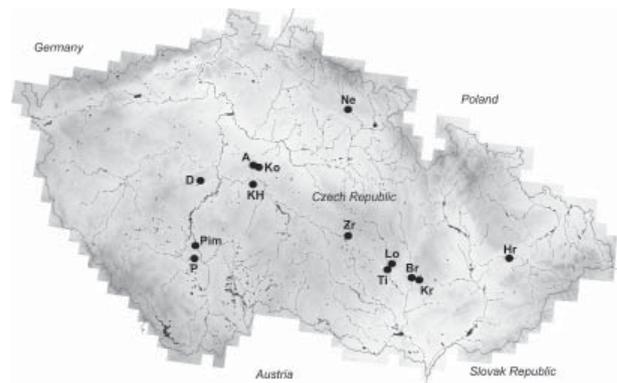


Fig. 1. Study site localization. Acronyms denote the names of localities

Kostelec nad Černými lesy – Ko; Aldašín – A; Komorní Hrádek – KH; D – Dobříš; Písek, school training forest – P; Písek, municipal forests – Pim; Hranice na Moravě – Hr; Křtiny, university forest 2011 – Kr; B, university forest 2012; Tišnov – Ti; Lomnice u Tišnova – Lo; Žďár n. Sáz. – ZR; Nemojov – Ne

Jaccard similarity coefficient) is based on the presence/absence of data, the second one – the Euclidean distance is calculated using transformed values of species representation (McCUNE, GRACE 2002). Distances were calculated from data on the herb layer. Differences in distances according to three groups of parallel plots were statistically tested by the one-way ANOVA (SPSS, Tulsa, USA).

Understorey (herb layer) species were grouped into bioindication groups such as acidophilous, mesophilous, nitrophilous, nitrophilous-to-ruderal and indifferent plants (Appendix 1). Nitrophilous species were divided into two groups due to different behaviour of these species. Distinctively nitrophilous species which often accompany human-affected localities such as *Urtica dioica*, *Chelidonium majus*, *Impatiens parviflora*, *Galium aparine* and *Geranium robertianum* belong to the nitrophilous-to-ruderal group. Other nitrophilous species were grouped to pure nitrophilous.

In the framework of present data processing, attention was paid to correlations between structural parameters of monitored plant communities and some significant dominant tree species. DBreleve package (MATĚJKÁ 2009) was used to calculate indices elucidating the community structure (MAGURRAN 2004) – i.e. species richness (equal to the number of species, S), Shannon-Wiener diversity index (*sensu* Shannon 1948; H') and equitability ($e = H'/\log_2 S$).

Taxonomical nomenclature was used according to KUBÁT et al. (2002).

RESULTS AND DISCUSSION

Difference in species composition under native trees and Douglas-fir

The increased frequencies of species were recorded under Douglas-fir compared to oak: *Oxalis acetosella* ($P = 0.0\%$), *Mycelis muralis* ($P = 0.1\%$), *Senecio ovatus*^(R) ($P = 0.1\%$), *Carex pilulifera* ($P = 0.2\%$), *Calamagrostis epigejos*^(R) ($P = 0.5\%$), *Rubus fruticosus* agg.^(R) ($P = 3.0\%$), *Cardamine impatiens* ($P = 3.6\%$), *Dactylis glomerata* ($P = 3.6\%$), *Euphorbia amygdaloides* ($P = 3.6\%$), *Dryopteris dilatata* ($P = 3.7\%$), *Urtica dioica*^(R) ($P = 4.4\%$), *Brachypodium sylvaticum* ($P = 5.3\%$), *Torilis japonica*^(R) ($P = 5.3\%$) and regenerating *Pseudotsuga menziesii* ($P = 0.6\%$). Species such as *Galeopsis pubescens* ($P = 4.3\%$), *Melica uniflora* ($P = 2.8\%$), *Quercus petraea* agg. ($P = 2.8\%$) and *Impatiens parviflora*^(R) ($P = 1.4\%$) showed decreased frequencies. Inter-

esting is a decreased frequency of the invasive neophyte *I. parviflora*. The listed species marked with^(R) can be considered as the species indicating a ruderalization process.

The dominating Douglas-fir leads to increased frequencies of several species compared to dominant beech: *Convolvulus arvensis*^(R) (error probability of t -test $P = 0.3\%$), *Glechoma hederacea*^(R) ($P = 0.3\%$), *Asarum europaeum* ($P = 0.4\%$), *Urtica dioica*^(R) ($P = 0.5\%$), *Dryopteris filix-mas* ($P = 0.7\%$), *Brachypodium sylvaticum* ($P = 0.7\%$), *Sambucus nigra*^(R) ($P = 0.9\%$), *Hordelymus europaeus* ($P = 1.8\%$), *Fragaria vesca* ($P = 2.7\%$), *Rubus idaeus*^(R) ($P = 2.7\%$), *Chelidonium majus*^(R) ($P = 3.5\%$), *Oxalis acetosella* ($P = 4.2\%$), *Carpinus betulus* ($p = 4.2\%$), *Senecio ovatus* ($P = 4.2\%$), *Viola reichenbachiana* ($P = 4.7\%$) and *Geranium robertianum*^(R) ($P = 4.9\%$). Conversely, decreased frequencies of two juvenile tree species *Acer platanoides* ($P = 4.2\%$) and *Quercus petraea* agg. ($P = 2.7\%$) were recorded.

Comparing Douglas-fir and both autochthonous broadleaved species, Douglas-fir leads to increase by more species (16 compared to beech in canopy and 14 compared to oak in canopy) than is the count of decreased species. Many species indicate ruderalization of the site. This process is obvious as some of archaeophytes increased (*Convolvulus arvensis* and *Chelidonium majus*). Regeneration of Douglas-fir is common under oak (at 46% of plots), but it is also present under beech (17% of plots).

Compared with the cultivated Norway spruce, dominance of Douglas-fir in the stand exhibited an increased frequency of species such as *Stellaria media* ($P = 0.1\%$), *Fraxinus excelsior* ($P = 1.9\%$), *Acer platanoides* ($P = 2.0\%$), *Galium odoratum* ($P = 2.2\%$), *Milium effusum* ($P = 3.2\%$), *Circaea lutetiana* ($P = 3.5\%$), *Dactylis glomerata* ($P = 3.5\%$), *Juncus effusus* ($P = 3.5\%$), *Prenanthes purpurea* ($P = 3.5\%$), *Impatiens parviflora* ($P = 3.9\%$), *Urtica dioica* ($P = 5.5\%$), *Viola reichenbachiana* ($P = 5.8\%$) and regenerating *Pseudotsuga menziesii* ($P = 4.6\%$). The decreased frequency was observed in *Abies alba* ($P = 5.1\%$), *Maianthemum bifolium* ($P = 4.0\%$), *Galeopsis pubescens* ($P = 2.8\%$) and *Quercus petraea* agg. ($P = 1.4\%$) in the herb layer. It points to a possibility of the growth of some species from natural potential vegetation under Douglas-fir compared to the cultivated spruce. However, this positive process is counterbalanced by the occurrence of Douglas-fir as a tree neophyte with potential high prosperity. In total 70% of comparable plots with Douglas-fir contains regeneration of this tree species.

Table 1. Pairs of parallel plots according to the distances in the pairs

Group of parallel plots with		<i>Quercus</i> sp.	<i>Fagus sylvatica</i>	<i>Picea abies</i>	<i>P</i>
Number of plot pairs		30	18	75	
Jaccard	distance (%)	73.6 ± 10.8	67.8 ± 11.5	67.7 ± 14.6	0.115
Euclidean		36.3 ± 15.1	26.2 ± 9.5	32.9 ± 18.8	0.142

significance of the one-way ANOVA test between three compared groups of the plots is marked by probability

Both the Jaccard and Euclidean distances for three groups of parallel plots show statistically insignificant differences (Table 1). The biggest distances were found when comparing Douglas-fir with oaks. Distances of the Douglas-fir sites to sites with European beech and Norway spruce are comparable.

It is necessary to comment that Norway spruce stands were largely unnatural, planted in lower forest altitudinal zones (2nd–4th), compared to the natural ones of the higher altitudes (VIEWEGH 2003). Norway spruce forests represent planted allochthonous stands in all our plots. Very preliminary look on it is proved by next two blocks of parallel plots (Douglas-fir–European beech and Douglas-fir–oaks), where Douglas-fir was planted in the first generation on localities with indigenous European beech and oak and

where the higher proportion of herbaceous species (understorey) corresponds with the autochthonous dominant tree species ecosystems.

Ecological groups of species

In Douglas-fir stands, mesophilous, nitrophilous and nitrophilous-to-ruderal species prevail in all three parallel groups of plots (Table 2). This fact is obvious on Douglas-fir–European beech parallel plots (Table 2), but the averages of frequency and the sum of abundances show an increased nitrophilous-to-ruderal group only. It could be a result of different light conditions under Douglas-fir and European beech stands. However, changed soil conditions in terms of

Table 2. Number of understorey species and their averages of frequency and sum of abundances in bioindication groups (see Appendix 1) in the pairs of parallel plots

Plots	Bioindication group	Number of species		Frequency (%)		Abundances (%)	
		<i>Quercus</i> sp.	<i>P. menziesii</i>	<i>Quercus</i> sp.	<i>P. menziesii</i>	<i>Quercus</i> sp.	<i>P. menziesii</i>
Douglas-fir (n = 26) – oaks (n = 17)	acidophilous	7	14	10	16	1.27	5.10
	mesophilous	31	36	19	15	15.39	14.98
	nitrophilous	16	21	15	12	4.68	5.43
	nitrophilous-to-ruderal	17	21	18	20	9.34	15.24
	indifferent	14	12	19	27	15.94	17.82
Douglas-fir (n = 18) – European beech (n = 18)	acidophilous	<i>F. sylvatica</i>	<i>P. menziesii</i>	<i>F. sylvatica</i>	<i>P. menziesii</i>	<i>F. sylvatica</i>	<i>P. menziesii</i>
	acidophilous	9	8	12	17	0.16	0.43
	mesophilous	25	32	21	21	14.93	10.93
	nitrophilous	8	18	18	15	4.99	2.25
	nitrophilous-to-ruderal	11	15	24	36	10.77	18.72
Douglas-fir (n = 40) – Norway spruce (n = 37)	acidophilous	<i>P. abies</i>	<i>P. menziesii</i>	<i>P. abies</i>	<i>P. menziesii</i>	<i>P. abies</i>	<i>P. menziesii</i>
	acidophilous	22	23	16	17	12.46	8.96
	mesophilous	29	39	7	9	2.00	6.14
	nitrophilous	20	23	6	9	0.43	2.38
	nitrophilous-to-ruderal	16	22	17	17	11.48	13.80
indifferent	17	22	21	17	10.51	18.48	

n – number of relevés

Table 3. Species diversity and equitability of the understorey (herb layer) according to groups of dominant tree species

Dominant tree species	Richness (S)					Species diversity (H')				Species equitability (e)			
	n	Min	Avg	Max	SD	Min	Avg	Max	Std	Min	Avg	Max	SD
Cover 60–90%													
<i>Pseudotsuga menziesii</i>	48	9	17.8	28	4.9	1.13	2.13	3.18	0.47	0.31	0.52	0.69	0.10
<i>Quercus</i> sp.	5	11	16.6	30	7.1	1.62	2.24	2.91	0.49	0.45	0.57	0.71	0.09
<i>Fagus sylvatica</i>	7	10	14.9	21	3.4	1.36	2.18	2.77	0.41	0.35	0.57	0.65	0.10
<i>Picea abies</i>	19	4	14.2	27	6.1	0.40	1.98	2.77	0.62	0.12	0.56	1.00	0.20
Cover 90–100%													
<i>Pseudotsuga menziesii</i>	8	11	16.1	19	2.4	1.23	2.06	2.83	0.44	0.35	0.51	0.71	0.10
<i>Quercus</i> sp.	4	10	13.3	17	2.6	1.59	2.10	2.52	0.41	0.48	0.56	0.66	0.07
<i>Fagus sylvatica</i>	5	9	15.4	23	5.1	1.12	2.05	3.09	0.71	0.32	0.52	0.68	0.12
<i>Picea abies</i>	5	7	12.6	17	3.3	1.36	2.03	2.82	0.64	0.39	0.57	0.77	0.17

n – number of relevés, min – minimal value, avg – mean, max – maximal value, SD – standard deviation

higher available soil nitrogen could be a more dominant factor than light conditions on the plot.

In spite of the above-mentioned prevailing mesophilous, nitrophilous and nitrophilous-to-ruderal species on Douglas-fir–Norway spruce parallel plots results of the average of frequency are not so clear. Results based on abundances describe differences between groups of stands better than those based on the pure species presence. A more distinct decrease of acidophilous species and increase of mesophilous, nitrophilous and nitrophilous-to-ruderal species abundances indicate changes in available nitrates in the soil.

The changes in frequency and abundance averages on Douglas-fir–oak parallel plots are not so much noticeable. It could be due to the higher naturalness of oak stands. However, it could also be seen that the frequency and abundance averages do not increase so much.

Species diversity

The species richness varies between 3 and 30 taxa per relevé (153 relevés in total). The total species diversity (using the Shannon-Wiener index) showed a broad interval from 0.33 to 3.18, and the equitability was between 0.11 and 1.00.

A comparison of the species diversity and equitability in groups of plots is shown in Table 3. According to such comparison, stands with one markedly dominant tree species, communities being dominated by Douglas-fir in the tree layer show the highest diversity, and conversely those with Norway spruce dominance show the lowest diversity. Species equitability is, however, influenced by a dominant tree

species minimally. Both species richness and diversity are highest on the plots under Douglas-fir and oaks with admixture other tree species.

The influence of species diversity parameters by Douglas-fir silviculture compared to other tree species is the basic issue. Species diversity and species richness changes reflected complex features of the whole community, so they were a result of the changes in species composition, which were described in preceding paragraphs. Douglas-fir presence in stands increases the species diversity of the herb layer, both overall and in cultural Norway spruce and European beech stands (Table 4). While Douglas-fir presence in Norway spruce stands (Fig. 2) could be assessed positively, since Douglas-fir increases similarity of the site conditions to natural stands, the increase of Douglas-fir

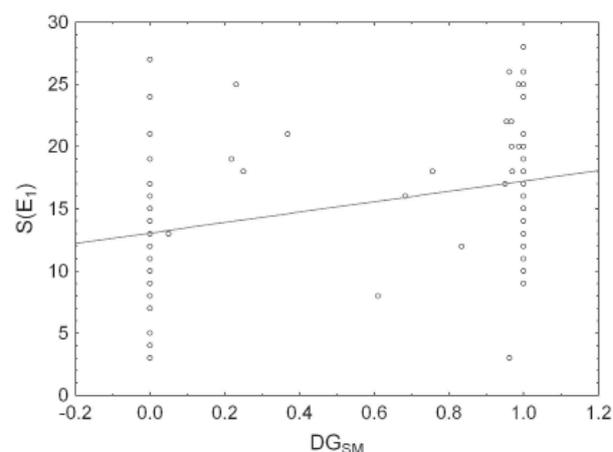


Fig. 2. Relative share of *Pseudotsuga menziesii* in the tree canopy of the cultural Norway spruce stands (DG_{SM}) influences species richness in the herb layer: $S(E_1) = 13.06 + 4.17 DG_{SM}$ ($r = 0.360$; $P = 0.0003$).

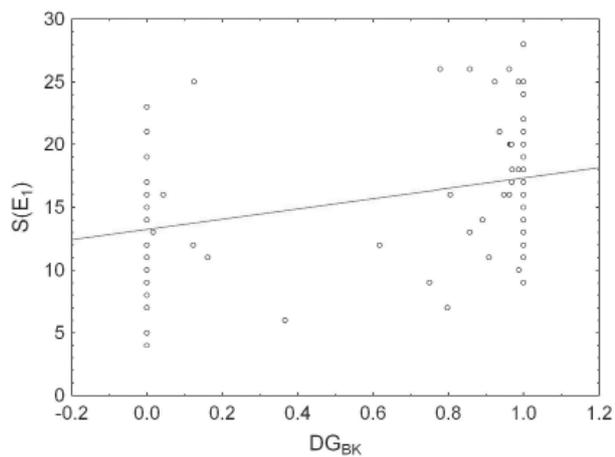


Fig. 3. Relative share of *Pseudotsuga menziesii* in the tree canopy of the stands with beech (DG_{BK}) influences species richness in the herb layer: $S(E_1) = 13.25 + 4.08 DG_{BK}$ ($r = 0.346$; $P = 0.0017$)

presence in European beech stands (Fig. 3) could be assessed negatively, since it promotes ruderalizing processes, when the species incoming to communities are not natural. However, it is necessary to pay attention to the observed increase in total canopy of the tree layer in mixtures of Douglas-fir with Norway spruce compared with just Norway spruce, which may result in a reduction in the light penetration, thus reducing the presence of some species in the herb and moss layers. Indeed, a reduction in total abundance of the moss layer (E_0) with an increasing proportion of Douglas-fir in the Norway spruce tree layer was demonstrated (Table 4).

In the forestry practice introduced tree species should be used with caution in new areas and research should reveal and prevent negative, even deleterious consequences (SCHMID et al. 2014). Douglas-fir is not excluded from this presumption although relevant information both in the Czech Republic and in Central Europe is missing. The available sources indicate very similar results with those documented by our team.

A similar pattern was documented by AUGUSTO et al. (2002), both in relation to broadleaved and Norway spruce stands. They studied Douglas-fir effects in the conditions of Northern France. They found no reduction in the species richness; on the contrary, they found the increase when Douglas-fir based ecosystems were compared with European beech stands. This is probably attributable to different light patterns in both stand types. Also BUDDE (2006) compared similar sets of forest stands in north-western Germany. He studied 50-years-old and older forest stands composed of

European beech, Scots pine, Douglas-fir and mixed stands. Also in this study it was concluded that the Douglas-fir and Douglas-fir–Norway spruce stands showed the highest tree species numbers (diversity) compared to other stand types. In general, Douglas-fir stands can host very similar communities compared to native species, especially the conifer ones. Also the stand age, as well as the composition and structure play an important role. On the other hand, the different plant ecological groups were not recorded, in slight contrast to our finding, where a tendency towards more nitrophilous, even ruderal vegetation was documented.

The combined effects of both the species composition and management practices (relict species, spatial heterogeneity, wind-throw gaps, skidding trails) were documented by LEITL (2001). He also documented the spreading of ruderal species, ascribing it rather to the forest management than to soil changes. VOLOSCUK (2012) did not document any remarkable changes in soil chemistry, overall soil, light, water and in general microclimatic conditions in Douglas-fir stands compared to native tree species. Despite this, there are some indications that Douglas-fir promotes more intensive nitrogen dynamics, which can be reflected by the trends of the ground vegetation towards more ruderal character (TRUM et al. 2011, KUPKA et al. 2013). In any case, more detailed research is necessary (SCHMID et al. 2014).

Table 4. Statistically significant correlations (Pearson's correlation coefficient) between different parameters of observed communities (significant at a level of $\alpha = 5\%$)

Parameter 1	Parameter 2	r
Total cover E_0	total cover E_3	-0.476
	DG_{SM}	-0.330
Total cover E_1	species richness E_1 (S)	0.363
	<i>P. abies</i> cover in E_3	-0.306
Total cover E_3	DG_{SM}	0.276
	<i>F. sylvatica</i> cover in E_3	0.356
	DG_{SM}	0.351
Species richness E_1 (S)	<i>P. menziesii</i> cover in E_3	0.323
	DG_{SM}	0.360
Total diversity E_1 (,H)	DG_{BK}	0.346
	<i>F. sylvatica</i> cover in E_3	0.090

Pseudotsuga menziesii relative presence in stands with Norway spruce $DG_{SM} = DG/(DG+SM)$ and *Pseudotsuga menziesii* relative presence in stands with European beech $DG_{BK} = DG/(DG+BK)$, where $DG = Pseudotsuga menziesii$ cover in E_3 , $SM = Picea abies$ cover in E_3 , $BK = Fagus sylvatica$ cover in E_3

CONCLUSIONS

As it is shown, Douglas-fir stands influence their habitats, which is indicated by species growing in the understorey. This tree species increases the species diversity of the stands, but decreases the abundance of some species. The most striking may be a comparison of Douglas-fir stands with managed Norway spruce stands, planted at lower altitudes. This fact is also confirmed by research in other European countries, where Douglas-fir stands are more common. The above-described differences in understorey are not so noticeable when European beech and oak stands are substituted by Douglas-fir once. However, even the significant phenomenon of striking nitrophilous species occurrence such as *Geranium robertianum*, *Urtica dioica* and *Galium aparine* manifests here. This indicates a high content of available nitrates in humus and top-soil horizons. However, detailed knowledge will be necessary to support this conclusion by soil analyses and thus to pertinently confirm the results of scarce studies performed until now. Induced higher N-dynamics can be one of the potential risks of Douglas-fir introduction.

Appendix

List of recorded species according to the nutrition groups:

Acidophilous species: *Anthoxanthum odoratum*, *Avenella flexuosa*, *Calamagrostis arundinacea*, *C. epigejos*, *C. villosa*, *Calluna vulgaris*, *Carex canescens*, *C. echinata*, *C. nigra*, *C. pilulifera*, *Dryopteris dilatata*, *Gymnocarpium dryopteris*, *Hieracium murorum*, *H. sabaudum*, *Luzula luzuloides*, *L. pallescens*, *L. pilosa*, *Melampyrum pratense*, *M. sylvaticum*, *Molinia arundinacea*, *Nardus stricta*, *Phegopteris connectilis*, *Picea abies*, *Pinus strobus*, *Prenanthes purpurea*, *Pteridium aquilinum*, *Senecio ovatus*, *Vaccinium myrtillus*, *Veronica officinalis*.

Mesotrophic species: *Acer campestre*, *Actaea spicata*, *Agrostis stolonifera*, *Anemone nemorosa*, *Asarum europaeum*, *Astragalus glycyphyllos*, *Athyrium filix-femina*, *Bromus benekenii*, *Campanula patula*, *C. persicifolia*, *C. trachelium*, *Carex digitata*, *C. ovalis*, *C. pairae*, *C. pallescens*, *C. pilosa*, *C. sylvatica*, *Clinopodium vulgare*, *Convallaria majalis*, *Dactylis polygama*, *Dentaria bulbifera*, *Dryopteris filix-mas*, *Euphorbia amygdaloides*, *Festuca drymeja*, *Galeobdolon luteum*, *Galium odoratum*, *G. sylvaticum*, *Hedera helix*, *Hepatica nobilis*, *Hypericum hirsutum*, *H. montanum*, *H. per-*

foratum, *Lathyrus niger*, *L. vernus*, *Melica nutans*, *M. uniflora*, *Milium effusum*, *Poa nemoralis*, *Polygonatum multiflorum*, *P. odoratum*, *Quercus robur*, *Ranunculus auricomus*, *Salvia pratensis*, *Sanicula europaea*, *Scrophularia nodosa*, *Sonchus arvensis*, *Sorbus torminalis*, *Stellaria graminea*, *S. holostea*, *Tilia cordata*, *Veronica chamaedrys*, *Viola reichenbachiana*, *V. sylvatica*.

Nitrophilous species: *Acer platanoides*, *A. pseudoplatanus*, *Agrostis capillaris*, *Ajuga reptans*, *Brachypodium sylvaticum*, *Cardamine impatiens*, *Circaea lutetiana*, *Cirsium vulgare*, *Corylus avellana*, *Dactylis glomerata*, *Digitalis grandiflora*, *Epilobium angustifolium*, *Festuca gigantea*, *Fragaria vesca*, *Frangula alnus*, *Fraxinus excelsior*, *Galeopsis pubescens*, *G. tetrahit*, *Holcus lanatus*, *Hordelymus europaeus*, *Impatiens noli-tangere*, *Lamium maculatum*, *Lysimachia nummularia*, *L. vulgaris*, *Mercurialis perennis*, *Moehringia trinervia*, *Myosotis sylvatica*, *Paris quadrifolia*, *Poa trivialis*, *Pulmonaria obscura*, *Ranunculus lanuginosus*, *R. repens*, *Rosa canina*, *Stachys sylvatica*, *Torilis japonica*, *Ulmus glabra*.

Nitrophilous-to-ruderal species: *Aegopodium podagraria*, *Alliaria petiolata*, *Arrhenatherum elatius*, *Atropa bella-donna*, *Conium maculatum*, *Convolvulus arvensis*, *Galeopsis speciosa*, *Galium aparine*, *Geranium robertianum*, *Geum urbanum*, *Glechoma hederacea*, *Grossularia uva-crispa*, *Humulus lupulus*, *Chaerophyllum temulum*, *Chelidonium majus*, *Impatiens parviflora*, *Mycelis muralis*, *Rubus fruticosus* agg., *R. idaeus*, *Rumex acetosella*, *R. conglomeratus*, *R. obtusifolius*, *Sambucus nigra*, *Solanum dulcamara*, *Stellaria media*, *Urtica dioica*.

Indifferent species: *Abies alba*, *Betula pendula*, *Carex brizoides*, *C. remota*, *Carpinus betulus*, *Deschampsia caespitosa*, *Euphorbia cyparissias*, *Fagus sylvatica*, *Juncus conglomeratus*, *J. effusus*, *Larix decidua*, *Maianthemum bifolium*, *Oxalis acetosella*, *Pinus sylvestris*, *Populus tremula*, *Prunus avium*, *Pseudotsuga menziesii*, *Quercus petraea* agg., *Q. rubra*, *Salix caprea*, *Senecio sylvaticus*, *Sorbus aucuparia*, *Stellaria nemorum*.

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