134. Jahrgang (2017), Heft 2, S. 99–118

Austrian Journal of Forest Science
Centralblatt für das gesamte Forstwesen

Foliage and fine root litter: A comparative study in young, natural regenerated stands of European beech and Norway spruce

Eintrag toter Biomasse aus Belaubung und Feinwurzeln: Eine vergleichende Studie in jungen, natürlich verjüngten Beständen aus Rotbuche und Fichte

Bohdan Konôpka [1,2]

Keywords: *Fagus sylvatica, Picea abies*, fine root necromass, aboveground litter, carbon and nitrogen content

Schlüsselbegriffe: *Fagus sylvatica, Picea abies*, tote Biomasse der Feinwurzeln, oberirdische Biomasse, Gehalt an Kohlenstoff und Stickstoff

Abstract

Our research was conducted in young growth stands of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) with similar stand characteristics. The aim of the work was to estimate quantity of aboveground (thin brunches, buds and foliage) and belowground (fine roots) necromass as well as annual input of aboveground and belowground litter. Moreover, to quantify carbon (C) and nitrogen (N) content within these compartments. Aboveground litter-fall was collected over five years (2009 – 2013) and annual input of necromass was estimated. At the same time, stocks of fine

[1] National Forest Centre, Forest Research Institute Zvolen, T.G. Masaryka 22, 960 92 Zvolen, Slovak Republic, Corresponding author: Bohdan Konôpka (bkonopka@nlcsk.org)
[2] Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 176, 165 21 Praha 6 – Suchdol, Czech Republic

root biomass and necromass at soil depth 0 – 30 cm were quantified by means of soil coring. Fine root production was measured by in-growth bags. Then fine root mortality was calculated with regard to differences between biomass stocks in consecutive years and annual production. Our study showed that annual aboveground and belowground litter together represented a large proportion of C input (nearly 3.0 t of C ha^{-1} per year in beech stand and 2.5 t ha^{-1} per year in spruce stand). Aboveground litter accumulated on the ground was significantly larger in spruce than in beech, however there was more aboveground necromass input in the beech stands. This is most likely due to different decomposition rate between the species and also residence time of C in aboveground litter. On the other hand, fine root necromass stock as well as necromass input of fine roots were similar in both species. As for ratio between quantities of fine roots to aboveground parts, higher value was found for necromass input than necromass standing stock in both species. These differences can be explained by faster decomposition of fine root necromass than aboveground necromass.

Zusammenfassung

Unsere Forschung wurde in Jungwuchsbeständen der Rotbuche (*Fagus sylvatica*) und der Fichte (*Picea abies*) mit ähnlichen Eigenschaften durchgeführt. Das Ziel der Arbeit war es die Menge des Eintrages an oberirdischer (dünne Zweige, Knospen und Belaubung) und unterirdischer (Feinwurzeln) Biomasse der aktuellen Situation ebenso wie der jährlichen Akkumulation an oberirdischer und unterirdischer toter Biomasse zu bestimmen. Darüber hinaus war es Ziel, den Gehalt an Kohlenstoff (C) und Stickstoff (N) in diesen Bestandteilen zu quantifizieren. Der oberirdische Anfall an Biomasse wurde über fünf Jahre (2009 – 2013) hinweg gesammelt und die jährliche Rate der Produktion an Biomasse wurde bestimmt. Im gleichen Zeitraum wurde die lebende und tote Biomasse aus Feinwurzeln in einer Bodentiefe von 0 – 30 cm mittels Bodenkernbohrungen quantifiziert. Darüber hinaus wurde die Produktion an Feinwurzeln durch den Einwuchs der Feinwurzeln in Taschen im Boden gemessen. Dann wurde die Mortalität der Feinwurzeln aus den Differenzen zwischen der Biomasse des aktuellen Bestandes in aufeinanderfolgenden Jahren und der Produktion berechnet. Unsere Studie zeigte dass der jährliche gemeinsame Eintrag an oberirdischer und unterirdischer toter Biomasse einen großen Anteil am Eintrag an Kohlenstoff entspricht (3.0 t an C ha^{-1} im Buchenwald und 2.5 t ha^{-1} im Fichtenwald). Oberirdischer Eintrag, der auf dem Boden akkumuliert war, war signifikant höher in Fichtenwäldern als in Buchenwäldern, jedoch war die oberirdische tote Biomasse in den Buchenbeständen höher. Dies kommt sicherlich von unterschiedlichen Zersetzungsraten zwischen den Arten und auch die unterschiedlichen Verbleibzeit von Kohlenstoff in der oberirdischen Streu. Andererseits war die tote Biomasse aus Feinwurzeln ebenso wie der Eintrag aus toter Biomasse aus Feinwurzeln ähnlich für beide Arten. In Bezug auf das Verhältnis der Menge an Feinwurzeln zu den oberirdischen Bestandteilen wurde

ein höherer Wert für den Eintrag an toter Biomasse als für die aktuelle Situation der Menge an toter Biomasse für beide Arten gefunden. Diese Differenzen können erklärt werden durch eine schnellere Zersetzung der Biomasse der Feinwurzeln als die der oberirdischen Biomasse.

1. Introduction

Changing climate conditions effect both natural and artificial environments, adding stress to already fragile ecosystems. The main contributors to these changes are emissions of greenhouse gases into the atmosphere, deforestation and deterioration of the carbon balance in natural ecosystems (e.g. Schelhaas and Nabuurs, 2001). Forests constitute the most important terrestrial ecosystem contributing to the global carbon cycle and to carbon sequestration (e.g. Dixon et al., 1994). Thus, forest ecosystems are not just passive receptors of the effects of climate change, but through several feedback loops, influence this phenomenon (Bonan, 2008) themselves.

In forest ecosystems, five main compartments in terms of carbon pools and cycling are usually recognized: aboveground biomass, belowground biomass, dead wood, litter layer and soil organic matter. Brunner and Godbold (2007) show that forests of central Europe bind approximately 110 tons of carbon per hectare (t C ha^{-1}) in tree biomass, about 27 tons of which is stored belowground as root biomass. Forest soils store a further 96 t C ha^{-1} in their mineral fraction. As for biomass, trees comprise of components which differ not only in their specific physiological tasks and anatomical properties but also in residence time of C contained within the organs. While woody parts, i.e. branches, coarse roots and stem, store C for a long period, foliage and fine roots cycle C within a few months to years. In fact, much of the previous research focuses on the role of aboveground litter (particularly foliage) when considering the process of C and N cycling (e.g. Scott and Binkley, 1997; Valentini et al., 2008; Takahashi et al., 2010; Xu et al., 2013). In contrast, few studies include information on belowground (prevailingly fine roots) litter in these processes (e.g. Sulzman et al., 2005; Leppälammi-Kujansuu et al., 2014).

This lack of information about fine roots, including stock, production and especially mortality (i.e. litter input) is due to their role in biochemical cycles being undervalued as well as the laborious procedures required for measurements. Helmisaari et al. (2002) showed that fine roots contributed between 43 – 60% of the net primary production and between 2 – 15% of the total tree biomass in pine plantations in Finland. Similarly, fine roots account for >40% of the total net primary production but only 3% of standing stock in a mature pine stand in Belgium (Curiel Yuste et al., 2005). Although fine roots are commonly negligible in terms of tree standing biomass, they are crucial for the quantification of primary production and therefore in the assessment of the forest carbon cycle (e.g. Tateno et al., 2004). Brunner and Godbold (2007) estimated that for the average conditions of Central Europe, 4.4 t of C ha^{-1} enter the forest soil each year, about 20% are contributed by fine roots. Recent meta-analysis of litter input in a variety of forest types showed that root litter quantity often prevails over leaf litter-fall (Freschet et al., 2013).

Slovakia has a high forest cover of nearly 45% and belongs to the European countries with a positive carbon balance in the terrestrial ecosystems (Janssens et al., 2004). European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) are the most common tree species in the country. While beech forests naturally occur at altitudes between ca. 300 and 1300 m a.s.l., spruce forest naturally grow at altitudes above ca. 600 m a.s.l. up to the tree line. The species frequently make up mixed forest stands (Pagan and Randuška, 1987). Spruce is more sensitive to drought stress (an inherent phenomenon of climate change) and on many sites appears allochtonously, beech seems to be a more resilient, therefore likely prospective species in Slovakia under current and future changing climate conditions (Minďáš and Škvarenina, 2003). Moreover, spruce having a shallow root system, is prone to and frequently damaged by storms as well as susceptible to a variety of pathogens e.g. Spruce Bark Beetle (*Ips typographus*) (Kunca et al., 2015).

The aim of this paper is to estimate the quantity of aboveground (thin branches, buds and foliage) and belowground (fine roots) necromass as well as the annual input of aboveground and belowground litter. Moreover, this study aims at quantifying C and N content of these compartments and elaborating inter-specific differences.

2. Material and methods

Research was conducted from 2009 to 2013 at Vrch Slatina (48° 38'' 50' N, 19° 36'' 12' E), approximately 10 km north-east of Hriňová, Slovakia. The site is located ca 960 m a.s.l. in the westernmost part of the Veporské Hills. Bedrock is prevailingly composed of granodioirite and the soil is Eutric Cambisol with a low percentage of coarse material. The texture is mostly sandyloam. The C/N ratio in the upper 10 cm of soil is about 17, pH (in $CaCl_2$) was 4.5, 5.3 and 4.5 at the depths of 0 – 10 cm, 10 – 35 cm and 35 – 65 cm, respectively. The site is situated within the ecological optimum range for beech growth and the southernmost frontier of naturally occurring spruce in Slovakia (for a detailed site description see also Konôpka et al., 2013).

Our measurements were done in nearly even-aged forest stands originating from natural regeneration and are composed exclusively of beech or spruce. Both stand types prevailingly developed after selective cuts between 1995 and 1996 under few old seed-producing trees. Then, the old trees were cut between 1996 – 1998. The beech and spruce stands are neighboring, and amongst the forest complexes are open areas colonized by grasses and herbs, dominated by bushgrass (*Calamogrostis* *epigejos*).

In early spring of 2009, five circular plots in beech and five plots in spruce were established and all trees inside the plots were marked with metal labels. Plots were established with radii between 0.7 and 1.0 m in order to measure stand density and included between 30 and 50 trees per plot. The trees were measured in March of each year for height and diameter at ground level (d_0 hereafter). We could not use the standard measurement of diameter at 130 cm (dbh) because some trees were shorter than this height. The recorded tree parameters were used to calculate basic stand characteristics (see Pajtík et al., 2013).

In March 2009, 30 plastic litter trays (35 x 35 cm) were placed within the stands with 3 litter trays located on each circular plot. The litter trays were 20 cm deep and thus, they were able to intercept aboveground litter from nearly all trees, including small ones. The litter was collected once every three months, ending in March 2014. The harvested litter was packed in paper bags, transported to the laboratory and sorted into two groups: foliage and other litter (that covered thin branches and buds) and were oven-dried at 95°C to achieve constant weight. Weight was measured with a precision ± 0.1 gram. The annual sum of litter collected was calculated for individual litter trays and the mean litter amount was expressed for both beech and spruce stands. Moreover, subsamples from the litter collected in 2011 were subject to chemical analyses (dry combustion method performed by elementary analyzer Flash EA 1112) in order to measure C and N contents. In summer 2011, samples of litter accumulated on the ground (15 square areas with 50 x 50 cm in both beech and spruce stands) were collected, oven-dried, weighed and C and N content was analyzed.

Estimation of fine root quantities in beech and spruce stands was done using two methods: (i) soil cores – aiming at establishing current stock and (ii) in-growth bags – to estimate annual production. Thus, each year between 2009 – 2013 (end of March), 15 soil cores from beech and 15 from spruce stands were randomly sampled from across the stands. A 30 cm (length), 7 cm (diameter) iron auger was used to collect the soil cores. The cores were split into three 10-cm-long columns and inserted in plastic bags. The samples were stored in a deep-freezer until further processing. All fine roots (diameter up to 2 mm) were separated by using tweezers. Roots over 2 mm and those which did not originate from beech or spruce (bushes and herbs) were excluded. The fine roots of target species were sorted as living (biomass) and dead (necromass). In order to distinguish live roots from dead, characteristics like: color, mechanical properties of tissues, cohesion between periderm and cortex, status of structure and morphology in root clusters were used. The sorted fine roots were carefully washed with distilled water and placed in paper envelopes, dried in an oven at 85°C for 24 hours. The dry roots were weighed with a precision of 10^{-4} grams. The weight of fine roots was expressed for soil depth 0 – 10 cm, 10 – 20 cm, and 20 – 30 cm and up-scaled into tons per hectare of stand area. In 2011, samples of fine root biomass and necromass were analysed for C and N contents. While chemical properties of fine root biomass were used to C and N quantities in current year litter (input), those of fine root necromass were used for C and N values fixed in the mass of dead fine roots.

In-growth bags were cylindrically shaped plastic nets with a mesh size of 2 x 2 mm, an inner diameter of 7 cm and a length of 30 cm. Each year in March, 30 in-growth bags were located within the beech stand and 30 bags in the spruce stand and were inserted inside 30 cm deep holes drilled using an auger. The bags were filled with quartz sand. Further, half the bags (15 pieces in beech and 15 in spruce stands) were harvested at the end of the vegetation period of the same year and half were collected at the end of the vegetation period of the consecutive year (1-year and 2-year bags, hereafter). The in-growth bags were inserted in plastic sacks and frozen. In-growth bags were analyzed similar to the soil cores however, and provided data on living fine roots only with the biomass of fine roots representing the approximate annual production of roots in the ecosystem. From previous experiments it was observed that beech and spruce have contrasting strategies in terms of colonizing new competition-free volume, therefore two series of in-growth bags were applied. The first approach was based on 1-year in-growth bags only. The second approach used the difference between fine root biomass production in 1-year bags and 2-year bags. Definitive production of fine roots was calculated as an average value for both methods.

Parallel data on fine root biomass and production in the period 2010 – 2013 enabled the calculation of the mortality of fine roots between 2010 – 2012. Under these assumptions, mortality may be calculated as follows:

$$M_x = B_x + P_x - B_{x+1}$$

where: M_x – fine root mortality in the year x,

B_x –biomass stock of fine roots in the year x,

P_x – fine root production in the year x,

B_{x+1} –biomass stock of fine roots in the year x+1.

The combined relationship of inter-annual and inter-specific differences on the studied variables were analyzed by ANOVA. Significant differences were found by Tukey's HDS test (for α = 0.05) and inter-specific differences between variables when the year was not considered as a factor were tested by Student's t-test (α = 0.05). Statistical analyses were performed in JMP 6.0 program (SAS Institute, Cary, NC, USA).

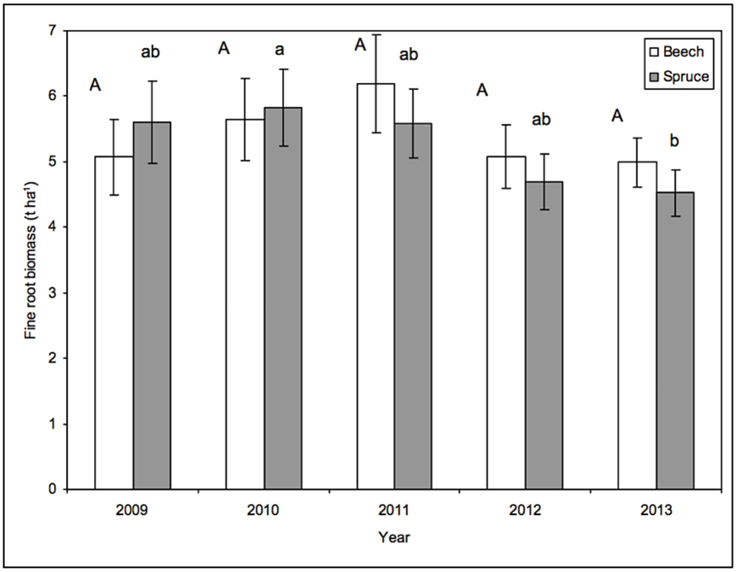
3. Results

In 2009, both beech and spruce stands had very similar characteristics (Table 1). Then, during the 2010 and 2011 variance in the number of trees (in favor of beech) and means stem volume (in favor of spruce) emerged. The most intensive inter-specific differentiation occurred between the years of 2012 and 2013, when the number of trees in the spruce stands were reduced by more than 50% due to competition, but the density of trees in the beech stands dropped by only 12%.

Table 1: Stand characteristics of the European beech and Norway spruce stands within the study period

Species	Stand characteristics	2009	2010	2011	2012	2013
European beech	Number of trees (10^3 ha^{-1})	157	150	136	125	110
	Lorey's tree height (cm)	225	272	323	373	485
	Mean diameter d_0 (cm)	1.89	2.13	2.43	2.67	3.17
	Mean stem volume (cm^3)	233	313	452	595	731
Norway spruce	Number of trees (10^3 ha^{-1})	176	154	134	98	48
	Lorey's tree height (cm)	172	212	242	301	423
	Mean diameter d_0 (cm)	1.88	2.29	2.71	3.23	4.68
	Mean stem volume (cm^3)	225	336	496	860	2212

Biomass stock of fine roots fluctuated slightly between the years (Fig. 1a). Minimum fine root biomass in beech stands (4.99 t ha^{-1}) was recorded in 2013, and the maximum biomass (6.19 t ha^{-1}) was observed in 2011. As for spruce stand, while the minimum fine root biomass (4.53 t ha^{-1}) was recorded in 2013, the maximum amount observed (5.83 t ha^{-1}) was in 2010. Inter-annual differences were not statistically significant except for the contrast in spruce fine root biomass between 2010 and 2013. No significant inter-specific differences were found within individual years. Quantity of necromass (Fig. 1b) of fine roots was approximately 7 times less than that observed for biomass in both species. In the beech stand, while minimum necromass (0.61 t ha^{-1}) was observed in 2012, maximum necromass (0.97 t ha^{-1}; statistically significant differences) was recorded in 2010. A similar situation was observed in the spruce stand, where minimum necromass (0.70 t ha^{-1}) was recorded in 2012 and maximum (1.13 t ha^{-1}) in 2010 (the minimum and maximum values were significantly different).



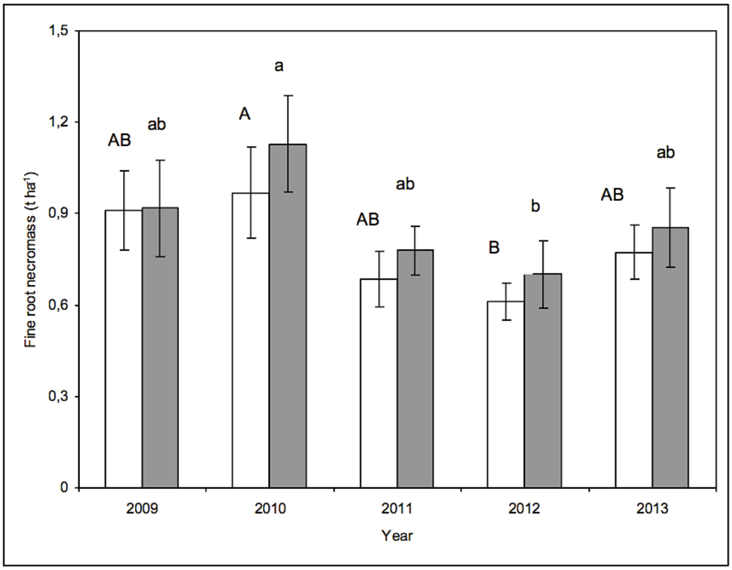


Fig. 1: Stocks of fine root biomass (upper graph) and fine root necromass (lower graph) in beech and spruce stands, by years (different letters, specifically capitals for beech and small for spruce, indicate significant inter-annual differences in each species; Tukey's HDS test on α = 0.05). Error bars show standard deviations.

In-growth bags indicated different fine root production in the first year with beech producing significantly more (between 1.42 and 2.73 t per ha and year) than spruce (between 0.58 and 0.86 t per ha and year; Table 2). On the other hand, during the second year, fine root production was more in spruce than beech. Thus, fine roots produced during the observation period of two-year incubation was similar in both species (between 2.39 and 4.23 t per ha and year in beech and 2.13 and 3.11 t per ha in spruce). The combination of the two approaches for estimation of fine root production provided very similar values for both species. Specifically, annual fine root production varied between 1.11 and 1.63 t per ha in beech and 0.95 and 1.54 t per ha in spruce (no significant inter-specific differences were found in the individual years). Similarly, fine root mortality showed about similar values for both species in the years of observation with the exception of 2010 (1.08 t per ha and year in beech against 1.78 t per ha and year in spruce). At the same time, the ratio between fine root production and mortality differed between the individual years of 2010, 2011, and 2012, more in beech (between 0.50 and 1.51) than in spruce (0.51 and 0.89). During the three years of 2010 – 2012, accumulated necromass of fine roots (4.76 t ha^{-1} in beech and 5.18 t ha^{-1} in spruce) prevailed over the accumulated fine root biomass (4.10 t ha^{-1} in beech and 3.88 t ha^{-1} in spruce).

*Table 2: Fine root biomass within in-growth bags incubated for 1 and 2 years in the beech and spruce stands as well as calculated fine root production and mortality (units: t ha^{-1}; * indicates significant differences between beech and spruce stand in the specific year; Tukey's HDS test on α = 0.05)*

Year	Fine root biomass (1 year-bag)		Fine root biomass (2 years-bag)		Fine root production		Fine root mortality	
	Beech	Spruce	Beech	Spruce	Beech	Spruce	Beech	Spruce
2009	2.731	*0.863	–	–	–	–	–	–
2010	1.760	*0.822	4.232	3.110	1.629	1.537	1.080	*1.779
2011	1.419	*0.580	2.551	2.132	1.112	0.951	2.221	1.847
2012	1.748	*0.601	2.389	2.749	1.362	1.388	1.454	1.554
2013	1.952	*0.708	3.150	2.563	1.467	1.230	–	–

Chemical analyses showed that both C and N contents were slightly higher in spruce than in beech stands in the aboveground litter trays, aboveground litter accumulated on ground, as well as fine root biomass and necromass (Table 3). Highest concentrations of C were found in fine root biomass (49.1% in beech and 52.2% in spruce), the lowest C values were recorded in aboveground litter accumulated on the soil (43.4% and 46.3% in beech and spruce, respectively). While the highest concentration of N

(1.87% in beech and 2.03% in spruce) was recorded in fine root necromass, and the lowest values of N (1.35% and 1.79%) were observed in current year`s aboveground litter.

Table 3: Carbon and nitrogen contents (%) of the individual tree components in the beech and spruce stands in 2011 (indicates significant differences between beech and spruce stand by component; Student's t-test on α = 0.05)*

Element content	Stand	Aboveground litter (accumulated)	Aboveground litter (current year)	Fine root biomass	Fine root necromass
Carbon	Beech	43.4	47.9	49.1	46.2
	Spruce	46.3	51.7	52.2	47.5
Nitrogen	Beech	1.42	1.35	1.83	1.87
	Spruce	*1.85	*1.79	1.95	2.03

As for stock of aboveground necromass (status for summer 2011; Table 4) much larger quantities accumulated in the spruce (11.53 t ha^{-1}) than in the beech (7.52 t ha^{-1}) stand. On the other hand, fine root necromass was similar in both tree species (0.79 t ha^{-1} in beech and 0.88 t ha^{-1} in spruce expressed by the mean for the period 2009 – 2013). Therefore, the aboveground litter was much more (nearly 10 times in beech and 13 times in spruce, see also Fig. 2) than fine root necromass in the soil. Surprisingly, while the amount of aboveground litter was larger in spruce than in beech stands, the opposite situation occurred for annual input of aboveground litter (Table 5). While the sum of aboveground litter recorded during the years 2009 – 2013 was 21.94 t ha^{-1} in the beech stand, the quantity in the spruce stand was 15.98 t ha^{-1} (Fig. 3). At the same time, annual input of aboveground necromass (litter) in beech stand was 2.7 times and 1.8 times larger than that of finer root necromass (Table 5). If we consider interspecific differences in necromass input by tree components (foliage, other aboveground litter, fine roots) per year, significant differences were found for all components in 2010 (Table 6). Moreover, litter of other aboveground tree parts significantly prevailed in the beech over the spruce stand in each year. In terms of inter-annul differences in total litter input, the largest (statistically significant) contrast was found in the spruce stand between 2010 and 2011, 3.92 t ha^{-1} against 5.90 t ha^{-1} (Fig. 4).

*Table 4: Stocks of aboveground and belowground necromass in beech and spruce stands (units: t ha^{-1}; *indicates significant differences between beech and spruce stand by tree part; Student's t-test on α = 0.05)*

Stand part	Species	Mass	Carbon	Nitrogen
Aboveground [a]	Beech	7.523	3.265	0.102
	Spruce	*11.527	*5.337	*0.206
Belowground [b]	Beech	0.789	0.365	0.015
	Spruce	0.876	0.416	0.018

[a] - includes foliage, buds, woody parts collected from the ground in summer 2011
[b] - includes dead fine roots - average for necromass determined in the period 2009-2013

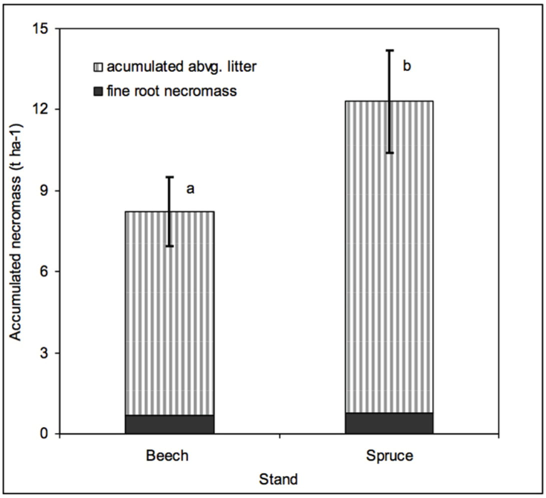


Fig. 2: Necromass stock including aboveground litter and fine roots in 2011 (total necromass was significantly different between beech and spruce stand; Student's t-test on α = 0.05). Error bars show standard deviations for total necromass.

*Table 5: Annual necromass input of aboveground and belowground tree parts in beech and spruce stands (units: t ha^{-1}; * indicates significant differences between beech and spruce stand by tree part; Student's t-test on α = 0.05)*

Stand part	Species	Mass	Carbon	Nitrogen
Aboveground [a]	Beech	4.298	2.059	0.058
	Spruce	*3.196	1.652	0.057
Belowground [b]	Beech	1.585	0.778	0.029
	Spruce	1.727	0.901	0.034

[a] - includes foliage, buds, and thin branches caught up by litter collectors in the period 2009-2013
[b] - includes dead fine roots - average for necromass determined in the period 2010-2012

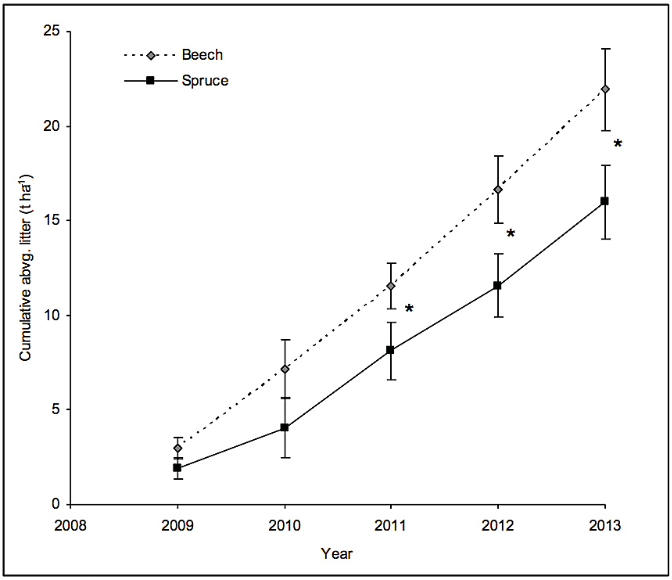
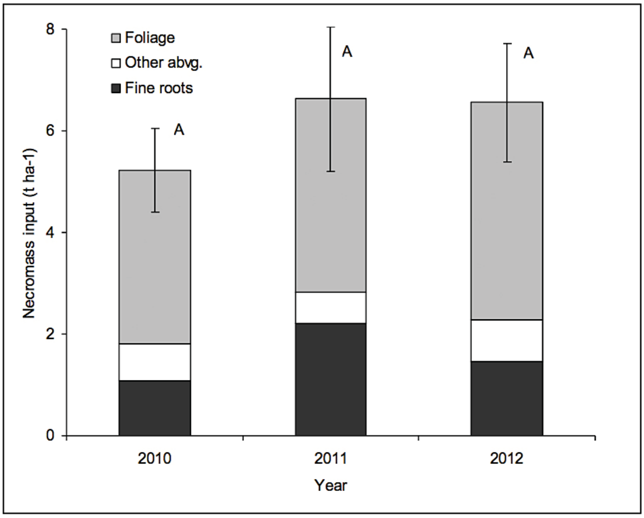


Fig. 3: Cumulative amount of aboveground necromas input during five years in beech and spruce stands (indicates significant differences between beech and spruce stand; Student's t-test on α = 0.05). Error bars show standard deviations for cumulative amount of necromass.*

Table 6: Statistical test for interspecific differences for annual necromass input by tree components in the specific year (indicates significant differences between the beech and spruce stand regarding component and year; Tukey's HDS test on α = 0.05).*

Component against year	2010	2011	2012
Foliage	*	---	---
Other aboveground	*	*	*
Fine roots	*	---	---
Together	*	---	---



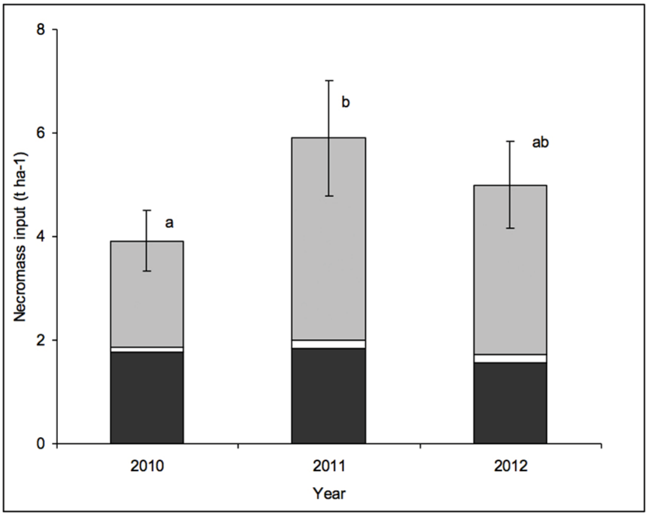


Fig. 4: Necromass input including aboveground litter and fine roots (different letters, specifically capitals for beech and small for spruce, indicate significant inter-annual differences in total input; Tukey's HDS test on α = 0.05) in beech (upper graph) and spruce (lower graph) stands. Error bars show standard deviations for total necromass input.

4. Discussion

Our study showed that annual aboveground and belowground litter combined represents a large C flux (nearly 3.0 t of C ha^{-1} in beech and 2.5 t C ha^{-1} in spruce) to soil. At the same time, the stock of annual aboveground and belowground necromasses together represented nearly 4.0 t C ha^{-1} in beech and 6.0 t C ha^{-1} in spruce. It should be noted that while our methods for quantification of aboveground necromass is relatively accurate, the method for estimating fine root necromass can result in underestimates. The underestimation is caused by our soil depth limitation to 30 cm (deeper soil layers are difficult to investigate, especially in terms of fine root production using in-growth bags). Other sources of underestimation for fine root necromass stock might be caused by omitting some fragmented or partly decomposed roots. Meta-analysis on the temperate zone forests in Europe (Finér et al. 2007) showed that fine root necromass varied between 0.8 and 3.5 t ha^{-1} in beech forests and from 0.4 to 3.1 t ha^{-1} in spruce forests. Thus, our values (0.8 t ha^{-1} and 0.9 t ha^{-1} in beech and spruce, respectively) are at the lower limit of the results from other European countries. Also, our method for calculating C input (fine root mortality) may underestimate the real values because we were not able to consider intra-seasonal changes (fluctuation) in biomass and necromass but only all-season change (see McClaugherty et al., 1982; Fairley and Alexander, 1985). Meta-analysis on data obtained by Maximum-Minimum method showed that under European conditions, mean fine root production in beech was 1.6 t ha^{-1} and in spruce 1.1 t ha^{-1} (Brunner et al. 2013). Thus, our results (1.4 t ha^{-1} in beech and 1.3 t ha^{-1} in spruce) are quite similar.

Even though some underestimation of absolute values in carbon fixed in fine root mass and input via fine root mortality in the stands is expected, our experiment provides reasonable results in terms of interspecific differences in these processes. Clearly, beech stands had a higher ratio (0.11) of carbon fixed in fine root necromass compared to that fixed in aboveground necromass in spruce stands (0.08). However, we found a higher ratio of carbon flux via fine root necromass compared to that of aboveground litter in spruce (0.55) than in beech (0.38) stands. For both species, the contribution of current C stock in necromass was much higher in accumulated litter on the ground than in fine roots, i.e. in the soil. In addition, while aboveground litter of the current year was less than the accumulated necromass, the opposite was found in fine roots for both beech and spruce stands. This indicates a faster decomposition rate in belowground (fine roots) than aboveground (e.g. foliage, buds and thin branches) tree components. According to Ostertag and Hobbie (1999) faster root than foliage decomposition in forests is typical especially in infertile sites, in part because of lower lignin to N ratio in roots than in leaf litter.

As for inter-specific differences belowground, the ratios between necromass input and necromass stock were very similar in both species (2.01 and 1.97 in beech and spruce, respectively). On the other hand, large differences in the ratio between necromass input and necromass stock (0.57 in beech and 0.28 in spruce) were found for aboveground tree components. This implies that aboveground litter in beech stands (prevailingly necromass of leaves) decomposed faster than in spruce stands (prevailingly needles). This statement is in accordance with the generally accepted, but however not exclusively valid knowledge, that litter decomposition is faster in broadleaved species than conifer species (Prescott et al., 2000; Berger and Berger, 2014). For instance, Prescott et al. (2004) showed in manipulation experiments that leaves of aspen (*Populus tremula*) decompose faster than spruce (*Picea engelmannii*) needles. Similarly Mo et al. (2006) showed faster decomposition of foliage in broadleaved forests stand than in pine stands. These differences are mostly associated with higher diversity of microbial decomposers in broadleaved than coniferous stands (He et al., 2007) as well as different lignin and nutrient contents between foliage and needles (Berger and Berger, 2014).

Finally, fine roots are a very important contributor to net primary production; thus also for biochemical processes including the carbon cycle of forest ecosystems (e.g. Helmisaari, et al. 2002; Matamala et al., 2003; Tateno at al., 2004; Van Do et al., 2015). In spite of this fact, we are still lacking precise information on fine root production and mortality in individual types of forests growing under a variety of climatic and soil conditions. Actually, methodological difficulties limit accurate quantification of fine roots and ectomycorhiza along the full soil profile. Thus, this field still provides much room for future research activities including both improvement of methods and data acquisition.

5. Conclusions

The study performed in young stands shows that aboveground litter (foliage, buds and thin branches) accumulated on the ground was significantly larger in spruce than in beech stands. The opposite situation was observed for aboveground necromass input (more in beech than in spruce). This discrepancy is most probably related to different decomposition rates of aboveground litter between the species. On the other hand, fine root necromass in the soil profile 0 – 30 cm as well as necromass input in the form of fine roots were similar in both species. What concerns the ratio between quantities of fine roots to aboveground compartments, higher values for necromass input was found than necromass stock in both species. These differences can be explained by faster decomposition of fine root necromass than aboveground necromass. Even though our method possibly underestimates fine root quantity, the results indicate the relevant role of tree component in the forest carbon cycle.

Acknowledgements

The research was supported by the projects APVV-0268-10, APVV-0584-12, and APVV-14-0086 from the Slovak Research and Development Agency in the Slovak Republic. With additional thanks to project No. QJ 1220316 supported by the Ministry of Agriculture of the Czech Republic. Dr. Jennifer Clear is acknowledged for valuable comments on the manuscript and also language revision of the text. Dr. Jörg Rößiger translated the abstract to German language.

References

Berger, T.W., Berger, P., 2014. Does mixing of beech (*Fagus sylvatica*) and spruce (*Picea abies*) litter hasten decomposition? Plant and Soil, 377, 217-23.

Bonan, G.B., 2008. Forest and climate change: forcings, feedbacks, and the climate benefits of forests. Science, 320, 1444-1449.

Brunner, I., Godbold. D.L., 2007. Tree roots in a changing world. Journal of Forest Research, 12:78-82.

Brunner I., Bakker M., Björk R.G., Hirano Y., Lukac M., Aranda X., Borja I., Eldhuset T.D., Helmisaari H.S., Jourdan C., Konôpka B., Lopez B.C., Miguel Pérez C., Persson H., Ostonen I., 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant and Soil, 362, 357-372.

Curiel Yuste, J., Konôpka, B., Janssens, I., Coenen, K., Xiao, C.W., Ceulemans, R., 2005. Contrasting net primary productivity and carbon distribution between neighboring stands of *Quercus robur* and *Pinus sylvestris*. Tree Physiology, 25, 701-712.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science, 263, 185-190.

Fairley, R.I., Alexander, I.J., 1985. Methods of calculating fine root production in forests. In: Fitter, A.H., Atkinson, D., Read, D.J., (eds): Ecological interactions in soil: plants, microbes and animals. Blackwell, Oxford, pp. 37-42.

Finér, L., Helmisaari, H.S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, E., Godbold, D., Grebenc, T., Konôpka, B., Kraigher, H., Möttönen, M.R., Ohashi, M., Oleksyn, J., Ostonen. I., Uri, V., Vanguelova, E., 2007. Variation in fine root biomass of three European tree species: beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst) and Scots pine (*Pinus sylvestris* L.). Plant Biosystems, 141: 394-405.

Freschet, G.T., Cornwell, W.K., Wardle, D.A., Elumeeva, T.G., Liu, W., Jackson, B.G., Onipchenko, V.G., Soudzilovskaia, N.A., Tao, J., Cornelissen, H.C., 2013. Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. Journal of Ecology, 101, 943-952.

He, X.-B., Song, F.-Q., Zhang, P., Lin, Y.-.H., Tian, X.-J., Ren. L.-L., Chen, Ch., Li, X.-N., Tan, H.-X., 2007. Variation in litter decomposition-temperature relationship between coniferous and broadleaf forests in Huangshan Mountain, China. Journal of Forestry Research, 18, 291-297.

Helmisaari, H.S., Makkonen, K., Kellomäki, S., Valtonen, E., Mälkönen, E., 2002. Belowand above-ground biomass, production and nitrogen use in Scots pine stand in eastern Finland. Forest Ecology and Management, 165, 317-326.

Janssens, I.A., Freibauer, A., Schlamadinger, B., Ceulemans, R., Ciais, P., Dolman, A.J., Heimann, M., Nabuurus, G.J., Smith, P., Valentini, R., Schulze, E.D., 2004. The carbon budget of terrestrial ecosystems at country-scale – a European case study. Biogeosciences Discussions, 1, 167-193.

Konôpka, B., Pajtík, J., Šebeň, V., Bošeľa, M., Máliš, F., Priwitzer, T., Pavlenda, P. 2013. The research site Vrchslatina – an experimental design and the main aims. Lesnícky časopis – Forestry Journal, 59, 203-213.

Kunca, A., Zúbrik, M., Galko, J., Vakula, J., Leontovyč, R., Konôpka, B., Nikolov, Ch., Gubka, A., Longauerová, V., Maľová, M., Kaštier, P., Rell, S., 2015. Salvage felling in the Slovak forests in the period 2004-2013. Lesnícky časopis – Forestry Journal, 61, 188-195.

Leppälammi-Kujansuu, J., Aro, L., Salemaa, M., Hansson, K., Kleja, B.D., Helmisaari, H.S., 2014. Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. Forest Ecology and Management, 326, 79-90.

Matamala, R., Gonzales-Meler, M.A., Jastrow, J.D., Norby, R.J., Sclesinger, W.H., 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science, 302, 1385-1387.

McClaugherty, C.A., Aber, J.D., Melillo, J.M., 1982. The role of fine roots in the organic-matter and nitrogen budgets of two forested ecosystems. Ecology, 63, 1481-1490.

Minďáš, J., Škvarenina, J., 2003. Globálne zmeny atmosféry a lesy Slovenska. EFRA, Zvolen, 128 p.

Mo, J., Brown, S., Xue, J., Fang, Y., Li, Z., 2006. Response of litter decomposition to simulated N deposition in disturbed, rehabilitated and mature forests in subtropical China. Plant and Soil, 282, 135-151.

Ostertag, R., Hobbie, S.E., 1999. Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. Oecologia, 121, 564-573.

Pajtík, J., Konôpka, B., Marušák, R., 2013. Above-ground net primary productivity in young stands of beech and spruce. Lesnícky časopis – Forestry Journal, 59, 154-162.

Pagan, J., Randuška, D., 1987. Atlas drevín. 1 (Pôvodné dreviny). Obzor, Bratislava, 360 p.

Prescott, C.E., Zabek, L.M., Staley, C.L., Kabzems, R., 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: Influences of litter type, forest type and litter mixture. Canadian Journal of Forest Research, 30, 1742-1750.

Prescott, C.E., Blevins, L.L., Staley, C., 2004. Litter decomposition in British Columbia forests: Controlling factors and influences of forestry activities. BC Journal of Ecosystems and Management. 5, 44-57.

Scott, N.A., Binkley, D., 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia, 111, 151-159.

Schelhaas, M.J., Nabuurs, G.J., 2001. Spatial distribution of regional whole tree carbon stocks and fluxes in Europe. Alterra-rapport, 300, Wageningen, 44 p.

Sulzman, E.W., Brant, J.B., Bowden, R.D., Lajtha, K., 2005. Contribution of aboveground litter, belowground litter, and rizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest. Biochemistry, 73, 231-256.

Takahashi, M., Ishizuka, S., Ugawa, S., Sakai, Y., Sakai, H., Ono, K., Hashimoto, S., Matsuura, Y., Morisada K., 2010. Carbon stock in litter, deadwood and soil in Japan's forest sector and its comparison with carbon strock in agricultural soils. Soil Science and Plant Nutrition, 56, 19-30.

Tateno, R., Hishi, T., Takeda, H., 2004. Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographic changes in soil nitrogen. Forest Ecology and Management, 193, 297-306.

Valentini, C.M.A., Sanches, L., de Paula, S.R., Vourlitis, G.L., Nogueira, J.S., Pinto, O.B., de Almeida Lobo, F., 2008. Soil respiration and aboveground litter dynamics of a tropical transitional forest in northwest Mato Grosso, Brazil. Journal of Geophysical Research, 113, 1:11.

Van Do, T., Sato, T., Saito, S., 2015. Fine-root production and litterfall: main contributions to net primary production in an old-growth evergreen broad-leaved forerst in southwestern Japan. Ecological Research, 30, 921-930.

Xu, S., Liu, L.L., Sayer, E.J., 2013. Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analyses of literfall-manipulation experiments. Biogeosciences, 10, 7423-7433.