Belowground biomass and its annual increment in a montane beech forest in Mavrovo National Park, north-west Macedonia

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ABSTRACT: The aim of this paper is to present the results of the investigation on belowground biomass and its annual increment in a beech ecosystem (*Calamintho grandiflorae-Fagetum*) in Mavrovo National Park, Republic of Macedonia. Belowground biomass was estimated in three layers of the ecosystem (tree, shrub and herb layers) for seven years during the period 1997–2005. Allometric regressions were established for the relationship of root biomass from volume index (D^2H, diameter squared × height) on a sample of 10 model trees and 13 model shrubs of European beech (*Fagus sylvatica* L.). Fine root biomass of trees and shrubs was estimated in soil samples to a depth of 145 cm and divided into live and dead fine roots and subdivided into thickness classes. Belowground biomass of the herb layer was assessed in 20 herb species. It was estimated that the total belowground biomass in the ecosystem was 57.75 $\cdot ha^{-1}$. The contribution of shrub and herb layers was insignificant (less than 0.2%). Biomass of the live fine roots was 10.16 $t \cdot ha^{-1}$, i.e. 18% of the total belowground biomass. Annual increment of trees and shrubs was 1.03 $t \cdot ha^{-1} \cdot y^{-1}$ and 4.6 $kg \cdot ha^{-1} \cdot y^{-1}$, respectively.

Keywords: root biomass; coarse roots; fine roots; trees; shrubs; beech ecosystem

Abbreviations: bd – basal root diameter; DBH – diameter at breast height; H – height of trees, h – height of shrubs; dag – diameter at ground level of shrubs; R/S – root/shoot ratio (ratio between belowground and aboveground biomass); D^2H – volume index (=$DBH^2 \cdot H$); B – total belowground biomass (B_t – of trees, B_s – of shrubs, B_h – of herbs); B_{cr} – biomass of coarse roots ($B_{cr\text{-}t}$ – of trees, $B_{cr\text{-}s}$ – of shrubs); FRB – fine root biomass (FRB_t – trees, FRB_s – shrubs); ΔB – total belowground annual increment (ΔB_t – in tree layer, ΔB_s – in shrub layer)

Belowground biomass in forest ecosystems is less investigated compared to aboveground biomass. This is due to the need of destructive and not-standardized methods, high labour consumption and costs, time-consuming methods and large variations in the root samples as well as lower economic interest in belowground biomass (Cairns et al. 1997; Brown 2002; Bolte et al. 2004). However, the knowledge of relationships between belowground biomass and dynamics and nutrient availability and absorption is very important for understanding forest functioning and terrestrial ecology (West et al. 2004). The needs for carbon sequestration estimation and forest responses to soil acidification put forward the significance of accurate measurements of belowground biomass (Power, Ashmore 1996; Pritchard et al. 2001; Chojnacky, Heath 2002; Zianis et al. 2005).

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Coarse roots (> 2 mm) account for 70% of the total belowground biomass (Cairns et al. 1997) and the development and use of allometric regressions are still the most convenient method for the estimation of their biomass. Fine roots (< 2 mm) represent a large and dynamic component of belowground biomass, a large pool of nutrients and they have high primary production in forest ecosystems. They represent the primary pathway for water and nutrient uptake – the same role as that the leaves play for carbon and energy uptake (McClaugherty et al. 1982). However, it has to be noted that the fine and coarse root division is not completely correspondent to the physiological or structural role of roots and it depends on the ecosystem characteristics (Hendrick, Pregitzer 1996; Pregitzer et al. 1997). It is considered that the carbon content of fine roots is more than 5% of the total carbon in the atmosphere and the nitrogen content makes 1/7 of the total nitrogen stored in terrestrial plants (Jackson et al. 1997).

There are several studies on belowground biomass in European beech forests (e.g. Le Goff, Ottorini 2001; Kodrík, Kodrík 2002; Curt, Prévosto 2003). Information on the belowground biomass of beech forests in the Balkans is not available despite the significance of beech forests for the Balkan region being among the widest spread and economically most important forests (Filipovski et al. 1996). In general, regression models for belowground biomass of European beech are very scarce (Zianis, Mencuccini 2005). These models were obtained in the ecosystems research in Western, Central and Northern Europe, and none of them in the Balkans.

Belowground net primary production consists of three components: annual increment (of roots and stumps), belowground litter production and heterotrophic consumption. However, primary production in forest ecosystems is usually divided into two components: production of coarse roots (corresponds to annual increment) and of fine roots (corresponds to litter production). This division is due to different methodological approaches, dynamics of these root fractions, physiological role, production rate and turnover. It is known that coarse roots have the lowest values for production compared to their biomass (~10%), higher are the values for shrubs and the highest for herb plants and fine roots of trees (Gill, Jackson 2000).

Long-term ecological studies of the montane beech ecosystem in Mavrovo National Park (north-west Macedonia) included the estimation of (aboveground and belowground) biomass and production of tree, shrub and herb layers, analyses of litter decomposition and hydrological cycle. The main objectives in the estimation of belowground biomass were:

- establishment of allometric equations for the dependence of DBH (diameter at breast height) of trees (or diameter at ground level for shrubs) and belowground coarse root biomass,
- estimation of coarse root biomass,
- annual increment,
- estimation of fine root biomass,
- estimation of the participation of tree, shrub and herb layers.

MATERIAL AND METHODS

Site description

The present study was conducted in a fenced site of 1 ha in the beech ecosystem (*Calamintho grandiflorae-Fagetum* Em 1968) in Mavrovo National Park (Bistra Mt.) near the village of Leunovo at the elevation of about 1,400 m a.s.l. Thinning was used as a primary method for wood exploitation by the National Park from the 1950s to the end of the 1980s. All of the destructive measurements (excavation of roots) were carried out outside of the fenced area at a variable distance. The DBH of trees was measured within the fenced site.

The community is developing on Dystric Cambisol soil type, with thick humus layer, high nitrogen content, but poor in other nutrients. The bedrock is composed of phyllitic schists (Petkovski et al. 2008). The area has a mountain continental climate with Mediterranean influences (Filipovski et al. 1996). The average annual temperature is 7.1°C. The minimal average monthly temperature (below 0°C) is registered during three winter months with the minimum of –2.2°C. The mean annual fluctuation of temperature is 18.7°C. The mean annual precipitation is 1,103 mm. It consists mainly of snow and smaller amounts of rain in the warmer seasons of the year. Permanent snow cover lasts for 30–110 days while the snow period is 166 days on average (Lazarevski 1993).

The forest is well structured into three main layers (strata): trees, shrubs and herbs. The tree layer can be subdivided into three sub-layers: dominant, co-dominant and suppressed trees.

Trees in the sub-layer of dominant trees have DBH of 25–35 cm and height between 20 and 25 m. The majority of dominant trees were 70 to 80 years old, although the thickest trees (DBH between 35 and 55 cm) were much older. Suppressed trees are dominant by their number (especially trees with DBH between 5 and 13 cm) and they form a sub-layer with the height of their crowns between 10 and 13 m. Beech (*Fagus sylvatica* L.) absolutely dominates the tree layer with density of 1,200 trees·ha^{-1}. Mean DBH of trees is about 16 cm (Melovski et al. 2003).

The shrub layer is represented mainly by shrubs (not higher than 3 m, usually multi-stemmed ones) of beech and Macedonian fir (*Abies borisii-regis* Mattf.). On average, there are 4,390 beech shrubs and about 60 fir shrubs per hectare.

The herb layer is poorly developed with the aboveground phytomass of less than 6 kg·ha^{-1}. The most abundant herb species are *Anemone nemorosa, Dentaria bulbifera, Carex* sp., *Brachypodium sylvaticum, Asperula odorata, Rubus* sp., *Actaea spicata, Pteridium aquilinum* etc. (Melovski et al. 2004a).

Aboveground annual litter fall biomass is 4.98 t·ha^{-1} while the average forest floor biomass is 20.8 t·ha^{-1} (Melovski et al. 2004b).

METHODS

Belowground biomass was estimated by methods described in Newbould (1967), later on elaborated by Vogt et al. (1998) and Makkonen and Helmisaari (1999). The research comprised field measurements (DBH, excavation of trees, shrubs and herbs) and mathematical and statistical analyses (establishment of allometric regressions, estimation of belowground biomass and annual increment).

Field measurements

Field measurements were carried out in the years 1997–2005. DBH of the trees in the fenced area was measured continuously. The measurements of the belowground biomass of selected trees, shrubs and herbs were performed within short-term field works.

Measurements of DBH of trees*.* DBH of all trees in the fenced area (ca 1,200 trees per ha) was measured at the end of the vegetation season in 1998, 1999, 2001, 2004 and 2005. All trees were numerated and their DBH was measured at a height of 130 cm (horizontal line marked in 1998). DBH was estimated as an average of three values: maximum diameter, minimum diameter and diameter derived from the perimeter of the tree at the red marker. The height (H) of trees was estimated using an allometric formula established for this site (Melovski et al. 2003).

Model roots. Model roots of different diameters were selected from the model trees and shrubs during the field work in September/October 2004. The model roots were extracted completely by following their branched parts all the way to diameter of 1 mm (a similar procedure was later described by Helmisaari et al. (2002)). Model roots were then thoroughly examined. Diameter at base was calculated: (1) as an average of the minimum and maximum diameter for "rounded" roots; (2) as an average of several measurements (3–6) for roots with irregular shape or (3) by calculation of idealized circle diameter with the surface equal to the cross-section surface of roots with very irregular shape. Their length was measured, the number of primary, secondary and tertiary branches (considered as individual model roots), their total weight as well as the weight of separate fractions (0.10 to 0.50 cm, 0.51–1.50 cm, 1.51–3.0 cm, 3.1–5.0 cm, 5.1–10.0 cm and > 10.0 cm) were determined. The weight was measured after drying at 105°C for 24 h at different precision depending on the root weight: 0.0001 g (up to 100 g), 0.1 g (up to 800 g), 0.5 g for the largest roots.

Allometric regressions were established with basal diameter as independent variable. Dependent variables were length and total biomass of roots.

Coarse roots in the tree layer. Coarse root systems of the trees and shrubs were extracted from the soil during the field work conducted in September and October 2004. In total, 10 trees were analyzed: seven trees were excavated and three trees were found uprooted by the wind. DBH of model trees varied between 5 and 38 cm (Table 1). Roots were cleaned; basal diameter was measured and weighed. It took 2–3 days to analyze the root system of a single large tree. Smaller trees (5 to 10 cm in DBH) required about half a day. The biomass and the length of broken roots were calculated by mathematical models which were obtained by the analysis of *model roots.* The same approach was used for estimation of the biomass of very coarse roots with diameters over 5 cm which were impossible to extract completely from the soil (for comparison see Le Goff, Ottorini 2001). Moisture content and bark/wood ratio were measured for all the fractions and tree stumps in replications from 3 to 5.

The total coarse root biomass of a single model tree (b_{cr}) was calculated as follows:

$$b_{cr} = m_{\text{stump}} + \sum_{1}^{n} m_n$$

where:

m_{stump} – biomass of the stump,

m_n – biomass of the root (estimated by field measurement or allometric regressions of model roots),

n – number of primary roots of the tree.

Allometric regressions for estimation of belowground biomass on the basis of D^2H were established.

Coarse roots in the shrub layer. $B_{cr\text{-}s}$ was estimated by allometric regressions similarly like for the trees. In total, 13 shrubs of *Fagus sylvatica* L. were completely excavated (dag varied between 0.4 and 4.5 cm) in the same period as the coarse roots of trees. Cleaned and rinsed model roots were divided into four fractions on the basis of their diameter: ≤ 2.0 mm, 2.1–5.0 mm, 5.1–15.0 mm and 15.1–30.0 mm. At the end allometric regressions describing the relationship between dag and root biomass were established.

Estimation of total belowground biomass and its annual increment at stand level

Trees. Allometric regressions of model trees were applied for all the trees in the fenced area for the period 1997–2005. The sum of the biomasses of all trees resulted in the value of B_t. Annual increment of coarse roots in the tree layer was estimated as a difference between biomasses of coarse roots in two consecutive years.

Table 1. Basic characteristics of the excavated (*model*) trees in the investigated beech ecosystem in Mavrovo

Tree No.	DBH (cm)	H (m)
1	4.605	3.423
2	12.800	14.480
3	5.950	6.500
4	37.250	24.000
5	21.350	24.430
6	24.150	19.760
7	21.500	19.150
8	8.950	10.480
9	14.850	14.460
10	18.500	27.720
Number of analyzed trees	10	
Number of analyzed model roots	59	
Shrubs		
Number of analyzed shrubs	13	
Diameter (at ground) range (cm)	0.4–4.5	
Number of analyzed model roots	107	

Shrubs. In 2002 and 2005 dag and h of shrubs were measured in 11 randomly chosen acres (100 m^2) in the fenced experimental area and allometric regressions of model shrubs were applied. B_t was estimated as the sum of calculated root biomasses of individual shrubs and corrected per 1 ha surface. Annual increment of coarse roots in the shrub layer was estimated as a difference between biomasses of coarse roots in 2002 and 2005 divided by 3.

Fine root biomass. Biomass of the fine roots (< 2 mm) was measured by taking soil samples by cylinders (100 cm^3) in September 2004 from three soil pits in three replications from the following depths: 0–5; 5–10; 10–15; 15–20; 20–25; 25–30; 30–35; 40–45; 50–55; 60–65; 70–75; 80–85; 90–95; 100 to 105; 110–115; 120–125; 130–135 and 140–145 cm. Collected samples were kept at a temperature of 4°C during the process of their analyses. Samples were rinsed with water and they were sieved in a series of sieves with mesh sizes of 0.5, 0.2 and 0.1 cm. Roots were separated under a stereomicroscope and ocular scale. A similar method was described by Burke and Raynal (1994). All the fine roots were divided into two categories: live and dead roots, on the basis of several criteria (a similar approach was described by McClaugherty et al. 1982):

– colour: live roots were reddish or brownish; dead roots had darker colour,
– compactness: live roots were compact; dead roots had the bark which easily detached from the wood,
– consistency: live roots were elastic; dead roots were soft and easily disintegrated,
– branching: live roots were branched; dead roots had no or few lateral roots and most of the finest roots were missing,
– mycorrhiza: live roots had distinct mycorrhiza; dead roots had a faint trace of mycorrhiza.

Live roots were divided into four fractions according to their diameter (≤ 0.20; 0.21–0.50; 0.51 to 1.0 and 1.1–2.0 mm). Dead roots were divided into two fractions (≤ 1.0 mm and 1.1–2.0 mm). All the fine roots were dried at a temperature of 105°C for 24 hours and weighed (0.0001 g).

During the separation of fine roots it was not possible to distinguish the roots of trees from the roots of shrubs. Thus, an approximation was applied in

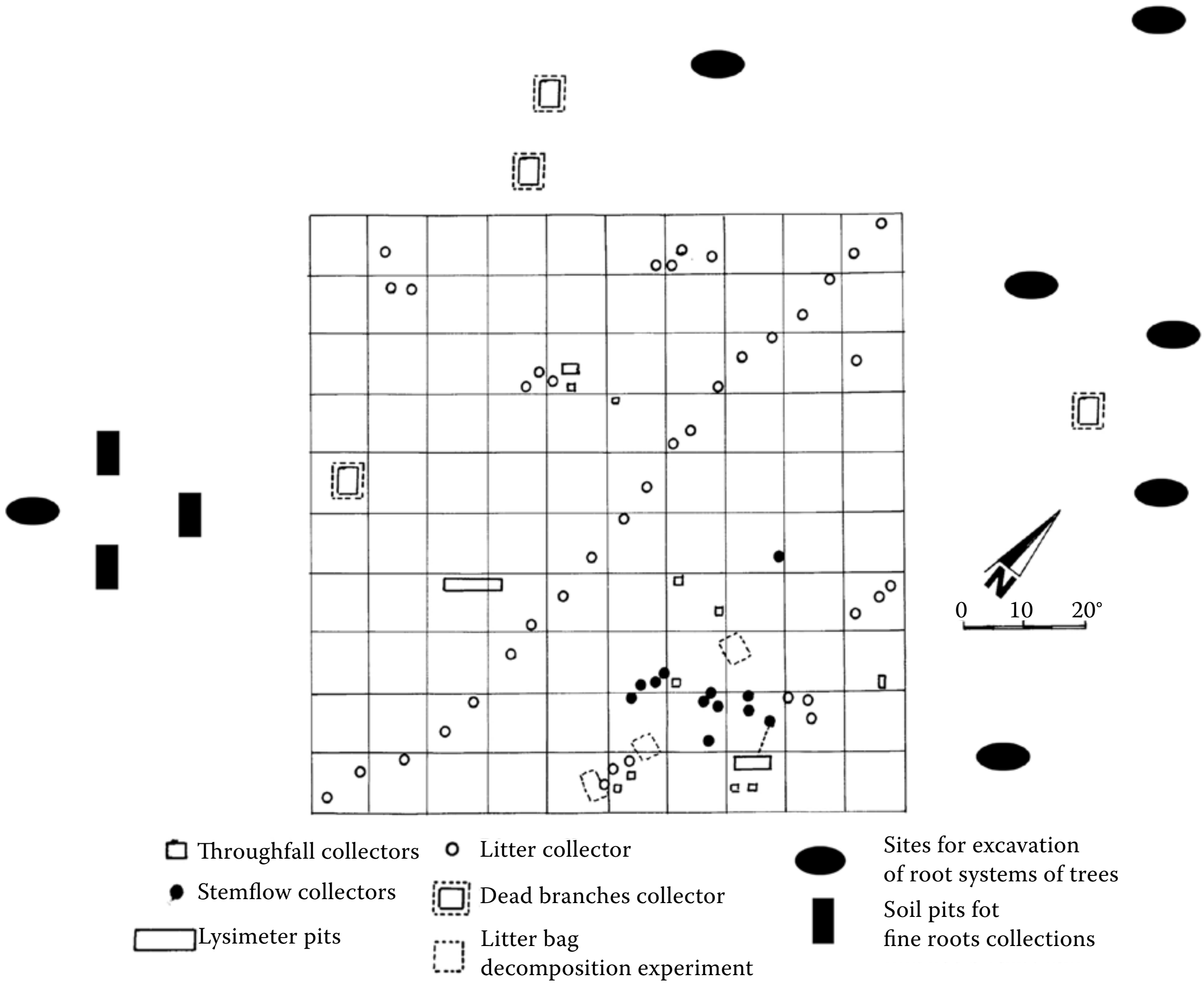

Fig. 1. Experimental layout of the investigated site in the beech ecosystem in Mavrovo. The distance of the excavation of root systems from the fenced area may considerably vary

order to calculate the fine root biomass of trees and shrubs, separately:

$$B_{cr\text{-}t}:B_{cr\text{-}s} = FRB_t:FRB_s$$

Belowground biomass in the herb layer. Belowground organs (roots, rhizomes, tubers) of 20 herb species were thoroughly excavated in June 2003, rinsed with water and weighed (0.0001 g) after air drying at 105°C for 24 h. The aboveground biomass of these plants was also measured. The R/S (root/shoot) value was calculated for each species as a ratio between belowground and aboveground biomass of the herb species. Data for aboveground biomass per hectare for the period 1998–2003 were found in Melovski et al. (2004a). Belowground biomass per hectare for each species (b_h) was estimated according to the following equation: b_h = R/S·aboveground biomass. B_h was calculated as the sum of b_h of all herb species.

Statistical analyses

Statistical regression analyses were performed in STATGRAPHICS for Windows 2.0. The best-fitted model was used and correlation coefficient (R^2), *P*-value and *F*-ratio were calculated. The following mathematical models were used: linear ($a + bx$), exponential ($e^{a + bx}$), reciprocal – Y ($1/(a + bx)$), logarithmic – X ($a + b{\cdot}\ln(x)$), multiplicative (ax^b), square root X ($a + bx^{0.5}$) and square root Y ($(a + bx)^2$).

RESULTS

Coarse root biomass of trees and shrubs

Allometric regressions for estimation of coarse root biomass in the tree layer (based on regressions for coarse model roots – Table 2) with D^2H as independent variable showed higher correlation

Table 2. Allometric regressions for the model roots of trees and shrubs in the investigated beech ecosystem in Mavrovo: correlation of length and mass with diameter at the base (dag)

Diameter at base	Variable	Model	*a*	*b*	*P*	R^2	*F*	*n*
dag ≤ 0.5 cm	length	ad^b	1.02806	1.4682	< 0.001	34.36	123.05	236
	total mass	ad^b	8.30013	2.5453	< 0.001	59.61	341.04	233
dag = 0.51–1.50 cm	length	a + bd	–0.0998	0.6652	< 0.001	44.01	16.51	23
	total mass	a + bd	–0.5159	3.4599	< 0.001	55.68	27.65	24
dag = 1.51–3.00 cm	length				n.s.			
	total mass	$(a + bd)^2$	–2.5985	4.7360	< 0.001	96.35	184.69	9
dag = 3.01–5.00 cm*	total mass	ad^b	9.1977	2.5566	< 0.001	84.70	38.76	27
dag = 5.01–10.00 cm	total mass	ad^b	39.5310	1.4917	< 0.004	48.33	12.16	15
dag > 10.00 cm	total mass	ad^b	43.5960	1.6779	< 0.022	86.62	19.41	10

a, *b* – regression coefficients, d – dag (diameter at ground); *roots with d = 1.51–3.00 and 5.01–10.00 cm were included in the analyses due to the low number of roots in the class 3.01–5.00 cm (only 3 model roots); *n* – number of individuals

coefficients than the regression with DBH as independent variable (Table 3.). $B_{cr\text{-}t}$ (root diameter over 1 mm) was estimated at 44.9 t·ha^{-1} in 1997 and increased to 53.3 t·ha^{-1} in 2005 (Fig. 2). The percent proportion of bark in root classes 0.51 to 1.50, 1.51–3.00, 3.1–5.0 cm, 5.1–10.0 cm and > 10.0 cm was 17.28, 13.67, 11.59, 8.37 and 5.70%, respectively. It clearly shows a decrease in the bark proportion with an increase in root diameter (Fig. 2). The coarsest roots with d > 10 cm accounted for 54.3% and tree stump for 33.6%. Diameter classes of trees between 23 and 35 cm had the highest proportion in the coarse root biomass in the tree layer (Fig. 3). $B_{cr\text{-}s}$ was estimated on the basis of allometric regressions for 13 model shrubs. Regressions for model roots (Table 2) were used to calculate different parameters of the roots of model shrubs (Table 4). Coarse root biomass in the shrub layer in 2002 was 66.32 kg·ha^{-1} (Table 5). The highest biomass was recorded for the diameter class with dag = 1.51–3.00 cm, followed by the class with dag = 0.51–1.50 cm (Table 5).

Fine root biomass (d < 2 mm) in tree and shrub layers

FRB in the investigated beech ecosystem was 10.16 t·ha^{-1}. The largest FRB was recorded in the soil layer of 0–5 cm (23.3%) and 5–10 cm (12.5%).

Table 3. Allometric regressions for the model trees with D^2H (*X*) as independent variable in the investigated beech ecosystem in Mavrovo

Fraction	Model	*a*	*b*	*P*	R^2	*F*	*n*
d ≤ 0.5	$1/(a + bx)$	0.0077	0.000054	< 0.001	99.37	469.94	5
d = 0.51–1.50	$a + b\ln(X)$	147.9900	–12.721900	< 0.015	80.83	16.86	6
d = 1.51–3.00	aX^b	793.0270	–0.184706	< 0.038	70.13	9.39	6
d = 3.01–5.00	aX^b	1.2023	0.780320	< 0.005	88.86	31.92	6
d = 5.01–10.00	aX^b	532.68	0.248340	< 0.003	96.65	86.58	5
d > 10.00	aX^b	8.9431	0.890650	< 0.001	94.43	84.72	7
Coarse roots total	$a + bX$	4,497.4000	3.545500	< 0.001	99.47	1,122.84	8
Stump	$a + bX$	860.5100	1.703800	< 0.001	98.44	441.04	9
Total biomass	$a + bX$	629.1600	5.228400	< 0.001	98.13	366.47	9

a, *b* – regression coefficients, d – root diameter (cm); $X = D^2H$

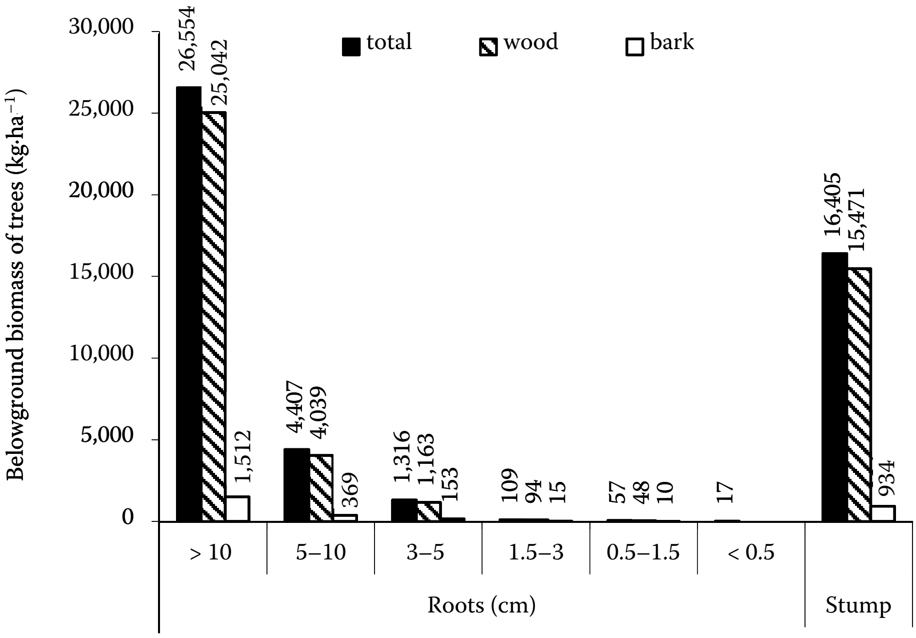

Fig. 2. Total average belowground biomass of coarse roots with diameter over 1 mm in the tree layer in the investigated beech ecosystem in Mavrovo in 2005 (kg·ha^{-1})

All the other layers had less than 5% of the FRB (the exceptions were 30–40 and 100–110 cm layers). The smallest percentage (less than 3%) was recorded in the deepest soil layers (Fig. 4). The decrease in percent proportion was statistically significant (Fig. 4). Similar results were obtained for fine root fractions with d ≤ 0.2 mm and d = 0.21–0.50 mm. Based on the mathematical calculation it was estimated that FRB_t is 10.15 t·ha^{-1} and FRB_s is 11.49 kg·ha^{-1}. The biomass of roots with d ≤ 1 mm in the tree layer by the same approximation was calculated at 8.78 t·ha^{-1} and 9.94 kg·ha^{-1} for shrubs. The last two values were added to the coarse root biomasses of trees and shrubs in order to estimate B. The corresponding values are 57.65 t·ha^{-1} for B_t and 83.14 kg·ha^{-1} for B_s.

Belowground biomass in the herb layer

Total belowground biomass in the herb layer was 16.6 kg·ha^{-1} (Table 6). Dominant plant forms were cryptophytes (*Anemone nemorosa, Pteridium aquilinum, Dentaria bulbifera, Asperula odorata*) and hemicryptophytes (*Daphne mezereum*).

Total belowground biomass and its annual increment in trees and shrubs

B was 57.75 t·ha^{-1} (Table 7). B_t accounted for 99.83% of B, while the values of B_s and B_h were 0.14% and 0.03%, respectively. Mean ΔB_t was estimated at 1,032.2 kg·ha^{-1}·year^{-1}. Stump and the

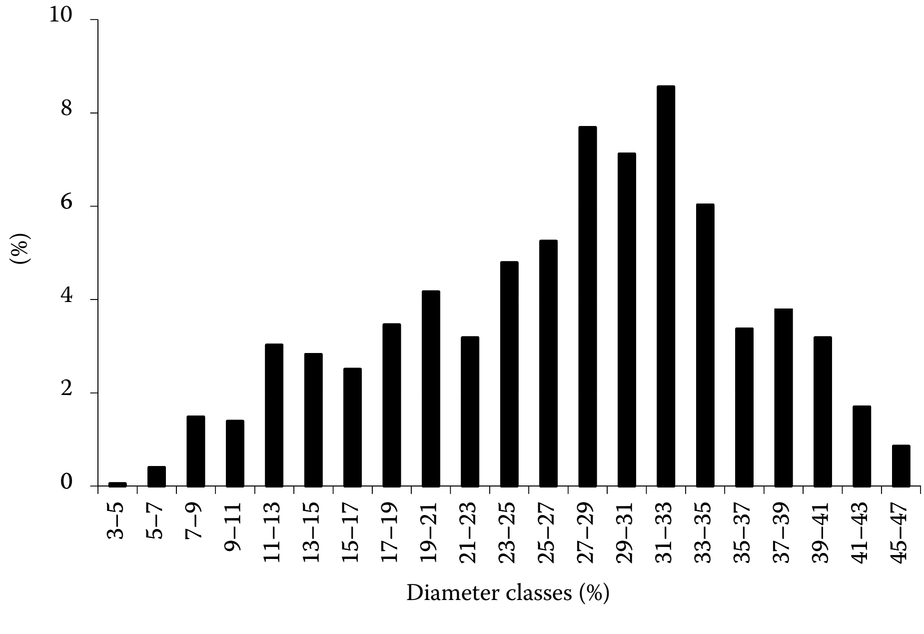

Fig. 3. Average percent proportions of diameter classes of trees in the total coarse root biomass in the tree layer in the investigated ecosystem in Mavrovo for the period 1997–2005

Table 4. Allometric regressions for the model shrubs with d^2H (x) as independent variable in the investigated beech ecosystem in Mavrovo

Biomass and R/S	Model	*a*	*b*	*P*	*r*	*F*	*n*
R/S (root/shoot ratio)	$1/(a + bx)$	1.46065	0.0347	< 0.001	81.34	47.96	13
Coarse roots	$(a + bx)^2$	1.78886	0.0403	< 0.001	98.84	1,038.95	13
Stump	$a + b$x	–14.23910	12.8410	< 0.001	98.19	599.57	13
d = 1.0–5.0 mm	$(a + bx)^2$	1.23767	0.1887	< 0.001	99.74	4,317.86	13
d = 5.1–15.0 mm	$(a + bx)^2$	2.25897	0.2844	< 0.001	94.48	136.71	10
d = 15.1–30.0 mm	e^{a+bx}	3.05284	0.0541	< 0.001	98.19	163.39	5

a, *b* – regression coefficients, d – root diameter (cm); $x = d^2H$

Table 5. Total belowground biomass of coarse roots in the shrub layer in the investigated beech ecosystem in Mavrovo in 2002 and 2005 ($kg{\cdot}ha^{-1}$)

Root diameter classes	Number of shrubs per ha	2002		2005	
		coarse roots biomass	participation (%)	coarse roots biomass	participation (%)
≤ 0.5 cm	882.0	1.11	1.67	0.85	1.06
0.51–1.50 cm	2,673.0	18.20	27.44	18.15	22.65
1.51–3.0 cm	391.0	30.44	45.90	39.37	49.13
3.1 –5.1cm	36.0	16.57	24.98	21.76	27.15
Total	3,981.8	66.32	100.00	80.14	100.00

coarsest roots had the greatest proportion in ΔB_t (Table 8). ΔB_s was 4.61 $kg{\cdot}ha^{-1}{\cdot}y^{-1}$ and it was almost negligible compared to ΔB_t. The smallest shrub classes (dag ≤ 1.5cm) showed the negative values of annual increment due to the die-off of the smallest shrubs. Shrub classes with dag over

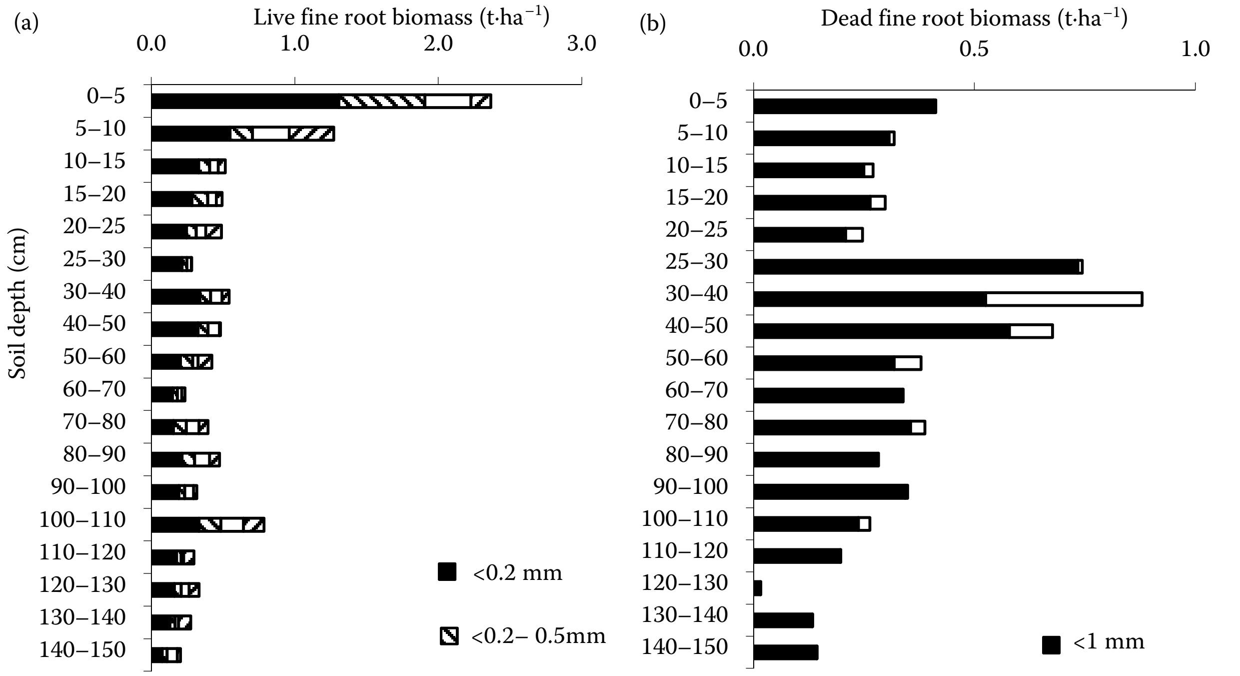

Fig. 4. Percent proportions of the soil layers in total FRB of live roots (a) ($FRB = 13.54{\cdot}dp^{-1.465}$; $R^2 = 61.65\%$, $P < 0.001$, $F = 25.72$, dp – soil depth) and dead roots (b) in the investigated beech ecosystem in Mavrovo in 2004

Table 6. Total belowground biomass in the herb layer in the investigated beech ecosystem in Mavrovo in 2003

Life form	Biomass (kg·ha^{-1})
Cryptophytes	15.244
Hemicryptophytes	1.348
Phanerophytes	0.010
Total	16.601

1.5 cm had increment values of 2.98 and 1.73 kg·ha^{-1}·y^{-1} (Fig. 5).

DISCUSSION

In most of the studies, DBH or D^2H was used as independent variable in allometric regressions for estimation of B. These models are based on the presumption that the growth of structural roots depends on stem diameter and the belowground and aboveground parts sustain the allometric balance of the trees (Drexhage, Colin 2001). Obtained allometric regressions for trees and shrubs in our study showed high correlation coefficients (Table 3) and they contribute to fill in the complete lack of such equations in the Balkan region. Allometric regressions for belowground biomass of beech shrubs in Europe are almost completely missing. There are only a few articles which correlated height and dag of shrubs (Collet et al. 2002; Prévosto, Curt 2004), but none of them correlated dag with B_s.

Broadleaved and subtropical forests have the values of belowground biomass between 70 and 100 t·ha^{-1}, with a maximal range between 2 and 200 t·ha^{-1} (Richardson et al. 2003). Values for B of beech forests in Europe vary between 15 and

Table 7. Total biomass in the investigated beech ecosystem in Mavrovo (presented as an average value for the period 1997–2005)

Layers	Belowground biomass (kg·ha^{-1})	Participation (%)
Tree layer	57,650.77	99.83
Shrub layer	83.14	0.14
Herb layer	16.60	0.03
Total	57,750.50	100

74 t·ha^{-1} (Le Goff, Ottorini 2001; Kodrík, Kodrík 2002; Bascietto et al. 2004). These large variations in natural forests are due to different tree species, age of forests, climate factors (temperature, humidity, precipitation and winds), length of the root growth season, relief, soil mechanical properties and nutrient availability, competition between tree species, silvicultural treatments (Le Goff, Ottorini 2001; Richardson et al. 2003). The investigated beech ecosystem in Mavrovo National Park falls well within these values. It is expected that B will increase with the maturing of the ecosystem due to the growth of coarse roots. According to Kodrík and Kodrík (2002) the growth of very coarse roots (d > 10 cm) is evident at the age of 60–80 years. This is the case in Mavrovo, where coarse roots and stump increased their proportion with an increase in DBH, i.e. with the age of trees.

Curt and Prévosto (2003) assumed that B_s accounted for less than 1% in different beech stands in France. B_s in the investigated beech ecosystem in Mavrovo amounted to 0.14% (Table 7) and we expect that this value will further decrease due to the faster root growth of trees, increase in B_t/B_s ratio

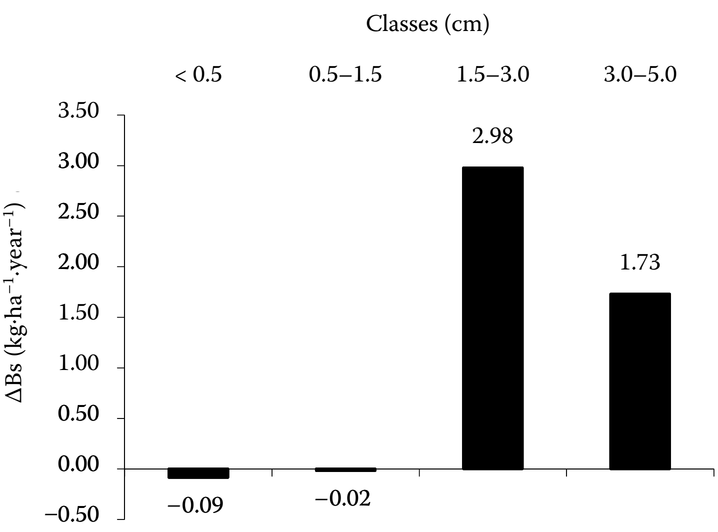

Fig. 5. Belowground increment in the shrub layer (excluding roots < 1 mm) in the investigated beech ecosystem in Mavrovo in the period 2002–2005

Table 8. Belowground annual increment (kg·ha^{-1}·year^{-1}) of coarse roots (> 1 mm) in the investigated beech ecosystem in Mavrovo in the period 1997–2005

Organs/fractions		1997	1998	1999	2000–2001	2002–2004	2005	Average
d > 10 cm	T	506.9	848.1	542.8	541.9	547.5	823.6	605.3
	W	478.0	799.8	511.9	511.0	516.3	776.7	570.8
	B	28.9	48.3	30.9	30.9	31.2	46.9	34.5
d = 5–10 cm	T	28.0	39.5	21.5	13.5	9.1	15.0	17.6
	W	25.7	36.2	19.7	12.4	8.3	13.8	16.1
	B	2.3	3.3	1.8	1.1	0.8	1.3	1.5
d = 3–5 cm	T	23.3	36.5	22.7	21.0	20.6	31.5	24.2
	W	20.6	32.2	20.1	18.6	18.2	27.8	21.4
	B	2.7	4.2	2.6	2.4	2.4	3.7	2.8
d = 1.5–3 cm	T	2.3	3.7	2.3	2.3	2.3	3.5	2.6
	W	2.0	3.2	2.0	2.0	2.0	3.0	2.2
	B	0.3	0.5	0.3	0.3	0.3	0.5	0.4
d = 0.5–1.5 cm	T	–0.5	–0.5	–0.3	–0.2	–0.7	–0.6	–0.5
	W	–0.4	–0.4	–0.2	–0.2	–0.6	–0.5	–0.4
	B	–0.1	–0.1	0.0	0.0	–0.1	–0.1	–0.1
d = 0.1–0.5 cm	T	–0.5	–0.3	–0.2	0.0	–0.3	–0.2	–0.3
Total roots	T	559.5	926.9	588.8	578.4	578.5	872.8	648.9
	W	525.4	870.6	553.2	543.7	543.9	820.6	609.9
	B	34.1	56.3	35.6	34.7	34.5	52.2	39.0
Stump	T	333.5	540.5	347.1	340.9	342.1	520.3	383.3
	W	314.5	509.8	327.4	321.5	322.6	490.7	361.5
	B	19.0	30.8	19.8	19.4	19.5	29.6	21.8
Belowground increment (ΔB)	T	893.0	1,467.4	936.0	919.4	920.6	1,393.1	1,032.2
	W	839.9	1,380.4	880.6	865.2	866.6	1,311.3	971.4
	B	53.1	87.0	55.4	54.1	54.0	81.8	60.9

(Rochow 1974) and dying off of the shrubs. The B_t/B_s ratio increased from 3.827 to 3.839 between 2002 and 2005.

B_h in the investigated beech stand was exceptionally low. It is due to the closed canopy, low density of herbs and less developed root systems (low R/S values). Ovington (1956) reported almost 10 times higher value of 162 kg·ha^{-1} for a beech stand in England.

More than 250 studies on FRB were published in the world by the end of the 20th century (Jackson et al. 1997). Most of them referred only to the surface soil (0–30 cm), which was a significant deficiency in the estimation of true FRB in forest ecosystems. FRB (live and dead) in the investigated beech ecosystem in Mavrovo was 16.50 t·ha^{-1}. It is a higher value than the average of 7.8 t·ha^{-1} for broadleaved temperate forests (Jackson et al. 1997). However, if only the values to a 30-cm depth are taken into account (7.7 t·ha^{-1} – Fig. 4), then the FRB of the beech stand in Mavrovo is comparable. Leuschner et al. (2001) reported the values of 0.2–2.3 t·ha^{-1} in the humus horizon for a mixed beech-oak forest (90% beech) in north-west Germany. This is comparable with 1.81 t·ha^{-1} estimated in the 0–5 cm layer in our study (Fig. 4).

The greatest FRB was estimated in the soil layers to a 30-cm depth (5.15 t·ha^{-1} of live and 1.61 t·ha^{-1} of dead roots). It is well known that the top 40 cm of the soil in beech and other forest ecosystems contain the greatest bulk of FRB (Hendrick, Pregitzer 1996; Curt et al. 2001; Curt, Prévosto

2003). This is even more pronounced in the Mediterranean ecosystems that contain 50% of FRB in the top 25 cm (López et al. 2001; Silva, Rego 2003). It should be taken into account that the FRB measured in the autumn season (before leaf fall) in temperate forests shows the highest values (Burke, Raynal 1994; Hendrick, Pregitzer 1996). Thus, we can assume that our field research was carried out during the highest FRB (September, 2004) and it should decrease during the winter season.

Obviously, total FRB and biomass of all fine root fractions decrease with the soil depth (Fig. 4). However, the finest roots (≤ 0.2 mm and 0.21–0.50 mm) are dominant in surface soil layers and their percent proportion decreases while the "coarser" fine roots (0.50–1.00 and 1.01–2.00 mm) increase their proportion with the soil depth. This indicates that the physiologically active roots are mostly found in the surface soil layers. Fine roots of the deeper layers were less branched and thus they play a less significant role in the absorption of water and nutrients. According to Fahey and Hughes (1994) a higher proportion of "coarser" fine roots in deeper soil layers is due to their resistance to soil pressures. There were no fine roots in the forest floor of the investigated beech ecosystem. The same conclusion was drawn by Hendriks and Bianchi (1995), although in other studies, fine roots were reported for the forest floor (Fahey, Hughes 1994).

The proportion of FRB in total belowground biomass was 19.34%. Bolte et al. (2004) summarized the results of five studies (Nihlgård 1972; DeAngelis et al. 1981; Bartelink 1998; Hertel 1999; Le Goff, Ottorini 2001) and concluded that the FRB proportion is less than 10%. However, Curt and Prévosto (2003) found a much higher value of 48%. The underlying cause for the estimation of a smaller FRB proportion is probably the omission of fine roots in deeper soil layers.

ΔB for beech stands in Europe varies between 0.8 and 2.4 $t \cdot ha^{-1}$ (Nihlgård, Lindgren 1977; Duvigneaud et al. 1977; Le Goff, Ottorini 2001). The value for the investigated beech ecosystem in Mavrovo (1.03 $t \cdot ha^{-1}$) is among the lowest ones. In general, root turnover (the ratio between belowground net primary production and belowground biomass) in forest ecosystems is very low (Gill, Jackson 2000). According to Kestemont (1982 in Gill, Jackson 2000) the turnover in one beech forest was only 0.022. Root turnover in the investigated beech forest in Mavrovo cannot be calculated since we miss the data on fine root production. However, the coarse root turnover (ΔB/B) shows a low value of 0.020. The low annual increment value in the beech forest in Mavrovo may increase with the stand age since older trees "invest" more in coarse root biomass than in FRB (Le Goff, Ottorini 2001). The aboveground biomass in the beech forest in Mavrovo has faster growth – the annual increment of 7.7 $t \cdot ha^{-1}$ (Melovski et al. 2003). This means that the belowground biomass will lag behind the aboveground biomass growth. This was also evident in the beech forest in Mavrovo during the investigation period. Belowground biomass of the stand steadily decreased its proportion in total biomass from 14.2% in 1998 to 13.8% in 2005.

Belowground net-primary production of the forest ecosystem is very difficult to assess. For the beech forest in Mavrovo we miss the data on fine root production and heterotrophic consumption. The knowledge of values and rates of consumed biomass by heterotrophs is generally insufficiently known (Fahey, Hughes 1994) and often neglected (Hendrick, Pregitzer 1992).

Belowground biomass of coarse roots in beech ecosystems can be easily estimated by allometric regressions showing the relationship of biomass to DBH. In terms of biomass and productivity, the most important are trees while shrub and herb layers are almost insignificant with the total proportion of 0.17%. Larger trees (diameter classes between 23 and 35 cm) have the greatest coarse roots, despite the low number of trees per hectare. Coarse root biomass is much smaller compared to the aboveground biomass, but it still represents an important storage of carbon and nutrients. FRB represents a large and dynamic fraction of the belowground biomass. The estimation of FRB should be carried out in the whole root zone since a significant part of FRB is present in deeper soil horizons. The most physiologically active (finest) roots are found in the top soil layers, while the "structural" fine roots are dominant in deeper soil layers.

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