130. Jahrgang (2013), Heft 1, S. 45 – 59

Austrian Journal of Forest Science
Centralblatt für das gesamte Forstwesen

Species-specific properties of forest floor under mountain conditions

Spezifische Eigenschaften der oberen Humusschicht in Abhängigkeit von der Baumart in Gebirgslagen

Dušan Kacálek [1,*], Ondřej Špulák [1], David Dušek [1], Ivan Kuneš [2], Vratislav Balcar [1]

Key words: Assimilatory tissues, forest floor, nutrients, conifers, broadleaves.

Stichworte: Assimilationsorgane, obere Humusschicht, Nährstoffe, Nadelbäume, Laubbäume.

Abstract

The ameliorative species are considered to keep soils fertile as they return nutrients via litter-fall. Contents of nutrients in assimilatory tissues, litter and forest floor under five tree species in comparison with two low-density treatments with dominance of grass were investigated. The objective of this study was to answer whether the species differ in chemical properties of plant assimilatory tissues` matter (leaves and current year needles) and properties of soil humus layers under 18-year-old plantations. Weight of dry mass of forest-floor vegetation (herbs and litter) was higher in grass and broadleaves treatments compared to conifers. Birch had more foliar phosphorus and nitrogen while Mountain ash had more foliar potassium, calcium, magnesium compared to the other species. Mountain ash litter was higher in calcium. Forest floor humus (fermentation and humification horizons) showed similar contents of base cations under grass and broadleaves. Humus under conifers was higher in phosphorus.

1 Forestry and Game Management Research Institute, Strnady, Opočno Research Station, Na Olivě 550, 51773 Opočno, Czech Republic; e-mail: kacalek@vulhmop.cz

2 Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, 16521 Prague 6 – Suchdol, Czech Republic; e-mail: kunes@fld.czu.cz

* Corresponding author

Zusammenfassung

Die Meliorationswirkung der Baumarten besteht in der Eigenschaft, die Bodenproduktion durch den Rückfluss der Nährstoffe durch Laubfall zu fördern. Im Rahmen dieser Studie wurden Nährstoffgehalte in Assimilationsorganen, Streu und Humus von fünf Baumarten untersucht, welche einerseits in Wäldern und andererseits in grasdominierten Bereichen mit niedrigerer Baumdichte wuchsen. Das Ziel der Studie war es herauszufinden, ob und wie sich achtzehnjährige Bestände der ausgewählten Holzarten in chemischen Eigenschaften der Assimilationsorgane (Blätter und einjährige Nadeln) und des Humus unterscheiden.

Das Gewicht der Trockenmasse des Pflanzmaterials in der Streuschicht (krautige Pflanzen und Streu) war in von Gras und Laubbäumen bedecken Bereichen höher als unter Nadelbäumen. Der Vergleich der Nährstoffe in den Blättern zeigte für die Birke die höchsten Konzentrationen an Phosphor und Stickstoff und wohingegen in den Blättern der Eberesche die höchsten Werte an Kalium, Kalzium und Magnesium gemessen wurden. Die Streu der Eberesche hatte im Vergleich der Baumarten die höchsten Konzentrationen an Kalzium.

In der oberen Humusschicht (Fermentations- (OF) und Humifizierungshorizont (OH)) unter Grasbedeckung und Laubbäumen wurden höhere Mengen von alkalischen Nährstoffen nachgewiesen als unter Nadelbäumen. Der Humus unter Nadelbäumen hatte höhere Konzentrationen an Phosphor als jener unter Laubbäumen.

Introduction

Nutrient supply in naturally poor acidic mountain soils has been impacted by acidic air pollution. As a result, a newly mandated practice was introduced in Czech forestry in order to restore or maintain the productive status of the soil. All new forest plantations must be a mixture of commercial tree species, such as Norway spruce, and ameliorative tree species (broadleaves).

Acid soils occur under conditions of high rainfall and free drainage, both of which favor leaching and the biological production of acids (Singer, Munns 1996). In addition to natural acidification, large forested areas were heavily affected by the air pollution during the 1970s and 1980s in the northern Czech mountains (Lomský et al. 2011). These forests were dominated by Norway spruce stands situated on naturally acidic soils (podzols) that have become even more acidified due to air pollution (Slodičák et al. 2009, Klimo et al. 2006, Borůvka et al. 2009). Excessive die-off of forests occurred across large areas, and these stands were then removed. Large clearings were covered with new dominant vegetation, *Junco effusi–Calamagrostietum villosae* (Krecek et al. 2010). Altered soil properties were known to constitute such a serious factor, impeding the successful restoration of forests. Aerial liming was conducted over large areas in order to add basic nutrients and to amend the low pH. Amending materials such as crushed limestone or dolomitic limestone are favored for liming (Singer, Munns 1996). Unlike the soils in the Ore Mountains, the soils in the Jizera Mountains were never influenced by bulldozing of the forest floor and topsoil layers (Podrázský et al. 2003, Vavříček et al. 2006). The natural arrangement of soil horizons therefore remained undisturbed.

Forest soils, however, evolve under trees, and tree species have species-specific effects on the nutrient cycle (Weand et al. 2010). For example, each species has a specific nutrient demand and returns nutrients to the soil via litterfall. The latter process seems to be very important on formerly polluted, excessively acidic mountain sites, which are characterized by leaching of base cations (Perry et al. 2008). We suppose that young forest stands are able to affect the soil environment even before canopy closure occurs. Five tree species and two grass-dominated treatments were considered in addressing the following questions: 1) Do forest floors of grass-dominated sites differ from those on sites covered with trees? 2) Do broadleaves improve forest floor conditions compared to conifers on acidic sites in mountains?

Material and methods

The experiment was established in the early 1990s in the Jizera Mountains of northern Bohemia in the Czech Republic. Tree species were planted on a large, clear-felled summit area to study their prosperity under the conditions of an air polluted site (Balcar, Podrázský 1994). The experimental site is situated at an altitude of 970 m a.s.l. The mean annual precipitation was 1135 mm during the period 1994–2010 (Balcar et al. 2012a); the mean annual temperature was 5.0 °C between 1997 and 2010 (Balcar et al. 2012b).

The completely randomized design of the experiment consists of seven treatments with four replications per treatment. The plantations include the following treatments: SB – silver birch (*Betula pendula* Roth.), MA – mountain ash (*Sorbus aucuparia* L.), MP – mountain pine (*Pinus mugo Turra*), NS – Norway spruce (*Picea abies* (L.) Karsten) and EL – European larch

Tab. 1: Mean heights and stand density, by treatment, in 2008

Tabelle 1: Durchschnittshöhe und Bestandesdichte unter einzelnen Varianten in 2008

Treatment	Tree species	Mean height (cm)	Density (per ha)
A	beech*	206	400
B	sycamore*	57	225
SB	silver birch	276	900
MA	mountain ash	302	3,175
EL	European larch	502	1,675
MP	mountain pine	210	2,825
NS	Norway spruce	379	2,325

* gap-dominated treatments
* Variante mir niedriger Dichte der Baumschicht; A Bergahorn; B Gemeine Buche; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte.

(*Larix decidua* Mill.). In addition, two treatments presently dominated by grass vegetation were studied (grass plots). The A treatment was planted with European beech and the B treatment was planted with sycamore maple. Both beech and maple have shown poor survival since the second half of the 1990s. Their plantations were so thin in 2008 (Table 1) that herbal vegetation still dominated there. Therefore, these gap-dominated sites have not been covered with any woody species canopy since the deforestation in 1990. The plantations are designed as 100 m^2 square plots. The tree species were planted at 2 × 1 m spacing.

Tab. 2: Dry mass concentrations (%) of macroelements and silicon in leaves and needles

Tabelle 2: Vertretung der Makroelemente und des Kiesels in der Trockenmasse von Blättern und Nadeln (%).

	N	P	K	Ca	Mg	S	Si
SB	2.43	0.14	0.63	0.61	0.249	0.186	0.05
MA	1.43	0.08	0.86	1.24	0.415	0.137	0.03
EL	1.70	0.09	0.41	0.60	0.249	0.198	0.44
MP	1.23	0.086	0.45	0.15	0.073	0.117	0.04
NS	1.32	0.065	0.53	0.52	0.086	0.124	0.21
SB (SD)	0.12	0.02	0.04	0.06	0.008	0.020	0.02
MA (SD)	0.16	0.01	0.12	0.25	0.043	0.010	0.01
EL (SD)	0.19	0.01	0.03	0.05	0.016	0.014	0.10
MP (SD)	0.05	0.010	0.05	0.04	0.011	0.022	0.01
NS (SD)	0.07	0.004	0.04	0.19	0.011	0.028	0.05

Captions: SB silver birch; MA mountain ash; EL European larch; MP mountain pine; NS Norway spruce; SD – standard deviation
Bemerkungen: SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte; SD – Standardabweichung

We sampled living assimilatory tissues from trees (leaves or current-year needles) in tree-dominated treatments. Surface herbal vegetation, including litter (L), was sampled in all treatments. As for soil layers, samples of forest floor (both fermentation and humus horizons [FH]) and mineral topsoil (A) were collected. Five soil cores per plot were taken using a cylindrical soil corer (6 cm in internal diameter). Subsequently, the layers (L, FH and A) were separated from one another and the cores from the same layer per one replication were mixed.

Surface organic matter of plant-tissue origin (leaves, needles, twigs and herbal matter of litter) was analyzed to compare the percentage of the elements' content in dry mass. After the mineralization of samples, phosphorus was analyzed using a colorimetric procedure. Both calcium and magnesium were analyzed using an atomic absorption method after the addition of lanthanum. Humus (FH) and mineral soil (A) levels were analyzed for pH (both measured in water and KCl), total humus content (Springel-Klee), total nitrogen content (Kjeldahl), sum of bases and base saturation (S and V values according to the Kappen method), and plant-available nutrients (P, K, Ca, Mg using Mehlich III) (*Zbíral 1995*).

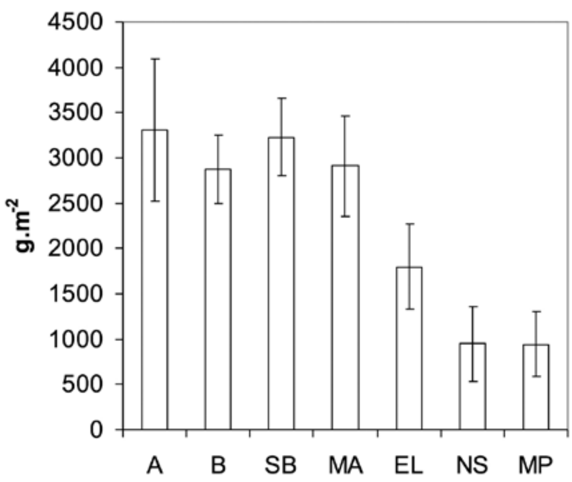

Figure 1: Dry mass weight of forest floor vegetation (herbs and litter), by treatment. A, B, low-density treatments; SB, silver birch; MA, mountain ash; EL, European larch; NS, Norway spruce; MP, mountain pine. Error bars denote standard deviation.

Abbildung 1: Gewicht der Trockenmasse der ebenerdigen Vegetation (Abfall und Krautmaterial) je nach Variante. Bemerkungen: A, B – Varianten mit niedriger Dichte der Baumschicht; A Bergahorn; B Gemeine Buche; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte. Die Fehlerbalken bezeichnen die Standardabweichungen.

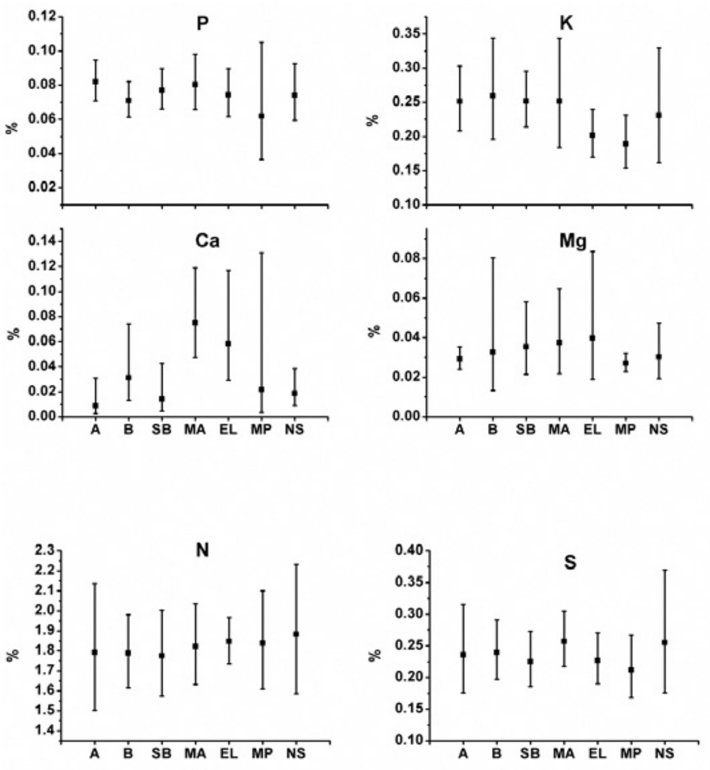

Figure 2: Nutrient contents in litter layer. A, B, gap-dominated treatments; SB, silver birch; MA, mountain ash; EL, European larch; NS, Norway spruce; MP, mountain pine. Error bars denote 95% confidence intervals.

Abbildung 2: Nährstoffgehalte im Abfallhorizont. Bemerkungen: A, B – Varianten mit niedriger Dichte der Baumschicht; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte. Fehlerbalken zeigen 95%-Konfidenzintervalle.

The data from the chemical analysis were evaluated by redundancy analysis (RDA), which is a canonical form of principal component analysis (*Legendre and Legendre 1998*). Canonical axes in the RDA ordination diagram correspond to the direction of the greatest variability in the data set, explainable by the level of a qualitative factor. Arrows show the direction in which the values of the given parameters increase. The angles between the respective arrows represent the correlation between the variables. Qualitative factors are displayed by means of symbols (Fig. 3). The data were processed using CANOCO software (*ter Braak and Šmilauer 2002*). Statistical significance of canonical axes in RDA was tested with a permutation test which can be considered a nonparametric counterpart of multivariate analysis of variance

(MANOVA). In spite of some advantages of the multivariate approach, there are some difficulties in interpretation of results, especially in treatment effect evaluation. Thus we also performed univariate ANOVA (or generalized linear model with gamma distribution and a logarithmic link for highly skewed data) for each variable and constructed 95% confidence intervals of mean. Since we doubted the usefulness of multiple comparison testing procedures such as the Tukey HSD test and things like that, we used linear contrasts for testing specific differences between coniferous and deciduous species.

Results

Birch leaves were higher in N and P compared to mountain ash and conifers. Mountain ash had more foliar K, Ca and Mg (Table 2) compared to the other tree species. Evergreen conifers were the same or lower in all nutrients compared to larch and broadleaves.

The treatments differ in terms of the dry mass weight of the litter. We found significantly lower values underneath conifers (European larch, Norway

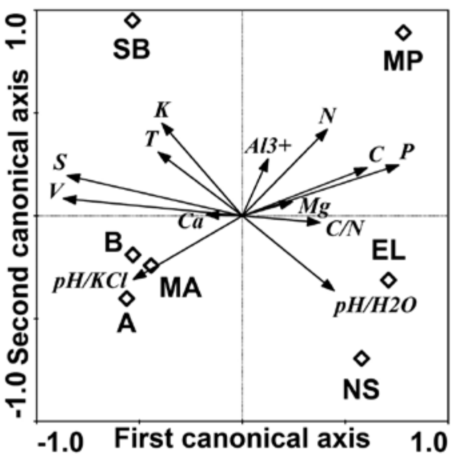

Figure 3: RDA shows different properties of forest floor humus (FH layer) under conifers vs. broadleaves. Qualitative factors: A, B, gap-dominated treatments; SB, silver birch; MA, mountain ash; EL, European larch; NS, Norway spruce; MP, mountain pine.

Abbildung 3: RDA stellt unterschiedliche Eigenschaften der Bodenhumusschicht (OF+OH-Horizont) unter Nadel- und Laubbäumen dar. Bemerkungen: Qualitative Merkmale: A, B – Varianten mit niedriger Dichte der Baumschicht; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte.

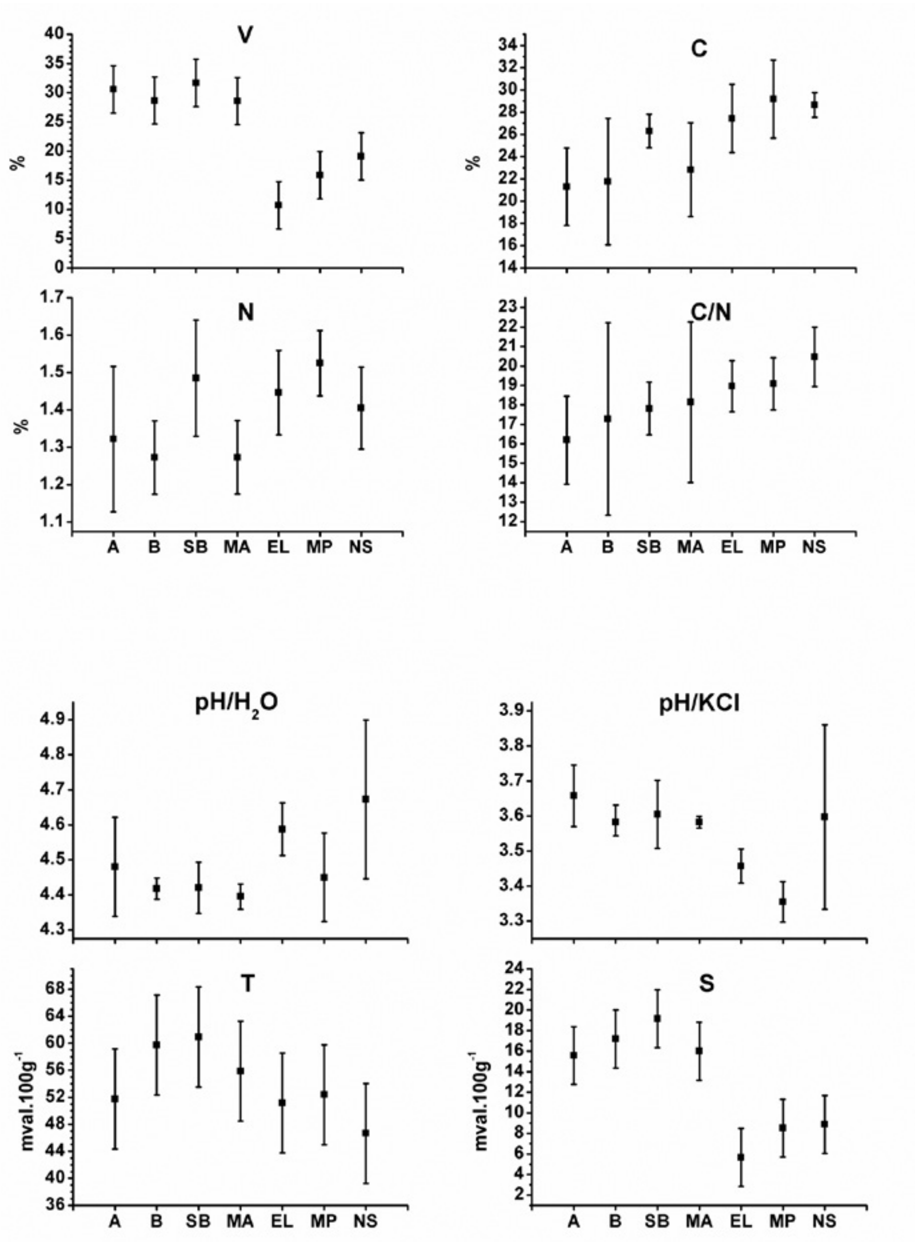

Figure 4: Properties of forest floor humus (FH) layers. FH layers in broadleaf and low-density treatments were higher in exchangeable base cations (S, V by Kappen) compared to those of conifers. A, B, gap-dominated treatments; SB, silver birch; MA, mountain ash; EL, European larch; NS, Norway spruce; MP, mountain pine. Error bars denote 95% confidence intervals.

Abbildung 4: Eigenschaften der oberen Humusschichten (OF+OH-Horizont). Die oberen Humusschichten bei Laubbäumen und bei Varianten mit niedriger Dichte des Holzbestandes haben im Vergleich zu den Nadelbäumen höhere Werte der austauschbaren Kationen (Werte S, V nach Kappen). Bemerkungen: A, B – Varianten mit niedriger Dichte der Baumschicht; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte. Die Fehlerbalken zeigen 95%-Konfidenzintervalle.

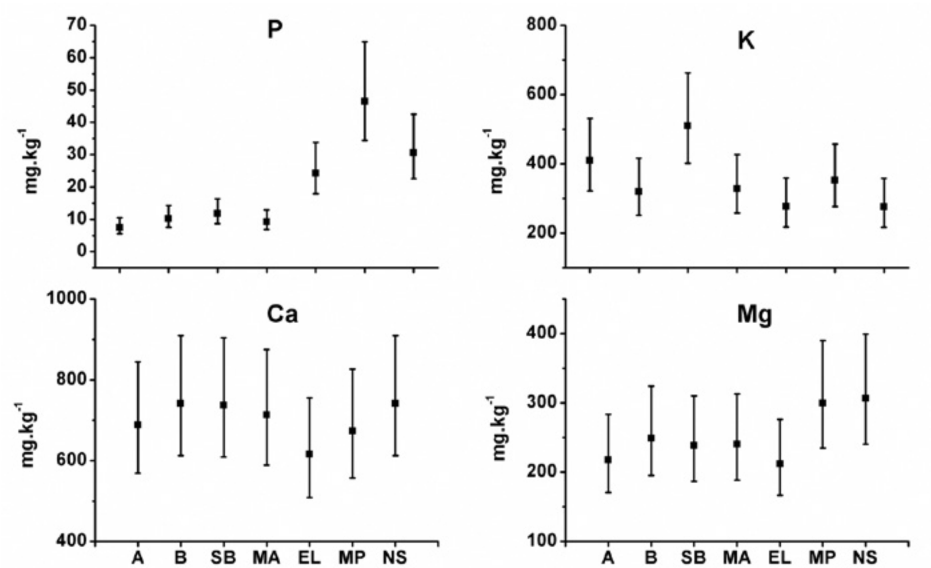

Figure 5: Forest floor humus layers in broadleaf and low-density treatments are lower in plant-available phosphorus (Mehlich III) compared to conifers. A, B, gap-dominated treatments; SB, silver birch; MA, mountain ash; EL, European larch; N,S Norway spruce; MP mountain pine. Error bars denote 95% confidence intervals.

Abbildung 5: Obere Humusschichten (OF+OH-Horizont) unter Laubbäumen und Varianten mit niedriger Dichte des Holzbestandes haben im Vergleich zu den Nadelbäumen eine niedrigere Vertretung des zugänglichen Phosphors (Mehlich III). Bemerkungen: A, B – Varianten mit niedriger Dichte der Baumschicht; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte. Fehlerbalken zeigen 95%-Konfidenzintervalle.

Tab. 3: Comparison of treatments using ANOVA

Tabelle 3: Vergleich der Varianten mithilfe von ANOVA

	Al^{3+}	C	N	pH H_2O	pH KCl	S	T	V	P	K	Ca	Mg	C/N
NS;MP;EL × A;B;SB;MA	0.639	**<0.001**	**0.019**	**0.011**	**0.012**	**<0.001**	**0.024**	**<0.001**	**<0.001**	**0.018**	0.444	0.198	**0.039**
A;B × SB;MA	0.618	0.151	0.275	0.341	0.427	0.413	0.489	0.807	0.295	0.345	0.889	0.836	0.490
SB × MA	0.388	0.143	**0.034**	0.554	0.658	0.134	0.353	0.300	0.306	**0.023**	0.817	0.964	0.886
A × B	0.766	0.894	0.659	0.407	0.177	0.437	0.150	0.521	0.185	0.189	0.607	0.471	0.699
NS;MP × EL	0.725	0.426	0.785	0.735	0.800	0.099	0.723	**0.014**	**0.037**	0.452	0.308	**0.035**	0.341
NS × MP	0.109	0.777	0.108	0.108	0.093	0.863	0.300	0.283	0.079	0.192	0.515	0.901	0.197

SB, silver birch; MA, mountain ash; EL, European larch; MP, mountain pine; NS, Norway spruce; A and B, gap-dominated treatments.
Bemerkungen: A, B – Varianten mit niedriger Dichte der Baumschicht; A Bergahorn; B Gemeine Buche; SB Weißbirke; MA Eberesche; EL Europäische Lärche; MP Bergkiefer; NS Gemeine Fichte.

spruce and mountain pine) compared to broadleaves (silver birch, mountain ash) and grass plots (A, B) (Fig. 1). All conifers showed denser canopies and initially accumulated litter on the soil surface.

As regards the nutrient contents (N, P, K, Ca, Mg and S) in the litter layer, we only found a difference underneath mountain ash. The mixture of herbs and mountain ash leaves was higher in Ca. With the exception of larch, the dry mass concentration of Ca in plant matter underneath mountain ash exceeded that of the other broadleaves and conifers (Fig. 2).

The RDA results show that the principal properties of the forest floor (FH layer) differ between two groups of treatments in concentrations of plant-available P and exchangeable alkaline nutrients (S and V values according to Kappen) (Fig. 3). Birch and mountain ash are similar in alkaline nutrients, but these broadleaves do not differ from the two grass treatments (Fig. 4). On the other hand, all conifers show increased P concentrations regardless of their being deciduous or evergreen species (Fig. 5). The multivariate model (RDA) explained about 42% of data variability with a high level of statistical significance ($p < 0.001$). The first ordination axe in the ordination graph is associated with substantial differences between coniferous species treatments and the others. The second axe shows the difference between the SB treatment and the MA, B, A treatments. The difference between coniferous treatments associated with the second axes is not so clear. The linear contrast used in ANOVA revealed statistically significant ($p < 0.05$) differences between coniferous treatments and the others in each tested variable, except of Al, Ca and Mg (Table 3).

Discussion

The composition of the herbal understory depends on the presence of particular trees in the overstory (Barbier et al. 2008). Herbal communities in both gap and broadleaved treatments showed more grass and herbal vegetation compared to conifer treatments. This accords with the findings of Chávez, Macdonald (2010) from boreal mixed forests. They attribute the differences to drier, cooler soils and darker conditions underneath a conifer overstory. Unlike broadleaved treatments, the conifers have already closed their canopies in our experiment. Thus, litter consisting of needles prevails in samples beneath conifers. Ayres et al. (2009) found higher soil temperature and moisture underneath stands of trembling aspen compared to lodgepole pine and Engelmann spruce. These conditions are also likely to occur under the other pioneer broadleaved tree species which form less dense canopies. Such conditions might promote litter mineralization and, along with litter composition, play a role in the lower accumulation of broadleaved litter on the soil surface in comparison to that of conifers.

As for the foliar nutrients' contents, Brandtberg et al. (2004) had found no difference in the capacity of birch (both silver and downy birch) and Norway spruce to take up calcium (they had applied ^{45}Ca) from the soil and forest floor. This factor is also likely to play a role in our experiment. We found the same dry-mass concentration of foliar Ca in both silver birch and Norway spruce. Birch, however, showed higher foliar P compared to the other species, and this also accords with Brandtberg et al. (2004). The results of their study indicated that birch had a higher demand for P than spruce did. In an earlier study, Brandtberg et al. (2000) had observed significantly higher concentrations of Ca and Mg in the LF (both litter and fermentation horizons) layer and of K, Ca and Mg in the H layer underneath stands with a birch admixture. Podrázský et al. (2013) and Ulbrichová et al. (2004) also found this positive effect of birch on humus chemical properties. In our study, the birch FH layer had a significantly higher amount of basic cations and basic saturation (S and V values from Kappen assays). We could not, however, exclusively attribute these increased values to birch, since mountain ash and even both grass-dominated treatments showed similar values.

Shiels and Sanford (2001) found different contents of plant-available phosphorus underneath two alpine krummholz tree-formed conifers (bristlecone pine and Engelmann spruce). In our study, all conifer FH layers were richer in plant-available phosphorus compared to broadleaf and grass-dominated treatments. Weand et al. (2010) reported species-specific relationships to the phosphorus cycle, observing differences in foliar, litter and root P concentrations of northern hardwoods and eastern hemlock. If the conifers were able to produce phosphorus-rich forest floors, this would be of great importance under conditions such as podzol soils. The experimental plot is situated in a part of the mountains where Slodičák et al. (2009) expect soils to be very low in phosphorus. The common forms of phosphorus in soil are phosphate salts (Binkley 1986, Perry et al. 2008), which are highly insoluble. The solubility of these salts is driven by pH. The very low pH of the soils in the Jizera Mountains is likely to affect the low availability of phosphorus, since low-pH soils are dominated by the least soluble $AlPO_4$ (Binkley 1986). Other species-specific factors are also known to influence concentrations of nutrients in the soil, such as the presence of fungi. For instance, Bending and Read (1995) found different extents of phosphorus depletion in FH layers colonized by two mycorrhizal fungi. One species (*Suillus bovinus*) showed significantly depleted phosphorus levels compared to an uncolonized treatment, while the other (*Thelephora terrestris*) showed no difference after 40 days of incubation. Read and Perez-Moreno (2003) pointed out that because so many species of fungi are capable of forming ectomycorrhiza, it is necessary to be cautious when generalizing on the basis of particular plant–fungus combinations. Whether humus conditions depend on the tree species itself or upon partnerships between tree species and fungus in the area of interest, is a new research question yet to be answered.

Conclusions

Comparing forest floor plant matter, humus and topsoil underneath 18-year-old experimental plantations, we can conclude the following:

- The weight of dry plant mass was higher in grass and broadleaves treatments compared to those of conifers. The reduced herbal vegetation was related to canopy closure in the conifers.
- Birch had more foliar phosphorus and nitrogen while mountain ash had more foliar potassium, calcium, and magnesium compared to the other species.
- The litter layer underneath mountain ash showed a higher calcium concentration than that of the other evaluated species did.
- Forest floor humus (FH) showed comparable properties underneath grass and broadleaves, i.e. the broadleaves still had a low effect on humus properties, while humus under conifers was higher in phosphorus.
- We suppose that silver birch and mountain ash will always play a temporary role in mountain forests' species composition, since they have different growth strategies compared to conifers such as Norway spruce and European larch. Different forest floor properties underneath conifers and broadleaves favor a restoration of mixed forests in formerly pollu-

ted mountains. Mountain pine is not a suitable species on sites capable of tree vegetation support.

Acknowledgements

The study was supported within the long-term research project MZe 0002070203 and NAZV project QH92087. Chemical analyses were conducted in the J. Tomáš Laboratory. We thank Gale Allen Kirking for editing the English text and we also thank Štěpánka Špuláková for translating the abstract and explanatory capture texts into German language.

References

Ayres, E., Steltzer, H., Berg, S., Wallenstein, M. D., Simmons, B. L., Wall, D. H., 2009. Tree species traits influence soil physical, chemical, and biological properties in high elevation forests. Journal PLoS ONE, June pp. e5964.

Balcar, V., Podrázský, V., 1994. Založení výsadbového pokusu v hřebenové partii Jizerských hor. Zprávy lesnického výzkumu, 39, 1–7.

Balcar, V., Špulák, O., Kacálek, D., Kuneš, I., 2012a. Klimatické podmínky na výzkumné ploše Jizerka – I. Srážky a půdní vlhkost. Zprávy lesnického výzkumu, 57, 74–81.

Balcar, V., Špulák, O., Kacálek, D., Kuneš, I., 2012b. Klimatické podmínky na výzkumné ploše Jizerka. II - teplota, vítr a sluneční svit. Zprávy lesnického výzkumu, 57, 160–172.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. Forest Ecology and Management 254, 1–15.

Bending, G. D., Read, D. J., 1995. The structure and function of the vegetative mycelium of ectomycorrhizal plants. V. Foraging behaviour and translocation of nutrients from exploited organic matter. New Phytologist 130, 401–409.

Binkley, D., 1986. Forest nutrition management. Wiley, New York, 290 pp.

Borůvka, L., Nikodem, A., Drábek, O., Vokurková, P., Tejnecký, V., Pavlů, L., 2009. Assessment of soil aluminium pools along three mountainous elevation gradients. Journal of Inorganic Biochemistry 103, 1449–1458.

Brandtberg, P. O., Lundkvist, H., Bengtsson, J., 2000. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. Forest Ecology and Management 130, 253–264.

Brandtberg, P. O., Bengtsson, J., Lundkvist, H., 2004. Distributions of the capacity to take up nutrients by *Betula spp*. and *Picea abies* in mixed stands. Forest Ecology and Management 198, 193–208.

Chávez, V., Macdonald, S. E., 2010. The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest. Forest Ecology and Management 259, 1067–1075.

Klimo, E., Materna, J., Lochman, V., Kulhavý, J., 2006. Forest soil acidification in the Czech Republic. Journal of. Forest Science, 52 (Special Issue), 14–22.

Krecek, J., Novakova, J., Horicka, Z., 2010. Ellenberg's indicator in water resources control: the Jizera Mountains, Czech Republic. Ecological Engineering 36, 1112–1117.

Legendre, P., Legendre L., 1998. Numerical Ecology – Second English edition. Elsevier, Amsterdam, 853 pp.

Lomský B., Šrámek V., Novotný R., 2011. Changes in the air pollution load in the Jizera Mountains: effects on the health status and mineral nutrition of the young Norway spruce stands. European Journal of Forest Research, online first

Perry D. A., Oren R., Hart S. C., 2008. Forest Ecosystems – 2nd Edition. The Johns Hopkins University Press, Baltimore, 606 pp.

Podrázský, V. V., Remeš, J., Ulbrichová, I., 2003. Biological and chemical amelioration effects on the localities degraded by bulldozer site preparation in the Ore Mountains - Czech Republic. Journal of Forest Science 49, 141–147.

Read, D. J., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? New Phytologist 157, 475–492.

Shiels, A. B., Sanford, R. L., Jr., 2001. Soil nutrient differences between two krummholz-form tree species and adjacent alpine tundra. Geoderma 102, 205–217.

Singer J. S., Munns D. N., 1996. Soils, an introduction. Prentice Hall, New Jersey, 480 pp.

Slodičák, M. et al., 2009. Lesnické hospodaření v Jizerských horách. Lesnická práce, Kostelec nad Černými lesy, 232 pp.

ter Braak, C. J. F., Šmilauer, P., 2002. CANOCO Reference manual and Cano-Draw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca (NY, USA), 500 pp.

Ulbrichová, I., Podrázský, V., Slodičák, M., 2004. Půdotvorná a půdoochranná funkce břízy v Krušných horách. Zprávy lesnického výzkumu 49, 32–34.

Vavříček, D., Šimková, P., Samec, P., Formánek, P., 2006. Soil aspects of forest site revitalization after windrow cultivation by heavy mechanization on the Krušné hory Mountains Plateau. Journal of Forest Science 52, 1–12.

Weand, M. P., Arthur, M. A., Lovett, G. M., Sikora, F., Weathers, K. C., 2010. The phosphorus status of northern hardwoods differs by species but is unaffected by nitrogen fertilization. Biogeochemistry 97, 159–181.

Zbíral, J., 1995. Analýza půd I (Jednotné pracovní postupy). Státní kontrolní a zkušební ústav zemědělský, Brno, 248 pp.