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BELOWGROUND PLANT BIOMASS OF GRASSLAND ECOSYSTEMS AND ITS VARIATION ACCORDING TO ECOLOGICAL FACTORS

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Abstract

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Total belowground plant biomass (TBB, comprising both living and dead plant parts), percentage proportion (PLBB) and amount of living biomass (LBB), as well as, yearly net belowground biomass production (BNBP) and root turnover (TO) were assessed and compared in various stands of grasslands studied in the Czech Republic, northeaster part of USA and in Cuban savannas. TBB assessed in 45 different grassland stands varied in a broad range of values. There was mostly only 1000 to 1500 g DM m^{-2} in fresh moist meadows and dry grasslands but 2500 to 3500 g DM m^{-2} in old wet and moist meadows. Higher values (up to 3000 g DM m^{-2}) were also found in mountain grasslands of clearcut areas. PLBB in TBB and LBB were also considerably variable (mostly ranged from 10 to 80% of living parts and from 260 to 2300 g DM m^{-2}). Values of PLBB and LBB gradually increase and TBB decrease from wet meadows through moist and fresh moist meadows to clearcut grasslands. The highest values of LBB were also recorded in the centre of soil moisture gradient of a natural meadow hydrosere (1500 to 1700 g DM m^{-2}). The lowest values of BNBP were recorded in unmowed *Polygalo-Nardetum* stands (750–950 g DM m^{-2} yr^{-1}) and the highest ones in unmowed *Polygono-Cirsietum palustris* (1300 g DM m^{-2} yr^{-1}). 500 g DM m^{-2} yr^{-1} was estimated in a savannas community. Obtained results suggest that TO period of total belowground plant mass is mostly about two to three years in mesophytic meadows and probably longer in stands growing in either dry or wet habitats. Meadow stands rich in plant species and with greater amount of LBB were more resistant to mowing, i.e., the decrease in both TBB and LBB was slower.

Key words: belowground net production, fertilization, living belowground biomass, mowing, seasonal fluctuation, turnover rate

Introduction

Belowground biomass of plants is a very important compartment of grassland ecosystems with respect to both structure and function. Root mass and rhizosphere represent the main pool of organic matter and geobioelements of grassland ecosystems. Stanton (1988) deduces that concretely 60 to 90% of net primary production (belowground plant parts) and 90% of secondary production (microoganisms and soil animals) is concentrated in soil of grassland ecosystems. Similarly, Titlyanova et al. (1999) reported that 70% of the living biomass is located in the soil and no less than 70% of the net primary production is allocated into belowground organs of Siberian meadows and steppes. Data on belowground biomass production of grassland ecosystems occurring at large geographical and temperate scales shown on broader range; they varied between 40 to 87% of total primary production (Hui, Jackson, 2005). Root turnover is a central component of ecosystem carbon and nutrient cycling. Decomposing dead roots enrich soil by organic matter and nutrients and influence substantially soil quality. In grasslands, these processes are particularly important and are considered as one of their main features (Rychnovská, 1983). Gill and Jackson (2000) found that root turnover rates increased exponentially with mean annual temperature for fine roots of grasslands. Therefore to learn patterns and controls of root turnover can be crucial for the evaluation of consequences of climate changes for the processes in grassland ecosystems.

Production of greater amount of living active roots (including greater amount of accumulated reserve substances) represents also higher resistance of stands to fluctuation of external conditions, different impacts, disturbances etc. (Fiala, 1997). Therefore a decrease in production and total amount of belowground plant matter, which can occur under the influence of external conditions, represents, with respect to their important role in ecosystem, a pronounced interference with the functioning of stands in landscape.

The first aim of this paper was to summarize and compare all data obtained in grassland ecosystems by the present author, partly in cooperation with other colleagues, during more than three decades and to answer especially the following questions:

1) How great is the amount of total, living and dead belowground plant parts in various grassland ecosystems?
2) What is the course of seasonal fluctuation of belowground biomass?
3) How is the annual production and turnover rate in belowground biomass?
4) What is the effect of human impact on belowground plant biomass in grassland ecosystems?

The second aim was to determine how our data fit the findings of several papers summarizing numerous data on belowground plant biomass, recorded nearly over the whole world (e.g., Gill, Jackson, 2000; Hui, Jackson, 2005), but mostly not including results of present studies.

Material and methods

Study sites

The examined grasslands were located in the Czech Republic in the Českomoravská vrchovina (Bohemian-Moravian highland) (studied total 21 mown and unmowed stands), in Southern Moravia (11 stands), in Moravian-Silesian Beskydy Mts (7 stands), in northeast part of the USA (8 stands) and in Cuba (7 stands). Twenty one stands located in the Bohemian-Moravian highland) comprised wet meadows (*Caricetum rostratae*, *Scirpetum silvatici*), moist meadows (*Sanguisorbo-Festucetum commutatae*, *Polygono-Cirsietum palustris*, *Polygalo-Nardetum*, *Junco-Molinietum*), fresh moist meadows (*Trifolio-Festucetum rubrae*, *Arrhenathretum elatioris*). In alluvium of southern Moravian lowland, stands belonging to *Glycerietum maximae*, *Phalaridetum arundinaceae* were also studied as well as stands dominated by *Serratula tinctoria* (*Molinion* alliance), *Cirsium canum* (*Cnidion*), *Alopecurus pratensis* (*Cnidion*) and expanding stands of *Calamagrostis epigejos* and *Arrhenatherum elatior*. On dry sites, stands of *Potentilo arenariae-Agrostietum vienalis* were also analyzed. Grass stands of deforested sites in the Beskydy Mts included *Avenella flexuosa*, *Calamagrostis arundinacea* and *C. villosa* stands. Wet meadows dominated by *Carex lasiocarpa*, *C. rostrata*, *C. trichocarpa*, *Cladium mariscoides* and *Eleocharis rostellata* were examined in the north-eastern part of USA. Natural savannas of Cuba represented stands of *Byrsonimo-Andropogenetum* and *Phyllantho-Aristidetum* and anthropic savannas dominated by *Axonopus compressus*, *Paspalum notatum* and *Panicum maximum*. For detailed description of studied sites see Fiala (1979, 1989, 1990a, b, 1998, 2000a, 2001), Fiala et al. (1991, 2004), Fiala, Herrera (1988), Bernard, Fiala (1986), Hernández, Fiala (1992), Seischab et al. (1985) and Tesařová, Fiala (1997).

Methodological approach

Traditional soil blocks and soil cores (see Fiala, 1990a) were taken to the depth of 150 (200) mm for quantitative determination of total belowground dry mass (TBB) since roots were mostly concentrated in upper soil layers. The vital staining method with a solution of Congo red, developed by Ward et al. (1978) and modified by Tesařová et al. (1982), was used to determine the proportion of living and dead roots (see also van der Maarel, Titlyanova, 1989). Living and dead rhizomes and shoot bases were distinguished visually according to their colour and mechanical consistency. We thus assessed the percentage proportion of living (PLBB) and dead (PDBB) belowground biomass as well as the dry mass (DM) of living (LBB) and dead (DBB) belowground biomass.

Methods using soil core technique, including three approaches, were also applied to estimate the annual belowground production (NBBP): (a) a series of TBB measurements were taken over the growing season and the increments of TBB were summed up (see Dahlman, Kutcera, 1965; Sims, Sing, 1978) and, (b) additional parallel soil cores were exposed in soil to assess the amount of decomposed root mass for the correction of NBBP (Titlyanova, 1971). (c) an ingrowth technique for the study of root and rhizome increments was also used (e.g., Persson,1978; Steen, 1984). Turnover values (TO) were calculated (NBBP/TBB). For detailed description of the method see also Fiala (2005).

Results

Amount of dry mass of total belowground plant parts

Data on TBB assessed in 45 stands of various grassland communities are summarized in Fig. 1 and demonstrate the broad range of their variability. Just values of TBB of several meadow stands of a natural hydrosere from the region of the Moravian-Bohemian highland showed a broad range of values (1600 to 3700 g DM m^{-2}). The highest values were recorded in stands belonging to the association of *Trifolio-Festucetum* and *Polygono-Cirsietum palustris* and the lowest values in an *Arrhenatheretum elatioris* stand. The most of the assessed values of TBB were over 2 kg DM m^{-2}. Ratios of TBB to aboveground biomass (TBB/AB ratios) fluctuated in broad range as well (3–12) (Fig. 2). Data on TBB assessed in meadow stands of the Dyje river alluvium after water management measures and elimination of floods, i.e., in the warmer and drier part of South Moravia, were only around 1300 to 1600 g DM m^{-2}. Similarly, lower values than 2 kg m^{-2} were mostly found in dry acidophilic grasslands and also in stands dominated by *Calamagrostis epigejos* expanding into grass stands of

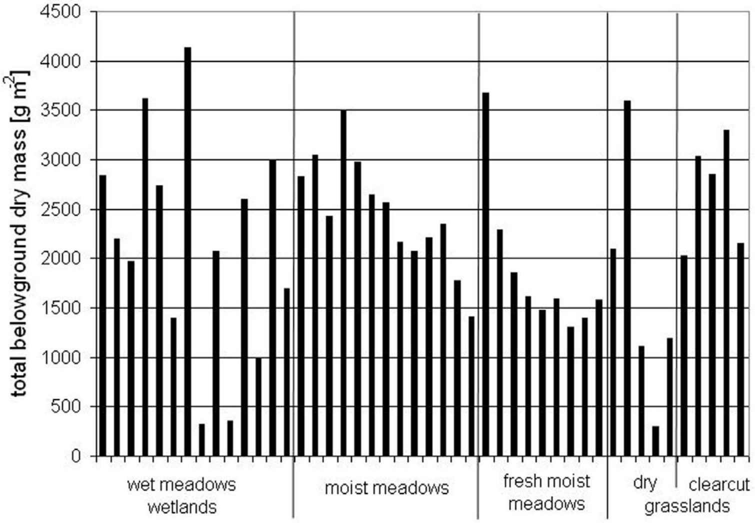


Fig. 1. Comparison of TBB dry mass of various meadow and grassland communities. For other details see Method – Study sites. Figure based on the data recorded by Seischab et al. (1985), Bernard, Fiala (1986), Fiala (1990a, b, 1997, 1998, 2001), Fiala, Zelená (1995), Fiala et al. (1989, 2004), Tesařová, Fiala, (1997).

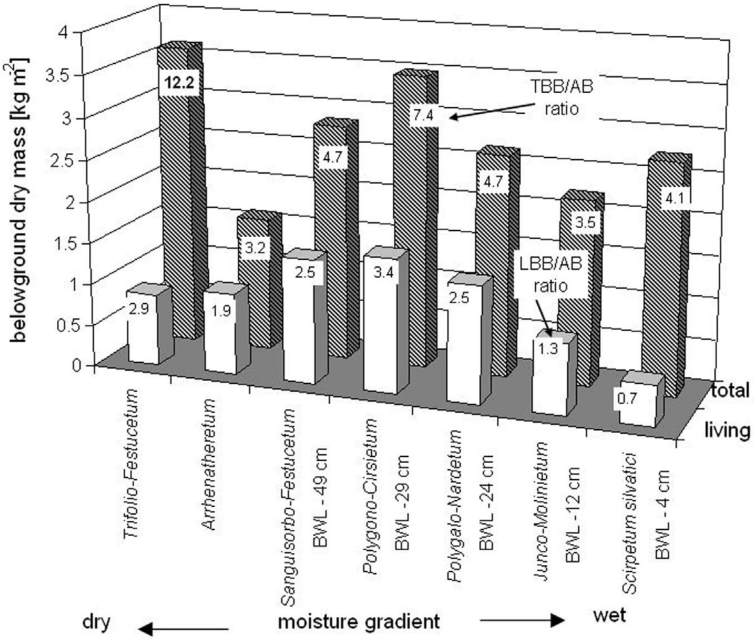


Fig. 2. Variation in TBB and LBB in different meadow stands of a natural hydrosere. BWL – mean belowground water level. Modified from Fiala (1990a) and Balátová et al. (1977).

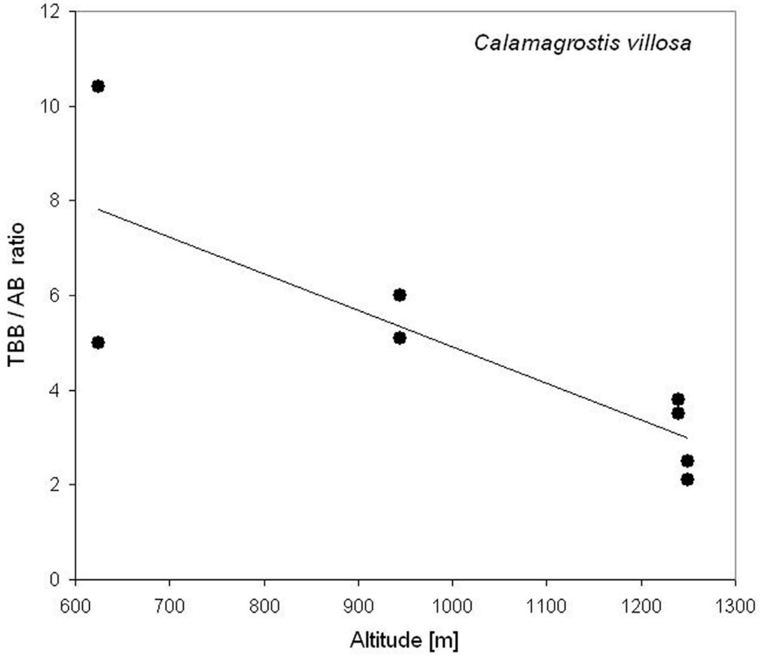


Fig. 3. TBB/AB ratios recorded in *Calamagrostis villosa* stands along an altitudinal gradient in the Moravian-Silesian Beskydy Mts. Modified from Fiala (1998).

southern Moravia. It follows from several studies of root biomass of *C. arundinacea* and *C. villosa* stands on different sites of damaged and deforested forest stands in the Beskydy Mts that TBB in these sites reached values around 2 to 3 kg DM m^{-2}. In *C. villosa* stands, TBB/AB ratio (2.0 to 10.5) decreased with increasing altitude, i.e., with increasing pollution impact (Fig. 3). Relatively high values of TBB (4460 a 4940 g DM m^{-2}) were recorded in wet meadows (in sedge stands) in the north-eastern part of USA. TBB/AB ratio attained in these stands 3.9 and 5.2. The TBB/AB ratio of 12.9 at 3.28 kg m^{-2} TBB was found in old *Eleocharis rostellata* stands in the same region. Considerable accumulation of TBB (about 3 kg m^{-2}) was also assessed in *Carex rostrata* stands in the Bohemian-Moravian highland. In contrast to temperate grasslands, TBB was lower and ranging mostly in a narrow range of values (from 700 to 1300 g DM m^{-2}) in stands of both natural and anthropogenic savannas of Cuba. TBB/AB ratios were also lower (1.3–2.2).

Amounts of living and dead belowground plant parts

Data about PLBB and PDBB were obtained in 35 stands of various types of plant communities. There were meadow stands in the Bohemian-Moravian highland, grass stands of deforested areas in the Beskydy Mts, communities of wetlands in north-eastern part of

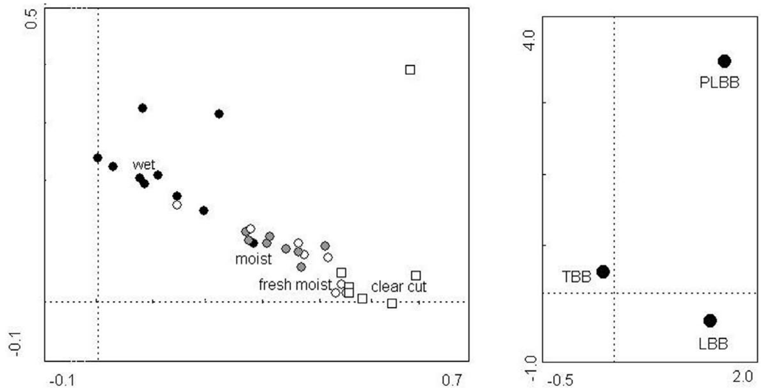


Fig. 4. Indirect gradient analysis (DCA) of data on belowground plant matter of various grassland communities (presentation of samples) (left). Interrelation of TBB, PLBB and LBB on a habitat gradient (relation of measured parameters) (right). Computed from data given by Bernard and Fiala (1986), Seischab et al. (1985) and Fiala (1990a, b, 1997, 1998).

the USA and grass stands of savannas in Cuba. Data recorded in meadow communities in the Bohemian-Moravian highland showed great differences in PLBB (Fig. 2). The greatest PLBB values (60 to 80%) were recorded in *Arrhenatheretum elatioris* and *Polygalo-Nardetum* stands. Enhanced soil moisture, respectively a waterlogged soil profile, resulted in a decrease in PLBB down to 28 and 18%. Similarly, in the relatively driest and in nutrients poor habitat (*Trifolio-Festucetum*), 24% of LBB in TBB was only assessed. Thus LBB of meadow communities of natural hydroseres mostly ranged only from 490 to 1610 g DM m^{-2} (Fig. 2). The highest values of LBB were recorded in stands in the centre of soil moisture gradient and the greatest amount of dry mass of DBB was recorded in the wettest and driest habitats. TBB of grass stands of deforested areas in the Beskydy Mts was formed mostly by living plant parts. In *Calamagrostis villosa* and *Avenella flexuosa* stands, 85% and 83–95% of LBB was found respectively. Assessment of living roots in wetlands of the north-eastern part of USA showed a very low PLBB (11.9 to 18.8%) and considerable accumulation of DBB of sedges (3000 to 3600 g DM m^{-2}). Similarly, only 9.7% (200 g DM m^{-2}) of living roots were found in the old *Eleocharis rostellata* stand. Described differences in TBB and LBB of studied grassland communities, and relationships between them, clearly demonstrate an indirect gradient analysis of all obtained data (Fig. 4). Values of PLBB and LBB gradually increase and TBB decrease from wet meadows, through moist and fresh moist meadows to clearcut grasslands. In natural savannas of Cuba, 430 and 520 g DM m^{-2} of LBB (34 and 50%) was found, whereas it reached to 740 g DM m^{-2} (74.1%) and 510 to 1120 g DM m^{-2} (39.2 to 64.7%) in anthropic ones (Fig. 5). Lower amount of living roots of *Paspalum notatum* (22%) were also estimated in more wet habitats in anthropic savannas.

Very different values of TBB, as well as of TBB/AB ratio, represent considerable difficulty in comparison of various types of stands if living and dead roots were not distinguished. Therefore ratios of LBB and aboveground biomass (LBB/AB) illustrate the biomass parti-

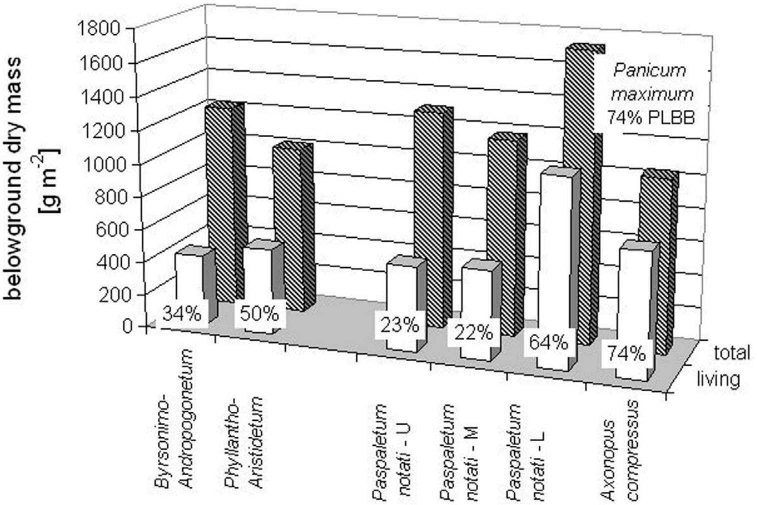


Fig. 5. Comparison of TBB and LBB of various savannas communities of Cuba. From the data recorded by Fiala and Herrera (1988) and Fiala et al. (1991).

tioning which is much closer to the real distribution of plant biomass. LBB/AB ratios were lowest in the wettest sites (0.2–0.9) and increased to 2.9 and 3.4 with decreasing soil moisture (Fig. 2). Higher values were recorded for grass stands of clearcut sites (5.6 and 8.1). In savannas, the highest ratios, 2.8 and 3.8, were recorded in natural savannas and the lower ones (0.9–2.4) in anthropogenic savannas.

Seasonal fluctuation of belowground biomass

The study of seasonal changes in dry mass of TBB of several meadow stands performed in the Bohemian-Moravian highland has shown mostly a typical increase of biomass during June and July, attaining up to 1 kg DM m^{-2}. However, in *Polygalo-Nardetum* stand, these values mostly did not reach over 400 to 600 g DM m^{-2}. Similar seasonal TBB dynamics was found in clear cut grass stands in the Beskydy Mts. The lowest values of PLBB were here usually assessed at the beginning and at the end of the growing season. Maximum daily root increments, assessed in *Polygalo-Nardetum* stand during several years by Titlyanova´s method, were also mostly recorded in June and July (13 g DM m^{-2} d^{-1} on the average), i.e., in a period when aboveground biomass values were the highest and climatic conditions were the most favourable (Fig. 6). When ingrowth core technique was used, maximum daily root increments were smaller (about 9 g DM m^{-2} d^{-1}) and were recorded even earlier (in May). In contrast to temperate grassland, determination of seasonal dynamics of root biomass in the savannas community *Paspaletum notati* in Cuba has shown conspicuous changes in values of TBB reflecting different soil moisture conditions (see Hernández, Fiala,

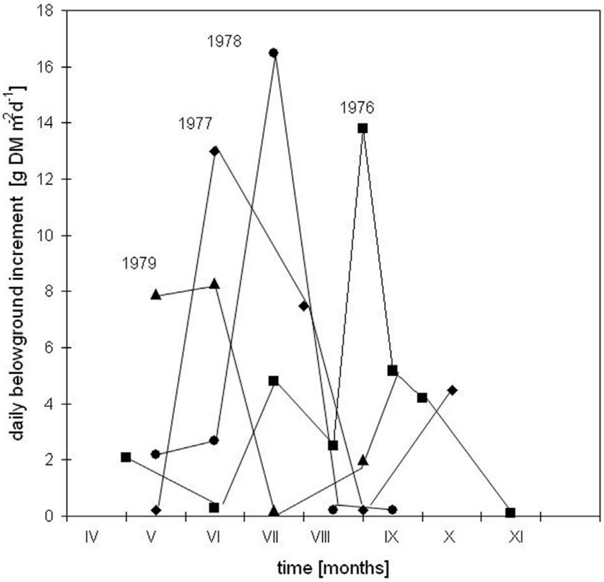


Fig. 6. Variation in daily increments of BB recorded in the course of four growing seasons in a *Polygalo-Nardetum* stand (Bohemian-Moravian highland). Assessed by Titlyanova´s method. From measurements by Fiala (1979, 1983).

1992). A pronounced decrease in TBB, i.e., to 33% of its recorded maximum of dry mass, was assessed during the raining period.

Yearly net production and turnover rate of belowground plant biomass

NBBP determined according to Titlyanova´s method ranged in the stand of *Polygalo-Nardetum* around 800 g DM m^{-2} yr^{-1} (Fig. 7). The average decomposition of 960 g DM m^{-2} of TBB in the course of one year was calculated by means of this method. Similar values were also reached in other unmanaged meadow stands in the same region and they were mostly two to three times higher than the primary production of aboveground parts (Fig. 8). However, data on the NBBP of *Polygono-Cirsietum* stands (both unfertilised or fertilised), estimated with the help of ingrowth technique, have shown lower values (220–330 g DM m^{-2} yr^{-1}) (Fig. 9). NBBP of grassland communities of clearcut areas, estimated from seasonal changes of their dry mass, was 620 g DM m^{-2} yr^{-1} in *C. villosa* stand and 630 g DM m^{-2} yr^{-1} in *Avenela flexuosa* stand, on the average (Fig. 8). Ingrowth technique was also used to determine differences in the yearly increase of roots and rhizomes of *Calamagrostis villosa* and *C. arundinacea* on habitats situated along the gradient of increasing altitude and impact of acidic depositions in the Moravian-Silesian Mts (Fig. 10). Close negative correlations were found between altitude and yearly increment of both roots and rhizomes

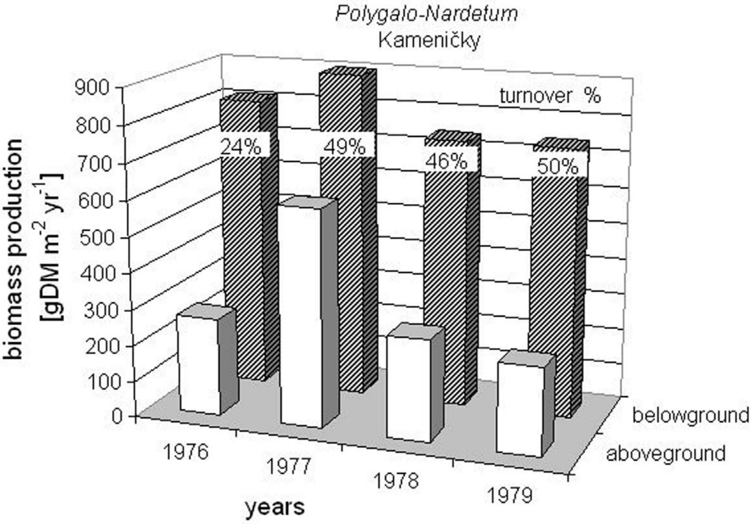


Fig. 7. Comparison of values of estimated BNBP and assessed ANBP. Recorded in the Bohemian-Moravian highland. After Fiala (1983, 1993) see also Jakrlová (1993).

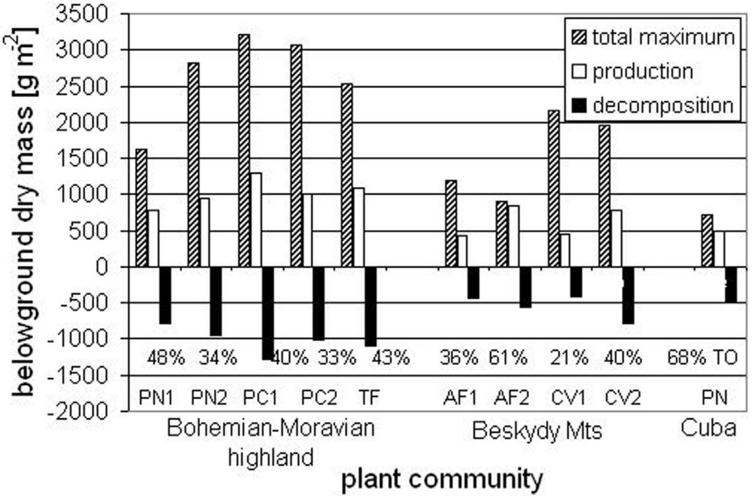


Fig 8. Comparison of maximal TBB, BNBP (max. – min. total dry mass) and amount of decomposed belowground dry mass (calculated from TO values) recorded in grasslands of the Bohemian-Moravian highland, Beskydy Mts. and in Cuba. After Vaněk and Fiala (1981), Hernández and Fiala (1992) and Fiala (1998), supplemented by data of Studený (unpublished).

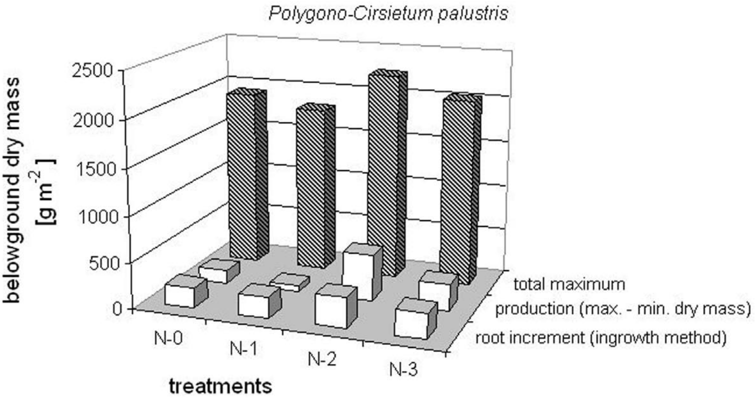


Fig. 9. Comparison of maximal TBB, BNBP (max. – min. total dry mass) and yearly root increments (ingrowth method) assessed in mowed and fertilized *Polygono-Cisietum palustris* stands (Bohemian-Moravian highland). N-0 – not fertilized, N-1 – 30 kg P/ha + 60 kg K/ha, N-2 - 90 kg N/ha + P and K, N-3 - 180 kg N/ha + N and P, all stands were mowed 3 times per year. Recorded by Fiala and Tůma (unpubl).

of *C. villosa*. Thus, results of this study have shown the reduction of yearly increments of roots and rhizomes of clearcut grasses growing in conditions of higher altitudes, i.e., in less favourable climatic conditions, and at a greater impact of pollution. For example, annual increment of *C. villosa* rhizomes attained 51 to 88 m $m^{-2} yr^{-1}$ at the locality of lower altitude (630 m a.s.l.), but only 0.9 and 7.6 m $m^{-2} yr^{-1}$ in stands growing near the mountain tops (1240 or 1250 m a.s.l).

Obtained data enable to evaluate TO of the belowground plant parts, estimated as the ratio between NBBP and maximal TBB values. In a *Polygalo-Nardetum* stand, they were mostly assessed as 0.48, i.e., 48% of TBB was decomposed during one year. However, values 0.24 to 0.55 were calculated for various meadow stands in the Bohemian-Moravian highland (Fig 8). Most of them corresponded to two to three years of TO time (TO period). The highest rates of root decomposition (from 5.3 to 19.1 g DM $m^{-2} d^{-1}$), assessed by Titlyanova´s method, were recorded during the first half of the growing season and also in its end, i.e., in more moist parts of the year. Mean TO values of belowground parts were in *C. villosa* and in *Avenella flexuosa* 0.3 and 0.6, respectively (Fig. 8). TO rate is probably faster in *Avenella flexuosa* (about 1.6 year) than that in *C. villosa* (3.3 years). Remarkable were the findings that in these stands of deforested areas about 600 g DM per m^2 of decomposed roots and rhizomes can come annually into the soil.

In a savannas community of *Paspaletum notati* in Cuba, the estimation of BNBP and amount of decomposed roots (calculated from statistically significant increments and decreases in dry mass of fine and coarse roots) was about 500 g DM $m^{-2} yr^{-1}$, however, the total decease in root dry mass represented 1070 g DM m^{-2} and pointed so to the very fast turnover of root biomass possible in the savannas (Fig. 8).

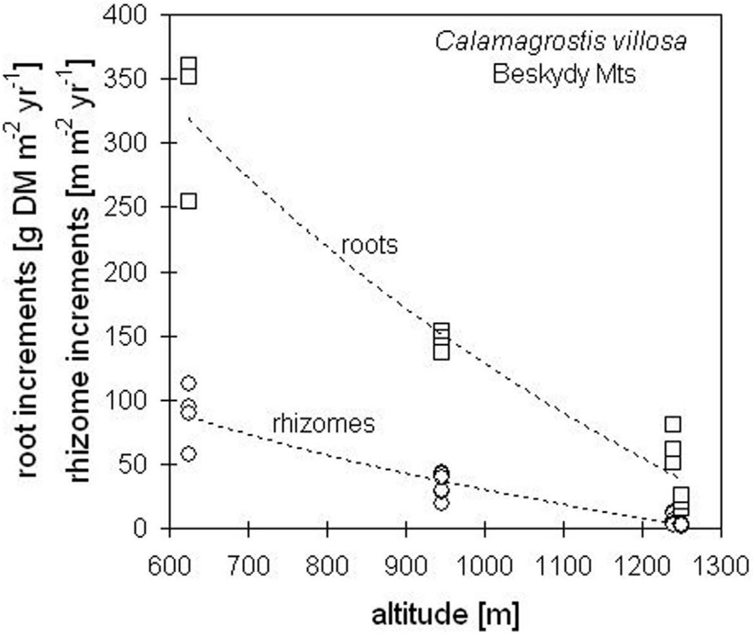


Fig. 10. Root and rhizome increments of *Calamagrostis villosa* recorded along the altitudinal gradient in the Moravian-Silesian Beskydy Mts. The data taken from Fiala (2000b).

Effect of human activities on belowground plant biomass

The effect of different frequency of mowing on root systems of various meadow stands of natural hydroseres, situated in the Bohemian-Moravian highland, was studied in the course of six years (1986 to 1991). Mowing applied once per year led to the greatest reduction of dry mass of TBB only in the third year of application. However, intensive mowing (three times per year) was displayed in the reduction of PLBB already from the first year of mowing (Fig. 11). A slower and smaller reduction of both PLBB and LBB was observed in *Polygalo-Nardetum* and *Arrhenatheretum elatioris* stands when intensive mowing was applied. A rapid and pronounced decrease in PLBB (down by 50 to 67% in comparison with unmown treatments) was recorded in *Caricetum rostratae* and *Junco-Molinietum* stands occurring in wet habitats (Fig. 12). In the contrary, termination of mowing after four years caused pronounced increase of PLBB in all studied stands. Nevertheless, the amount of LBB of stands of wet habitats (*Caricetum rostratae*, *Junco-Molinietum*) did not reach values recorded in unmown stands.

Results of studies of the effect of agrotechnical measures (mowing, fertilization, renovation) on root systems, above all on LBBB and DBB, indicate that the application of lower

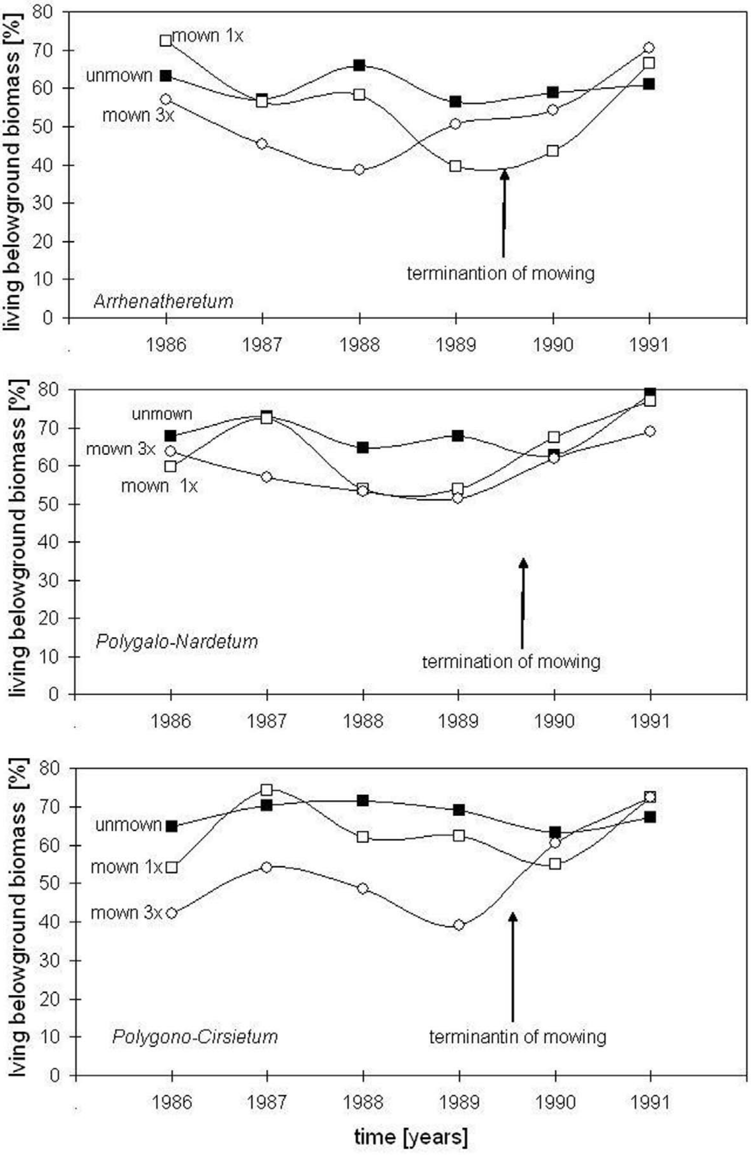
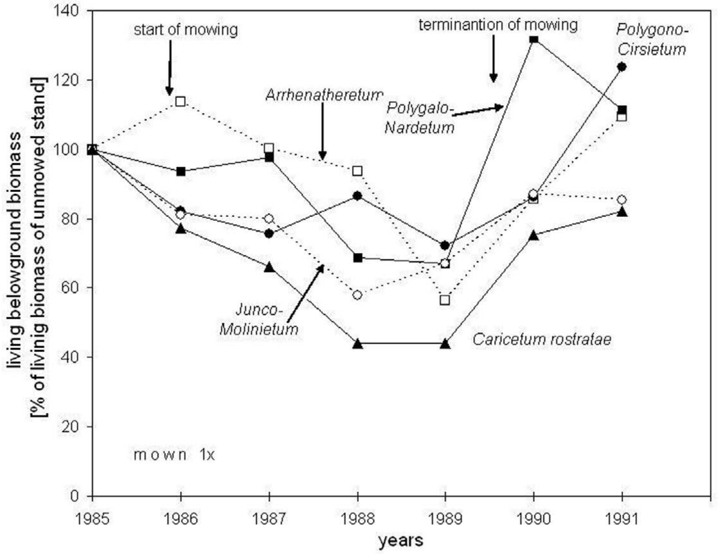


Fig. 11. Changes in PLBB in TBB in meadow stands with different intensities of mowing in the course of 1986 to 1991. Recorded in the Bohemian-Moravian highland. From the data recorded by Fiala (1997).

doses of fertilization (100 kg N ha^{-1}) resulted in seminatural meadow stands (*Polygalo-Nardetum*) in an increase of TBB (e.g., from 2620 to 3310 g DM m^{-2}) (Fig. 13). Application of



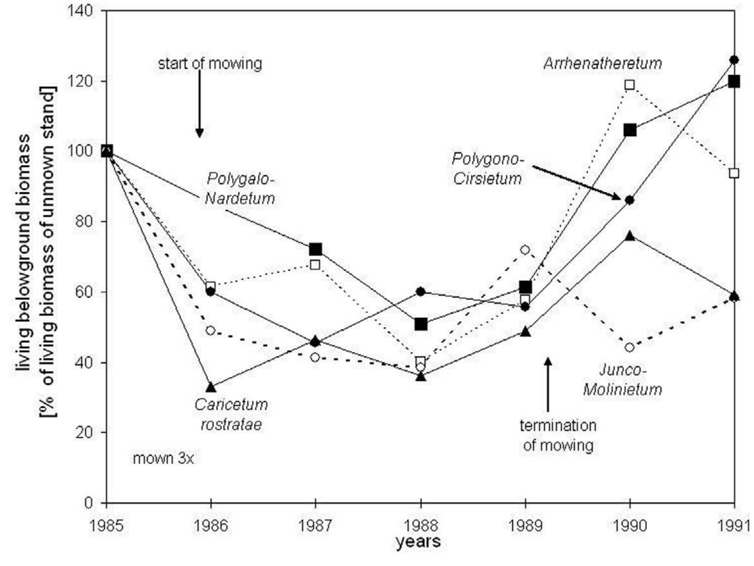


Fig. 12. Comparison of changes in the dry mass of LBB of mowed meadow stands (expressed as a percentage of living belowground of unmowed plots). Recorded in the Bohemian-Moravian highland. Computed from data given by Fiala (1997).

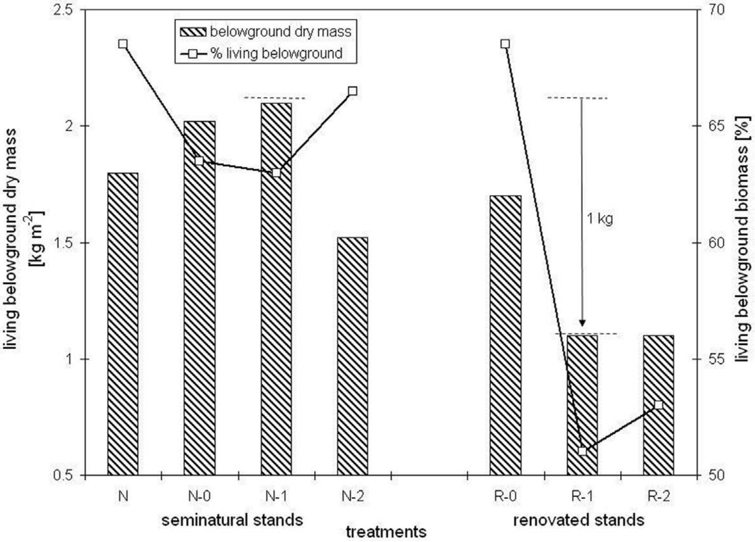


Fig. 13. Comparison of PLBB and amount of LBB assessed in moved and fertilized seminatural *Polygalo-Nardetum* stands (Bohemian-Moravian highland). N-0 – not mown and fertilized stands, N-1 – not fertilized stands, N-2 – fertilized by 100 kg N/ha + 22 kg P/ha + 41.5 kg /ha, N-3 – N, P, K were at the double of previous rate, treatments N-1, N-2 and N-3 were mown 2 times per year. Renovated stands (R-0, R-1 and R-2) were treated in the same way as seminatural stands and mown 3 times per year. Modified from Tesařová et al. (1982) and Fiala and Studený (1987).

double doses of fertilizers caused a decrease in TBB (2360 g DM m^{-2}). In renovated (man made) stands, even the first level of fertilization caused a decrease in TBB (from 2430 to 2290 g DM m^{-2}) while the double dose even down to 2050 g DM m^{-2}. In the renovated stand, the first level of fertilization resulted in an already marked decrease in LBB. Difference in LBB between seminatural and renovated stands attained, at the lower level of fertilization, nearly 1 kg m^{-2} of dry mass. Application of higher doses of fertilizers resulted also in a decrease in TBB, as well as in NBBP in *Polygono-Cirsietum* stands (Fig. 9).

Discussion

Amount of dry mass of total belowground plant parts

The results of studies of numerous grassland communities have shown that the TBB varied in a broad range of values: it often reached 2500 to 3500 g DM m^{-2} in old wet and moist meadows, while mostly only 1000 to 1500 g DM m^{-2} in fresh moist meadows and dry grasslands. Higher values were also found in mountain grasslands of clearcut areas. Published data indicate that generally the highest TBB was recorded in wet meadows and marshes, varying from 2 to 4 and even to 5 and 6 kg DM m^{-2} (e.g., Vagina, 1962; Evdokina, Grishina, 1968; Jakrlová, 1971; Vagina, Shatochina, 1972; Kotańska, 1973, 1975b; Saunders et al., 2006). Studies of mesophytic meadows have shown that their TBB mostly ranges between 0.9 and 2 kg DM m^{-2}. Data on dry grasslands usually fall outside this range, towards lower values (0.5 to 1.5 kg DM m^{-2}), although TBB values of about 3 were also found (e.g., Máthé et al., 1967; Kotańska, 1967; Simon, Kovács-Láng, 1976). High values were also reported from grasslands of mountain regions of Central Slovakia and the Krkonoše Mts, (4.7 kg DM m^{-2} in *Agrostietum rupestris* and 5.8 kg DM m^{-2} in *Polygono-Deschampsietum flexuosae*) (Pecháčková, Krahulec, 1995; Krajčovič, 1988). In addition, it follows from studies of root distribution on grassland sites differing in soil moisture content that TBB increased with increasing moisture of the sites and the highest total root dry mass was recorded around the middle of the studied moisture gradient (Harrach, Kunzmann, 1983). The results of the present study show that the TBB of moist meadows may be even higher than the upper limits indicated in the studies mentioned above. Data for grasslands of the warmer and drier region of southern Moravia represent on average only lower values than those recorded in meadow stands of the Bohemian-Moravian highland (see also Pilát, 1969; Jakrlová, 1971).

The following general rules can be deduced if we summarize findings of both present and previously published studies: Water surplus or deficiency, acid soil reaction and nutrient deficiency impede the decomposition of dead plant parts and increase TBB. Therefore, TBB can be very high under conditions which reduce the decomposition rate and thus cause a build up of undecomposed dead plant material.

Amount of living and dead belowground plant parts

PLBB in TBB varied in studied grasslands over a wide range (10–80%). The lowest values (10–40%) were found in wet meadows and wetlands. The highest PLBB (66–95%) were recorded by present author in grasslands of clearcut mountain areas at higher altitudes. Scanty published data on PLBB of similar types of meadows are mostly in accordance with here presented results. They ranged between 50 to 91% in various grassland communities and from 10 to 52% in wet meadows and wetlands (e.g., Plewcyńska-Kuraś 1976; Kotańska, 1975a; Berendse et al., 1987; Vagina, Shatochina, 1972; Shaver, Billings, 1975; Muc, 1977). Both recorded decreases and increases in soil moisture in temperate and Cuban grasslands can be associated with a decrease of PLBB, reflecting enhanced accumulation of undecomposed dead roots. Similarly, Harrach and Kunzmann (1983) found lower PLBB values either in the wettest or the driest habitat. Titlyanova et al. (1999) investigated 10 Siberian grasslands (meadows and steppes) during 15 years and reported that PLBB ranged from 47–66% and was highest in the mesophytic meadow. The PLBB in TBB and DBB reflects also specific differences in the life span of roots, root mortality and differences in the decomposability of dead belowground plant parts under different conditions of habitats, such as soil moisture and fertility. Roots may live longer in cool environments and thus root longevity is higher in higher altitudes (Eissenstat, Yanai, 1997). There are considerable differences among the life span of grass roots; e.g., *Nardus stricta* and *Molinia coelurea* have relatively long living roots (Troughton, 1981). Plant species growing in low-productive habitats with a low relative growth rate do indeed have both longer-lived leaves and roots (Ryser, 1996). Therefore in European meadows characteristic by nutrient-poor sites can occur plants with longer root life-span than those adopted to nutrient-rich sites. Thus the amount of LBB mostly depends on the type of plant community characterized by specific differences in the life-span of roots, and root mortality of present species. PLBB in TBB and DBB reflect differences in the decomposition rate of DBB under different conditions of habitat such as soil moisture and temperature.

The TBB/AB ratio varies between 1.8 to 12.9 for studied temperate meadows, if all parts (living and dead belowground parts) are considered. Werger (1983) reported the highest TBB/AB 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 similar data published by Evdokinova, Grishina, 1968; Kotańska, 1967, 1975a, b; Jakrlová 1971, 1975). Low temperatures also tend to promote belowground accumulation (Titlyanova et al., 1999). Similar broad range of values of TBB to AB was recorded in the desert grassland (TBB/AB = 2), mixed prairies (3–6) montane grassland (6) and in shortgrass prairie (13) (Sims, Coupland, 1979). Because of a low decomposition rate and accumulation of undecomposed dead roots in both dry and wet habitats, the estimation data based on TBB are somewhat misleading, making thus a comparison of these values rather difficult. Thus, mean LBB/AB values can be substantially lower than the values calculated from TBB and such values can be much closer to the real distribution of plant biomass. Results of the present studies are in accordance with the abovementioned environmental factors of habitats, i.e., these ratios were lowest in the studied wettest sites (0.2–0.9) and increased to 2.9 to 3.4 with decreasing soil moisture. In clearcut mountain sites, these ratios reached higher values (5.6 and 8.1). In savannas, the highest ratios, 2.8 and 3.8, were recorded in natural savannas, when only living biomass was taken into account. Lower values of the ratio were found for anthropic savannas (0.9–2.4).

Seasonal fluctuation of belowground biomass

Seasonal fluctuations of TBB of studied temperate seminatural meadows were characterized by their increase, mostly during the first half of the growing season. The maximum daily increments of belowground biomass (6 to 14 g DM m^{-2} d^{-1}) were recorded in the *Polygalo-Nardetum* in June and July. The rate of decomposition of belowground plant biomass was higher in the first half and also at the end of the growing season: the maximum values varied mostly between 5.3 and 19.1 g DM m^{-2} d^{-1}. According to Titlyanova et al. (1999), the fastest growth of belowground organs of various grassland species can occur early in spring, in the middle (July) or even at the end of the growing season (late August). They reported that wet/dry and warm/cool conditions can change substantially seasonal changes of TBB of *Festuca pratensis* in a mesophytic meadow. That is why the active growth of different organs of plant species may occur at different times of the season and vary from year to year according to climatic conditions.

The effect of climatic conditions (soil moisture and temperature, particularly) is displayed not only in different root dynamics in the course of one growing season but also in the course of several years (Fiala, 1997). Thus, in the framework of multi-annual changes in TBB, considerable differences (up to about ± 1.5 kg DM m^{-2}) were observed in the community of *Polygalo-Nardetum* in the Bohemian-Moravian highland between years in 1976–1983 and 1986–1991 (Titlyanova, Tesařová, 1991; Fiala, 1997). However, in some grasslands TBB may drastically change also during the season. In a steppe-meadow, LBB varied from 500 to 1080 g DM m^{-2} and PLBB from 34 to 72% (Titlyanova et al., 1999).

In Cuban savannas, a pronounced decrease in TBB can occur during raining season following a drought period. There was a close negative linear relationship between soil moisture and TBB, indicating fast decomposition processes in favourable soil moisture conditions. In the contrary, dry conditions appear to induce root death (Speidel, 1976; Pielota, Smucker, 1995). A large disappearance of roots and consequently the decrease in root biomass could thus have resulted from a low rainfall. Titlyanova et al. (1997) reported, that the highest PLBB was recorded at the beginning or in the middle of summer and the lowest percentage in autumn. The number of living root tips recorded in a *Festuca rubra* stand was characterized by a seasonal periodicity with two peaks (in early summer and in autumn) (Speidel, 1976). PLBB can change not only during the growing season but also during years. Szanser (1991) reported that PLBB decreased with the age of meadows. Summarized data indicate that there is a considerable fluctuation of TBB in grassland ecosystems involving changes in PLBB and the amount of DBB given by differences in the intensity of root increments and root decomposition, both in the course of single growing seasons and in the course of several years, which are determined by climatic conditions (soil moisture and temperature, particularly).

Yearly net production and turnover rate of belowground plant biomass

Although the TBB of plants of studied various seminatural grassland communities fluctuated within broad range of values, estimates of their BNBP made by different methods mostly varied within a narrower range, i.e., from the lowest values, recorded in unmowed *Polygalo-Nardetum* stands (750–950 g DM m^{-2} yr^{-1}), and the highest ones in unmowed *Polygono-Cirsietum palustris* (1300 g DM m^{-2} yr^{-1}). The assessed BNBP of studied savannas communities reached only 500 g m^{-2} yr^{-1}. Our estimations fall mostly into the range of data published by several authors. Rychnovská (1993) summarized data recorded in 13 different temperate seminatural grasslands of Eurasia and mentioned that their BNBP has been found to vary between 240 and 1370 g DM m^{-2} yr^{-1}. However, values of yearly root increments estimated by the present author using the ingrowth technique may be substantially lower than those calculated mostly from seasonal changes of total belowground dry mass (see Fiala, 1998; Ostonen et al., 2005). Hui and Jackson (2005) concluded from a large collection of field biomass measurements that BNBP varied from 228 to 2147 g DM m^{-2} yr^{-1} from savannas to cold desert steppes. Humid temperate and alpine meadows had intermediate mean values and small interannual variability in this fraction. They also found that proportion of BNBP in the total net primary production was negatively correlated with means of annual temperature and precipitation across sites. However, in the intensively studied meadow stand of *Polygalo–Nardetum*, the highest BNBP was found in a relatively warm and moist year (1997), when the highest aboveground biomass production was also recorded. Similarly, BNBP can differ in *Elytrigia* steppe with a large reduction in the dry year (Titlyanova et al., 1999). Andrzejewska (1991) recorded the highest yearly root increment (1303 g DM m^{-2} yr^{-1}) on an undrained swamp, while lower root increments were characteristic of drained, cultivated and managed meadows (173–567 g DM m^{-2} yr^{-1}). Negative effect of pollution (soil acidification, nitrogen excess, etc.) on root and rhizome production occurring in deforested areas of the uppermost mountain zone can be also intensified by other unfavourable factors of environment of such sites (cf. Pyšek, 1993; Koppish, 1994; Persson et al., 1995; Eissenstat, Yanai, 1997; Fitter et al., 1998). The assessed lower BNBP in studied Cuban savanna stand can be in reality higher, and likewise higher than that in temperate regions, since faster TO can mask root increments (see e.g., Menaut, Cesar, 1982).

The average daily increment of belowground biomass was 4.7 g DM m^{-2} d^{-1} for four growing seasons in *Polygalo-Nardetum*, and this value was approached by the average daily decomposition of the belowground biomass, i.e., 4.1 g DM m^{-2} d^{-1}, indicating TO values closely below 50%. Calculated data on TO rate of TBB of studied stands of the temperate region, estimated as the ratio of BNBP related to the recorded maximum TBB, varied from 0.24 to 0.61 (about 24 to 61% of total belowground biomass was renewed annually, 38% on average). Similar data were also assessed in different types of grassland of the temperate region (e. g., Dahlman, Kucera, 1965; Kotańska, 1967, 1975a, b; Sims, Singh, 1978; Tomaškin, 2003) varying mostly between 0.25 to 0.50. Nevertheless, Titlyanova (1971) recorded that about 80 to 90% of the belowground plant matter in a temperate grassland was exchanged during a year. Data on TO values recorded over the whole world were reviewed by Gill and Jackson (2000). They concluded that there is a strong positive exponential relationship between root TO in grasslands and the mean annual temperature. There was no clear relationship between precipitation and TO. They reported that the mean annual TO for roots of grasses was 55%. Lower TO values of 24% and 21–36% were recorded, respectively, in studied meadow stands in the Moravian-Bohemian highland and in clearcut grass stands in the Beskydy Mts in warm and dry years. Gill and Jackson (2000) reported that root TO decreased from tropical to high-latitude systems. Thus the highest value was calculated for the studied Cuban savannas (68%), but this value can be still underestimated and probably not reflecting a real situation.

Obtained results suggest that the BNBP of grassland communities can attain mostly two to three times higher values than the aboveground biomass production and represents so a very important part of primary production of these ecosystems. The TO period of TBB mostly lasts about two to three years in mesophytic meadows and probably longer in stands growing in either dry or wet habitats. However, the resulting estimates of annual root production should be used with caution, because the data were obtained with some methodological problems (cf. Singh et al., 1984; Vogt et al., 1986; Cheng et al., 1990; Lauenroth et al., 2006).

Root biomass is considered as the most important stabilizing element in grasslands. Therefore, the information on the extent of variation in the amount of belowground plant biomass, compared with biomass values of unmown stands, provides the possibility to evaluate the resistance of plant communities to human impact, i.e., the ability of a system to avoid displacement during a stress period. Fiala (1997) summarized data on the effect of mowing on TBB published by several authors and concluded that these activities usually resulted in a decrease of TBB, however the response of TBB does not follow the same tendency in all communities. Similarly, Milchunas et al. (1993) deduced from multiple regression analysis performed on worldwide data set that TBB displayed both positive and negative values in response to grazing. Mowing impact resulted in studied stands in a decrease in PLBB in TBB and also in a reduction of the amount of LBB. Results of other studies showed that TBB of *Agropyron dasystachyum* was even reduced by 30% after 3 years of defoliation repeated at 6-week intervals (Zhang, Romo, 1994). Similarly, 26 to 45% of the root length and 17% to 28% of root biomass produced by grasses during the year was reduced by cutting (Guo et al., 2005; Chandra, Tanaka, 2006). Titlyanova et al. (1988) reported that PLBB were mostly lying between 57 and 65% in ungrazed grasslands, and they varied, respectively, from 38 to 62% and from 21 to 63% in the moderately and overgrazed communities. Mowing negatively affects the span of root life (Troughton, 1981). Thus the higher DBB was recorded in grazed (1054–1246 g m^{-2}, Titlyanova et al., 1988) and mowed grasslands (Benning, Seastedt, 1997), which were similar to the studied meadow stands. The higher amount of LBB and TBB was also recorded at a moderately grazed site. The increase in aboveground productivity, induced by moderate grazing, may account for this results (cf. Parton, Risser, 1979; Detling, 1979; Maarel, Titlyanova, 1989; Titlyanova et al., 1988). A higher species diversity of meadow stands offers more possibilities – thanks to the mobilization of various compensation mechanisms – for the stabilization of their production. For example, fluctuations in the abundance of species with different adaptive modes may be a mechanism stabilizing the community function in varying environments (Rychnovská, Jakrlová, 1990). McNaughton (1983) listed meristem number and location as critical factors of a plant´s ability to tolerate defoliation. In addition, the ability of roots to survive for prolonged periods of time and to form a larger active root system, together with physiological links between various generations of shoots in the tufts of perennial grasses during relatively long periods, can lead to their rapid regeneration and to an increase in their resistance to changes in ecological conditions.

Results of the present author also demonstrate that the effect of the mowing impact on meadow stands, which consist of greater amount of living belowground biomass and were more rich in plant species, were more resistant to mowing and they return faster to the initial state, i.e., to the amounts of dry mass of living belowground biomass recorded in unmown stands. This fact is clearly demonstrated by calculated stability of LBB (see Titlyanova, 1979), pointing to a higher K_Q parameters assessed for *Polygalo-Nardetum*, *Polygono-Cirsietum* and *Arrhenatheretum* stands (Fig. 14) involving plant species with a high regenerative ability (Fiala, 1997).

Increased levels of fertilization, and available nitrogen particularly, generally bring about the growth of aboveground plant parts rather than roots. Nevertheless, the absolute amount

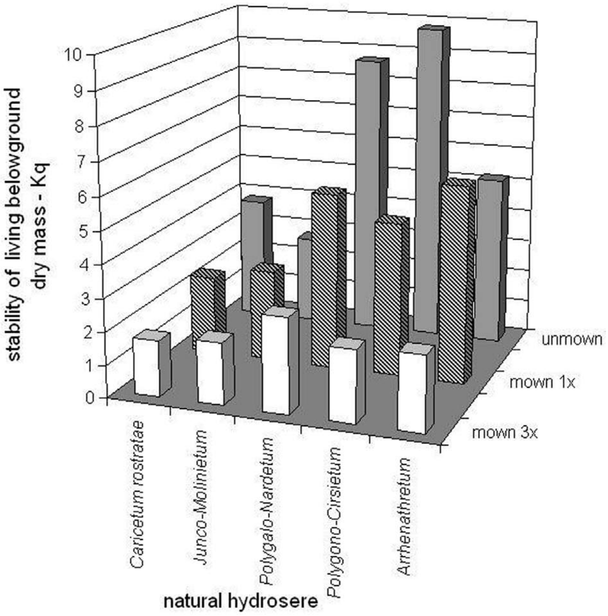


Fig. 14. Changes in the stability of LBB (expressed as changes in K_Q parameters) of meadow stands under the influence of different frequencies of mowing. Figure based on the data given by Fiala (1997). K_Q = mean biomass value of several years / average of biomass differences from mean value of several years.

of root biomass can increase due to fertilization (see summarized data published by Velich, 1986; Fiala, Studený, 1987; Gáborčík, Kohoutek, 1999). Mowing and lower level of fertilization resulted in studied seminatural stands in enlargement of LBB, however, higher doses of fertilization led to a pronounced decrease in LBB. These findings of present author are supported by results of several authors (e.g., Lorenz, 1977; Steen, 1984; Gáborčík, 1985; Li, Redman, 1992) who reported, that TBB decreased at the highest nitrogen level. Lower PLBB (58%) and LBB (370 g DM m^{-2}) were also found in a two years renovated and fertilized stand (Tesařová et al., 1982). Similarly, Gáborčík and Kohoutek (1999) mention that TBB, in comparison with seminatural grasslands, decreased in renovated stands by 57%. Data indicating lower TBB and BNBP in studied renovated than in seminatural fertilized stands were supported by the other data on belowground biomass. Daily increments measured by means of the ingrowth method were smaller in renovated (6.1–6.8 g DM m^{-2} d^{-1}) than in the seminatural stands (7.4–7.6 g DM m^{-2} d^{-1}) (Vachovec, 1983). This fact can be associated with higher mortality and rapid decomposition of dead roots and faster TO of belowground biomass in renovated fertilized stands (see also Tomaškin, 2003). Presented data are also in accordance with findings of Tesařová (1993) who found the lower amount of total carbon content in renovated stands exposed so to disturbance and aeration of the soil profile, resulting in changes of soil moisture and temperature, and, consequently, in the loss of carbon from the soil. We can conclude that mowing and higher doses of fertilization can result in reduction of the amount of LBB, in renovated stands particularly, i.e., in a deterioration of stand resistance to unfavourable impact of environment.

Conclusion

The above-discussed dependences of the amount of living and dead belowground plant parts of grassland ecosystems on conditions of habitats, different anthropogenic impacts and on plant features are summarized in the following schema which is based on results obtained by present author and supported by literature data (e.g., Boot, 1989; Eissenstat, Yanai, 1997; Ryser, 1998; Person, et al., 1995). Such a schematic generalization of very complicated relations represents certain simplifications, nevertheless it can demonstrate, in a short way, how many factors influence the belowground plant biomass in grass stands.

For example the first line below says that an increase or decrease of soil moisture resulted in a reduction of decomposition rate which led to greater total belowground dry mass.

↑↓water (soil moisture) = ↓decomposition = ↑ TBB (living + dead)
↑ temperature = ↑respiration ↑mortality = ↑decomposition dead roots ↑TO =
↓ TBB
↓ nutrients (N) = ↓ decomposition ↓ TO = ↑ TBB
↑ nutrients (N) = ↑ decomposition ↑ TO = ↓ TBB
↓ altitude = ↓ temperature ↓ respiration ↑ root life span = ↑ LBB
↑ altitude = ↓ temperature ↓ decomposition of dead roots ↓TO = ↑ TBB
↑ altitude = ↓ temperature ↑ acid depositions = ↓ root production ↑ root mortality
= ↓ R/S ratio
exposure (southern) = ↑ temperature ↓ mortality ↑TO = ↓ LBB and TBB (+ effect of soil moisture)
↑ irradiation ↑length of growing season = ↑ BNBP
↑ mowing = ↓ carbohydrate supply = ↑ mortality ↑ dead root decomposition = ↑ TO =
↓ TBB
↑ temperature, ↑ respiration, ↑ drought, ↑ frost, ↑ damage by herbivores and pathogens = ↑
mortality ↓ life span of roots
↓ irradiation ↑ shading) = ↓ carbohydrate supply = ↑ mortality
plant species of nutrient-poor habitats = ↑ life span of roots = ↑ LBB
plant species of nutrient-rich habitats = ↓ life span of roots = ↓ LBB

Translated by author

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References

Andrzejewska, L., 1991: Root production of some grass communities on peat soil in river valleys of Biebrza and Narew. Pol. Ecol. Stud., 17: 63–72.

Balátová- Tuláčková, E., Tesařová, M., Zelená, V., 1977: Synökologische Charakteristik einiger wichtiger Wiesentypen des Naturschutzgebietes „Ždárské vrchy". Rozpravy Československé Akademie Věd, 87: 1–115.

Benning, T.L., Seastedt, T.R., 1997: Effect of fire, mowing and nitrogen addition on root characteristics in tall-grass prairie. J. Veg. Sci., 8: 541–546.

Berendse, F., Beltman, B., Bobbink, R., Kwant, R., Schmitz, M., 1987: Primary production and nutrient availability in wet heathland ecosystems. Acta Oecol., 8: 265–279.

Bernard, J.M., Fiala, K., 1986: Distribution and standing crop of living and dead roots in three wetland *Carex species*. Bulletin of the Torrey Botanical Club, 113: 1–5.

Boot, R.G.A., 1989: The significance of size and morphology of root systems for nutrient aquisition and competition. In Lambers, H. et al. (eds), Causes and consequences of variation in growth and productivity of higher plants. The Hague, p. 299–311.

Chandra,D.S., Tanaka, N., 2006: Harvesting aerial shoots of *Zizania latifolia* at different growth strategy: Effects on belowground biomass, regrowth, and rhizome morphology. J. Freshw. Ecol., 21: 583–591.

Cheng, W., Coleman D.C., Box, J.E., 1990: Root dynamics, production and distribution in agroecosystems on the Georgia Piedmont. J. Appl. Ecol., 27: 592–604.

Dahlman, R., Kucera, C. L., 1965: Root productivity and turnover in native prairtie. Ecology, 46: 84–89.

Detling, J.K., 1979: Processes controlling blue grama production on the shortgrass prairie. Ecol. Stud., 32: 25–42.

Eissenstat, D.M., Yanai, R.D., 1997: The ecology of root lifespan. In Begon, M., Fitter, A.H. (eds), Advances in ecological research. San Diego, 27: 1–60.

Evdokinova, T.I., Grishina, L.A., 1968: Productivity of root systems of herbaceous vegetation on flood plain meadows and methods for its study. In Rodin, L.E. (ed.), Methods of productivity studies in root systems and rhizosphere organisms. Leningrad, p. 24–27.

Fiala, K., 1979: Estimation of annual increment of underground plant biomass in the *Polygalo-Nardetum*. Folia Geobot. Phytotax., 14: 1–10.

Fiala, K., 1983: Annual production and turnover rate of underground plant biomass in a grasland stand – *Polygalo-Nardetum*. In Böhm, W., Kutschera, L., Lichtenegger, E. (eds), Root ecology and its practical application. Int. Symp. Gumpenstein, Irdning, p. 447–452.

Fiala, K., Studený, V., 1987: Cutting and fertilization effect on the root system in several grassland stands. I. Impact on the living and dead root biomass. Ekológia (ČSSR), 6: 389–402.

Fiala, K., Herrera, R., 1988: Living and dead belowground biomass and its distribution in some savanna communities in Cuba. Folia Geobot. Phytotax., 23: 225–237.

Fiala, K., 1989: Underground biomass of three typical grass stands growing on areas deforested by air-pollution. Ekológia (ČSSR), 8: 105–115.

Fiala, K., Jakrlová, J., Zelená, V., 1989: Biomass partitioning in two *Calamagrostis villosa* stands on deforested sites. Folia Geobot. Phytotax., 24: 207–210.

Fiala, K., 1990a: Live and dead underground plant biomass in a natural meadow hydrosere. Folia Geobot. Phytotax., 25: 113–135.

Fiala, K., 1990b: Underground plant biomass of seminatural meadows amd its variation according to ecological factors. Ekológia (ČSSR), 9: 171-191.

Fiala, K., Hernández, L., Pérez, E., Cárdenas, A., 1991: Biomass partitioning in *Paspalum notatum* stands on slope relief in the anthropic savanna of Cuba. Preslia, 63: 269–289.

Fiala, K., 1993: Underground biomass in meadow stands. In Rychnovská, M. (ed.), Functioning of meadow ecosystems. Academia, Praha, p. 133–153.

Fiala, K., Zelená, V., 1995: Stand structure and aboveground biomass partitioning in three populations of *Calamagrostis arundinacea*. Preslia, 66: 323–335.

Fiala, K., 1997: Underground plant biomass of grassland communities in relation to intensity. Acta Sc. Nat. Brno, 31, 6: 1–54.

Fiala, K., 1998: Variation in belowground biomass of grass stands in deforested areas affected by air pollution in the Beskydy Mts. Ekológia (Bratislava), 17, Suppl. 1: 256–278.

Fiala, K., 2000a: Proportion of living biomass in total dry mass of belowground organs of various plant communities. Preslia, 72: 73–85.

Fiala, K., 2000b: Root and rhizome growth of grasses *Calamagrostis arundinacea* and *C. villosa* on deforested sites in response to pollution and climatic impacts. Biológia, Bratislava, 55: 91–98.

Fiala, K., 2001: The role of root system of *Calamagrostis epigejos* in its successful expansion in alluvial meadows. Ekológia (Bratislava) 20: 292–300.

Fiala, K., Záhora, J., Tůma, I., Holub, P., 2004: Importance of plant matter accumulation, nitrogen uptake and utilization in expansion of tall grasses (*Calamagrostis epigejos* and *Arrhenatherum elatius*) into acidophilous dry grassland. Ekológia (Bratislava), *23*, p. 225-240.

Fiala, K., 2005: Determination of seasonal changes in root growth and their annual production (in Czech). Zprávy Čes. Bot. Společ., 40: 13–24.

Fitter, A.H., Graves, J.D., Self, G.K., Brown, T.K., Bogie, D.S., Taylor, K., 1998: Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation. Oecologia, 114: 20–30.

Gáborčík, H., 1985: The study of the production processes in a grassland stand and possibilities of its regulation from the point of view of quantitative and qualitative production (in Slovak). PhD. Thesis. Grassland Research Institute, Banská Bystrica.

Gáborčík, N., Kohoutek, D., 1999: Reaction of root system of permanent and renovated grass swards on mineral fertilization (in Slovak). Agrochémia, 3: 4–6.

Gill, R.A., Jackson R.B., 2000: Global patterns of root turnover for terrestrial ecosystems. New Phytol., 147: 13–31.

Guo, L.B., Halliday, M.J., Siakinotu, S.J.M., Gifford, R.M., 2005: Fine root production and litter input: its effects on soil carbon. Plant Soil, 272: 1–10.

Harrach, T., Kunzman, G., 1983: Wurzelverteilung von Grünlandgesellschaften in verschiedenen Böden unterschiedlichen ökologischen Feuchtegrades. In Böhm, W., Kutschera, L., Lichtenegger, E. (eds), Root ecology and its practical application. Int. Symp. Gumpenstein, Irdning, p. 335–342.

Hernández, L., Fiala, K., 1992: Root biomass dynamics in the savanna community of *Paspaletum notati* in Cuba. Ekológia (ČSFR), 11: 153–166.

Hui, D., Jackson, R.B., 2005: Geographical and interannual variability in biomass partitioning in grassland ecosystems: a synthesis of field data. New Phytol., 169: 85–93.

Jakrlová, J., 1971: Flooded meadow communities. An analysis of productivity in a dry year. Folia Geobot. Phytotax., 6: 1–27.

Jakrlová, J., 1975: Primary production and plant chemical composition in flood-plain meadows. Acta Sci. Nat. Brno, 9: 1–52.

Jakrlová, J., 1993: Primary producers of the natural stands. In Rychnovská, M. (ed.), Functioning of meadow ecosystems. Academia, Praha, p. 99–132.

Koppish, D., 1994: Nährstoffhaushalt un Populationsdynamik von *Calamagrostis villosa* (Chaix.) J.F.Gmel., einer Rhizompflanze des Unterwuchses von Fichtenwälder. Forum Ökologie, 12: 1–187.

Kotańska, M., 1967: Biomass dynamics of underground plant organs in some grassland comminities of the Ojców National Park. Bull. Acad. Pol. Sci., Ser. Sci. Biol., 15: 625–631.

Kotańska, M., 1973: Productivity of underground plant organs on some meadow and marsh communities of the Niepolomice forest (Southern Poland). Bull. Acad. Pol. Sci., Ser. Sci. Biol., 21: 555–560.

Kotańska, M., 1975a: Primary productivity in the meadow of the *Hieracio-Nardetum strictae* association in the Gorce mountains (Southern Poland). Bull. Acad. Pol. Sci., Ser. Sci. Biol., 23: 623–627.

Kotańska, M., 1975b: Seasonal changes in biomass of underground plant organs in some meadow communities (in Polish). Zeszyty Naukowe Uniw. Jagellońskiego. Prace Botaniczne, 395: 23–47.

Krajčovič, V., 1988: Production and non-production changes in grass ecosystems under different intensity of fertilization. In Krajčovič, V. (ed.), Teória a prax v odvetví lúkárstva, pasenkárstva a trávnych porastov. Banská Bystrica, p. 225–234.

Lauenroth, W.K., Wade, A.A., Williamson, M.A., Ross, B.E., Kumar, S., Cariveau, D.P., 2006: Uncertainty in calculations of net primary production for grasslands. Ecosystems, 9: 843–851.

Li, Y.S., Redman, R.E., 1992: Growth-responses to ammonium-N, nitrate-N and defoliation in *Agropyron-Dasystachyum* from the Canadian mixed grassland. Am. Midl. Nat., 127: 300–308.

Lorenz, R., 1977: Changes in root weight and distribution in response to fertilization and harvest treatment of mixed prairie. In Marshall, J.K. (ed.), The belowground ecosystem: A synthesis of plant-associated processes. Range Sci. Dep. Sci. Ser. No. 26, Colorado State Univ., Fort Collins, p. 63–71.

Maarel van der, E., Titlyanova, A., 1989: Above-ground and below-ground biomass relations in steppe under different grazing conditions. Oikos, 56: 364–370.

Máthé, I., Précsényi, I., Zólyomi, B., 1967: Phytomass investigations in different ecosystems at Újszentmargita. Acta Bot. Acad. Sci. Hung., 13: 239–257.

Menaut, J.C., Cesar, J., 1982: The structure and dynamic of a West African savannas. Ecol. Stud., 42: 80–100.

McNaughton, S.J., 1983: Compensatory plant growth as a response to herbivory. Oikos, 40: 329–336.

Milchunas, D.G., Lauenroth, W.K., 1993: Quantitative effects of grazing on vegetation and soil over a global range of environments. Ecol. Monogr., 63: 327–366.

Muc, M., 1977: Ecology and primary production of sedge-moos meadow communities. Truelove Lowland. In Bllis, L.C. (ed.), Truelove lowland, Devon island, Canada: A high arctic ecosystem. Univ. of Alberta Press, Alberta, p. 157–184.

Ostonen, I., Lohmus, K., Pajuste, K., 2005: Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. Forest Ecol. Manag., 212: 264–277.

Parton , W.J., Risser, P.G., 1979: Simulated impact of management practices upon the tallgrass prairie. Ecol. Stud., 32: 135–155.

Pecháčková, S., Krahulec , F., 1995: Efficient nitrogen economy: Key to the success of *Polygonum bistorta* in an abandoned mountain meadow. Folia Geobot. Phytotax., 30: 211–222.

Persson, H., 1978: Root dynamics in a young Scots pine stand in Central Sweden. Oikos, 30: 508–519.

Person, H., Majdi, H., Clemensson, A., 1995: Effects of acid depositions on tree roots. Ecol. Bull., 44: 158–167.

Pielota, L.M., Smucker, J.M., 1995: Fine root dynamics of alfalfa after multiple cuttings and during a late invasion by weeds. Agron. J., 87:. 1161–1169.

Pilát, A., 1969: Underground dry weight in the grassland communities of *Arrhenathererum elatioris alopecuretosum pratensis* R. Tx. 1937 and *Mesobrometum erecti stipetosum* Vicherek 1960. Folia Geobot. Phytotax., 4: 225–234.

Plewcyńska-Kuraś, U., 1976: Estimation of biomass of the underground parts of meadow herbage in the three variants of fertilization. Pol. Ecol. Stud., 2: 63–74.

Pyšek, P., 1993: What do we know about *Calamagrostis villosa*? A review of the species behaviour in secondary habitats. Preslia, 63: 9–20.

Rychnovská, M., 1983: Grasslands: A multifunctional link between natural and man-made ecosystems. Ekológia (ČSSR), 2: 337–345.

Rychnovská, M., Jakrlová, J., 1990: Alternating dominance: a manifestation of ecological strategy in a seminatural *Nardus stricta* grassland. In Krahulec, F., Agnew, A.D.Q., Willems, J.H. (eds), Spatial processes in plant communities. Praha, p. 185–189.

Rychnovská, M., 1993: Temperate semi-natural grasslands of Eurasia. In Coupland, R.T. (ed.), Ecosytems of the world. Grassland ecosystems, Vol. 2, Amsterdam, p. 125–166.

Ryser, P., 1996: The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologicaly contrasting grasses. Funct. Ecol., 10: 717–726.

Ryser, P., 1998: Intra- and interspecific variation in root length, root turnover and the underlying Parameters. In Lambers, H., Poorter, H., van Vuureen, M.M.I. (eds), Inherent variation in plant growth physiological mechanismus and ecological consequences. Leiden, p. 442–465.

Saunders, C.J., Megonical, J.P., Reynolds, J.F., 2006: Comparison of belowground biomass in C-3- and C-4- dominated mixed communities in a Chesapeske Bay brackish marsh. Plant Soil, 280: 305–322.

Seischab, F.K., Bernard, J.M., Fiala, K., 1985: Above and belowground standing crop partitioning of biomass by *Eleocharis rostellata* Torr. in the Byron-Bergen Swamp, Genesee County, New York. Am. Midl. Nat., Notre Dame, 114: 70–76.

Shaver, G.R., Billings, W.D., 1975: Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology, 56: 401–409.

Simon, T., Kovácz-Láng, G.E., 1976: Phytomass production and environmental conditions of grasslands on sand soil at Csévharaszt (IBP experimental area in Hungary). Pol. Ecol. Stud., 2: 121–127.

Sims, P.L., Sing, J.S., 1978: The structure and function of ten western north American grasslands. II. Intra-seasonal dynamics in primary producers compartments. J. Ecol., 66: 547–572.

Sims, P.L., Coupland, R.T., 1979: Producers. In Coupland, R.T. (ed.), Grassland ecosystems of the world: analysis of grassland and their uses. Cambridge, p. 49–73.

Singh, J.S., Lauenroth, W.K., Hunt, H.W., Swift, D.M., 1984: Bias and random errors in estimators of net root production: a simulation approach. Ecology, 65: 1750–1764.

Speidel, B., 1976: Primary production and root activity of a Golden Oat meadow with different fertilizer treatments. Pol. Ecol. Stud., 2: 77–89.

Stanton, N.L., 1988: The underground in grasslands. Ann. Rev. Ecol. Syst., 19: 573–589.

Steen, E., 1984: Variation of root growth in a grass ley studied with a mesh bag technique. Swedish. J. Agric. Res., 14: 93–97.

Szanser, M., 1991: Production and dynamics of belowground plant biomass of all-aged *Arrhenatheretalia* meadows (in Polish). In Kajak, A., Wasiliewskaja, L. (eds), Różnorodność i jej Konsekwencje dala ekosystemu lakowego. Inst. Ekol. Pol. Akad. Nauk, Dzieanów Leśny, p. 79–93.

Tesařová, M., Fiala, K., Studený, V., 1982: Live and dead roots – their mass ratio in several grassland stands. Folia Geobot. Phytotax., 17: 427–430.

Tesařová, M., 1993: Carbon cycling in grassland ecosystems. In Rychnovská, M. (ed.), Functioning of meadow ecosystems. Academia, Praha, p. 265–275.

Tesařová, M., Fiala, K., 1997: Impact of water management measures on the sate and biodiversity of plant, animals and microbial communities of meadow ecosystems. Final Report, Programme GEF Biodiversity Protection in the Czech Republic, Institute of Pedology and Microbiology, Mendel University of Agriculture and Forestry, Brno.

Titlyanova, A.A., 1971: Study of the biological cycling in biogeocoenoses. Methodological manual (in Russian). Nauka, Novosibirsk.

Titlyanova, A.A., 1979: Stability of biological cycling in natural ecosystems (in Russian). In Ružička, M. (ed.), V. Intern. Symp. Probl. Ecol . Land. Res., 19.–23.11.1979, Vysoké Tatry, ÚEBE SAV, Bratislava, p. 137–156.

Titlyanova, A. A., Rusch, G., Maarel Van der E., 1988: Biomass structure of limestone grasslands on Öland in relation to grazing intensity. Acta Phytogeogr. Suec., 76: 125–134.

Titlyanova, A.A., Tesařova, M., 1991: Regimes of biological cycle (in Russian). Nauka, Novosibirsk.

Titlyanova, A.A., Kosich, N.P., Mironiczeva-Tokareva, N.P., Romanova, I.P., 1997: Underground plant organs of grassland ecosystems (in Russian). Nauka, Novosibirsk.

Titlyanova, A.A., Romanova, I.P., Kosykh, N.P., Mironycheva-Tokareva, N.P., 1999: Pattern and process in aboveground and below-ground components of grassland ecosystems. J. Veg. Sci., 10: 307–320.

Tomaškin, J., 2003: Accumulation and production of root systems of grassland ecosystems in different mineral nutrition in relation to aboveground biomass (in Slovak). PhD. Thesis. SPU, Nitra.

Troughton, A., 1981: Length of life of grass roots. Grass Forage Sci., 36: 117–120.

Vachovec, Z., 1983: A study of the annual growth cycle of the root system in a grass stand in the Bohemian Moravian Upland (in Czech). Diploma Thesis, University of Agriculture, Faculty of Agronomy, Brno.

Vagina, T.A., 1962: Baraba meadows (in Russian). Nauka, Novosibirsk.

Vagina, T.A., Shatochina, N.G., 1972: Features of phytomass accumulation in different types of herbaceous vegetation of the Barabinsk complex forest steppe. In Kuminova, A.V. (ed.), Geobotanical studies in Western and Middle Siberia. Novosibirsk, p. 163–190.

Vaněk, V., Fiala, K., 1981: Production of aboveground and underground parts of the Polygono-Ciursietum palustris grass stand in the alluvium of the Fryšávka brook in the Bohemian-Moravian uplands. Report on the Kameničky Projekt, IB ASCR, Brno, 29, p. 1–5.

Velich, J., 1986: A study of the development of the production potential of permanent grass stands and of the forming process and its optimalization under a long-term fertilization (in Czech). University of Agriculture, Praha.

Vogt, K.A., Grier, C.C., Gower, S.T., Sprugel, D.G., Vogt, D.J., 1986: Overestimation of net root production: a real or imaginary problem? Ecology, 67: 577–579.

Ward, K.J., Klepper, B., Rickman, R.W., Allmaras, R.R., 1978: Quantitative estimating of living wheat-root length in soil cores. Agron. J., 70: 675–677.

Werger, M.J.A., 1983: Wurzel/Spross-Verhaltnis als Merkmall der Pflanzenstrategie. In Böhm, W., Kutschera, L., Lichtenegger, E. (eds), Root ecology and its practical application. Int. Symp. Gumpenstein, Irdning, p. 323–334.

Zhang, J., Romo, J.T., 1994: Defoliation of a northern wheatgrass community – aboveground and belowground phytomass productivity. J. Range. Manage., 47: 279–284.