Arch. Biol. Sci., Belgrade, 64 (3), 1181-1195, 2012 DOI:10.2298/ABS1203181K

THE EFFECTS OF FORTY YEARS OF SPRUCE CULTIVATION IN A ZONE OF BEECH FOREST ON MT. MALJEN (SERBIA)

OLGA KOSTIĆ, MIROSLAVA MITROVIĆ, SNEŽANA JARIĆ, L. DJURDJEVIĆ, GORDANA GAJIĆ, MARIJA PAVLOVIĆ and P. PAVLOVIĆ

Department of Ecology, Institute for Biological Research "Siniša Stanković", University of Belgrade, 11060 Belgrade, Serbia

Abstract - This study investigates the effects of the forty-year cultivation of *Picea abies* on the floristic composition, physical and chemical soil characteristics, and the intensity of organic matter decomposition in a zone of mountainous beech forest (Mt. Maljen, northwestern Serbia). The long-term cultivation of conifers in a deciduous habitat has caused a reduction in biodiversity, as well as changes in the soil which were most pronounced in the top soil layer. There were found to be lower soil moisture levels ($p<0.05$), lower active ($p<0.01$) and substitutional acidity ($p<0.001$), depletion of the adsorption complex in base cations ($p<0.001$), and lower levels of N, P and K ($p<0.001$) in the spruce stand in relation to the beech stand (control). The higher C/N ratio of spruce litter ($p<0.001$) caused its lower decomposition rate in comparison to beech litter ($p<0.01$). All these changes have led to degradation and a reduction in this ecosystem's productivity.

Key words: Degraded habitat, spruce plantation, beech, soil characteristics, biodiversity, Mt. Maljen, Serbia

INTRODUCTION

Soil acidification across Europe has prompted research into the influence of various woody species on soil characteristics, particularly over the last two decades (Nihlgard, 1971; Ranger and Nys, 1994; Derome et al., 2001; Oulehle et al., 2007, 2010). It has been proven that vegetation composition, and in particular the composition of woody species, has varying effects on the chemical characteristics of soil and the processes in it (Pavlović, 1998; Dinić et al., 2001; Augusto et al., 2002; Klimo et al., 2006; Moukoumi et al., 2006; Kostić, 2007). Despite these effects being the result of the interaction between all the components of an ecosystem, the primary factor in these processes is the litter of the dominant woody species and its quality (Facelli and Pickett, 1991; Bonifacio et al., 2008; Bagherzadeh et al., 2008). Leaf litter is the largest single source of organic matter in soil (Aber et al., 1990; Kuzyakov and Domanski, 2000), and its decomposition is a key process in the functioning of forest ecosystems (Swift et al., 1979). The intensity of leaf litter decomposition is influenced by the environmental conditions in which decay takes place, the chemical composition of the leaf litter, and the decomposer community structure (Polyakova and Billor, 2007; Berg and McClaugherty, 2008). Forest litter acts as an input-output system for nutritious material in which the processes of nutrient cycling, primary production and maintaining soil fertility in the ecosystem vary according to the intensity of litter influx and the intensity of its decomposition (Sariyildiz and Anderson, 2003; Pandey et al., 2007; Wang et al., 2008). The negative input-output budgets for some nutrients promote higher soil acidification and a decrease in pH (Augusto et al., 2002). Tree species with different litter quality can cause a diverging impact on humus type, nutrient availability and acidification of the top soil (Ritter et al., 2003). Different woody species on the same soil type can condition the formation of mull, moder or mor humus types (Klinka et al., 1981; Doleman and Eijsackers, 2004). Woody species which have litter rich in base cations, particularly calcium, such as beech litter (Berger et al., 2008), might direct the humus development towards mull types, while woody species which have litter that abounds in acidic cations, such as *Picea abies*, condition the formation of moder or mor humus types (Rothe et al., 2002; Berger et al., 2004; van Oijen et al., 2005; Berger et al., 2008). Plant species with litter characterized by a higher content of nutrients and base cations impact on higher base saturation (V%), cation exchangeable capacity (T), pH, soil fauna activity, decomposition rate, total porosity and lower C/N ratios (Binkley and Valentine, 1991; Neirynck et al., 2000; van Oijen et al., 2005). A decrease in pH leads to changes in many other soil characteristics, such as the concentration of bio-available P (Carreira et al., 1997). Spruce litter, which is well-protected both chemically (a high content of polyphenols and tannin) and mechanically (lignins, waxes and resins), decomposes very slowly, and hence the accumulation of organic matter on the surface of the forest soil causes the sequestration of nutrients, the acidification of top soil, reduced activity of soil macro fauna, and shallow rooting (Berger et al., 2008).

Research into plantations in temperate zones that are up to 30 years old, has shown that changes in the characteristics of soil that are under the influence of plant species first appear in the surface layer (Raulund-Rasmussen and Vejre, 1995; Alriksson and Eriksson, 1998; Vesterdal and Raulund-Rasmussen, 1998; Vesterdal et al., 2002; Hagen-Thorn et al., 2004). As the stand ages, this influence becomes more and more marked, and after 40-50 years the influence of the dominant woody species can be noted in the deeper soil strata as well (Binkley and Valentine, 1991; Norden, 1994).

Besides determining the litter type and modifying soil characteristics, woody species also have an impact on changes in the light regime in a forest stand (Berbier et al., 2008), which, as a whole, influences the composition of understory vegetation. Past research has mainly studied the relationships between trees and soil, or soil and the understory, while studies that have included both interactions are rare (Pigott, 1989; Van Ojen et al., 2005).

Under natural conditions, Serbia is a country of deciduous trees, and beech (*Fagus moesiaca* (Domin, Maly) Czeczott) is the most widespread tree species. It dominates in the forest reserves of Serbia, accounting for 60% of the volume of trees and 31% of the surface area it occupies. Coppice forests and shrubs comprise 52.56% of the total area populated by beech (Medarević et al, 2003). Such a high proportion of coppice and degraded forests, which are often unable to make use of the production potential of the habitat, meant that the need arose for the melioration of these forests in order to improve their quality (Jovanović et al., 1983). As such, in the mid-20th century, a program of intensive afforestation was begun, and according to data from the National Inventory of Forests, the surface area of silviculture in Serbia today totals 174,800 ha, 71.4% of which comprises coniferous plantations (European black pine, spruce, Douglas fir, Eastern white pine, etc.) (Banković et al., 2008). When it came to choosing coniferous species for the melioration of degraded forest areas and for the afforestation of barren land, their productive capabilities were of the greatest importance. However, they were also planted in localities that, due to the ecological conditions, would have been naturally inhabited by deciduous species. Hence, for example, Norway spruce (*Picea abies* (L) Karst.), which was planted at mid and low altitudes, found itself completely outside its natural distribution area, occupying some of the best habitats for deciduous species in Serbia.

The aim of this work was to establish whether the forty-year cultivation of spruce in a montane belt of beech forest in northwest Serbia has affected floristic composition, physical and chemical soil characteristics, and the metabolism of this habitat, and if so, to what degree.

MATERIALS AND METHODS

Site description

Research was undertaken in the northwest of Serbia, on Mt. Maljen (Lat./Lon. $44^0$10'N / $20^0$5'E), in the locality of Kaona (880 m.s.l.), which is situated in a climatoregional area of montane beech forests (*Fagetum montanum* s. lat.). The climatic conditions of this area are moderate continental (mean annual temperature is 9.16^{0}C, average temperature during the vegetation period is 15^{0}C, and mean annual precipitation is 890 mm).

Description of experimental areas

Forty years ago, in a beech forest of root sprout origin, clear-cutting of beech trees was carried out in 20 m-wide strips. Spruce stands were established in these clearings, with these strips alternating with areas populated by beech. Our experimental areas were a spruce stand strip and a strip of autochthonous beech forest (control). The criterion for their being selected was that they were situated on the same soil type (dystric cambisol), formed on the same bedrock (diabase), with the same exposure (west) and almost the same terrain incline (5-10^0).

Floristic composition of the experimental areas

Phytocoenological research was conducted according to the Westhoff and Van der Marrel method (1973) in 20 x 20 m plots. For each area, three phytocoenological releves were taken. The plant species were established on the basis of The Flora of Serbia (Josifović et al., 1970-1980) and Ikonographie Der Flora Des Südöstlichen Mitteleuropa (Javorka and Csapody, 1975).

Litter and soil analysis

For the litter samples (OLF and OH horizon-layer, n=7), dried to a constant weight and ground to pass a 0.5mm sieve, the pH was determined in deionized water (0.6 g of plant material/15 ml H_2O) and in 1N KCl (0.6 g of plant material/15 ml 1N KCl + 1.2 g $BaSO_4$). The total carbon and nitrogen content in the litter was determined from the same sample using the Anstet method, modified by Ponomareva and Nikolaeva (1975).

Soil moisture was determined in the period from April to October at 10 cm increments up to a depth of 50 cm, with three replications. Moisture levels were established gravimetrically, using a Chyo IB 30 type hygrometer. The results are presented in the form of the average levels of soil moisture during the vegetation period.

The chemical characteristics of the soil were determined at soil depths of 0-10, 10-20, 20-50 cm with 7 replications (n=7). The samples were dried at 65^{o}C to a constant weight and sieved. The acidity of the soil (active and substitutional) was determined potentiometrically, with a glass electrode, using a mixture of soil/deionized water and soil/1 N KCl (1:2.5, w/v). Soil adsorptive complex characteristics were determined according to Kappen as follows: the content of exchangeable bases (S, mg ekv*100 g^{-1}), hydrolytical acidity, the sum of acidic cations (T-S, mg ekv*100 g^{-1}) through calculation using hydrolytical acidity, and cation exchangeable capacity (T, mg ekv*100 g^{-1}) was established through calculation. The saturation of the adsorption complex with bases (V%) was determined through calculation, according to Hissink. The total organic carbon content (C%) in soil was determined by potassium dichromate oxidation using the Simakov modification of the Turin method (1957), and the total nitrogen content (N%) using the semimicro-Kjeldahl method. The C/N ratio was determined through calculation. Available phosphorus (P_2O_5, mg/100 g) and potassium (K_2O, mg/100g) were extracted with ammonium acetate-lactate (A-L solution, pH 3.7, ratio 1:20) and determined by flame photometry (Egner et al., 1960).

Litter decomposition

In order to determine the intensity of the decomposition of the leaf litter of the species examined, the 'Litter bag method' was used (Bocock and Gilbert, 1957; Wieder and Lang, 1982; Albers et al., 2004). Decomposition intensity for the organic matter of beech and spruce was determined 6 months and 12 months after the start of decomposition. Freshly fallen leaves and needles from the species examined were collected on plastic nets spread out on the surface of the forest soil. Leaf litter (20 g), dried at a temperature of 65°C to a constant weight, was enclosed in a bag (20 x 20 cm) made of plastic netting with a mesh size of 1 mm. In October, ten bags were randomly placed for each species on the surface of the forest floor. After six months, in April of the following year, five of the bags were sampled for each species (n=5), and after twelve months, in October, the remaining five bags were collected (n=5) from both plots. Once soil and roots had been removed, all the collected bags were dried at 65°C to a constant weight, in order to determine the remaining weight of the organic matter.

Based on Olson's decomposition model and Olson's rate constant of loss (Olson, 1963), the prognosis for the decomposition of organic matter from beech and spruce was calculated using the formula:

$$\frac{Mt}{Mo} = e^{-kt}$$

where M_0 is the initial mass of the organic matter, M_t is the mass of the organic matter after a year (t) of decomposition and k is Olson's rate constant of loss after 12 months of decomposition; $k_{1/2}$ represents the decomposition coefficient after 6 months. According to this exponential model, half of the decomposition time $t_{1/2}$=0.639*k, and the time constant k is equal to 0.368 of 1/e. The time required (in years) for the decomposition of 95% of the organic matter was calculated using 3/k, and the time required (in years) for the decomposition of 99% of the organic matter, using 5/k.

Statistical analysis

One-way analyses of variance (ANOVA) were performed to test the differences between the spruce stand and the beech stand as the control in terms of the physical and chemical characteristics of the soil, as well as the litter characteristics. Soil moisture, the acidity of the soil and litter (active and potential), characteristics of the adsorptive complex of the soil (cation exchangeable capacity – T, content of exchangeable bases – S, the sum of acidic cations – T-S, saturation of the adsorption complex with bases – V), total nitrogen content, available P and K in soil, as well as the C/N ratio in soil and litter were compared. The intensities of the decomposition of spruce and beech organic matter after 6 and 12 months were also compared, as were the decomposition constants ($k_{1/2}$ and k) and decomposition prognosis constants (3/k and 5/k) for the organic matter from these species (subsequent tests of normality using the Shapiro-Wilk W test and Levene's test of homogeneity of variances showed non-significant values for all the reported ANOVA breakdowns).

RESULTS

Floristic composition

The only layer that was identified in the spruce stand was a tree layer, with spruce being the only trees present (*Picea abies* (L.) Karst.) /9/ (Table 1). There has been no tending at the site, so trees with an average height of 12 m and a trunk diameter of approximately 20 cm cover 100% of the surface area. There is a complete absence of a shrub layer and herbaceous cover within the stand, while the surface of the soil is covered with a layer of needles densely intertwined with fungal hyphae. Isolated specimens of the species *Cardamine bulbifera* (L.) Crantz., *Rubus hirtus* W et K. and *Fagus moesiaca* (Domin, Maly) Czeczott were noted on the very edge of the spruce stand. At the control site (the beech stand), three layers were identified. In the tree layer, beech trees were present (*Fagus moesiaca* (Domin, Maly) Czeczott) /8/, accounting for 75% of the total. The trees are approximately 80 years old with an average height of 18-20 m and trunk diameter of 35-40 cm. The shrub layer covers 10% of the surface area, while the layer of herbaceous plants covers 100% (Table 1).

Litter and soil analysis

Average soil moisture levels at the research sites dur-

Table 1. Analysis of floristic composition in Norway spruce (plantation) and beech forest (control)

Community	***Picea abies* - plantation**			***Fagetum montanum* - control**		
Releve number	1	2	3	4	5	6
Locality	Maljen - NW Serbia (Kaona)					
Altitude (m)	880					
Exposition	W	W	W	W	W	W
Slope (^{0})	8	10	10	5	5	5
Bedrock	Diabase-chert formation					
Soil	Acid brown earth					
Average dbh (cm)	20	20	20	35	40	35
Average height (m)	12	12	12	18	20	18
Size of sample area (m)	20x20					
Tree layer						
Fagus moesiaca (Domin, Maly)Czeczott				7	9	8
Picea abies (L.) Karst	9	9	9			
Shrub layer						
Fagus moesiaca (Domin, Maly)Czeczott				3	3	3
Carpinus betulus L.				2		3
Crategus monogyna Jacq.				2		3
Corylus avellana L.				2		3
Acer pseudoplatanus L.				3		
Rubus hirtus W. et K.					2	
Prunus avium L.						
Cornus mas L.					2	
Betula pendula Roth					2	
Sambucus nigra L.					2	
Salix caprea L.					2	
Herb layer						
Rubus hirtus W et K.	2			8	7	7
Cardamine bulbifera (L.) Crantz.	2			3	3	3
Viola silvestris Lam.				3	3	3
Galeobdolon luteum Hudson				2	3	3
Fagus moesiaca (Domin, Maly)Czeczott	2			3	5	5
Pteridium aquilinum (L.) Kuhn.				2	2	5
Mycelis muralis (L.) Dum				3	2	3
Sambucus nigra L.					2	
Galium odoratum (L.) Scop.				5	5	3
Asperula taurina L.				3	2	
Acer pseudoplatanus L.				2	2	2
Allium ursinum L.				3	2	3
Heleborus odorus W. et K.				2	2	2
Epilobium montanum L.					2	2
Stachys silvatica L.				2		
Crataegus monogyna Jacq.						2
Quercus cerris L.						2
Circaea lutetiana L.				2		
Clinopodium vulgare L.				2		3
Moehringia trinervia (L.) Clariv.				2		3
Glechoma hirsuta W. et K.				3		3
Carpinus betulus L.				2		2
Corylus avellana L.				2		2
Sanicula europaea L.				3		2
Galium silvaticum L.						2
Carex silvatica Hudson						2
Euphorbia amygdaloides L.						3
Aremonia agrimonoides (L.) Neck.						2
Poligonatum multiflorum (L.) All.				2		2
Symphytum tuberosum L.				2		2
Scrophularia nodosa L.				2		2
Veronica chamedrys L.					2	2
Clematis vitalba L.						2
Urtica dioica L.						2

ing the vegetation period were highest in the surface layer of the soil (0-10 cm), with this layer being drier (28.63±2.96%) in the spruce stand in relation to the control site in the beech stand (31.13±2.84%), ($p<0.05$). Moisture content decreased in the deeper layers of soil at both sites, but no differences were noted between the spruce stand and the control site, except at a depth of 40-50 cm. At this depth, the soil was found to be moister in the spruce stand than in the control site (20.32±3.32% : 18.10±2.62%, $p<0.05$) (Fig.1).

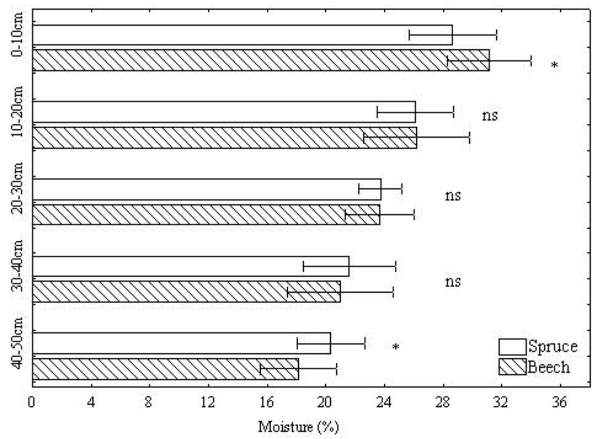

Fig. 1. Soil moisture (ANOVA, n=7, level of significance: *$p<0.05$, ns - not significant)

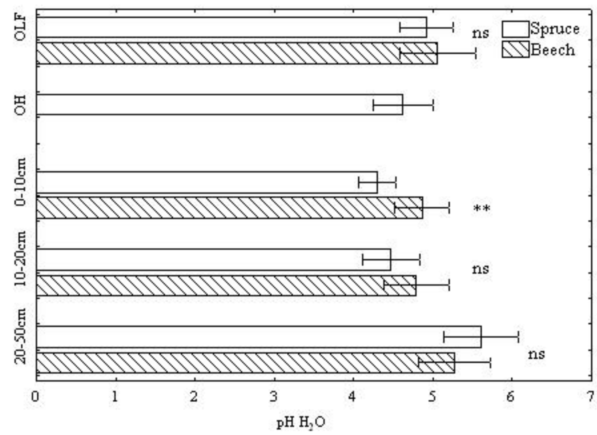

Fig. 2. Active acidity (ANOVA, n=7, level of significance: **$p < 0.01$, ns - not significant)

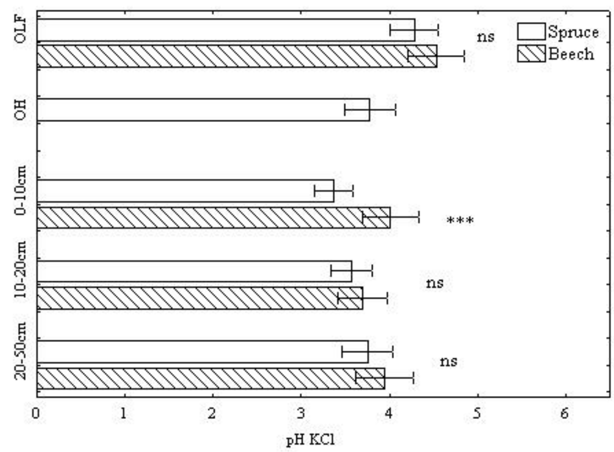

Fig. 3. Substitutional acidity (ANOVA, n=7, level of significance: ***$p<0.001$, ns – not significant)

The levels of active acidity of the soil, both in the litter layer and in all the investigated soil layers, were higher than those of substitutional acidity (Figs. 2 and 3). Statistically significant differences for active and also for substitutional acidity were only noted at a depth of 0-10cm, with lower values found in the spruce stand than in the control site (active acidity 4.30±0.24 : 4.86±0.35, $p<0.01$; substitutional acidity 3.37±0.22 : 4.01±0.32, $p<0.001$). In the litter layer, as well as in the deeper layers of soil, no differences between the sites were noted in terms of active and substitutional acidity (Figs. 2 and 3).

The cation exchangeable capacity (T) was lower in the spruce stand than in the control site at a soil depth of 0-10 cm (56.96±3.75 : 62.75±4.26, $p<0.01$), and at a depth of 10-20 cm (46.38±4.22 : 51.18±4.86, $p<0.05$). There were no differences between the sites at a soil depth of 20-50 cm (Fig. 4). Lower levels of the content of exchangeable bases (S) were recorded in the surface layer of soil in the spruce stand in comparison to the control site (11.61±1.35 : 20.66±1.98, $p<0.001$). No differences were noted at a depth of 20-30 cm, while at a soil depth of 20-50cm the values of S were higher in the spruce stand than in the control site (12.39±1.13 : 4.72±0.45, $p<0.001$) (Fig. 5). The sum of acidic cations (T-S) in the surface layer of soil was higher in the spruce stand (45.35±3.40 : 42.09±3.37, $p<0.05$), although at a depth of 10-20cm, the sum of acidic cations was lower in the spruce stand than in the

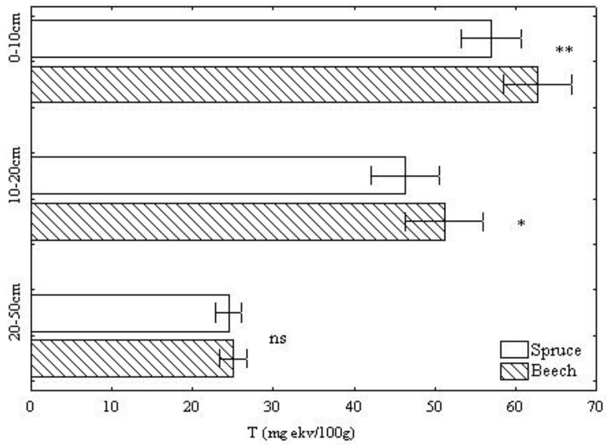

Fig. 4. Cation exchangeable capacity (T), (ANOVA, n=7, level of significance: *p<0.05, **p<0.01, ns – not significant)

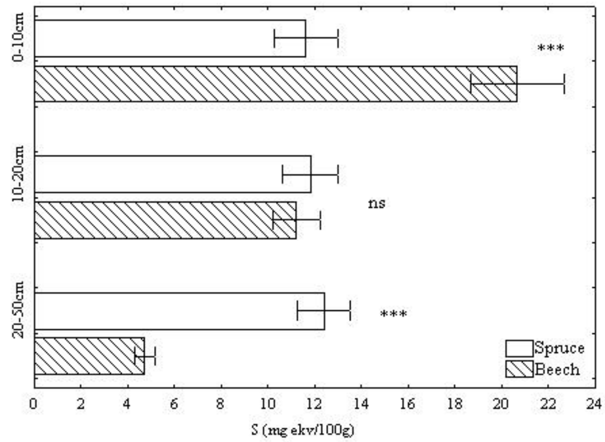

Fig. 5. Content of exchangeable bases (S), (ANOVA, n=7, level of significance: ***p<0.001, ns – not significant)

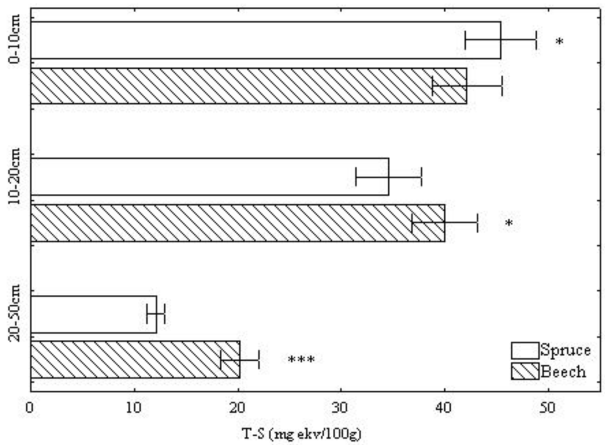

Fig. 6. Sum of acidic cations (T-S), (ANOVA, n=7, level of significance: *p<0.05, ***p<0.001)

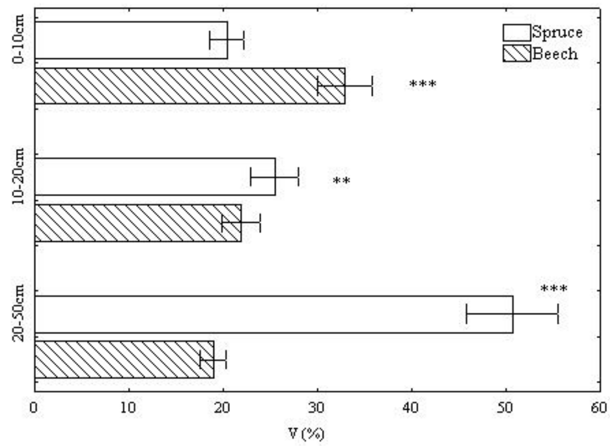

Fig. 7. Saturation of the adsorption complex with bases (V), (ANOVA, n=7, level of significance: **p<0.01, ***p<0.001)

control site (34.58±3.17 : 39.97±3.14, p<0.05). At a depth of 20-50 cm, the sum of acidic cations was also lower in the spruce stand than in the control site (12.07±0.85 : 20.23±1.86, p<0.001) (Fig. 6). In the surface layer of soil (0-10 cm), lower levels of the degree of saturation of the adsorption complex with bases (V%) were noted in the spruce stand (20.38±1.86 : 32.92±2.95, p<0.001) (Fig. 7). As the depth increased, the degree of saturation of the adsorption complex with bases in the spruce stand grew and, in the deeper layers of soil (20-50 cm), it became greater than at the control site in the beech stand (50.65±4.86 : 18.92±1.33, p<0.001).

Based on an analysis of essential nutrients (total N and available P and K), we found that the levels of these elements were lower in the soil in the spruce stand than in the control site, regardless of depth (p<0.001) (Figs. 8, 9, 10). These levels decreased with depth at both sites. In the soil at the spruce stand, the presence of available P was not found at a depth of 10-20 cm or 20-50 cm (Fig. 9).

The C/N ratio at both sites was highest in the litter layer and decreased with the depth of the profile (Fig. 11). A higher C/N ratio was found in the leaf litter at the spruce stand than at the control site

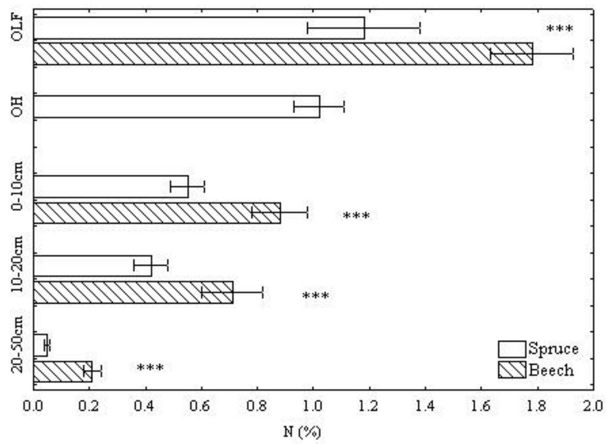

Fig. 8. Nitrogen concentrations (N) (ANOVA, n=7, level of significance: ***p<0.001)

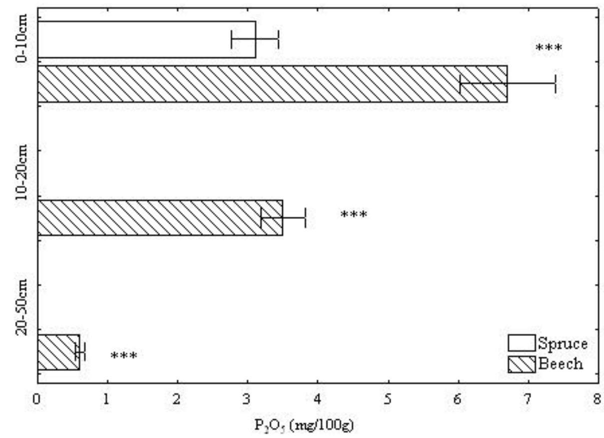

Fig. 9. Concentration of available phosphorus (P2O5) (ANOVA, n=7, level of significance: ***p<0.001)

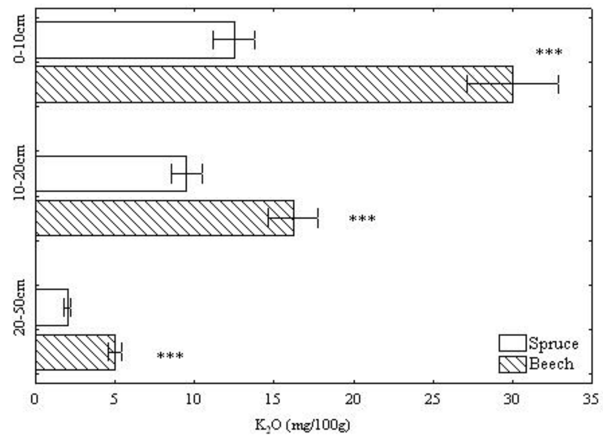

Fig. 10. Concentration of available potassium (K2O) (ANOVA, n=7, level of significance: ***p<0.001)

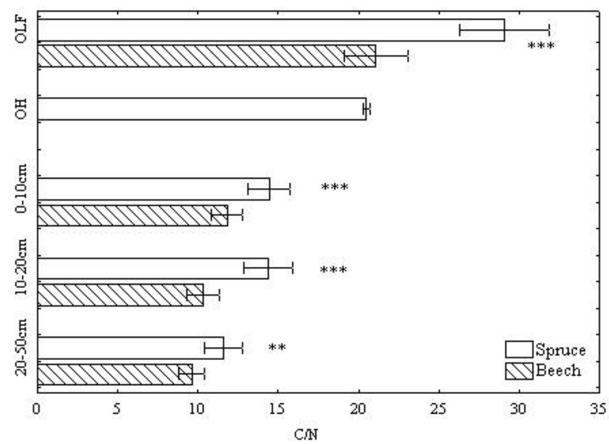

Fig. 11. Ratio of C to N (ANOVA, n=7, level of significance: **p<0.01, ***p<0.001)

(29.08±2.76 : 21.09±1.98, p<0.001), as was the case for all the soil layers examined.

Litter decomposition

The slower decomposition of spruce organic matter in comparison to beech organic matter was observed throughout the entire experiment (Table 2). After six months, the spruce matter had decomposed 7.60±2.69% in comparison to 18.2±0.7% for beech matter (p<0.001). After a year, spruce organic matter had decomposed 23.38±3.21%, as opposed to 32.76±3.57% for beech matter, (p<0.01). An analysis of the decomposition constants (k½ and k) and decomposition prognosis (3/k and 5/k) showed that at each stage of the experiment the organic matter from spruce decomposed more slowly than that of beech (Table 3).

The intensity prognosis for the decomposition of spruce and beech organic matter, on the basis of Olson's decomposition model, showed that it will take 11.499±2.064 years for 95% of spruce leaf litter to decompose as opposed to 7.639±0.951 years for beech organic matter. 19.166±3.440 years will be necessary for 99% of spruce organic matter to decompose, whereas it will take 12.732±1.586 years for the organic matter from beech (Fig. 12).

Table 2. Intensity of the decomposition of beech and spruce organic matter

Plot	6 months M ± SD (%)	F coef.	12 months M ± SD(%)	F coef.
Beech	18.2 ± 0.7	72.537 ***	32.76 ± 3.57	19.073 **
Spruce	7.60 ± 2.69		23.38 ± 3.21	

ANOVA, n=5, values are mean (S.D.), levels of significance: **p<0.01, ***p<0.001

Table 3. Analysis of the decomposition constants (k1/2 and k) and prognosis constants (3/k and 5/k) for the organic matter of beech and spruce

Plot	$k_{½}$ M±SD	F coef.	k M±SD	F coef.	3/k M±SD	F coef.	5/k M±SD	F coef.
Beech	0.402±0.017	11.666 ***	0.398±0.054	1.697 **	7.639±0.951	4.706 **	12.732±1.586	4.707 **
Spruce	0.159±0.058		0.267±0.041		11.499±2.064		19.166±3.440	

ANOVA, n=5, values are mean (S.D.), levels of significance: **p<0.01, ***p<0.001

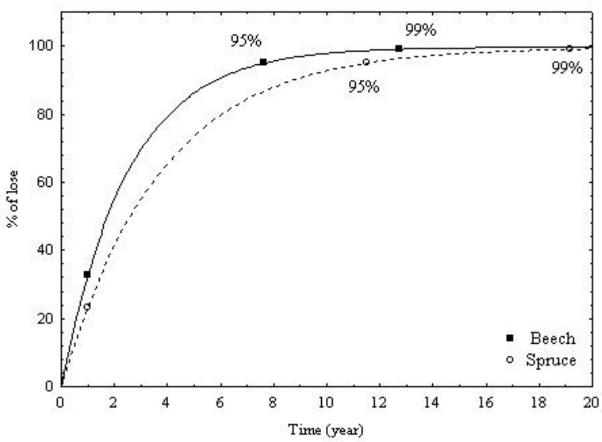

Fig. 12. Model of the process of beech and spruce organic matter decomposition

DISCUSSION

Through phytocoenological research, we established that there was a complete absence of herbaceous plants within the spruce stand. It is known that species in the tree layer influence the composition of herbaceous plants and their abundance and cover in the ground layer. Namely, trees have an effect on the plants in the herbaceous layer by altering the quantity and quality of light (Rackham, 1980; Tinya et al., 2009), the water balance and microclimate (Augusto et al., 2002), soil porosity (Nys et al., 1987), litter characteristics and the chemical characteristics of the soil (Van Oijen et al., 2005; Wulf and Naaf, 2009), as well as through leaching toxic compounds (Djurdjević et al., 2010). The high amount of litter as a consequence of the slow decomposition of spruce litter inhibits the germination of herbaceous plants (Sydes and Grime, 1981), while the spruce's shallow plate-like root system, which mainly extends in the surface layer of soil, affects below-ground competition for water and nutrients (Faliński and Falińska, 1986). The dense planting of spruce and the lack of tending in the form of sanitary cutting and thinning, has led to a reduction in the quantity and quality of light at the research site in the spruce plantation, which further explains the lack of a ground layer of plants in this area. Namely, past research has shown that after the intensive thinning of spruce plantations created in deciduous habitats, ground flora forms that does not differ significantly from the ground flora in deciduous forests (Hill, 1987). The absence of a ground layer of plants in the spruce plantation suggests that the planting of spruce has had a negative effect on the floristic composition, i.e. the biodiversity of this habitat.

An analysis of average soil-moisture levels during the vegetation period showed that the surface layer of soil (0-10 cm) is drier, while soil at a depth of 20-50 cm is moister in the spruce stand than in the control site. This drier surface layer of soil in coniferous forests compared to deciduous ones has been determined by other authors, too (Nihlgard, 1971; Augusto and Ranger, 2001). The degree of interception in coniferous forests is most often greater when compared to deciduous ones and has a positive correlation to the density of the stand (Parker, 1983; Komatsu et al., 2008). This means less precipitation passes through the dense coniferous canopy and reaches the forest soil (Augusto and Ranger, 2001). It should also be added that transpiration begins in conifers in early spring before new leaf growth starts in deciduous trees, meaning the period of transpiration during the year is longer for coniferous trees (Rothe, 1997). In addition, the structure of the root system of these two species has an effect on soil moisture. Spruce, which has a shallow, plate-like root system, takes water from the upper layer of soil and dries it out, while beech draws water from the deeper layers of soil with its strong taproot (Augusto et al., 2002; Schume et al., 2004). All this explains why drier soil is found in the surface layers at the experimental spruce stand site, while the deeper layers of soil are drier in the beech stand (control site).

Soil acidification is a continuous process, the intensity of which is reflected in changes to various soil characteristics, including pH. It is believed that through measuring the substitutional acidity of soil, the impact of some species on soil acidity can be determined much more precisely than by merely measuring active acidity (Alfredson et al., 1998). Some authors highlight the need to analyze the adsorption complex, particularly the degree of saturation of the adsorption complex with bases, as in this way the advance of the acidification process is much more noticeable (Porbeska et al., 2008). Our research highlights a signification reduction in all these parameters in the spruce stand when compared to the beech stand (control). This reinforces the results of earlier research indicating that spruce acts as a markedly acidificatory species, and also that these changes are most pronounced at a soil depth of 0-10 cm (Nihlgard, 1971; Ranger and Nys, 1994; Augusto et al., 2003; Hagen-Thorn et al., 2004; Bagherzadeh et al., 2008; Fabianek et al., 2009; Podrazsky et al., 2009).

The maintenance of certain nutrient reserves represents a fundamental prerequisite for the stability of any ecosystem. Namely, for deciduous trees (beech, oak, birch), the input-output budget of nutrients is in equilibrium, while for conifers (spruce), it is negative (Bergkvist and Folksen, 1995; Fichter et al., 1998; Augusto et al., 2002). This is a consequence of a higher concentration of nutrients in deciduous litter compared to conifers, as well as the fact that the loss of nutrients through leaching is two to four times greater in spruce stands compared to beech (Ranger and Nys, 1994; Rothe, 1997; Rothe et al., 2002; Berger et al., 2009). Deciduous litter contains 10-50% more N and P, and 100-400% more Ca, Mg, and K than coniferous litter (Augusto et al., 2002). We found significantly lower levels of nitrogen and available forms of phosphorus and potassium in the soil at the spruce stand compared to the beech stand (the control), whatever the depth of the examined soil profile ($p<0.001$), which means that the planting of spruce in a beech habitat has led to a reduction in nutrients at the habitat. Besides the factors already mentioned, the higher content of these nutrients in the surface horizon-layer of the soil at the control site is also a result of the dense ground cover of herbaceous plants, which is intensively involved in the cycling of these nutrients (Podrazsky et al., 2009), as well as beech acting as a pump which recycles nutrients from deeper soil horizons through its deeper root system (Berger et al., 2006). The lower potassium content in soil populated by conifers compared to soil populated by deciduous forest has also been confirmed by other authors (Brandentberg et al., 2000; Hagen-Thorn et al., 2004; Bagherzadeh et al., 2008). As far as phosphorus is concerned, general findings on the influence of different species on the levels of this nutrient are quite limited and contradictory (Augusto et al., 2002). Spruce causes an increase in the content of total P in the surface layer of soil (Hagen-Thorn et al., 2004). However, bearing in mind the fact that phosphorus is found in soil in various organic and inorganic forms, the content of available phosphorus does not depend on its total content. The significant decrease in available phosphorus which we found in the spruce stand when compared to the control site coincides with the findings that an increase in soil acidity causes a decrease in the content of available P (Van Breemen et al., 1983; Pare and Bernier, 1989; Carreira et al., 1997).

The content of N and the C/N ratio are important parameters for determining the impact of plant species on the functioning of the ecosystem (Vesterdal et al., 2008). The variability of C/N is closely linked to changes in the composition of plant cover (Lovett et al., 2002), and the C/N ratio in litter represents one of the indicators of the intensity of the organic matter decomposition process in the ecosystem (Swift et al., 1979; Sariyildiz and Anderson, 2003). Our research highlighted a reduction in N content in the soil of the spruce stand in relation to the control site, which led to an increase in the C/N ratio in the spruce stand. Decomposition of organic matter will take place uninhibited if the C/N ratio is less than 25 at the initial organic source (Swift et al., 1979; Waring and Schlesinger, 1985). The higher C/N ratio found in spruce litter when compared to the litter at the control site (29.08 : 21.09) was the first indicator of the future deceleration of organic matter decomposition in the spruce stand.

The slower process of organic matter decomposition in the spruce stand in comparison to the control site, and thereby the slower process of nutrient cycling, was also confirmed by the litter bag experiment. The research that was conducted by studying the transformation of the litter showed that the physicochemical environment, litter quality, and the composition of the decomposer community are the three main factors that influence the rates of decomposition and nutrient cycling (Swift et al., 1979). In addition to the regional climatic influence and the local influence of the litter quality (Meentemeyer, 1984), microenvironmental conditions are also of great importance for the intensity of the decomposition process (soil moisture, pH, temperature, and fertility) (Swift et al., 1979). In habitats at the same altitude and with the same temperature, a greater degree of decomposition was noted in moister habitats (Vitousek et al., 1994). It was also observed that the pH of the litter and soil regulates the decomposition process as it has a direct influence on the microorganism decomposers and an indirect one on the solubility and thus availability of the individual nutrients (Berg and McClaugherty, 2008). Our research shows that the planting of spruce has caused changes in the microenvironmental conditions (a decrease in moisture, pH, and a reduction in nutrients in the soil), which has led to the deceleration of the decomposition of organic matter in the spruce stand. Litter quality, i.e. its chemical composition, influences the decomposition process, as the early phase of decomposition has a positive correlation with initial litter N and P contents, while later decomposition rates are affected more by lignin concentrations in the litter (Berg et al., 1995). Research by Berger et al. (2009) showed that beech litter is characterized by higher nutrient concentrations. On the other hand, spruce needles and organic layers in spruce forests are characterized by their high polyphenol contents (Gallet and Lebreton, 1995), the initial levels of which correlated negatively with decomposition intensity (Loranger et al., 2002).

The slower decomposition of spruce needles led to the accumulation of non-decomposed organic matter and the sequestration of nutrients. This resulted in differences in the fertility of the habitats (lower levels of some essential nutrients at the spruce stand in comparison to the control site), which can lead to further deceleration of the decomposition process. Namely, at habitats with very low levels of available P, Ca and Mg in the top soil, the accumulation of amounts of carbon (humus) is much more pronounced than at sites with higher nutrient amounts (Swift et al., 1979; Vesterdal and Raulund-Rasmussen, 1998). Furthermore, plants that grow at nutrient poor sites are often characterized by greater nutrient resorption, which leads to even poorer litter quality (Rejmankova and Sirova, 2007). The decomposition prognosis for the organic matter of spruce (11.49 years and 19.16 years, respectively) points to the fact that nutrients will be excluded from the cycling process for a lengthy period of time. It should be added that spruce is characterized by modest nutrient requirements when compared to beech and by a shallow root system, and that it will not use nutrients from lower soil layers (Berger et al., 2006), only from the surface layers. Retarded litter decomposition leads to the production of organic acids and also delays the return of base cations to the soil sorption complex (Hagen-Thorn et al., 2004), and might result in further acidification of soil (Mertens et al., 2007). All this points to the fact that this habitat will continue to degrade further in terms of productivity.

CONCLUSION

Based on the results of our research, we can conclude that the forty-year cultivation of spruce has resulted in a reduction in the biodiversity of the beech habitat. The results of the analysis of the surface layer of soil have shown that certain degradation processes began after the planting of the spruce trees. These are reflected above all in the drainage of the soil, acidification, and a decrease in the concentrations of the most important nutrients in the soil. The changes are most pronounced in the surface layer, which is a result of differences in the amount and quality of the litter and the processes that occur on the surface of the forest soil. The planting of conifers has led to a deceleration of the metabolism of the beech ecosystem on Mt. Maljen. This all suggests that the planting of spruce trees should be avoided in habitats where beech is found in optimal ecological conditions.

Acknowledgments - This work was supported by the Ministry of Education and Science of Serbia, grant No 173018. The authors would like to thank Dr. Anka Dinić, a retired Senior Scientist IBISS, for her extensive help during field research.

References

Aber, J.D., Mellilo, J.M. and *C.A. McClaugherty* (1990). Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Bot.* **68**, 2201–2208.

Albers, D., Migge, S., Schaefer, M. and *S. Scheu* (2004). Decomposition of beech leaves (Fagus sylvatica) and spruce needles (Picea abies) in pure and mixed stands of beech and spruce. *Soil Biol. Biochem.* **36** (1), 155-164.

Alfredson, H., Condron, L., Clarholm, M. and *M. Davis* (1998). Changes in soil acidity and organic matter following the establishment of conifers on former grassland in New Zeland. *Forest Ecol. Manag.* **112** (3), 245-252.

Alriksson, A. and *H.M. Eriksson* (1998). Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. *Forest Ecol. Manag.*, **108**, 261–273.

Augusto, L. and *J. Ranger* (2001). Impact of tree species on soil solutions in acidic conditions. *Ann. Forest Sci.* **58**, 47–58.

Augusto, L., Ranger, J., Binkley, D. and *A. Rothe* (2002). Impact of several common tree species of European temperate forests on soil fertility. *Ann. Forest Sci.* **59**, 233-253.

Augusto, L., Dupouey, J.L. and *J. Ranger* (2003). Effects of tree species on understory vegetation and environmental conditions in temperate forests. *Ann. Forest Sci.* **60**, 823-831.

Bagherzadeh, A., Brumme, R. and *F. Beese* (2008). Impact of tree species on nutrient stocks in the forest floors of a temperate forest ecosystem. *Pakistan Journal of Biological Sciences* **11** (9), 1258-1262.

Banković, S., Medarević, M., Pantić, D. and *N. Petrović* (2008). National Forest Inventory of the Republic of Serbia. *Forestry,* Belgrade **3**, 1-16. (in Serbian)

Berbier, S., Gosselin, F. and *P. Balandier* (2008). Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. *Forest Ecol. Manag* **254**, 1-15.

Berg, B., Calvo de Anta, R., Escudero, A., Gärdenäs, A., Johansson, M.B., Laskowski, R., Madeira, M., Mälkönen, E., McClaugherty, C., Meentemeyer, V. and *A. Virzo de Santo* (1995). The chemical composition of newly shed needle litter of Scots pine and other pine species in a climatic transect. X. Long-term decomposition in a Scots pine forest. *Can. J. Bot.* **73**, 1423–1435.

Berg, B., and *C. McClaugherty* (2008). Plant litter: Decomposition, Humus Formation, Carbon Sequestration. Springer-Verlag, Berlin Heidelberg, pp. 338.

Berger, T.W., Köllensperger, G. and *R. Wimmer* (2004). Plant-soil feedback in spruce (*Picea abies*) and mixed spruce–beech (*Fagus sylvatica*) stands as indicated by dendrochemistry. *Plant Soil* **264**, 69–83.

Berger, W.T., Swoboda, S., Prohaska, T. and *G. Glatzel* (2006). The role of calcium uptake from deep soils for spruce (*Picea abies*) and beech (*Fagus sylvatica*). *Forest Ecol. Manag.* **229**, 234-246.

Berger, W.T., Untersteiner, H., Shume, H. and *G. Jost* (2008). Throughfall fluxes in a secondary spruce (*Picea abies*), a beech (*Fagus sylvatica*) and a mixed spruce – beech stand. *Forest Ecol. Manag.* **255**, 605-618.

Berger, W.T., Untersteiner, M.T. and *C. Neubauer* (2009). Nutrient fluxes in pure and mixed stands of spruce (*Picea abies*) and beech (*Fagus sylvatica*). *Plant Soil* **322**, 317-342.

Bergkvist, B. and *L. Folkeson* (1995). The influence of tree species on acid deposition, proton budgets and element fluxes in south Swedish forest ecosystems. *Ecol. Bull.* **44**, 90–99.

Binkley, D. and *D. Valentine* (1991). Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. *Forest Ecol. Manag.* **40**, 13–25.

Bocock, K.L. and *O.J. Gilbert* (1957). The disappearance of leaf litter under different woodland conditions. *Plant Soil* **9**, 179-185.

Bonifacio, E., Santoni, S., Cudlin, P. and *E. Zanini* (2008). Effect of dominant ground vegetation on soil organic matter quality in a declining mountain spruce forest of central Europe. *Boreal Environ. Res.* **13**, 113-120.

Brandtberg, P.O., Lundkvist, H. and *J. Bengtsson* (2000). Changes in forest-floor chemistry caused by birch admixture in Norway spruce stands. *Forest Ecol. Manag.* **130** (1-3), 253-264.

Carreira, J.A., Harrison, A.F., Sheppard, L.J. and *C. Woods* (1997). Reduced soil P availability in a Sitka spruce (*Picea sitchensis* (*Bong*) *Carr*) plantation induced by applied acid-mist: Significance in forest decline. *Forest Ecol. Manag.* **92**, 153-166.

Derome, J., Lindroos, A. and *M. Lindgren* (2001). Soil acidity parameters and defoliation degree in six Norway spruce stands in Finland. *Water Air Soil Poll.* **1**, 169–186.

Dinić, A., Pavlović, P., Mitrović, M., Djurdjević, L. and *O. Kostić* (2001). The effects of the spruce silviculture on the beech forest habitat on Maljen Mt. In Western Serbia. In: *Proceedings of International Conference: Forest Research: A Challenge for an Integrated European Approach*, Vol. II, (Ed. K. Radouglu), 559-565, Thessaloniki, Greece.

Djurdjević, L., Mitrović, M. and *P. Pavlović* (2010). The effect of phenolic compounds on soil properties. In: *Soil Phenols* (Eds. A. Muscolo, and M. Sidari), 31-62. Nova Science Publishers, New York, USA.

Doleman, P. and *H. Eijsackers* (2004). Vital soil: function, value and properties. Elsevier, Amsterdam, p. 358.

Egner, H., Riehm, H. and *W.R. Doming* (1960). Untersuchungen uber die chemishe bodenanalyse als grundlage fur die beurteilung des nahrstoffzustandes der boden. II. Chemische extraktions-methoden zu phosphor – and kalimbestimmung kungl. Lantbrukshoegsk. *Ann.* **26**, 204-209.

Fabianek, T., Menšik, L., Tomaškova, I. and *J. Kulhavy* (2009). Effects of spruce, beech and mixed commercial stand on humus conditions of forest soils. *J. For. Sci.* **5** (3), 119-126.

Facelli, J.M. and *S.T.A. Pickett* (1991). Plant litter: its dynamics and effects on plant community structure. *Bot. Rev.* **57**(1), 1-32.

Faliński, J.B. and *K. Falińska* (1986). Vegetation dynamics in temperate lowland primeval forests. Ecological studies in Bialowieza forest. Geobotany 8. Junk, Dordrecht, NL.

Fichter, J., Dambrine, E., Turpault, M.P., and *J. Ranger* (1998). Base cation supply in spruce and beech ecosystems of the Strengbach catchment (Vosges mountains, N-E France). *Water Air Soil Poll.* **105**, 125–148.

Gallet, C. and *P. Lebreton* (1995). Evolution of phenolic patterns in plants and associated litters and humus of a mountain forest ecosystem. *Soil Biol. Biochem.* **27**, 157-165.

Hagen-Thorn, A., Callesen, I., Armolaitis, K. and *B. Nihlgard* (2004).The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. *Forest Ecol. Manag.* **195**, 373-384.

Hill, M.O. (1987).Opportunities for vegetation management in plantation forest. In: *Environmental aspects of plantation forestry in Wales*, (Ed. J.E.G. Good), 64–69. Institute of Terrestrial Ecology, UK.

Javorka, S. and *V. Csapody* (1975). Ikonographie Der Flora Des Südöstlichen Mitteleuropa. Akademiai Kiadó, Budapest.

Josifović, M. (1970-1980). The Flora of the Socialist Republic of Serbia I-X, Serbian Academy of Science and Arts, Belgrade. (in Serbian)

Jovanović, B., Stojanović, Lj. and *N. Jović* (1983). Some thoughts and terms connected to converting low and degraded forests in silvicultural form. *Forestry*, Belgrade **2**, 3-13. (in Serbian)

Klimo, E., Materna, J., Lochman. V. and *J. Kulhavy* (2006). Forest soil acidification in the Czech Republic. *J. For. Sci.* **52**, 14-22.

Klinka, K., Green, R.N., Trowbridge, R.L. and *L.E. Lowe* (1981). Taxonomic classification of humus forms in ecosystems of British Columbia. First approximation. Land Management Report 8, Ministry of Forests, Province of British Columbia, Vancouver, Canada 54 p.

Komatsu, H., Kume, T. and *K. Otsuki* (2008). The effect of converting a native broadleaved forest to a coniferous plantation forest on annual water yield: a paired-catchment study in northern Japan. *Forest Ecol. Manag.* **255**, 880–886.

Kostić, O. (2007). The influence of a monoculture of spruce and Douglas fir on pedogenesis and soil characteristics on Mt.

Maljen. Master's thesis. Faculty of Forestry, Belgrade University, Belgrade. 1-136. (in Serbian)

Kuzyakov, Y. and *G. Domanski* (2000). Carbon input by plants into the soil. Review. *J. Plant Nutr. Soil Sci.* **163**, 421–431.

Loranger, G., Ponge, J.F., Imbert, D. and *P. Lavelle* (2002). Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. *Biol. Fert. Soils* **35**, 247–252.

Lovett, G.M., Weathers, K.C. and *M.A. Arthur* (2002). Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. *Ecosystems* **5**, 712–718.

Medarević, M., Banković, S. and *D. Pantić* (2003). The condition of beech forests in Serbia. Special issue: Managing beech forests. *Forestry*, Belgrade **1-2**, 5-23. (in Serbian)

Meentemeyer, V. (1984). The geography of organic decomposition rates. *Ann. Assoc. Am. Geogr.* **74**, 551-560.

Mertens, J., Van Nevel, L., De Schrijver, A., Piesschaert, F., Oosterbean, A., Tack, F.M.G. and *K. Verheyen* (2007). Tree species effect on the redistribution of soil metals. *Environ. Pollut*. **149**, 173-181.

Moukoumi, J., Munier-Lamy, C., Berthelin, J. and *J. Ranger* (2006). Effect of tree species substitution on organic matter biodegradability and mineral nutrient availability in temperate topsoil. *Ann. Forest Sci*. **63**, 763-771.

Neirynck, J., Mirtcheva, S., Sioen, G. and *N. Lust* (2000). Impact of *Tilia platyphyllos* Scop., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Quercus robur* L. and *Fagus* sylvatica L. on earthworm biomass and physicochemical properties of loamy topsoil. *Forest Ecol. Manag.* **133**, 275-286.

Nihlgard, B. (1971). Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. *Oikos* **22**, 302–314.

Norden, U. (1994). Influence of tree species on acidification and mineral pools in deciduous forest soils of South Sweden. *Water Air Soil Poll.* **76**, 363–381.

Nys, C., Bullock, P. and *A. Nys* (1987). Micromorphological and physical properties of a soil under three different species of trees. *Proceedings of the VIIth international working meeting on soil micromorphology* (Paris, July 1985), 459-464.

Olson, J.S. (1963). Energy storage and balance of producers and decomposer in ecological systems. *Ecology* **44**, 322-331.

Oulehle, F., Hofmeister, J. and *J. Hruška* (2007). Modelling of the long-term effect of tree species (Norway spruce and European beech) on soil acidification in the Ore Mountains. *Ecol. Modell.* **204**, 359-371.

Oulehle, F., Hleb, R., Houska, J., Samonil P., Hofmeister J. and *J. Hruška* (2010). Anthropogenic acidification effects in primeval forests in the Transcarpathian Mts. Western Ukraine. *Sci. Total Environ.* **408**, 856-864.

Pandey, R.R., Sharma, G., Tripathi, S.K. and *A.K. Singh* (2007). Litterfall, litter decomposition and nutrient dynamics in a subtropical natural oak forest and managed plantation in north-eastern India. *Forest Ecol. Manag*. **240**, 96–104.

Pare, D. and *B. Bernier* (1989). Phosphorus fixing potential of Ah and H horizons subjected to acidification. *Can. J. Forest Res.* **19**, 132–134.

Parker, G.G. (1983). Throughfall and stemflow in the forest nutrient cycle. *Adv. Ecol. Res*. **13**, 57–133.

Pavlović, P. (1998). Pedological components of the metabolism of some forest communities on Mt. Maljen. Doctoral dissertation, Faculty of Biology, Belgrade University, Belgrade. 1-268. (in Serbian)

Pigott, C.D. (1989). The growth of lime *Tilia cordata* in an experimental plantation and its influence on soil development and vegetation. *Quat. J. For*. **83**, 14-24.

Podrazsky, V., Remeš, J., Hart, V. and *W.K. Moser* (2009). Production and humus form development in forest stands established on agricultural lands – Kostelec nad Černymi lesy region. *J. For. Sci.* **55** (7), 299-305.

Polyakova, O. and *N. Billor* (2007). Impact of deciduous tree species on litterfall quality, decomposition rates and nutrient circulation in pine stands. *Forest Ecol. Manag*. **253**, 11–18.

Ponomareva, V.V. and *T.A. Plotnikova* (1975). Simultaneous determination of overall C and N content in peat soils using the Anstet method, modification Ponomareva and Nikolaeva. In Methods of determination of humus content and composition in soils (mineral and peat) in Russia. Federal Academy of Agricultural Sciences V. I. Lenin. Central Pedology Museum V.V. Dokucaev, Leningrad, 79–83.

Porbeska, G., Ostrowska, A. and *J. Borzyszkowski* (2008). Changes in the soil sorption complex of forest soils in Poland over the past 27 years. *Sci. Total Environ.* **399**, 105-112.

Rackham, O. (1980). Ancient woodland; its history, vegetation and uses in England. Edward Arnold, London, UK.

Ranger, J. and *C. Nys* (1994). The effect of spruce (Picea abies Karst.) on soil development: an analytical and experimental approach. *Eur. J. Soil Sci.* **45**, 193–204.

Raulund-Rasmussen, K. and *H. Vejre* (1995). Effect of tree species and soil properties on nutrient-immobilization in the forest floor. *Plant Soil* **168/169**, 345–352.

Rejmankova, E. and *D. Sirova* (2007). Wetland macrophyte decomposition under different nutrient conditions: relationships between decomposition rate, enzyme activities and microbial biomass. *Soil Biol. Biochem*. **39**, 525-538.

Ritter, E., Vesterdal, L. and *P. Gundersen* (2003) Changes in soil properties after afforestation of former intensively managed soils with oak and Norway spruce. *Plant Soil* **249**, 319–330.

Rothe, A. (1997). Influence of tree species composition on rooting patterns, hydrology, elemental turnover and growth in a mixed spruce–beech stand in Southern Germany Höglwald. Ph.D. Thesis, University of Munich Forstliche Forschungsberichte München, Bd. 1-163.

Rothe, A., Huber, C., Kreutzer, K. and *W. Weis* (2002). Deposition and soil leaching in stands of Norway spruce and European beech: results from the Höglwald research in comparison with other European case studies. *Plant Soil* **240**, 33-45.

Sariyildiz, T. and *J.M. Anderson* (2003). Interactions between litter quality, decomposition and soil fertility: a laboratory study. *Soil Biol. Biochem*. **35**, 391-399.

Schume, H., Jost, G. and *H. Hager* (2004). Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *J. Hydrol*. **289**, 258–274.

Simakov, V.N. (1957). The use of phenylanthranilic acid in the determination of humus by Tyurins method. *Pochvovedenie,* **8**, 72-73.

Swift, M.J., Heal, O.W. and *J.M. Anderson* (1979). Decomposition in terrestrial ecosystems. (Eds. D.J. Anderson, P. Greig-Smit and F.A. Pitelka) 1-372. Blackwell, Oxford.

Sydes, C. and *J.P. Grime* (1981). Effects of tree leaf litter on herbaceous vegetation in deciduous woodland I: Field investigations. *J. Ecol.* **69**, 237–248.

Tinya, F., Marialigeti, S., Kiraly, I., Nemeth, B. and *P. Odor* (2009). Restoration of oak forest: effects of former arable land use on soil chemistry and herb layer vegetation. *Scand. J. Forest Res.* **23**, 513-521.

Van Breemen, N., Mulder, J. and *C.T. Driscoll* (1983). Acidification and alkalinization of soils. *Plant Soil* **75**, 283–308.

Van Oijen, D., Feijen, M., Hommel, P., den Ouden, J. and *R. de Waal* (2005). Effects of tree species composition on within-forest distribution of understorey species. *Appl. Veg. Sci.* **8**, 155–166.

Vesterdal, L. and *K. Raulund-Rasmussen* (1998). Forest floor chemistry under seven tree species along a soil fertility gradient. *Can. J. Forest Res*. **28**(11), 1636–1647.

Vesterdal, L., Ritter, E. and *P. Gundersen* (2002). Change in soil organic carbon following afforestation of former arable land. *Forest Ecol. Manag*. **169**, 137-143.

Vesterdal, L., Schmidt, K.I., Callesen, I., Nilsson, O.L. and *P. Gundersen* (2008). Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecol. Manag*. **255**, 35-48.

Vitousek, P.M., Turner, D.R., Parton, W.J. and *R.L. Sanford* (1994). Litter Decomposition on the Mauna Loa Environmental Matrix: Hawaii. Patterns, Mechanisms, and Models. *Ecology* **75**, (2), 418-429.

Wang, Q., Wang, S. and *Y. Huang* (2008). Comparisons of litterfall, litter decomposition and nutrient return in a monoculture Cunninghamia lanceolata and a mixed stand in southern China. *Forest Ecol. Manag.* **255**, 1210-1218.

Waring, H.R. and *H.W. Schlesinger* (1985). Forest Ecosystems. Concepts and Management. Academic Press, San Diego, 1-340.

Weshoff, V. and *E. Van der Maarel* (1973). The Braun-Blanquet approach. In: *Handbook of vegetation science* V. Classification and ordination of communities. (Ed. R. H. Whittaker) 617-726. Junk, The Hague.

Wieder, R.K. and *G.E. Lang* (1982). A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* **63**, 1636-1642.

Wulf, M. and *T. Naaf* (2009). Herb layer response to broadleaf tree species with different leaf litter quality and canopy structure in temperate forests. *J. Veg. Sci.***20**, 517-526.