EFFECTS OF NATURAL BROADLEAVED REGENERATION VS CONIFER RESTORATION ON THE HERB LAYER AND MICROCLIMATE

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Abstract: This study was carried out on the Vidlič Mountain, eastern Serbia. The herb layer was surveyed in permanent plots on two localities: in a naturally regenerated beech forest and in a Douglas-fir plantation, in spring, summer and autumn 2011, 2012 and 2013. Air temperature, air humidity and soil moisture were measured. Species richness, Shannon's diversity index and Pielou's evenness index were calculated for each plot. Comparison of the abundances of species common to both forest stands was done using the Mann-Whitney U-test. The compositional gradient of the species data was examined using detrended correspondence analysis (DCA), and the species-environment relationship was analyzed by canonical correspondence analysis (CCA). Soil moisture and the total herb cover significantly differed in the naturally regenerated beech forest and Douglas-fir plantation. Floristic similarity between the surveyed forest stands was 28.12%. Although the dominant canopy species is known to be the strongest predictor of the herb layer, the model that includes all of the analyzed environmental factors explains the largest amount of the species variability. The species best fitted to this model are *Dryopteris filix-mas, Galium odoratum, Pulmonaria officinalis, Sanicula europaea*, *Pteridium aquilinum* and *Rubus caesius*. The analyzed forest stands are examples of two different post-disturbance regeneration strategies. Having in mind the limitations of this study, we can conclude that the naturally regenerated beech forest recovers faster: its herbaceous layer indicated nearly natural conditions, with only a few pioneer and disturbance-tolerant species. The herb layer in the Douglas-fir stand is still in the early seral stage, i.e. establishment.

Key words: beech; Douglas-fir; overstory effect; temperate forests

INTRODUCTION

Understory vegetation diversity and composition is largely influenced by the identity and composition of tree species, due to their dominant position in forests and their impact on various ecological gradients [1-3]. Therefore, tree species composition and diversity are considered a biodiversity indicator [4].

Conifer reforestation, if applied to a deciduous tree-species stand, causes a whole network of changes on different levels of the forest ecosystem structure and functionality. According to Nihlgård [5], the pedological effects of stand replacement of beech by spruce are: (i) changes in the physical properties of the upper soil horizon – the organic matter accumulates and humus forms on the soil surface; (ii) a decrease in the amount of available water, resulting in less rainwater to supplement the underground water; (iii) less available exchangeable K and Ca, but more Fe, PO_4 and acidic substances, resulting in the acidification of the upper soil layer to a depth of more than 50 cm; and (iv) less nitrification and greater mobilization of NH_4. Buck and St. Clair [6] found similar differences in the soil properties of aspen and conifer forests, which led them to a conclude that changes in the disturbance regimes, climate scenarios that favor conifer expansion, or the loss of aspen (or in our case beech), will decrease soil resource availability, which will have an important effect on the plant community development.

The ecological significance of the herb layer has been the focus of numerous studies, syntheses and reviews [7-10]. It has significant role in the structure and function of forest ecosystems in numerous ways and its importance is disproportionate to its minimal biomass and visibility in the forest landscape [11]. The ecological roles of the herb layer and their importance could be summarized by five aspects: (i) contribution to forest biodiversity; (ii) as the site of initial competitive interactions important to the regeneration of dominant canopy species; (iii) its link with the overstory; (iv) its role in ecosystem functions (e. g. energy flow, nutrient cycling); and (v) its abilities to respond to various disturbances, both natural and induced by direct and indirect human activities [11]. A large number of species, easy assessment in the field, specific site requirements and the ability to respond to disturbances and different forest management decisions make the forest herb layer the most suitable indicator of the forest site conditions, environmental changes, forest dynamics and human impact [5,6,12-24]. Numerous site-related factors, both biotic and abiotic, affect herbaceous plant communities in forests [3,25-29]. Among abiotic factors, soil moisture was found to be the most important [6,17,29-34]. Leuschner and Lendzion [17] found that air humidity influences the abundance of some species independently of soil moisture.

There are numerous ways in which the herbaceous layer is defined in the literature. Usually the definition emphasizes height rather than the growth form of the forest vegetation. In the most commonly used, so-called inclusive definition, the herbaceous stratum is composed of all plants that are up to 1 m in height. This definition combines true herbaceous species or “resident species” (plants that generally cannot grow higher than 1 m), and “transient species” (seedlings, sprouts, young saplings of woody species) that occur in the herb layer temporarily and have the ability to grow into higher strata. Variations in this definition are height distinction and the inclusion or exclusion of non-vascular or woody species [11]. In our study, the definition applied excludes non-vascular plants (mosses, liverworts) and transient species.

Over 50 years ago, a large part of the Balkan beech forest complex (*Fagus moesiaca* (K. Maly) Czecz.) was burned in a wildfire. One part of the burned area was reforested with Douglas-fir, while the rest of the area regenerated naturally. Douglas-fir is commonly grown for timber production throughout Europe. In this particular case, Douglas-fir seedlings were available in the largest quantity at the time, and they were used to reforest the more accessible part of the burned area, while the rest was left to regenerate naturally. Today, both stand types are managed extensively.

The aim of this study is to examine the effect of such stand replacement on herbaceous vegetation. In order to do this, we compared the features of the herb layer, as well as the microclimate and soil moisture. Since there are no data on the herbaceous vegetation and environmental conditions in the forest before the fire and reforestation, we have used the observed differences to estimate the environmental effects of the post-disturbance regeneration strategy applied.

MATERIALS AND METHODS

Study site

Our study was conducted on Mt. Vidlič, in eastern Serbia. The study site was chosen due to the fact that after the initial disturbance (the wildfire that happened over 50 years ago), two regeneration strategies were applied to the burned area that once constituted part of the same forest stand. The natural forest community of the surveyed area is *Fagetum moesiacae montanum* Jov. 1953 (non Rudski 1949). After the fire in 1962, one part of the large Balkan beech forest (*Fagus moesiaca* (K. Maly) Czecz.) burned to the ground. That area was reforested with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The study was done on two localities: one situated in the area reforested with Douglas-fir (central point 43°10'51.17"N, 22°42'31.05''E, altitude 1015 m a.s.l., NE exposure), and the other in the forest stand of Balkan beech that regenerated naturally (central point 43°10'42.27''N, 22°42'54.01''E, altitude 1015 m a.s.l.; NE exposure). The climate of Vidlič is moderately continental, with transitional changes to submountain and mountain at altitudes above 600 m a.s.l, a mean annual temperature of 7.8°C and mean annual rainfall of 858.5 mm at 1000 m a.s.l. The bedrock is mainly Jurassic limestone overlaid by a skeletal brown soil.

Herb layer survey, microclimate and soil moisture measurements

The survey of the forest herb layer was performed in May, July and September of 2011, 2012 and 2013 in the beech forest stand and Douglas-fir plantation. Three plots per stand type, each of 1 ha (100 x 100 m), were set. The initial plot in each stand, set in May 2011, was chosen randomly, while the positions of the other two were determined systematically, as well as the positions of plots surveyed in consecutive years (Fig. 1). In this way, the same plot was surveyed three times per year in order to rule out seasonal effects, and the effect of pseudo replication was minimized. To ensure a satisfactory level of accuracy in the plant-cover inventory and assessment, each 1 ha plot was divided into subplots (1 x 1 m). The cover of each species was estimated according the Braun-Blanquet extended cover-abundance nine-level scale transformed to ordinal transformed values (OTV) according to van der

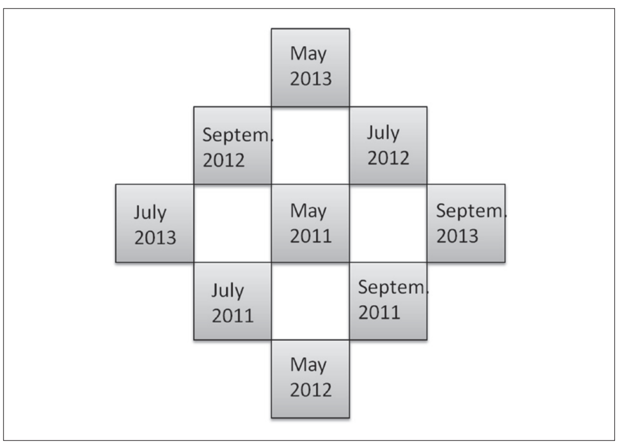

Fig. 1. Sampling scheme applied in both forest stands.

Maarel [35,36]. The sum of estimated OTVs was used as a measure of the total cover of herbaceous vegetation in one plot. The herbaceous species diversity in each plot was numerically expressed as species richness (S), Shannon's diversity index (H') and Pielou's evenness index (J'). Thermo button micro-weather stations, positioned 0.5 m above ground, were used to measure air temperature (range -40-85°C, sensitivity 0.1°C) and air humidity (range 0-100%, sensitivity 1%). Soil moisture (% mass) was determined at a soil depth of 20 cm, based on three randomly selected locations in each plot in May, July and September of 2011, 2012 and 2013.

Statistical analysis

In order to determine the differences in measured abiotic factors, as well as features of the herb layer (total cover, species richness, Shannon's diversity index and Pielou's evenness index) between plots in the Douglas-fir plantation and beech forest stand, the *t*-test was performed. The correlation between measured abiotic factors at each locality was assessed by the correlation coefficient, with a significance threshold of $p \leq 0.05$. Comparison of the abundances of species common to both forest stands was performed using the Mann-Whitney *U*-test. All the above-mentioned statistical analyses were performed using the STATISTICA 12 software package (www.statsoft.com). As the measure of floristic similarity, Sørensen's coefficient, expressed as percentage, was used. The ordination software package CANOCO 4.5 (www.canoco5.com) was used to perform multivariate analyses in order to describe basic vegetation patterns and their relationship with available environmental data. The unconstrained ordination, detrended correspondence analysis (DCA) was used to obtain a basic overview of the compositional gradients in the vegetation data. The length of the first axis was 3.193, suggesting that both linear and unimodal ordination methods could be applied. Since we expected qualitative changes in species composition, as well as the existence of a species optima with regard to the studied environmental factors, we chose to apply constrained ordination to the unimodal response model, canonical correspondence analysis (CCA) [37]. The significance of the relation to environmental variables was tested using the Monte Carlo permutation test (under full model and 999 permutations). In order to test the significance of the effect of each environmental factor, the marginal and conditional effects of environmental factors in CCA were analyzed. To reveal the number of canonical axes that effectively contribute to the explanation of herb vegetation variation, the effects of individual constrained axes were tested using partial CCA [37].

RESULTS

Environmental conditions

In order to assess the differences in environmental conditions between the Douglas-fir plantation and beech forest, we used the *t*-test. It showed that microclimate conditions (air temperature and air humidity) are not significantly different in the beech- and Douglas-fir-dominated plots (Table 1), while soil moisture is the abiotic factor that separates these two forest stands.

Species compositional gradient and response to environmental conditions

A total of 50 species was recorded: 29 in the beech-dominated plots, 41 in the Douglas-fir-dominated plots. Eighteen species were found to be common to both forest stands. In the beech forest stand, there are 11 distinct species, while in the Douglas-fir stand the number of characteristic species is 23. Floristic similarity between beech and Douglas-fir habitat types was 28.12%. *Pulmonaria officinalis, Glechoma hirsuta, Galium odoratum, Cardamine bulbifera* and *Aegopodium podagraria* had significantly higher values of total cover in the beech forest stand, while *Pteridium aquilinum* and *Fragaria vesca* had significantly higher values of OTVs in the Douglas-fir plantation (Table 2).

Numerical indicators of species diversity in the herb layer (species richness, Shannon's diversity index and Pielou's evenness index) did not differ significantly between the two analyzed forest stands. The total cover of herbaceous species in the plot, expressed here as the sum of OTVs, was the feature of vegetation that significantly differentiated the beech and Douglas-fir forest stands. The highest total cover values were recorded in the Douglas-fir-dominated plots (Table 1). Nine species (*Arum maculatum, Carex sylvatica, Clematis vitalba, Geum urbanum, Oxalis acetosella, Pastinaca sativa, Rumex acetosella, Sonchus asper, Urtica dioica*) out of the total 50, occurred with the lowest OTV of 1, and were recorded only once in one plot, and therefore they were excluded from further analyses.

In order to observe the vegetation patterns and their relationship to available environmental data, multivariate analyses were performed. First, unconstrained ordination – DCA, was applied. The first gradient was the longest (3.193), explaining about 24% of the total species variability. The first axis correlated very well with the environmental data (r=0.975), and the correlation for the other axes was considerably lower. The species-samples biplot of the DCA revealed a clear distinction between the plots surveyed in the Douglas-fir plantation (Fig. 2; circles) and in the beech forest stand (Fig. 2; squares). There was less variation in species composition in the plots surveyed in the beech stand (squares are grouped together) than in the Douglas-fir stand. The projection of environmental variables revealed that the first axis correlated

Table 1. Environmental variables, cover and diversity: differences between ~50-year-old beech and Douglas-fir plantation that regenerated after wildfire.

	Environmental variables			Cover	Diversity		
	ta [°C]	ha [%]	sm [%]	sumOTV	S	H'	J'
Beech	14.99 (4.17)	74.04 (9.05)	27.59 (7.65)	21.33 (7.76)	10.5 (2.15)	2.25 (0.25)	2.33 (0.22)
Douglas-fir	14.67 (4.33)	74.83 (8.90)	18.67 (6.8)	30.38 (7.05)	11.95 (3.38)	2.28 (0.30)	2.44 (0.30)
P	0.8214	0.7951	0.0008	0.0002	0.1179	0.6581	0.1686

ta – air temperature; ha – air humidity; sm – soil moisture; S – species richness; H' – Shannon's diversity index; J' – Pielou's evenness index. Mean values are given; standard deviation is in brackets. Differences were calculated using t-test ($p<0.05$ in bold type)

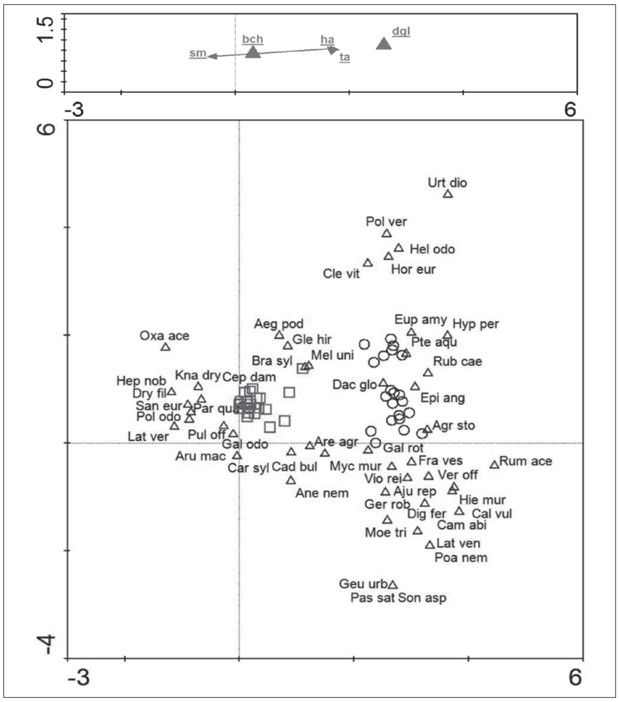

Fig. 2. The species-samples biplot of the DCA of the whole data set in the lower diagram (triangles – species; circles – plots in the Douglas-fir plantation; squares – plots in the beech stand), and retrospective projection of the environmental variables in the upper diagram (sm – soil moisture; ta – air temperature; ha – air humidity; bch – Beech forest stand; dgl – Douglas-fir plantation).

negatively with the soil moisture (sm) gradient, and positively with the air temperature (ta) and air humidity (ha). According to their effect on species composition, soil moisture and air temperature correlated negatively, while air humidity had a very short gradient showing its weak influence. The correlation matrix allows closer inspections of the relations among environmental variables (Table 3). Correlation between air temperature and air humidity was not statistically significant in either of the analyzed forest stands. A positive correlation was recorded between soil moisture and air humidity, and was strongest in the beech stand (beech: r=0.554; Douglas-fir: 0.506). Negative correlation was found between soil moisture and air temperature, and again the highest value of correlation coefficient was recorded in the beech stand (beech: r=-0.622; Douglas-fir: r=-0.501).

In order to directly extract the variation that is explainable by the measured environmental variables, CCA was done. The significance of the constrained ordination model was tested using the Monte Carlo permutation test. Both the test on the first axis and tests of all axes were found to be highly significant (p=0.002). However, the *F* value was much higher for

Table 2. Species list, abbreviations and comparative cover (sumOTV) using the Mann-Whitney *U*-test.

Species	Abbr.	Cover		
		bch	**dgl**	***P***
Aegopodium podagraria L. 1753	Aeg pod	17	3	**
Agrostis stolonifera L. 1753	Agr sto	0	27	
Ajuga reptans L. 1753	Aju rep	0	3	
Anemone nemorosa L. 1753	Ane nem	15	3	*ns*
Aremonia agrimonoides (L.) DC. 1825	Are agr	14	4	*ns*
Arum maculatum L. 1753	Aru mac	1	0	
Brachypodium sylvaticum (Huds.) P.Beauv. 1812	Bra syl	14	2	*ns*
Campanula patula L. subsp. *abietina* (Griseb.) Simonk 1887	Cam abi	0	4	
Cardamine bulbifera (L.) Crantz 1769	Cad bul	32	11	**
Carex sylvatica Huds. 1762	Car syl	2	0	
Cephalanthera damasonium (Mill.) Druce 1906	Cep dam	7	2	*ns*
Clematis vitalba L. 1753	Cle vit	0	2	
Clinopodium vulgare L. 1753	Cli vul	0	3	
Dactylis glomerata L. 1753	Dac glo	0	8	
Digitalis ferruginea L. 1753	Dig fer	0	20	
Dryopteris filix-mas (L.) Schott 1834	Dry fil	41	0	
Epilobium angustifolium L. 1753	Epi ang	0	37	
Euphorbia amygdaloides L. 1753	Eup amy	0	20	
Fragaria vesca L. 1753	Fra ves	2	29	**
Galium odoratum (L.) Scop. 1771	Gal odo	73	11	***
Galium rotundifolium L. 1753	Gal rot	2	8	*ns*
Geranium robertianum L. 1753	Ger rob	2	13	*ns*
Geum urbanum L. 1753	Geu urb	0	1	
Glechoma hirsuta Waldst. & Kit. 1802-1803	Gle hir	80	28	***
Helleborus odorus Waldst. & Kit. 1809	Hel odo	0	13	
Hepatica nobilis Schreb. 1768	Hep nob	4	0	
Hieracium murorum L. 1753	Hie mur	0	8	
Hordelymus europaeus (L.) Harz 1885	Hor eur	3	16	*ns*
Hypericum perforatum L. 1753	Hyp per	0	13	
Knautia drymeia Heuff. 1856	Kna dry	7	0	

Table 2. continued

Lathyrus venetus (Mill.) Wohlf. 1892	Lat ven	0	3	
Lathyrus vernus (L.) Bernh. 1800	Lat ver	31	0	
Melica uniflora Retz. 1779	Mel uni	59	35	*ns*
Moehringia trinervia (L.) Clairv. 1811	Moe tri	2	10	*ns*
Mycelis muralis (L.) Dumort. 1827	Myc mur	13	16	*ns*
Oxalis acetosella L. 1753	Oxa ace	1	0	
Paris quadrifolia L. 1753	Par qua	3	0	
Pastinaca sativa L. 1753	Pas sat	0	1	
Poa nemoralis L. 1753	Poa nem	0	5	
Polygonatum odoratum (Mill.) Druce 1906	Pol odo	9	0	
Polygonatum verticillatum (L.) All. 1785	Pol ver	0	6	
Pteridium aquilinum (L.) Kuhn 1879	Pte aqu	7	115	***
Pulmonaria officinalis L. 1753	Pul off	31	4	***
Rubus caesius L. 1753	Rub cae	0	111	
Rumex acetosella L. 1753	Rum ace	0	1	
Sanicula europaea L. 1753	San eur	36	0	
Sonchus asper (L.) Hill 1769	Son asp	0	1	
Urtica dioica L. 1753	Urt dio	0	1	
Veronica officinalis L. 1753	Ver off	0	25	
Viola reichenbachiana Jord. ex Boreau 1857	Vio rei	4	15	*ns*

Nomenclature follows Flora Europaea (http://rbg-web2.rbge.org.uk/FE/fe.html). bch – beech forest stand; dgl – Douglas-fir plantation; *** – p≤0.001; ** – p≤0.01; *ns*-not significant.

Table 3. The correlation between environmental parameters; ta – air temperature; ha – air humidity; sm – soil moisture. Correlation coefficient values significant at p <0.05 are in bold type.

	Total		Beech		Douglas-fir	
	ha	sm	ha	sm	ha	sm
ta	-0.370	-0.473	-0.350	-0.622	-0.401	-0.501
ha		0.384		0.554		0.506

Table 4. Marginal and conditional effects of environmental factors in CCA.

Marginal Effects			Conditional Effects				
Variable	Var.N	Lambda1	Variable	Var.N	LambdaA	P	F
bch	4	0.62	bch	4	0.62	0.002	15.90
dgl	5	0.62	ta	1	0.10	0.002	2.48
sm	3	0.32	sm	3	0.07	0.012	1.88
ta	1	0.09	ha	2	0.06	0.024	1.70
ha	2	0.05					

bch – dominant canopy species is beech; dgl – dominant canopy species is Douglas-fir; ta – air temperature; ha – air humidity; sm – soil moisture

the test on the first axis (*F*=15.026) than for the test on the trace (*F*=5.758). Analysis of the explained variability also confirmed this pattern: the first axis (0.624) explains more than the second (0.122), third (0.067) and fourth (0.047) axes together. The percentage variance explained by the first axis was very close to that explained by the first axis in the unconstrained DCA (23.5 in comparison with 24.3), and the species-environment correlation was only slightly higher (73.4 in comparison with 70.4), suggesting that the measured environmental variables were those responsible for species composition variation.

The independent effect of dominant canopy species (i.e. its marginal effect) is the most important for species composition, followed by soil moisture (Table 4). The last two variables, air temperature and air humidity, have relatively small marginal effects (Lambda1 was 0.09 and 0.05, respectively).

In the applied CCA, the dominant canopy species was first environmental factor added to the model since it explains the largest amount of variability in species data. The next factor added was air temperature, which increased the amount of explained variability from 0.62 to 0.72 (Table 4, Conditional Effects). Soil moisture and air humidity follow, explaining an additional 0.07 and 0.06 variability, respectively. The effects of all examined environmental variables are statistically significant (at p<0.05).

Partial CCA was done to test the significance of the individual effects of higher canonical axes. It was found that, in addition to the first, the second and third canonical axes effectively contributed to the explanation of herb vegetation variation. The test on the second axis was highly statistically significant (p=0.002), while the *F* value was much lower than for the test on the first axis (3.138 in comparison with 15.026). The individual effect of the third axis was significant (p=0.021), and the *F* value was 2.563. Therefore, the first axis, although clearly dominant, was not sufficient to explain the species-environment relationship in our data.

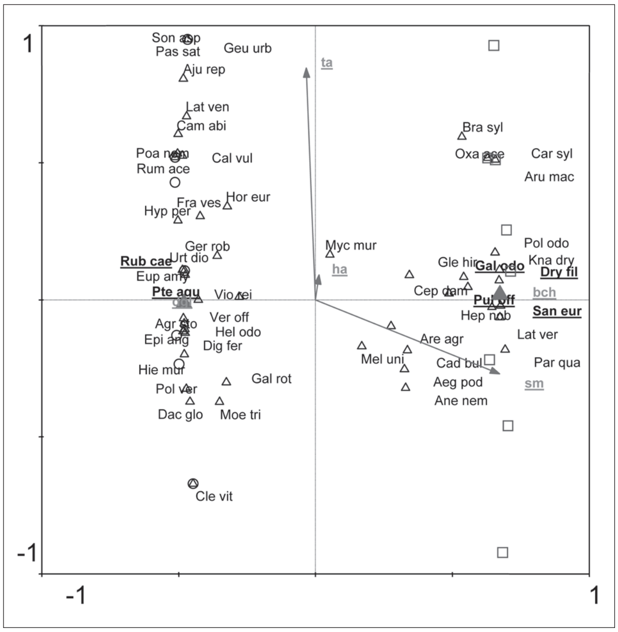

Fig. 3. The species-environmental variables-samples triplot of CCA. Species with the highest weight are underlined and in bold (triangles – species; circles – plots in the Douglas-fir plantation; squares – plots in the beech stand; sm – soil moisture; ta – air temperature; ha – air humidity; bch – Beech forest stand; dgl – Douglas-fir plantation).

In the ordination diagram obtained from the CCA, the herbaceous species are clearly divided into two groups, and this division follows the pattern of the main gradient (the dominant canopy species) – beech or Douglas-fir (Fig. 3). The pattern of the soil moisture gradient had a similar effect: the plots in the beech forest stand had higher soil moisture than those in the Douglas-fir plantation. The gradient of air temperature did not divide samples or species according to the dominant canopy species, but induced the heterogeneity in each of the forest habitat types. Air humidity was the factor with the shortest gradient, and it influenced the optimal distribution of only a few species, those whose positions on the ordination diagram could be projected on the arrow that represents this gradient. Species with the highest weight in this model are as follows: *Dryopteris filix-mas, Galium odoratum, Pteridium aquilinum, Pulmonaria officinalis, Rubus caesius* and *Sanicula europaea*. Optimal conditions for *Pteridium aquilinum* and *Rubus caesius* are in the Douglas-fir plantation habitat type, with low soil moisture and lower air temperature values. While *Rubus caesius* is indifferent to air humidity, this environmental factor influences the occurrence and abundance of *Pteridium aquilinum*. Species with optimal growth in the beech forest habitat type, and under the condition of high soil moisture, are *Dryopteris filix-mas, Galium odoratum, Pulmonaria officinalis* and *Sanicula europaea.* Unlike *Pulmonaria officinalis* and *Sanicula europaea, Galium odoratum* and *Dryopteris filix-mas,* are indifferent to air humidity.

DISCUSSION

Taking into account limitations due to the lack of information on herbaceous vegetation prior to the disturbance that occurred and its immediate environmental effects, as well as the possibility that the surveyed sites were not similar before the fire and reforestation with Douglas-fir, the obtained results enabled us to draw some conclusions about the environmental effects of the regeneration strategies applied, which are reflected in the features of the recent herb layer and of the measured abiotic factors.

Comparison of air temperature, air humidity and soil moisture in the naturally regenerated beech forest and in the Douglas-fir plantation revealed that the soil moisture is significantly different: in Douglas-fir stand it is much lower. This is consistent with the results of studies dealing with stand replacement of deciduous trees by conifer species [5,6]. The canopy architecture and leaf persistence through winter in deciduous and evergreen forests is different: deciduous stands have significantly greater snowpack accumulation [6,38]. Also, duff accumulation in the conifer stands is known to exhibit significant water repellency, which negatively influences the penetration and retention of water in the upper soil layers [6,38]. Minderman [39] emphasized the significance of the humus layer to the water regime of a forest, and Nihlgård [5] found that the transition from mull to mor in the pedological profile results in podsolization that produces a leaching horizon further down. Leaching processes were found to be faster in conifer stands [5]. Accumulation of organic matter in the surface soils, which was found in, for example, spruce forests [5], changes some of their physical properties (e. g. specific gravity, bulk density, porosity, water holding capacity). Ellenberg [40] pointed out the interesting fact that rainfall easily runs down the smooth beech bark, causing local wetting and incidentally a higher acidity where it reaches the soil, while with the conifers no water runs down the trunks. As expected [17], the soil moisture correlated positively with air humidity and negatively with air temperature, both in the beech-dominated and Douglas-fir-dominated plots.

The next significant difference between the beech and Douglas-fir stands was the total cover of herb layer. It was found to be better developed in the Douglas-fir stand. Also, the total number of recorded herbaceous species was higher in this stand type. Conifers are generally considered to be less favorable to understory diversity than deciduous trees [3]. However, Ellenberg and Leuschner [41] found that the increasing beech proportion in forests interferes with herb layer productivity due to the fine root network in the topsoil and its strong competitiveness for water and nutrients. Herb layer productivity increases with increased light availability [24,42,43]. The tree canopy architecture of the beech stand negatively influences light availability, which has a negative impact on herbaceous plants' productivity and diversity [24]. If we observe the reforestation of the former beech stand with Douglas-fir as one form of the stand disturbance, or in this case its hemeroby [44], which could not be distinguished from the immediate environmental effects of the fire that preceded reforestation, according to the disturbance hypothesis [45-47] the higher number of species found in the Douglas-fir stand was to be expected. Disturbances maintain high species richness and limit competitive exclusion [47-49]. Therefore, the number of species is not a good enough indicator of diversity; the quality or functional aspects of the species within a forest ecosystem can give much better insight into its naturalness, disturbances or its hemerobic state [44,50-54]. Comparison of the numerical expressions of diversity (species richness, Shannon's diversity index and Pielou's evenness index) on the plot-level did not reveal significant differences between the studied stand types. Therefore, these features of the herb layer could not be used as indicators of stand differentiation.

Floristic similarity between the herb layer in the naturally regenerated beech forest and the herb layer in Douglas-fir stand is only 28.12%, with 18 species common to both stands, 22 characteristics for Douglas-fir, and 9 found only in the beech stand. The quantitative relations of 8 species found in both stand types differ significantly: *Pulmonaria officinalis, Galium odoratum, Cardamine bulbifera* and *Aegopodium podagraria* have a better developed cover in the beech forest stand, while *Pteridium aquilinum* and *Fragaria vesca* are more abundant in the Douglas-fir stand. Ground flora in the Douglas-fir plantation is a mixture of species usually found in the beech forests of the region and species that are more characteristic of other forest communities, or are indifferent to the vegetation type where they occur [40,55,56]. Also, 14 out of 40 species recorded in the Douglas-fir forest stand are disturbance-tolerant pioneer elements of the secondary successions (e. g. *Pteridium aquilinum, Rubus caesius, Epilobium angustifolia).* Features of the herb layer in the Douglas-fir stand indicate the early-seral stage of the post-disturbance succession [57]. The herb layer in the beech forest stand has features that put this stand type in the mid-seral succession stage, the so-called stem exclusion phase or thinning [57,58]. These features are: the number of species decreases during understory establishment and growth declines compared with the Douglas-fir plantation, and the domination of shade-tolerant species characteristic of beech forests [55,56]. Although current insight into reforestation with indigenous trees emphasizes its important role in biodiversity conservation [23,59-61], we have not recorded any non-indigenous herbaceous plant species in the Douglas-fir plantation. Therefore, regarding the naturalness of the herb layer, in the modern and sustainable forest management the decision to use the conifer species on former deciduous species soil is much more important than the decision to reforest with native or non-indigenous tree species.

In addition to the dominant canopy species of beech or Douglas-fir, soil moisture was found to be one of the most important factors influencing the herb layer in the surveyed forest stands. A similar dependence of the herb layer on soil moisture was recorded in other similar studies [17,29-32]. According to Leuschner and Lendzion [17], air humidity is also an important predictor of herb distribution pattern in temperate broadleaf forests, although our study did not confirm its high importance. Air temperature, on the other hand, showed its importance in inducing both the heterogeneity of the surveyed plots and of herb layer, regardless of stand type. The dominant canopy species forms the forest stand and dictates light availability (and therefore air temperature and air humidity), soil chemical reaction, nutrient content in the soil, water availability, etc. [3,21]. We have found that the dominant canopy species influences soil moisture, but only when the effects of the air temperature and air humidity are added; this model explains herb layer variability. According to our results, the characteristic species of the herb layer of the naturally regenerated beech forest stand are *Dryopteris filix-mas, Galium odoratum, Pulmonaria officinalis* and *Sanicula europaea*. These species are typical for the beech forests in the region [56]. In the herb layer of the area reforested with Douglas-fir, the most prominent are *Pteridium aquilinum* and *Rubus caesius*, both plants of disturbed habitats [62]. We can conclude that the naturally regenerated beech forest recovers faster: its herbaceous layer indicates nearly natural conditions, with only a few pioneer and disturbance-tolerant plant assemblages. The herb layer in the Douglas-fir plantation is still in the phase of establishment. When analyzing the diversity and structure of the herb layer, reforestation with Douglas-fir seems to be an unsustainable post-disturbance strategy. The high number of recorded species found in the herb layer is the consequence of disturbance, and will last as long as the establishment phase lasts. Therefore, when using the herb layer as an indicator of environmental conditions, it is much more important to know which species are present than how many of them there are. In this particular case (the study took place in an area with very frequent wildfires), stand replacement of beech by Douglas-fir carries very serious environmental risks, since the Douglas-fir stand is a wildfire-prone area with its domination of coniferous, resin-producing tree species and a herb layer in which the most abundant plants are those that produce a large biomass that dries out at the end of the growing season, forming a fuel bed.

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