PROPORTION OF ROOT PRODUCTION IN SEVERAL TEMPERATE GRASSLANDS OF CENTRAL EUROPE

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Abstract

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Variability in f_{RNPP} defined as the fraction of root net primary productivity (RNPP) to total net primary productivity (TNPP) [above-ground net primary productivity (ANPP) + RNPP] were examined through synthesis of 40 samples from available field biomass data assessed by in-growth core and obtained at 13 grassland sites situated in different altitudes in the Czech and Slovak Republics. Results indicate that f_{RNPP} varied from 0.05 to 0.59 across the compared sites. Submontane wet meadows had larger f_{RNPP} and dry lowland grasslands had smaller f_{RNPP} . However, extreme conditions of mountain sites were reflected in a decrease of f_{RNPP} . Thus the relationship between values of f_{RNPP} at different sites and altitudes was indicated by quadratic regression with the highest f_{RNPP} coefficients in middle altitudes, where there were sufficient amounts of precipitation together with not so extremely cold temperatures. Results also indicate a high variability in f_{RNPP} at a regional scale and along increasing altitude. These data show how important and different roles grasslands can play in accumulation and turnover of root biomass.

Key words: altitude, biomass partitioning, grassland, net primary productivity, precipitation, temperature.

Introduction

Root systems are a fundamental part of grassland vegetation, because root mass and rhizosphere represent here the main pool of organic matter and geobioelements (e.g. Rychnovská, 1983; Stanton, 1988; Hui, Jackson, 2006). It is important to understand how habitat variability affects soil carbon (C) pools/fluxes, particularly, as these ecosystems store up to 30% of the world below-ground C (see Risch et al., 2007). Therefore, grasslands play a significant role in the global C cycle.

Net primary productivity and biomass partitioning are strongly influenced by climate (e.g. Melillo et al., 1993; Gill, Jackson, 2000; Ni, 2004). For example, above-ground net

primary productivity (ANPP) is positively correlated and showed a significant linear relationship with mean annual precipitation (MAP) in grasslands (e.g. Köchy, Wilson, 2004; Yahdjian, Sala, 2006; Fay et al., 2008). However, contradictory data on root growth and below-ground biomass in dry conditions were published. Root biomass and total fine root length were significantly higher at the dry site than at the humid site (e.g. Ibrahim et al., 1997; Bakker et al., 2006; Qaderi et al., 2006). On the other hand, results of other authors indicate that root biomass and root length were lower in the drought year than in the wet year (e.g. Hayes, Seastedt, 1987; Andrzejewska, 1991; Titlyanova et al., 1999). Also Hui and Jackson (2006) found strong negative relationships of root fraction with mean annual temperature (MAT) and MAP across sites, however, temporal relationships of root fraction and climatic variables within sites were more complicated and site-specific. They synthesised 94 site-year field biomass data at 12 grassland types around the world from net primary productivity database and from the literature. This analysis provides the first synthesis of geographical variability and its relationships with climatic variables for grassland roots. Their results showed that the fraction (f_{BNPP}) of below-ground net primary productivity (BNPP) to TNPP varied from 0.40 to 0.86 across analyzed sites (mainly from USA, China and Russia). But there were only a few data from Europe and no data were included from central part of Europe. Hui and Jackson (2006) deduced from their comparison that f_{BNPP} was negatively correlated with MAT and MAP. However, results of some authors (see text above) indicated an opposite relationship. Nevertheless, Hui and Jackson (2006) noticed that it is still unclear how large the impact of climate change will be on terrestrial C sequestration and cycling, and that additional data on geographical and interannual variability in below-ground biomass components are greatly needed. Thus a gap in knowledge still exists in comparison of root growth in various grasslands situated at different condition of various regions. This fact inspired us to study the role of the various temperate grasslands, their root production, in the regional C cycles.

Therefore, the aim of our study was to compare impacts of various grassland communities occurring in different regions on their root production, which was assessed by in-growth soil core technique. Applied the same methodological approach enables us to compile available data on field biomass measurements occurring in temperate grasslands of the Czech and Slovak Republics (Central Europe). Forty site-year field root biomass data at 13 grassland types were gathered from published original papers (see Material and methods). Thus a large collection of root samples, performed in the same way, enable us to determine the patterns and potential mechanisms of variation in f_{RNPP} for these grassland ecosystems. We were particularly interested in altitudinal variability in f_{RNPP} and relationships with MAT and MAP.

We hypothesised that: (1) As dry and warm conditions can cause reductions in root growth, we expected to find the lower root increments and lower biomass allocation into root biomass in drier condition at warmer sites in contrary to wet and cool highlands and mountains. (2) We expected that root production will be a simple linear function of altitude, precipitation and temperature. (3) We presume that analyzed study sites can be clustered, at least, into three main groups based on variability in f_{RNPP} associated with regions and given by climatic parameters.

Material and methods

Study site

The 40 site-year samples of roots, collected along altitudinal gradient and reflected large differences in MAT and MAP, encompassed several major grassland types or regions, including temperate dry grasslands, alluvial meadows, submontane wet meadows, mountain clear-cut grasslands and expanding grass stands dominated by *Calamagrostis epigejos* (Tables 1 and 2). The data set used in this study was obtained from mostly available recent publications (see Table 2) and data originate from natural growing field conditions. All sites were dominated by C3 species. Sites were not fertilised, only some of them were extensively mowed.

T a b l e 1. Location and characteristics of the nine grassland sites in Czech (CR) and Slovak (SR) Republics.

Site (region)	Latitude longitude	Altitude (m a.s.l.)	Grassland types	MAT (°C)	MAP (mm)	Soil type (bedrock)
Lednice, CR (Flood plain South Moravia)	48° 49' 16" 48'	160	Alluvial meadow	9.0	524	Gleyed soil (alluvial sediments)
Nejdek, CR (Flood plain South Moravia)	48° 48' 16" 47'	160	Alluvial meadow	9.0	524	Gleyed soil (alluvial sediments)
Havraníky–Podyjí National Park, CR (Etchplain S. Moravia)	48° 48' 15" 59'	320	Dry acidophilous grassland	8.5	471	Ranker (granit)
Suchý vrch, SR (Kremnické hills)	48° 44' 19" 09'	460	Montane Trisetum meadow	7.7	853	Dystric Cambisol (disintegrated andesite)
Kamenický, CR (Bohemian-Moravian Highland)	49° 43' 15" 58'	624	Submontane wet meadow	6.8	786	Brown acid gleyed soil (crystalline rocks)
Černá Ostravice valley, CR (Beskydy Mts.)	49° 28' 18" 30'	630	Montane clear-cut grassland	7.1	869	Dystric planosol (sandstone)
Bílý Kříž, CR (Beskydy Mts.)	49° 30' 18" 32'	945	Montane clear-cut grassland	6.5	948	Spodo-dystric cambisol (sandstone)
Kněhyně hill, CR (Beskydy Mts.)	49° 30' 18" 18'	1240	Montane clear-cut grassland	3.7	1102	Spodo-dystric cambisol (sandstone)
Smrk hill, CR (Beskydy Mts.)	49° 30' 18" 22'	1250	Montane clear-cut grassland	3.6	1146	Ferro-humic podzol (sandstone)

Notes: MAT - mean annual temperature; MAP - mean annual precipitation.

Data analysis

In order to assess yearly root increments (root production), the in-growth core technique (Milchunas, 2012) was used in all sites (see Fiala, 1998, 2000, 2001; Fiala et al., 2009, 2012; Holub et al., 2013a, b; Tomaškin, Tomaškinová, 2012). The same method used in all sites enables us to compare reliably summarised data. For comparison of the amount of produced roots in various grasslands, f_{RNPP} coefficient was used (see Hui, Jackson, 2006). The f_{RNPP} was calculated using the equation:

$$f_{\text{RNPP}} = \text{RNPP}/(\text{ANPP} + \text{RNPP}),$$

where RNPP is root net primary productivity and ANPP is above-ground net primary productivity. For calculations of f_{RNPP} we used ANPP data, where sum of peak live biomass and fresh litter were estimated and available (Jakrllová, 1996; Holub, 2002; Hrabě et al., 2002; Fiala et al., 2004; Holub et al., 2012; Tomaškin, Tomaškinová, 2012). Method was applicable at all of the sampling sites. Root in-growth estimates performed in dense meadow stands represented more suitable method, mainly for comparison of root growth in various conditions. To study the relationships of f_{RNPP} with climatic variables, MAT and MAP were collected for these sites (Table 1).

Statistical analysis

The regression analysis was conducted on relationships of root increments with altitude, MAT and MAP to determine whether these parameters are related. All statistical analyses were performed using statistical package STATISTICA 9 (Statsoft Inc., Tulsa, OK, US).

T a b l e 2. TBDM (in g DM m⁻² yr⁻¹), root increments (RNPP in g DM m⁻² yr⁻¹) and relationships of the fraction of RNPP to TNPP (f_{RNPP}) recorded on different sites (see also Table 1).

Site	Region	Dominant species	Year	TBDM	RNPP	f_{RNPP}
Lednice ¹	Flood plain	<i>Cirsium canum</i> ,	1998–1999	1562	98	0.20
	South Moravia	<i>Deschampsia cespitosa</i>		1601	66	0.12
Lednice ¹	Flood plain	<i>Calamagrostis epigejos</i>	1998–1999	1306	71	0.11
	South Moravia			1552	61	0.07
Nejdek ¹	Flood plain	<i>Serratula tinctoria</i> , <i>Poa pratensis</i>	1998–1999	1322	41	0.13
	South Moravia			1462	92	0.14
Nejdek ¹	Flood plain	<i>Calamagrostis epigejos</i>	1998–1999	1576	56	0.06
	South Moravia			1576	61	0.07
Havraníky–Podyjí National Park ²	Etchplain	<i>Festuca ovina</i> , <i>Avenella flexuosa</i> , <i>Pimpinella saxifraga</i>	2001–2005	1051±86	100±26	0.21±0.05
	South Moravia					
Suchý vrch ³	Kremnické hills	<i>Trisetum flavescens</i> , <i>Poa pratensis</i>	1991–1998	831±93	244±73	0.37±0.15
Kameničky ⁴	Bohemian-Moravian highland	<i>Cirsium palustre</i> , <i>Deschampsia cespitosa</i>	1992	1917	157	0.24
Kameničky ⁵	Bohemian-Moravian highland	<i>Cirsium palustre</i> , <i>Deschampsia cespitosa</i>	2001–2005	1821±146	163±24	0.25±0.04
Černá Ostravice valley ⁶	Beskydy Mts.	<i>Calamagrostis villosa</i>	1994–1995	1998	359	0.51
					319	0.33
Bílý Kříž ⁶	Beskydy Mts.	<i>Calamagrostis villosa</i>	1994–1995	2234	136	0.27
					135	0.24
Bílý Kříž ⁷	Beskydy Mts.	<i>Nardus stricta</i> , <i>Avenella flexuosa</i>	2001–2005	1620±181	162±46	0.27±0.06
Kněhyně hill ⁶	Beskydy Mts.	<i>Calamagrosatis villosa</i>	1994–1995	2592	80	0.14
					35	0.05
Smrk hill ⁶	Beskydy Mts.	<i>Calamagrostis villosa</i>	1994–1995	875	20	0.06
					22	0.06

Year, measurements included in the analysis were made during these years. SE values are shown where available. Dominant species occurring in grasslands are also given. RNPP data were obtained by Fiala 2001⁽¹⁾; Fiala et al., 2012⁽²⁾; Tomaškin, Tomaškinová, 2012⁽³⁾; Fiala et al., 2013⁽⁴⁾; Fiala et al., 2009^(5,7); Fiala, 1998, 2000⁽⁶⁾. ANPP data published by Holub, 2002⁽¹⁾; Fiala et al., 2004⁽²⁾; Holub et al., 2012^(2,7); Tomaškin, Tomaškinová, 2012⁽³⁾; Hrabě et al., 2002⁽⁴⁾; Holub unpubl.⁽⁵⁾; Jakrllová, 1996⁽⁶⁾ were used (see Material and Methods).

Results

Variations in below-ground plant parts on different sites

Summarised data on field biomass measurements, obtained in unfertilised temperate grasslands in the Czech and Slovak Republics (Central Europe), showed that root biomass data are rather variable (Table 2). Total below-ground dry mass (TBDM) varied in large range of values (from 831 to 2592 g DM m⁻²). Highland and mountain sites had higher amount of TBDM surpassed 2 kg of dry matter per m².

Yearly root increments, estimated by in-growth core technique, were used to calculate f_{RNPP} i.e. proportion of root production in relation to TNPP. The RNPP fluctuated from 20 to 359 g DM m⁻² yr⁻¹ on compared sites. Differences in RNPP values were also reflected in assessed f_{RNPP} . Values varied from different geographical sampling locations (Table 2). Across all sites, f_{RNPP} ranged between 0.06 and 0.51 (Table 2). Grasslands growing in dry habitats (41–100 and 0.06–0.21 g DM m⁻², respectively) and in the highest mountain sites (20–162 and 0.05–0.27 g DM m⁻², respectively) tended to have the lowest yearly root increments and f_{RNPP} as well. In contrast, highland and mountain sites at a lower altitude (Kamenický, Suchý vrch and Černá Ostravice valley sites) had higher yearly root increments and f_{RNPP} coefficients (157–359 and 0.24–0.51 g DM m⁻², respectively).

Relationships of f_{RNPP} and climatic factors

Results from different regions of sampling locations indicated that the f_{RNPP} values did not simply increased or decreased with altitude, MAT and MAP. The relationship of f_{RNPP} with these factors was nonlinear. Nevertheless, quadratic regressions showed that these factors significantly affected f_{RNPP} coefficients (Figs 1–3). The f_{RNPP} partly tended to increase with increasing climatic factors, but subsequently this coefficient (proportion of root production) decreased in sites with the highest altitude, MAT or MAP (Figs 1–3).

Fig. 1. Relationship of the fraction of root net primary productivity to total NPP (f_{RNPP}) and altitude (ALT).

Fig. 2. Relationship of the fraction of root net primary productivity to total NPP (f_{RNPP}) and mean annual precipitation (MAP).

Fig. 3. Relationship of the fraction of root net primary productivity to total NPP (f_{RNPP}) and mean annual temperature (MAT).

Discussion

Variations in below-ground plant parts on different sites

The pattern of biomass partitioning may be the results of plant species adaptation and responses to both internal and environmental stimuli (Hui, Jackson, 2006). Their results indicate that plants maintain a certain response to growth and biomass partitioning with annual environment of each habitat. The results of this study also indicate that recorded values of the TBDM, RNPP and f_{RNPP} varied in geographical locations of sampling and type of grassland. In this study, TBDM across analyzed sites ranged between 831 and 2592 g DM m⁻² yr⁻¹, which is consistent with results summarised by Hui and Jackson (2006). They reported that mean TBDM varied from 228 to 2147 g DM m⁻² yr⁻¹. In addition, the highest values of TBDM in this study were lower than values estimated previously in moist meadows (Fiala, 1993, 2010).

Also RNPP values presented in this paper (20–359 g DM m⁻² yr⁻¹) confirm with other available published data on the root production in meadow stands of various regions assessed by in-growth technique and compiled by Fiala (1997, 2010). These data ranged mostly between 173 and 567 g m⁻² yr⁻¹. Our data, gathered previously in alluvia of the warmer and drier region of southern Moravia, supported results of this study, because below-ground biomass production average only 40% of the below-ground biomass production in meadow stands of Bohemian-Moravian Highland (e.g. Pilát, 1969; Jakrlová, 1971). Thus, the present data confirmed our first assumption because lower allocation of root biomass was recorded in drier conditions at warmer sites on the contrary to larger root formation in wet and cool highland sites. However, data assessed with the help of in-growth core technique collected roots, but did not contain rhizomes and below-ground grass shoot bases. Thus, for example, productions of *Calamagrostis* rhizomes and shoot bases were not included in our calculation. Therefore data concerning *Calamagrostis* (four site-year samples) are partly underestimated. Effect of above-mentioned environmental factors on root and rhizome production can also

be intensified by negative impact of pollution (soil acidification, nitrogen excess, etc.) occurring in deforested areas of the uppermost mountain zone (e.g. Pyšek, 1993; Koppisch, 1994; Fiala, 2000).

Relationships of f_{RNPP} and climatic factors

By summarizing 40 field biomass estimations, we try to evaluate regional and altitudinal variability in f_{RNPP} and the relationships of f_{RNPP} with climatic variables. In contrast to data found by Hui and Jackson (2006) we did not find that f_{RNPP} was negatively correlated with MAT and MAP across sites. Altitude can determine values of these climate factors. However, Fitter et al. (1998) deduced from their field experiment that neither root production nor root death rate was a simple function of altitude. They noticed that increased root accumulation in summer was a function of changes in the length of the growing season, not of soil temperature.

Our data indicate, in accordance with our assumptions, that lower amount of precipitation and higher temperature can be associated with low root increments in South Moravia sites. On the other hand, the low temperature and the influence of wet acid deposition can be reflected in lower root production in the Beskydy Mts (Kněhyně and Smrk hills). Thus we found quadratic relationships between f_{RNPP} and studied climatic variables. Other different geographical and temporal responses of plants to climatic variables have been described in literature. For example, results showed that above-ground biomass production was more controlled by rainfall than by other factors. However, both the positive and negative relationships of BNPP (or RNPP) to climatic variables have been found (see Introduction). Experimentally obtained data (Fiala et al., 2009, 2012) showed that there was positive effect of precipitation on root growth in various grasslands during 5 years. Similarly, water availability was the most limiting factor for f_{RNPP} in tall prairie (Xu et al., 2012).

Ni (2004) summarised that productivity correlation implied that above-ground productivity is more controlled by rainfall, whereas below-ground and total productivity is more influenced by temperature in the temperate grasslands of northern China. The greater influence of temperature on below-ground productivity might be due to the high temperature in the growing season and the influence of soil temperature on the root system (Ni, 2004). The high correlation between MAT and below-ground biomass was also confirmed in the temperate and tropical grassland worldwide (Gill et al., 2002). They found that below-ground biomass was inversely related to MAT, while there was a poor relationship between below-ground biomass and MAP. According to Hui and Jackson (2006) the geographical relationships could be the result of long-term plant adaptation to local climates, and reflect the contribution of vegetation to variation in f_{RNPP} . Temporal relationships of f_{RNPP} and climatic variables within sites can be more complicated and could be site-specific.

As temperature continues to increase and precipitation decrease, plants may allocate relatively less below-ground, decreasing f_{RNPP} . Such decrease can probably influence the storage of C below-ground, as well as C turnover (Hui, Jackson, 2006). They summarised a larger data set and stated that advantages and limitations of data synthesis occur. One is the availability of measurements and second variation of data quality across sites; therefore estimates of BNPP remain the limiting step in most.

Cluster of regions based on f_{RNPP}

We found distinct patterns of variability in f_{RNPP} across regions, and divergent responses of f_{RNPP} to climatic variables. Our results showed that 13 sites could be clustered into three groups based on their variability in f_{RNPP} (Figs 1–3). Dry acid grasslands and meadows with eliminated floods in lowland had the smallest values of f_{RNPP} . Similarly lower f_{RNPP} values were found on the opposite site of altitudinal gradient, i.e. in cooler conditions of the upper sites of mountains. The third larger group, submontane and mountain meadows, situated approximately in the central part of altitudinal gradient, had large values of f_{RNPP} . Our data partly corresponded with results summarised by Ni (2004) because he recorded the high BNPP in meadow and alpine grasslands and the low BNPP in desert and steppes. Typical plant species growing in a region tend to adjust to local environment through their biomass-partitioning strategies (Hui, Jackson, 2006). For example, plants growing in wet submontane meadows usually have proportionally more roots and larger f_{RNPP} (Fiala, 1997, 2010). Thus our last presumption was confirmed since studied grassland sites can be clustered into three main groups.

Conclusion

Relationships of f_{RNPP} and climatic variables were rather more complicated than was presented by other authors (Ni, 2004; Hui, Jackson, 2006) and this knowledge represent new and important findings of this study. We did not find a simple negative linear relationship between f_{RNPP} and MAT or MAP across sites, how it was described by above mentioned authors. Our results rather indicate quadratic regressions, because a smaller root production was recorded in relation to above-ground biomass production in both dry and warm conditions of lowland and very cool mountain sites affected by air pollution. Our results provide useful information in several respects. They provide cover of f_{RNPP} across geographical and altitudinal scale. The geographical regression curve and climatic variables could also be used in modelling to improve model of C outputs in grasslands. Results can help in regional modelling studies and to the possible site-specific temporal responses to climatic variables.

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References

- Andrzejewska, L. (1991). Root production of some grass communities on peat soil in river valleys of Biebrza and Narew. *Polish Ecological Studies*, 17, 63–72.
- Bakker, M.R., Augusto, L. & Achat D.L. (2006). Fine root distribution of trees and understory in mature stands of marine pine (*Pinus pinaster*) on dry and humid sites. *Plant Soil*, 286, 37–51. DOI: 10.1007/s11104-006-9024-4.
- Fay, P.A., Kaufman, D.M., Nippert, J.B., Carlisle, J.D. & Harper C.W. (2008). Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. *Global Change Biology*, 14, 1600–1608. DOI: 10.1111/j.1365-2486.2008.01605.x.

- Fiala, K. (1993). Underground biomass in meadow stands. In M. Rychnovská (Ed.), *Functioning of meadow ecosystems* (pp. 133–153). Praha: Academia.
- Fiala, K. (1997). Underground plant biomass of grassland communities in relation to mowing intensity. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno*, 31, 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. (2000). Root and rhizome growth of grasses *Calamagrostis arundinacea* and *C. villosa* on deforested sites in response to pollution and climatic impacts. *Biologia*, 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., Tüma, 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, 225–240.
- Fiala, K., Tüma, I. & Holub P. (2009). Effect of manipulated rainfall on root production and plant belowground dry mass of different grassland ecosystems. *Ecosystems*, 12, 906–914. DOI: 10.1007/s10021-009-9264-2.
- Fiala, K. (2010). Belowground plant biomass of grassland ecosystems and its variation according to ecological factors. *Ekológia (Bratislava)*, 29, 182–206. DOI: 10.4149/ekol_2010_02_182.
- Fiala, K., Tüma, I. & Holub P. (2012). Interannual variation in root production in grasslands affected by artificially modified amount of rainfall. *The Scientific World Journal*, Article ID 805298, 10 pages. DOI: 10.1100/2012/805298.
- Fitter, A.H., Graves, J.D., Self, G.K. & Brown T.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. DOI: 10.1007/s004420050415.
- Gill, R.A. & Jackson R.B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytol.*, 147, 13–31. DOI: 10.1046/j.1469-8137.2000.00681.x.
- Gill, R.A., Kelly, R.H., Parton, W.J., Day, K.A., Jackson, R.B., Morgan, J.A., Scurlock, J.M.O., Tieszen, L.L., Castle, J.V., Okima, D.S. & Zhang X.S. (2002). Using simple environmental variables to estimate belowground productivity in grasslands. *Glob. Ecol. Biogeogr.*, 11, 79–86. DOI: 10.1046/j.1466-822X.2001.00267.x.
- Hayes, D.C. & Seastedt T.R. (1987). Root dynamics of tallgrass prairie in wet and dry years. *Can. J. Bot.*, 65, 787–791. DOI: 10.1139/b87-105.
- Holub, P. (2002). The expansion of *Calamagrostis epigejos* into alluvial meadows: comparison of aboveground biomass in relation to water regimes. *Ekológia (Bratislava)*, 21, 27–37.
- Holub, P., Fabšičová, M., Tüma, I., Záhora, J. & Fiala K. (2013a). Effects of artificially varying amounts of rainfall on two semi-natural grassland types. *J. Veg. Sci.*, 24(3), 518–529. DOI: 10.1111/j.1654-1103.2012.01487.x.
- Holub, P., Tüma, I. & Fiala K. (2013b). Effect of fertilization on root growth of submontane Polygono-Cirsietum meadow. *Plant, Soil and Environment*, 59, 342–347.
- Hrabě, F., Straka, J. & Rosická L. (2002). Produkční a strukturální změny polopřirozeného a nově setého lučního společenstva v oblasti CHKO Žďárské vrchy. In V. Krajčovič. (Ed.), *Ekológia trávneho porastu VI.* (pp. 220–227). Banská Bystrica: Výskumný ústav trávnych porastov a horského poľnohospodárstva.
- Hui, D. & Jackson R.B. (2006). Geographical and interannual variability in biomass partitioning in grassland ecosystems: a synthesis of field data. *New Phytol.*, 169, 85–93. DOI: 10.1111/j.1469-8137.2005.01569.x.
- Ibrahim, L., Proe, M.F. & Cameron A.D. (1997). Main effects of nitrogen supply and drought stress upon whole-plant carbon allocation in poplar. *Can. J. For. Res.*, 27, 1413–1419. DOI: 10.1139/x97-080.
- Jakrlová, J. (1971). Flooded meadow communities. An analysis of productivity in a dry year. *Folia Geobot.*, 6, 1–27.
- Jakrlová, J. (1996). Variability of aboveground production of *Calamagrostis villosa* in localities exposed to emissions in the region of the Beskydy Mts. In K. Fiala (Ed.), *Grass ecosystems of deforested areas in the Beskydy Mts* (pp. 75–82). Brno: ASCR, Institute of Landscape Ecology.
- Köchy, M. & Wilson S.D. (2004). Semiarid grassland responses to short-term variation in water availability. *Plant Ecol.*, 174, 197–203. DOI: 10.1023/B:VEGE.0000049098.74147.57.
- Koppisch, D. (1994). Nährstoffhaushalt und Populationsdynamik von *Calamagrostis villosa* (Chais.) J.F. Gmel, einer Rhizompflanze des Unterwuchses von Fichtenwäldern. *Bayreuther Forum Ökologie*, 12, 1–187.
- Melillo, J.M., McGuire, A.D., Kicklighter, A.W., Moore, B.I., Vorosmary, C.J. & Schloss A.L. (1993). Global climate-change and terrestrial net primary production. *Nature*, 363, 234–240. DOI: 10.1038/363234a0.
- Milchunas, D.G. (2012). Biases and errors associated with different root production methods and their effects on field estimates of belowground net primary production. In S. Mancuso (Ed.), *Measuring roots: An updated ap-*

- proach* (pp. 303–339). Berlin: Springer. DOI: 10.1007/978-3-642-22067-8_16.
- Ni, J. (2004). Estimating net primary productivity of grasslands from field biomass measurements in temperate northern China. *Plant Ecol.*, 174, 217–234. DOI: 10.1023/B:VEGE.0000049097.85960.10.
- Pilát, A. (1969). Underground dry weight in the grassland communities of *Arrhenatheretum elatioris alopecuretosum pratensis* R. Tx. 1937 and *Mesobrometum erecti stipetosum* Vicherek 1960. *Folia Geobot.*, 4, 225–234.
- Pyšek, P. (1993). What do we know about *Calamagrostis villosa*? A review of the species behaviour in secondary habitats. *Preslia*, 63, 9–20.
- Qaderi, M.M., Kurepin, L.V. & Reid D.M. (2006). Growth and physiological responses of canola (*Brasica napus*) to three components of global climate changes: Temperature, carbon dioxide and drought. *Physiologia Plantarum*, 128, 710–721. DOI: 10.1111/j.1399-3054.2006.00804.x.
- Risch, A.C., Jurgensen, M.F. & Frank D.A. (2007). Effects of grazing and soil micro-climate on decomposition rates in a spatio-temporally heterogeneous grassland. *Plant Soil*, 298, 191–201. DOI: 10.1007/s11104-007-9354-x.
- Rychnovská, M. (1983). Grasslands: A multifunctional link between natural and man-made ecosystems. *Ekológia (ČSSR)*, 2, 337–345.
- Stanton, N.L. (1988). The underground in grasslands. *Annu. Rev. Ecol. Syst.*, 19, 573–589. DOI: 10.1146/annurev.es.19.110188.003041.
- Titlyanova, A.A., Romanova, I.P., Kosykh, N.P. & Mironycheva-Tokareva N.P. (1999). Pattern and process in above-ground and below-ground components of grassland ecosystems. *J. Veg. Sci.*, 10, 307–320. DOI: 10.2307/3237060.
- Tomaškin, J. & Tomaškinová J. (2012). The ecological and environmental functions of grass ecosystems and their importance in the elimination of degradation processes in agricultural landscape. *Carpathian Journal of Earth Environmental Sciences*, 7, 71–78.
- Xu, X., Niu, Sh., Sherry, R.A., Zhou, X. & Zhou J. (2012). Interannual variability in responses of belowground net primary productivity (NPP) and NPP partitioning to long-term warming and clipping in a tallgrass prairie. *Global Change Biology*, 18, 1648–1656. DOI: 10.1111/j.1365-2486.2012.02651.x.
- Yahdjian, L. & Sala O.E. (2006). Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, 87, 952–962. DOI: 10.1890/0012-9658(2006)87[952:VSCPJR]2.0.CO.