Proportion of living biomass in the total dry mass of belowground organs of various plant communities

Zastoupení živých podzemních orgánů ve veškeré podzemní biomase různých rostlinných společenstev

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Dedicated to Jiří Vicherek on the occasion of his 70th birthday

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Proportion of living belowground plant biomass estimated for various types of meadows, grass stands of clear-cut areas, sedge stands of wetlands and for Cuban savannas and forests is reviewed. Analysis was done using a staining technique and laborious visual separation of living belowground biomass from soil cores and blocks. The differences in the amount of living belowground plant biomass are mostly associated with the type of plant community. The highest amounts of living belowground biomass (1100 to 2300 g·m^{-2}) were recorded most frequently in the unmown moist meadow stands (percentage of living belowground biomass was over 60 %) and in mountain grass stands of clear-cut sites (66–95%). A lower percentage and amount of living biomass was found in the driest habitat (23 %, 860 g·m^{-2}) and in several wetlands (10–13 %, about 500 g·m^{-2} or less). Mown meadows were characterized by a lower percentage of living belowground biomass and lower dry mass of total and living belowground plant parts. Living belowground biomass of 433 and 517 g·m^{-2} (34 and 50 %) was recorded in natural savannas, while 745 (74 %), and 512 to 1122 g·m^{-2} (39–65 %) was recorded, respectively, in the anthropogenic savanna stands dominated by *Axonopus compressus* and *Paspalum notatum*. The percentage of living fine roots in the total dry mass of fine roots of Cuban forests varies considerably: 41 and 47 % (554–758 g·m^{-2}) in mangrove forests, 30 and 56 % (64–90 g·m^{-2}) in evergreen broad-leaved mountain forests and 23 and 49 % (87–200 g·m^{-2}) in semideciduous lowland forests. Both the proportion of living plant organs in total belowground dry mass and the amount of belowground plant necromass vary greatly, which may reflect differences in root mortality and the decomposition rate of dead belowground plant parts associated with various habitat conditions.

Keywords: Living roots, belowground biomass, meadows, wetlands, savannas, Cuban forests

Introduction

Belowground biomass, mainly that of roots, rhizomes and shoot bases, is the most important stabilizing element in grasslands (Titlyanova 1979, Fiala 1997). It is very often the bulkiest biotic structural ecosystem compartment (Rychnovská 1983, Stanton 1988). The share of living roots represents an active element in energy and mineral nutrient flow through the plant cover. The remaining dead necromass undergoes decomposition and contributes to the soil humus. Fine roots of tropical forests have been shown to contribute to the fast and efficient cycling of nutrient elements in an environment where the potential for nutrient leaching is high and nutrient availability can be low (Stark & Jordan 1978, Silver & Vogt 1993).

Belowground plant organs of perennial plants are able to live for prolonged periods of time and form extensive root systems acting as physiological links between various generations of shoots produced over several growing periods. This ability leads to the rapid regeneration of perennial plants and to the increase of their drought resistance. Therefore, the knowledge of the amount of living belowground organs provides data for comparing the stability of diverse plant stands and their adaptability to changes in their environment and to various disturbances (Fiala 1997).

Relatively high percentages of living biomass (50–80 %) in total belowground dry mass were mostly recorded in grassland communities (Vagina & Shatochina 1972, Singh & Coleman 1973, 1977, Titlyanova & Shatochina 1974, Kotańska 1975, 1977, Midorikava et al. 1975, Bystrickaya & Kovácz-Láng 1991). Titlyanova et al. (1997) reported on the percentage of living belowground biomass in meadows and grassy marshes of Siberia ranging from 17 to 58 % and the proportion of living belowground plant organs decreasing in zonal grass ecosystems along the gradient of continentality (from western to central Asia). Her results provide an evidence for a lower rate of decomposition of dead roots under cooler temperature regime. The percentage of living roots changes during the growing season (Titlyanova et al. 1997, Fiala 1998). Within a species, cohorts of roots produced at different times of the year can differ greatly in life span. In temperate climates, the lifespan is often shorter for roots produced in late spring (Eissenstat & Yanai 1997). Szanser (1991) found the proportion of living roots to decrease with the age of meadows from 53.2 % (one year old human-made stand of *Dactylis glomerata*) to 48.8 % (eight years old stand belonging to *Arrhenatheretalia*) and even to 37.1 % in a permanent meadow stand of *Anthyllidi-Trifolietum montani*.

The determination of living and dead roots remains one of the principal problems in root studies. Recent technological advances, especially developments in minirhizotrone techniques and video-processing with personal computers, have made it more feasible to observe and quantify the demography of roots under field conditions (Richards 1984, Cheng et al. 1990, Pielota & Smucker 1995). However, root lifespan may be overestimated with minirhizotrons and root length densities can be considered lower than estimates based on soil coring (Eissenstat & Yanai 1997).The determination of the percentage of living roots in various plant communities studied (i. e. different types of meadows, wetlands, clear-cut areas, Cuban savannas and forests) involved staining and laborious visual separation of living belowground plant parts. The same method was used by Titlyanova et al. (1988) and van der Maarel & Titlyanova (1989) in order to assess the effect of different grazing conditions on belowground biomass in steppe vegetation. Our results contribute to the knowledge of differences in the dry mass of living and dead belowground plant organs in various habitats. Therefore the aim of this paper is to summarize and compare all the data obtained by the present author, partly in cooperation with other colleagues, during more than one decade.

Methods

The proportion of living belowground plant biomass was estimated for various types of meadows in the Bohemian-Moravian Uplands (Czech Republic), grass stands of clear-cut areas in the Moravian-Silesian Beskydy Mts (Czech Republic), sedge stands of wetlands in western New York (USA), and savannas and forests in Cuba.

Table 1. – The size of soil blocks (SB) or the diameter (D) of soil cores and number of replicates (given in the brackets) taken for the determination of total belowground dry mass and living biomass of belowground plant organs except roots (A) and for assessing the proportion of living roots in total root dry mass (B). Numbers of stands correspond to Tables 2 and 3.

Type of stand (No.)	Size of samples in mm (n)		Soil layer (mm)	Sampling time
	A	B		
Wet meadows				
(1–3)	D 70 (10)	D 20 (5)	0–150	October 1989
(5)	D 90 (10)	D 20 (5)	0–150	August 1983
Wetland stands				
(4, 6–10)	SB 200 × 200 (10)	SB 50 × 50 (3–4)	0–200	August, September 1982
(8)	SB 250 × 250 (6)	SB 50 × 50 (3)	0–200	September 1982
(9–10)	SB 125 × 125 (8)	SB 50 × 50 (3)	0–200	September 1982
Fresh moist meadows				
(11, 14)	D 90 (10)	D 20 (5)	0–150	August 1983
(12, 13, 15)	D 70 (10)	D 20 (5)	0–150	October 1989
Moist meadows				
(16, 18, 21, 25)	D 90 (10)	D 20 (5)	0–150	August 1983
(17, 19, 20, 22–24, 26–28)	D 70 (10)	D 20 (5)	0–150	October 1989
Grass stands of clear-cuts areas				
(29, 31, 32)	D 70 (10)	D 20 (3)	0–200	September 1987
(30, 35)	D 50 (10)	D 20 (3)	0–200	June 1991
(33, 34)	D 50 (5)	D 20 (5)	0–300	September 1986
Savannas				
(1–3)	SB 100 × 100 (10)	D 50 (3–5)	0–150	October,
(7)	–	D 50 (2)	0–150	November 1984
(4–6)	D 50 (10)	D 50 (3)	0–200	September 1989
Forests				
(9–11)	SB 100 × 100 (10)	D 50 (5)	0–150	October, November 1984
Mangroves				
(12–13)	D 50 (20)	D 25 (3)	0–250	October 1989

Samples were taken in soil blocks or soil cores mostly to the depth of 150 (200) mm (Table 1). Approximately 90 % (in meadows) and 80 % (in savannas) of both living and total belowground dry mass was concentrated in the upper 0–150 and 0–200 mm soil layers, respectively (Fiala & Ricardo 1988, Fiala 1990a). In Cuban semideciduous and evergreen broad-leaved forests, about 70 % of fine roots were mostly concentrated in the upper 0–100 mm soil layer (Fiala & Hernández 1993). Simultaneously with sampling for the assessment of total belowground biomass, additional smaller soil samples were collected in order to estimate the percentage of living and dead roots (Table 1). After washing of large samples, belowground biomass was visually separated into total roots, living and dead rhizomes, tubers and belowground shoot bases according to their colour and mechanical consistency. The method developed by Ward et al. (1978) and modified by Tesařová et al. (1982) was used to determine the proportion of living and dead roots. After washing of small samples, living and dead roots were distinguished by vital staining with a 1% aqueous solution of Congo red which stains living roots from dark pink to bright red. All samples were then dried at 70–80 °C and weighed. Data on total belowground dry mass, assessed from large samples, and data on the proportion of living and dead roots and other belowground plant organs were used to estimate both the amount of living and dead belowground plant parts per m^2.

Results

Dry mass of total belowground plant parts in temperate grasslands ranges mostly between 2000 and 3000 $g{\cdot}m^{-2}$. Higher values were recorded in wetlands (sedge stands), and/or meadow communities of dry habitats (*Trifolio-Festucetum rubrae*), reaching even 4000 $g{\cdot}m^{-2}$. The highest percentage of both living roots and living belowground biomass was recorded most frequently in unmown moist meadows of *Polygono-Cirsietum palustris* and *Polygalo-Nardetum* (52–69 %) and in grass stands of clear-cut sites (66–95 %). The highest values of living belowground biomass were also recorded in these unmown stands (1100–2 300 $g{\cdot}m^{-2}$ – Fig. 1, Table 2). The proportion of living roots in total root dry mass did not differ much from the proportion of living belowground biomass in total belowground dry mass. The proportion of living plant organs in total belowground dry mass decreased below 50 % with increasing soil moisture content or waterlogging of the soil, i. e. in wet meadows and wetland stands. Only 10–13 % of living belowground biomass was found in total belowground standing crop of several wetland stands, representing about 500 $g{\cdot}m^{-2}$ (Table 2). Similarly, a very low percentage of living belowground plant parts (23 %) was found on the opposite side of the soil moisture gradient (*Trifolio-Festucetum rubrae*), i. e. in the driest habitat with a relatively low rate of decomposition of organic matter (Balátová et al. 1977). Thus, the

Fig. 1. – Dry mass of living belowground biomass and percentage of living belowground biomass (% L) in total belowground dry mass in wetlands, meadows and grass stands of clear-cut sites.

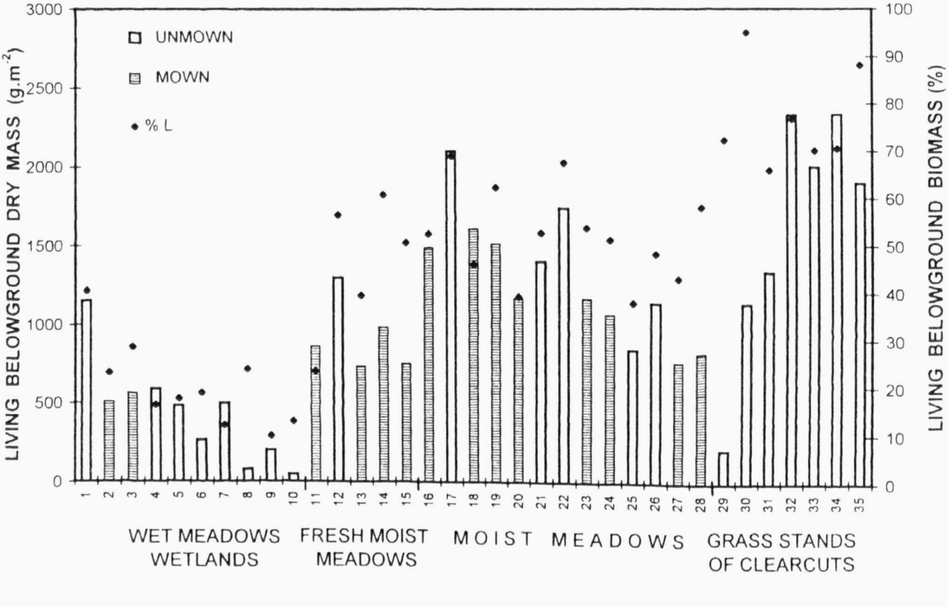


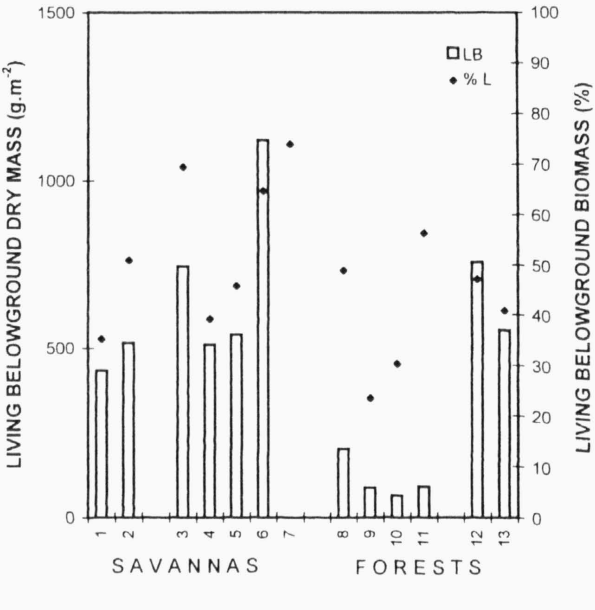
Table 2. – Dry mass of living, dead and total belowground plant parts and proportion of living roots in dry mass of total roots (mean values ±1S.E.) in various plant communities. Ratios of total belowground to aboveground dry mass (TR/TS) and live belowground to aboveground dry mass (LR/LS) are given.
Location: Moravian-Bohemian Uplands, Czech Republic (1–3, 5, 11–28), The Moravian-Silesian Beskydy Mts, Czech Republic (29–35), Inlet Valley, Ithaca, New York, USA (4, 6, 7), Byron-Bergen Swamp, New York, USA (8–10). Source: 5, 11, 14, 16, 19, 21, 25 – Fiala (1990a); 1–5, 12, 13, 15, 17, 18, 20, 22–24, 26–28 – Fiala (1997); 4, 6, 7 – Bernard, Fiala (1986); 8–10 – Seischab et al. (1985); 29, 31, 32 – Fiala (1989); 33, 34 – Fiala et al. 1989; 30, 35 – Fiala (1998). A – alluvial, L – lowland, U – upland, M – mountainous; unmown (UM) and mown stands (M1x – once a year, M2x – twice a year, M3x – three times a year).

	Type of stands and location	Belowground dry mass			Living	TR/TS
		Living ($g \cdot m^{-2}$)	Dead ($g \cdot m^{-2}$)	Total ($g \cdot m^{-2}$)	roots (%)	and LR/LS
	Wet meadows, wetlands					
1	*Caricetum rostratae* UM, U	1151 ±51	1692 ± 63	2843 ± 96	37.0 ±0.5	
2	*Caricetum rostratae* M1x, U	508 ±43	1686 ±128	2195 ±155	20.5 ±1.6	
3	*Caricetum rostratae* M3x, U	562 ±39	1402 ± 80	1964 ±113	27.3 ±0.4	
4	*Carex rostrata* UM, A	589 ±40	3030 ±209	3619 ±249	16.2 ±1.6	3.9/ 0.7
5	*Scirpetum sylvatici* UM, U	480 ±70	2260 ±350	2740 ±430	17.5 ±3.6	4.1 / 0.7
6	*Carex trichocarpa* UM, A	263 ±16	1135 ± 69	1398 ± 85	18.8 ±6.0	1.8 / 0.2
7	*Carex lasiocarpa* UM, A	496 ±17	3638 ±127	4134 ±144	11.9 ±2.3	5.2 / 0.7
8	*Eleocharis rostellata* – wet site, L	77 ±32	245 ±102	322 ±134	23.8 ±4.2	1.59 / 0.2
9	*Eleocharis rostellata* – old stand, L	201 ±61	1869 ±574	2069 ±635	9.7 ±1.4	12.9 / 0.9
10	*Eleocharis rostellata* – marl, L	45 ± 7	307 ± 46	352 ± 53	12.8 ±2.1	3.9 / 0.33
	Fresh moist meadows					
11	*Trifolio-Festucetum rubrae* M1x, U	860 ± 60	2810 ±210	3670 ±270	23.4 ±8.7	12.2 / 2.9
12	*Arrhenatheretum elatioris* UM, U	1296 ± 57	998 ± 45	2294 ± 95	63.7 ±4.7	
13	*Arrhenatheretum elatioris* M1x, U	732 ± 51	1124 ± 94	1856 ±134	39.1 ±1.9	
14	*Arrhenatheretum elatioris* M2x, U	980 ±120	630 ± 80	1610 ±210	60.7 ±2.3	3.2 / 1.9
15	*Arrhenatheretum elatioris* M3x, U	749 ± 61	732 ± 61	1481 ±116	50.6 ±8.2	
	Moist meadows					
16	*Sanguisorbo-Festucetum commutatae* M2x, U	1490 ± 70	1340 ± 60	2830 ±140	52.6 ±1.6	4.7 / 2.5
17	*Polygono-Cirsietum palustris* UM, U	2099 ±217	944 ± 77	3043 ±253	59.7 ±4.2	
18	*Polygono-Cirsietum palustris* M1x, U	1513 ±154	916 ± 45	2429 ±176	57.5 ±3.2	
19	*Polygono-Cirsietum palustris* M2x, U	1610 ±170	1880 ±190	3490 ±360	46.1±8.5	7.4 / 3.4
20	*Polygono-Cirsietum palustris* M3x, U	1167 ± 87	1811 ±139	2978 ±214	37.7± 8.3	
21	*Polygalo-Nardetum strictae* UM, U	1400 ±200	1250 ±180	2650 ±390	52.8 ±4.3	4.7 / 2.5
22	*Polygalo-Nardetum strictae* UM, U	1738 ±117	832 ± 65	2570 ±143	63.9 ±1.2	
23	*Polygalo-Nardetum strictae* M1x, U	1167 ± 97	992 ± 69	2169 ±145	53.3±10.3	
24	*Polygalo-Nardetum strictae* M3x, U	1065 ± 69	1009 ±197	2074 ±132	58.9 ±1.4	
25	*Junco-Molinietum coeruleae* UM, U	840 ± 40	1370 ± 70	2210 ±120	38.0 ±3.8	3.5 / 1.3
26	*Junco-Molinietum coeruleae* UM, U	1140 ± 94	1213 ±145	2353 ±230	42.9 ±5.1	
27	*Junco-Molinietum coeruleae* M1x, U	764 ± 45	1008 ± 75	1772 ±118	42.4 ±3.9	
28	*Junco-Molinietum coeruleae* M3x, U	820 ± 49	590 ± 44	1410 ± 82	64.4 ±1.8	
	Grass stands of clear-cut areas					
29	*Avenella flexuosa* UM, M	211 ± 28	81 ± 11	292 ± 39	72.3	
30	*Avenella flexuosa* UM, M	1130 ± 76	72 ± 6	1190 ± 79	95.0	
31	*Calamagrostis arundinacea* UM, M	1334 ±165	687 ± 97	2021 ±252	66.0	
32	*Calamagrostis villosa* UM, M	2327 ±136	705 ± 67	3032 ±158	76.7	
33	*Calamagrostis villosa* UM, M	2000 ±110	850 ± 70	2850 ±190	77.0 ±1.2	8.0 / 5.6
34	*Calamagrostis villosa* UM, M	2330 ±200	970 ±100	3300 ±290	76.0 ±1.8	10.3 / 8.1
35	*Calamagrostis villosa* UM, M	1897 ±105	254 ± 20	2151 ±173	88.2	

highest dry mass of undecomposed dead belowground plant matter (over 300 g·m^{-2}) was recorded in extreme habitats (*Trifolio-Festucetum rubrae* and several wetland stands). In most of the studied meadows (with an exception of grass stands of clear-cut areas) the belowground necromass exceeded 1000 g·m^{-2} (Table 2). Mowing reduced the amount of total belowground dry mass, namely that of its living component, as well as the percentage of living parts in the total belowground dry mass. The dry mass of living belowground plant parts mostly decreased by more than 500 g. m^{-2} in meadows mown three times a year (Fig. 1, Table 2).

In the Cuban savanna communities under study, the total dry mass of belowground plant organs varied mostly around 1000 g·m^{-2}. However, great variation was found in the proportion of living belowground organs in total belowground dry mass. The percentage of living roots in total dry mass of roots was lower in natural savanna communities (33.8 and 50.4 %, Table 3) than in the anthropogenic savanna stands dominated by *Axonopus compressus* (74.1 %) and *Panicum maximum* (67.6 %). In natural savanna stands, 433 and 517 g·m^{-2} of living belowground biomass was recorded, while in anthropogenic savanna stands dominated by *Axonopus compressus* it was 745 g·m^{-2}, i. e. nearly twice as high. Relatively great differences were found in the percentage of living belowground biomass (including both roots and rhizomes) in the total belowground dry mass in anthropogenic savanna dominated by *Paspalum notatum* growing on the slope. The highest value (64.7 %) was found in the *Paspalum* stand growing in the lowest part of the slope under favourable conditions as evidenced by a high proportion of living rhizomes, whereas the lowest value (39.2 %) was found on the upper part of the slope. However, the percentage of living roots in total root dry mass was substantially lower, ranging between 21.9 to 23.5 % (Table 3). The *Paspalum notatum* stand on the lower part of the slope had the highest amount of both total (1735 g·m^{-2}) and living (1122 g·m^{-2}) belowground dry mass, i. e. by 600 and 400–500 g·m^{-2}, respectively, more than the other stands

Fig. 2. – Dry mass of living belowground biomass (LB) and percentage of living belowground biomass (% L) in total belowground dry mass in Cuban savannas and forests. Data on Cuban forests represent only fine living roots.



studied. The more favourable the habitat (i. e. more wet and nutrient-rich) the greater was the rhizome and shoot growth of *Paspalum* and the smaller was the root production.

Results from various Cuban forests display a great variation in dry mass of fine roots (< 1 mm – Fig. 2, Table 2). Nevertheless, they indicate that specific root biomass accumulation occurs in individual types of studied forests and in the proportion of fine living roots as well. The highest total dry mass of fine roots was found in mangrove forests (1400–1600 $g \cdot m^{-2}$) while the lowest values were recorded in evergreen broad-leaved forests (160–212 $g \cdot m^{-2}$). In semideciduous forests, the dry mass of fine roots was about 400 $g \cdot m^{-2}$, i. e. about twice as high as in evergreen broad-leaved forests. However, the percentage of living fine roots in the total dry mass of fine roots of Cuban forests varies considerably: 23 and 49 % living roots were recorded in semideciduous forests, 30 and 56 % in evergreen broad-leaved forests, and 41 and 47 % in mangrove forests. Thus, the highest values of living fine root biomass were found in the mangrove forests (554–758 $g \cdot m^{-2}$) while the lowest dry mass of fine roots, ranging between 64–90 $g \cdot m^{-2}$, was found in both studied evergreen broad-leaved forests in the mountain area.

Table 3. – Dry mass of living, dead and total belowground plant parts and proportion of living roots in dry mass of total roots (mean values ±1S.E.) in Cuban savannas and forests. Ratios of total belowground to aboveground dry mass (TR/TS) and live belowground to aboveground dry mass (LR/LS) of savanna stands are also given. In Cuban forest, only data on fine roots are shown. Location: Yaguaramas, Cienfuegos Province (1, 9), Isla de Pinos (2, 8,), Biosphere Reserve of Sierra del Rosario, Pinar del Rio Province (3–6, 10, 11), Habana, Habana Province (7); Majana, Habana Province (12, 13). A – alluvial, L – lowland, M – mountainous. Community: [a]*Bursera simaruba-Pithecellobium lentiscifolium*, [b]*Lysiloma bahamense-Bursera simaruba*, [c]*Pseudolmedia spuria-Matayba apetala*, [d]*Hybiscus elatus*. Source: 1–3, 7 – Fiala & Herrera (1988); 4–6 – Fiala et al. (1991); 8–11 – Fiala & Hernández (unpubl.); 12–13 – Fiala & Hernández (1993).

	Type of stands, location	Belowground dry mass Living ($g \cdot m^{-2}$)	Dead ($g \cdot m^{-2}$)	Total ($g \cdot m^{-2}$)	Living roots (%)	TR/TS and LR/LS
	Natural savannas					
1	*Byrsonimo-Andropogonetum* L	433 ± 37	798 ± 63	1231 ± 99	33.8 ±4.5*	1.8 / 2.8
2	*Phyllantho-Aristidetum* L	517 ± 51	498 ± 48	1015 ± 98	50.4 ±3.6*	2.2 / 3.8
	Anthropic savannas					
3	*Axonopus compressus* L	745 ± 62	327 ± 25	1073 ± 87	74.1 ±2.1*	1.7 / 2.4
4	*Paspaletum notati* – upper slope part L	512 ± 78	795 ± 78	1307 ±134	23.5 ±1.6	1.9 / 1.3
5	*Paspaletum notati* – midde slope part L	541 ± 54	641 ±107	1182 ±134	22.2 ±3.4	1.9 / 0.9
6	*Paspaletum notati* – lower slope part L	1122 ±176	613 ±128	1735 ±247	21.9 ±0.6	1.3 / 1.7
7	*Panicum maximum* L	–	–	–	73.9*	
	Forests					
8	Semideciduous broad-leaved forest [a] L	200 ± 24	209 ± 25	409 ± 48	48.8 ±0.4	
9	Semideciduous narrow-leaved forest [b] L	87 ± 12	284 ± 39	371 ± 50	23.4 ±4.5	
10	Evergreen broad-leaved forest [c] M	64 ± 6	148 ± 14	212 ± 19	30.2 ±3.2	
11	Evergreen broad-leaved forest [d] M	90 ± 9	70 ± 7	160 ± 16	56.3 ±6.1	
	Mangrove forests					
12	*Rhizophora mangle* A	758 ± 42	851 ± 49	1606 ± 90	47.1 ±0.4	
13	*Avicennia germinans* A	554 ± 30	804 ± 45	1358 ± 75	40.8 ±1.5	

* Data on the proportion of living belowground biomass are given.

Discussion

The proportion of living biomass in total belowground dry mass varied in studied grasslands over a wide range (23–80 %). The lowest values (10–40 %) were found in wet meadows and wetlands. Dry conditions appear to increase root mortality (Speidel 1976, Pielota & Smucker 1995) hence the large disappearance of roots and consequent decrease in both living and total root dry mass results from the decrease of soil moisture content. On the other side, both decreased and increased soil moisture can be associated with a decrease of the proportion of living biomass, reflecting enhanced accumulation of undecomposed dead roots. Therefore the highest amount and proportion of living belowground biomass was noted in moist meadows situated around the middle of the soil moisture gradient (Fiala 1990a, b, 1997). Similarly, Harrach & Kunzmann (1983) found, regardless of the type of plant community, a lower proportion of living belowground biomass either in the wettest or the driest habitat.

The scanty literature data on the percentage of living biomass in the total belowground dry mass of similar types of meadows are in accordance with our results: 87–91 % (630–750 $g{\cdot}m^{-2}$) and 57 % (850 $g{\cdot}m^{-2}$) of living belowground biomass were recorded in stands of *Arrhenatheretum* and *Hieracio-Nardetum* (Plewczyńska-Kuraś 1976, Kotańska 1975). Similarly, very low proportion of living biomass in total belowground dry mass was found in wet meadows and wetlands such as in the stands of *Carex gracilis* (10–27 % – Vagina & Shatochina 1972) and *Carex aquatilis* (25 % – Shaver & Billings 1975). However, living biomass in sedge-moss meadow communities attained 52 % of total belowground dry matter (Muc 1977). Living belowground biomass varied around 400 $g{\cdot}m^{-2}$ (27 and 36 % of total dry mass) in the *Molinia*-community of wet heathland (Berendse et al. 1987).

The present study found a greater amount of living belowground biomass (1200–2100 $g{\cdot}m^{-2}$) in moist meadows of *Polygalo-Nardetum* and *Polygono-Cirsietum* growing on habitats with lower soil nutrient content (cf. Balátová et al. 1977, Fiala 1990a, 1997). Nutrient deficiency increases the amount of roots and prolongs their life span (Speidel & Weiss 1972, Speidel 1976). Throughton (1981, 1983) reported considerable differences between the life span of grass roots of various species. For example, *Nardus stricta* growing in nutrient-poor conditions had relatively long-living roots. This is also in agreement with the generalization that root longevity is greater in infertile habitats (Chapin 1980, Nadelhoffer et al. 1985, Cheng et al. 1990). Similarly, our data indicate that fertilization mostly resulted in a decrease of the percentage of living biomass in total belowground dry mass (Fiala & Studený 1987, Fiala 1990b).

The highest proportion of living roots was recorded at the beginning or in the middle of the summer and the lowest in the autumn (Titlyanova et al. 1997, Fiala 1998). The belowground plant biomass was often sampled at the end of the vegetation period (Table 1), but the percentage of living belowground biomass in meadows studied might be higher during the summer.

Frequent mowing and grazing has been reported to decrease the proportion of living belowground parts (Titlyanova et al. 1988, Fiala 1997) and belowground biomass (Schuster 1964, Richards 1984, Fiala & Studený 1987, Pielota & Smucker 1995, Klimešová & Čížková 1996). Our results strongly support this hypothesis (Fig. 1, Table 2). However, the higher amount of living and total roots was also recorded in mown and moderately grazed sites (Svejcar & Christiansen 1987, van der Maarel & Titlyanova 1989, Benning & Seastedt 1997).

In the mountains, the proportion of living belowground organs found in grass stands of clear-cut sites was usually quite high (66–95 %) and values of both living and total belowground dry mass in *Calamagrostis villosa* stands were very high in comparison with other studied grass stands. *Calamagrostis villosa* has a very dense rhizome and root systems (Fiala 1989). In addition, the biomass of belowground organs and R/S ratio increase with decreasing temperature (Davidson 1969, Sims & Singh 1971). Eissenstat & Yanai (1997) reported that roots may live longer in cooler environments and that root production was greater at lower altitudes. However, root longevity was higher in higher altitudes.

Data on the living and total belowground dry mass of savanna stands also vary considerably due to various soil moisture regimes (Hernández & Fiala 1992, Fiala et al. 1991). Different rates of decomposition of dead belowground plant material are therefore reflected in different accumulation rates of not yet fully decomposed plant parts affecting considerably the amount of dead and total belowground plant matter.

In Cuban forests, the percentage of living fine roots was lower than reported by Silver & Vogh (1993) for wet forest in Puerto Rico (60–70 %, ranging around 200 $g \cdot m^{-2}$). The estimates of mangrove living and total fine root biomass are, in the majority of cases, the largest reported so far for tropical and temperate forests (Lugo & Snedaker 1974, Persson 1978, Komiyama et al. 1987, 1988, Sagué & Hernández 1978, Hernández et al. 1992). Komiyama et al. (1988) noted that living roots represented 39 to 46 %, and the amount of living fine root biomass, ranging between 420 to 910 $g \cdot m^{-2}$ in Indonesian mangroves, was very similar to the results we obtained in Cuban mangrove forests. Mangroves can allocate much of their net primary production to roots. These roots provide for respiration and nutrient uptake in unstable and anaerobic alluvium. A high amount of total fine root dry mass (670 $g \cdot m^{-2}$) was also found in Cuban rain forests (Hernández et al. 1992).

Most studies published on the belowground biomass of grasslands give total dry mass of belowground plant organs. Wide ranges for both total belowground plant matter and R/S values published in literature illustrate the difficulty of comparing these values obtained in different types of stands as well as by different studies. This is mostly caused by inconsistent way of separating living and dead roots. This fact is clearly demonstrated by R/S values calculated by using dry mass of both total and living belowground plant parts. The ratio varies between 1.8–12.9 for studied temperate meadows, if all parts (living and dead) are considered (Table 1). Werger (1983) reported the highest R/S values for dry (3.0–6.0) and wet grasslands (7.0–12.4) whereas the value found in fresh meadows was as low as 1.5 (see also Evdokimova & Grishina 1968, Kotańska 1967, 1975, Jakrlová 1971, 1975). Because of a low decomposition rate and accumulation of undecomposed dead roots in both dry and wet habitats, the estimated data based on total dry mass of belowground plant parts are somewhat misleading, making thus comparisons of these values rather difficult (Fiala 1990a). Ratios of living belowground and aboveground biomass (except of litter) illustrate biomass partitioning which is much closer to the real distribution of plant biomass. R/S values estimated from living root biomass are substantially lower then R/S values based on dry mass of total belowground organs, and this was more pronounced in meadows of dry and wet habitats (Table 2). These ratios were lowest in the wettest sites (0.2–0.9) and increased to 2.9 and 3.4 with decreasing soil moisture (Fiala 1990a). Higher values were recorded for grass stands of clear-cut sites (5.6 and 8.1). In savannas, no great differences exist between belowground to aboveground biomass ratios if all parts are considered (1.3–2.2). However, the highest ratios, 2.8 and 3.8, were recorded in natural savannas, when only living biomass was taken into account. The lower values of this ratio were found for anthropogenic savannas (0.9–2.4).

The conclusions of the present paper are in accordance with most of the data published in literature. However, they show that both the living and total dry mass of belowground plant parts of moist meadows may be even higher than the upper limits indicated by previous studies. Management, i.e. fertilization and frequent mowing of grass stands, influences substantially (mostly negatively) both the percentage of living roots and living belowground plant biomass. Belowground plant matter of the savanna stands reported here is approximately average in terms of literary data (Fiala & Herrera 1988, Fiala et al. 1991).

The amount of living belowground plant biomass mostly depends on the type of plant community. The proportion of living plant organs in the total dry mass of belowground plant parts and the amount of root necromass reflects mainly specific differences in the life span of roots, root mortality and differences in the decomposition rate of dead belowground plant parts under different conditions of habitats such as soil moisture and fertility.

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Souhrn

Práce shrnuje a hodnotí výsledky získané při studiu zastoupení živých podzemních částí rostlin ve veškeré podzemní biomase u různých typů lučních společenstev, ostřicových porostů mokřadů, travinných porostů odlesněných ploch a některých kubánský savan a lesů. Ke stanovení živých kořenů bylo užito barvicí techniky a náročného vizuálního třídění podzemní biomasy, která byla odebírána z půdních monolitů. Rozdíly v množství živé podzemní biomasy souvisely většinou s typem rostlinného společenstva. Největší množství živé podzemní biomasy (1000 až 2300 g·m^{-2}) bylo nečastěji stanoveno u společenstev nekosených vlhkých luk *Polygono-Cirsietum palustris* a *Polygalo-Nardetum* (přes 60 % živé podzemní biomasy) a u travinných porostů horských lesních mýtin v oblasti Beskyd (66–95 %). Menší procentuální podíl i množství živé podzemní biomasy (23,4 %, 860 g·m^{-2}) bylo také na nejsušším stanovišti u společenstva *Trifolio-Festucetum rubrae* a u několika porostů mokřadů (10–13 %, okolo 500 g·m^{-2} nebo i méně živé podzemní biomasy). Kosené luční porosty charakterizoval nižší procentuální podíl živé podzemní biomasy a nižší hmotnost sušiny živých i veškerých podzemních částí. 433 a 517 g·m^{-2} (34 a 50 %) živé podzemní biomasy bylo zaznamenáno v porostech přirozených savan, zatímco její hmotnost sušiny dosáhla až 745 g·m^{-2} (74.1 %) a 512 až 1122 g·m^{-2} (39,2–64,7 %) v porostech antropických savan s dominantními druhy *Axonopus compressus* a *Paspalum notatum*. Procentuální zastoupení živých jemných kořenů ve veškeré hmotnosti jemných kořenů kubánských lesů bylo dosti variabilní: 41 a 47 % (554–758 g·m^{-2}) v mangrovových lesích, 30 a 56 % (64–90 g·m^{-2}) ve vždyzelených širokolistých lesích a 23 a 49 % (87–200 g·m^{-2}) u poloopadavých lesů. Poměry hmotnosti sušiny živé podzemní a nadzemní biomasy, které lépe charakterizují distribuci biomasy než R/S poměry zahrnující živé i mrtvé části rostlin, byly nejnižší u porostů mokřadů (0,2–0,9) a antropických savan (0,9–2,4) a nejvyšší u temperátních čerstvě vhkých a vlhkých luk (2,9–3,4) a přirozených společenstev savan (2,8–3,8). Procentuální zastoupení živé podzemní biomasy ve veškeré hmotnosti podzemních rostlinných částí a množství mrtvých kořenů bylo značně variabilní, což může odrážet rozdíly v mortalitě kořenů a v rychlostech dekompozice odumřelých částí, které souvisejí s vlastnostmi stanoviště (především vlhkostními poměry a zásobou živin v půdě).

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Vegetace Chráněné krajinné oblasti a Biosférické rezervace Křivoklátsko
1. Vývoj krajiny a vegetace, vodní, pobřežní a luční společenstva

Agentura ochrany přírody Praha a Botanický ústav AV ČR Průhonice 1999, 232 str., cena 400,– Kč [Kniha je v knihovně ČBS.]

Jiří Kolbek inicioval v 80. letech rozsáhlý botanický výzkum Křivoklátska. Výsledky tohoto výzkumu začínají v posledních letech „zahlcovat" knižní trh botanických publikací: Mapa potenciální vegetace, první díl Květeny a recenzovaný první díl Vegetace již byly publikovány. Jednou z výhod často kritizovaného grantového financování výzkumu v České republice je tlak na řešitele, aby byly výsledky práce publikovány. Osobně považuji tento zisk za jednu z největších předností, zejména tváří v tvář množství výzkumných prací v minulosti, které nebyly nikdy zakončeny kvalitní publikací. Navíc, ty správy CHKO a národních parků, kterým se podařilo pracovně zaangažovat některé přírodovědecké pracovní týmy, získávají v posledních letech nesmírně cenné podklady pro svou práci. Recenzované dílo je zahájením řady věnované vegetaci, která je plánována do tří dílů.