ORIGINAL ARTICLE

Seasonal dynamics of macronutrients in aboveground biomass of two herb-layer species in a beech forest

Martin Kubov[1,2] · Branislav Schieber[1] · Rastislav Janík[1]

Abstract

The content of six macronutrients (N, P, K, S, Ca, Mg) in the aboveground biomass of two forest plants representing different life forms (*Carex pilosa*, a hemicryptophyte, and *Dentaria bulbifera*, a geophyte) was analysed in relation to selected phenological phases. The ability of the plants to accumulate nutrients from the soil into the biomass was studied using transfer coefficients (TCs). Additionally, we examined the temporal changes in nutrient ratios for both species. The study was performed in a beech ecosystem in central Slovakia (Kremnické vrchy Mountains). The content of available nutrients in the soil (Eutric Cambisol) decreased as follows: N > Ca > S > Mg > K > P. A higher ability to accumulate all elements into the biomass was found for *Dentaria bulbifera* in comparison to *Carex pilosa*. We found different patterns of nutrient accumulation between *Dentaria bulbifera* (N > K > S > Ca > Mg > P) and *Carex pilosa* (K > N > Ca > S > Mg > P). Temporal changes in the content of nutrients were more noticeable in *Dentaria bulbifera*, especially for N, S and P – the content of these nutrients diminished. On the other hand, the content of K and Ca in *Carex pilosa* rose over time. For both species, the highest TC was detected in the case of P and K. Clear temporal variability was also revealed in some nutrient ratios, e.g., [N:K] and [Ca:P]. We confirmed that the nutrient content, nutrient ratio and transfer of macronutrients from the soil to plant biomass vary throughout the growing season in relation to the phenological phases of the plants. Similarly, the dynamics of both nutrient content and the accumulation of macronutrients in the biomass are related to the life form of the plant.

Keywords *Carex pilosa* · *Dentaria bulbifera* · Nutrient ratio · Phenological phases · Transfer coefficient

Introduction

Forest ecosystems are complex systems in which both abiotic and biotic components are directly involved in energy flow and nutrient cycles throughout their continual interaction. Decomposition of organic matter, with subsequent release of nutrients into the soil, is crucial for the nutrition base of plants and significantly affects the production of biomass (Chatzistathis and Therios 2013). The supply and availability of nutrients may shape plant-microorganism-soil interactions in forest ecosystems (Lang et al. 2017). Six elements, nitrogen (N), phosphorus (P), potassium (K), sulphur (S), calcium (Ca) and magnesium (Mg), are the most essential for proper plant growth. These elements affect one another, so balance between the nutrient requirements of plants and the nutrient supply in the soil is essential. The excess of a certain element can cause a deficiency in another element. For example, excess potassium results in Mg and Ca deficiency. However, a sufficient supply of N has a positive effect on the intake of Ca (Page and Mitchell 2008). The availability of Ca shapes tree species composition, which can subsequently affect the content of nutrients in the soil and its chemistry (Binkley and Giardina 1998; Chirino-Valle et al. 2016). In general, the qualitative content of elements in a plant corresponds to the content in the soil, but significant quantitative differences in the content of individual elements in plant biomass exist (Singh and Schulze 2015).

The most relevant studies dealing with the problems regarding nutrients in plants are related to agriculture (Dobermann and Cassman 2002; Torma et al. 2018) and gardening (Reickenberg and Pritts 1996; Yang et al. 2011). There are fewer papers focusing on forest ecosystems (Falkengren-

✉ Branislav Schieber
   schieber@ife.sk

[1] Institute of Forest Ecology of the Slovak Academy of Sciences, Štúrova 2, 96053 Zvolen, Slovak Republic

[2] Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka, 24 Zvolen, Slovak Republic

Grerup 1994, 1995; Mussche et al. 1998; Iivonen et al. 2001; Sigurdsson 2001; Weih and Karlsson 2001; Wielgolaski 2001; Fleischmann et al. 2004; Jamnická et al. 2007, 2013; Papa et al. 2014). The temporal dynamics of macroelement content and nutrient ratios in relation to phenological phases within forest ecosystems have rarely been examined. In this context, papers have mainly dealt with the analysis of assimilation by organs of herbs or trees (Milla et al. 2005). Several studies have reported that the [N:P] ratio is key in effectively determining the potential for plant growth and biomass production within plant communities (Koerselman and Meuleman 1996; Rossatto et al. 2015). The [N:K] ratio plays an important role during the transition from vegetative to generative phenophases. If this ratio is too high, flower production by plants is markedly reduced, and they create more vegetative parts (Fiedler and Höhne 1987). The intake of P is considerably affected by the [K:Mg] ratio (Graeme 2003). Ca improves soil aeration, while Mg promotes the adhesion of soil particles. In addition, if the [Ca:Mg] ratio reaches low values, the soil becomes less permeable, which can lead to plant damage (Schulte and Kelling 2004). The aforementioned papers focused mainly on the actual nutrient supply at the moment of biomass harvest. They do not allow us to evaluate the dynamics of the nutrients across phenological stages or to identify the limiting values (min/max) of the nutrient supply. Therefore, it is necessary to address the various phenological phases of plants throughout the entire growing season. Additionally, the determination of the transfer coefficient (TC), reflecting the ability of plants to take up nutrients from growth media (soil) into the biomass, is also important to understand the interrelations between abiotic and biotic components. The results of these interactions are reflected in the composition, biomass production and functioning of plant communities (Güsewell 2004).

Based on the above, our hypotheses were the following: a) the nutrient content, nutrient ratio and transfer of macronutrients from the soil to plant biomass are not static but can oscillate throughout the growing season in relation to the phenological phases of plants and b) the dynamics of both nutrient content and the accumulation of macronutrients in plant biomass can depend on the life form of the plant. For this reason, we focused on the vegetative and generative phenophases of two common plant species with different life forms growing in the beech forest understory (*Dentaria bulbifera* –geophyte, *Carex pilosa* –hemicryptophyte).

Materials and methods

Study site

This study was conducted at the Ecological Experimental Station (EES), which is included in the Long-Term Ecosystem Research in Europe (LTER) network located in the Kremnické vrchy Mountains (central Slovakia), Suchá dolina valley (48°38'N, 19°04'E), with an altitude of 450–520 m a.s.l. on a southwest slope of 5–15°. A Eutric Cambisol with skeleton contents ranging from 10% to 60% was developed from the andesite tuffaceous agglomerates. Both moderate acid reactions and relatively low humus levels are characteristic of this type of soil (Kukla et al. 1998; Gašová et al. 2017). European beech (*Fagus sylvatica*), 120 years in age on average, is the dominant tree species. Fir, oak and hornbeam are the associated species. The vegetation cover consists mostly of patches of *Carici pilosae-Fagetum* Oberd. 1957 and *Dentario bulbiferae-Fagetum* (Zlatník 1935) Hartmann 1953 phytocoenoses with permanent elements such as *Carex pilosa*, *Carex digitata*, *Carex sylvatica*, *Dentaria bulbifera*, and *Galium odoratum*. Two ferns, *Athyrium filix-femina* and *Dryopteris filix-mas,* are also present. The area of the EES belongs to a moderately warm region and a moderately warm and humid hilly land subregion (Lapin et al. 2002). The long-term mean (1951–1980) of the annual air temperature is approximately 6.8 °C, with a mean of 17.0 °C in the warmest month (July) and − 4.0 °C in the coldest month (January). The mean annual precipitation is 780 mm (Střelec 1992). An increasing positive deviation of +1.1 °C (from 6.8 °C to 7.9 °C) of the mean annual air temperature was observed during the last two decades. However, the mean annual precipitation did not change significantly (Schieber et al. 2017).

Nomenclature of plant *species follows* the checklist of Marhold and Hindák (1998).

Plant species characteristics

For the purpose of our study, the selection of herb-layer species was based on the following three criteria: a) common plant species in a beech ecosystem, b) dominant species within the plant community, and c) different life forms. The first criterion was important to obtain a sufficient number of individuals for sampling. Although the life cycles, behaviour and ecological-production characteristics have been previously studied (e.g., Klötzli and Walther 2000; Schieber and Kováčová 2000, 2002), we have no information about the temporal dynamics of macronutrients in the biomass of these plants. In addition, temporal changes in macronutrients may differ among plant life forms. Therefore, we selected two species, *Carex pilosa* and *Dentaria bulbifera*, which frequently grow in the herb layer of beech-dominated stands in the study region.

Dentaria bulbifera (*Brassicaceae*) is a perennial herb (geophyte) that mostly grows within the beech communities of northern and central Europe. The species demands both relatively high soil moisture and a relatively high nutrient supply. Vegetative reproduction via axillary buds is the basic

form of dispersal. Generative reproduction is not common, and seeds are rarely produced (Gustafsson et al. 2002).

Carex pilosa (Cyperaceae) is a dark green perennial graminoid (hemicryptophyte) with broad ecological amplitude. It can grow in forests dominated by many different broad-leaved and coniferous species but also tolerates a continental climate (Rejzková et al. 2008). This evergreen sedge with clonal growth reproduces both vegetatively, with offshoots and creeping rhizomes, and via generative methods.

Phenological observations

The methodology of phenological observations was based on the methodology of the Slovak Hydrometeorological Institute, which is commonly used for the long-term monitoring of forest plants (Braslavská and Kamenský 1996). The determination of selected phenological phases was performed according to the BBCH scale (Meier 2001). Thirty individuals per species were harvested in each phenophase during the growing season in 2014. For *Dentaria bulbifera*, the following phenophases were taken into account: BBCH 11 –developed leaf, BBCH 51 –flower buds visible, BBCH 65 –full flowering and BBCH 95 –general yellowing of the leaves. In the case of *Carex pilosa,* we examined these phenophases: BBCH 10 –offshoot top opening, BBCH 11 –first leaves (on sterile shoots), BBCH 14 –fully developed leaves (on sterile shoots), BBCH 60 –first flowers, BBCH 65 –full flowering, BBCH 90 –start of leaf yellowing (on young sterile shoots), BBCH 97 –fully yellow plant (on 2-year-old senile shoots).

Content of macronutrients in the soil

Sampling was carried out over an area of 400 m^2 in March and October 2014. Six samples of mineral topsoil (3–8 cm) were taken along two line transects (contour and fall line with lengths of 10 and 15 m, respectively) at regular distances of 5 m. We found no significant differences in nutrient content between the spring and autumn samples. The collected soil samples were dried at 105 °C to a constant weight. Subsequently, the samples were milled into fine dust using the Planetary Micro Mill (Fritsch, Germany). We determined the total N and S content with a FLASH 1112 CNS analyser (Hanau, Germany). Available forms of the other macronutrients (Ca, Mg, K, P) were extracted according to Mehlich II, and then the samples were analysed using an atomic emission spectrometer (AES-ICP), type LECO ICP-3000 (USA).

Content of elements in plant species

The samples of aboveground biomass, consisting of 30 shoots per species, were obtained by random sampling across an area of 400 m^2 during the selected phenophases. Subsequently, the plant material was dried for 48 h in the laboratory at 105 °C.

Dry matter was then milled in a Fritsch Planetary Micro Mill into a powder. The total nitrogen and sulphur content was determined with a FLASH 1112 CNS analyser. The determination of Ca, Mg, K, and P in the selected phenological phases was performed after mineralization of the samples in concentrated HNO_3 using microwave decomposition (UniClever type, Plazmatronika, Poland). The content of P was measured with an atomic emission spectrometer (AES-ICP), while Ca, Mg and K were analysed on an SensAA atomic absorption spectrometer (GBC, Australia).

We calculated the TCs as the ratio of the nutrient content in the plants and soil, indicating the nutrient flux between them. We utilized this relationship to determine the ability of the species to accumulate the nutrients from a soil subsystem into the plant biomass throughout the growing period. Additionally, seven of the most frequently examined nutrient ratios in research studies (N/P, N/S, N/K, K/Mg, K/Ca, Ca/P and Ca/Mg) were evaluated to determine the variation in the relative availability of the macronutrients.

Statistical analysis

Statistical analyses were performed in R (R Core Team 2017). The significance of the differences was assessed by ANOVA followed by a post hoc test (Tukey's HSD test, with significance level $\alpha = 0.05$). Homogeneity of variance was evaluated with Bartlett's test.

Results

Nutrient content in the soil

The N content in the mineral topsoil (3–8 cm) showed the highest values (2.52 g kg^{-1}) among all macronutrients. A significantly lower content was found for Ca (1.43 g kg^{-1}) and S (1.38 g kg^{-1}). The content of other macronutrients (Mg, K and P) did not exceed 0.2 g kg^{-1} (Table 1).

Table 1 The content of nutrients (g kg^{-1}) in cambisol (depth 3–8 cm, $n = 6$)

Nutrient	Mean ± SD	Min	Max	CV
N	2.52[a] ± 0.69	1.92	3.57	29.98
Ca	1.43[b] ± 0.39	0.81	1.88	56.57
S	1.38[b] ± 0.19	1.11	3.38	13.76
Mg	0.19[c] ± 0.06	0.11	0.29	31.05
K	0.17[c] ± 0.08	0.11	0.32	45.29
P	0.01[c] ± 0.004	0.01	0.02	40.00

The differences are indicated at the significance level $\alpha = 0.05$
(one-way ANOVA, Tukey's HSD test)

Nutrient content in the plants

The analysis of the aboveground biomass of *Dentaria bulbifera* showed that during all phenological phases, N was mostly accumulated, while the lowest values were found for P, and the content of all of the macronutrients showed the following order: N > K > S > Ca > Mg > P (Fig. 1). We noted statistically significant variability in nutrient content among the phases. The highest content of the nutrients was observed in the following phenophases: BBCH 11 (Mg), BBCH 51 (N, K, S and P) and BBCH 95 (Ca).

In the biomass of *Carex pilosa*, the highest content was found for K, and other nutrients showed a lower content in the following order: K > N > Ca > S > Mg > P (Fig. 2). Temporal analysis showed that during the vegetative development of this species (BBCH 10), the contents of N, Mg and P were the highest. On the other hand, the accumulation of S culminated during the full flowering (BBCH 65) phenophase. At the time of plant senescence (BBCH 90), the content of Ca increased, similar to what was observed for *Dentaria bulbifera*.

Regarding the participation of herbs in the biogeochemical cycles of nutrients, we analysed the TC, which reflects the temporal accumulation of nutrients during the growing season. The highest values of the TC among all elements were detected for K and P, while the lowest values were found for Ca and S for both species (Table 2). The ability to take up P and K was more than 40–80 times higher in comparison to the transfer of Ca. For N and Mg, the coefficients were more than 10 times lower within both species. The temporal dynamics of the coefficients, expressed through the phenological phases, were closely related to the nutrient content in the plant biomass.

Relationships between nutrient ratios and phenological phases

During the selected phenological phases in the two investigated species, the [N:P] ratio ranged from 19.1 to 29.8 and from 16.4 to 28.8, respectively (Table 3). The highest or nearly highest [N:P] ratio was detected during the full flowering
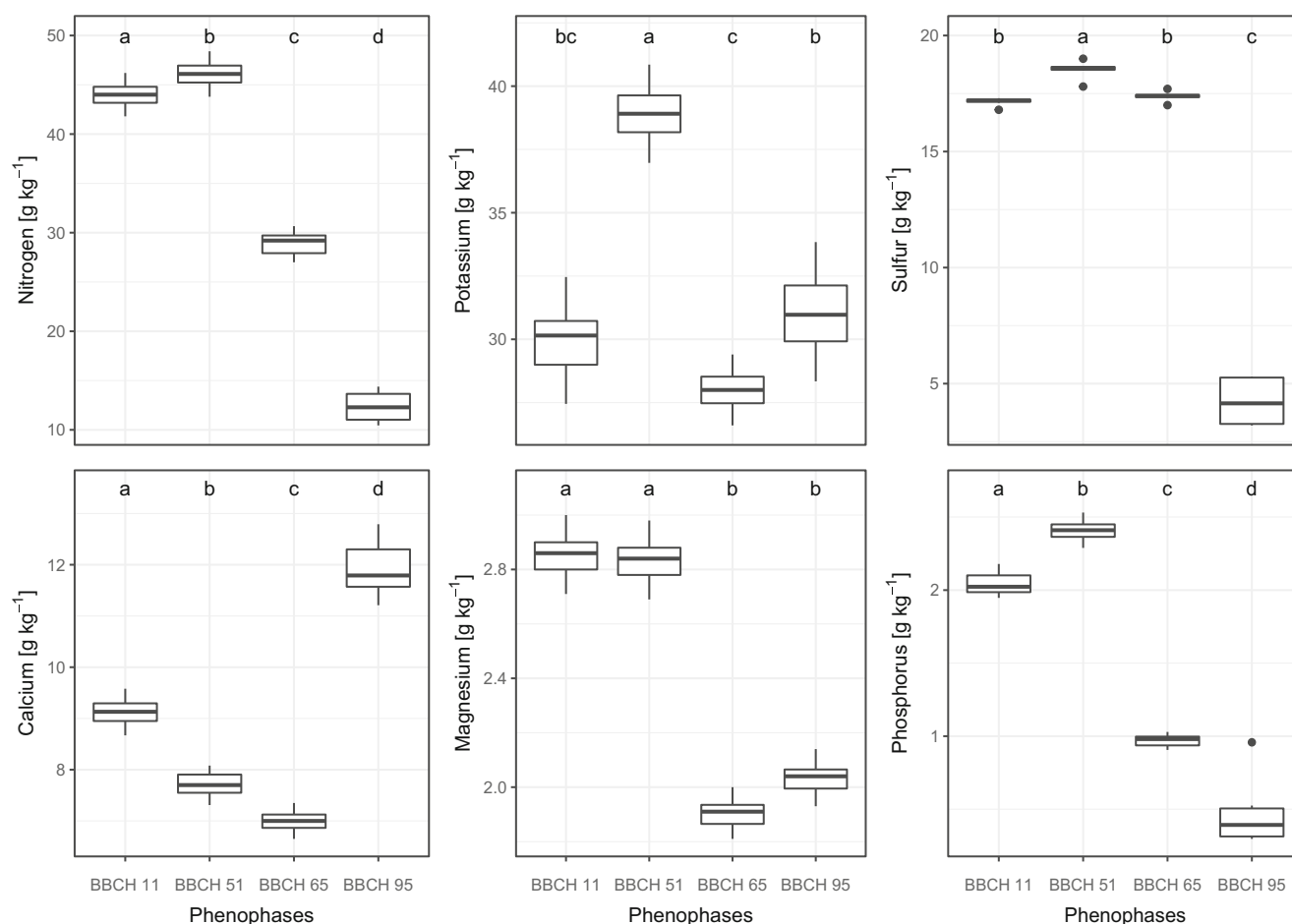

Fig. 1 Temporal changes in the content of nutrients in aboveground biomass of *Dentaria bulbifera* (n = 30). The letters indicate differences in elements contents at the significance level α = 0.05 (one-way ANOVA, Tukey's HSD test). BBCH 11 – vegetative phenophase, BBCH 51 and 65 – generative phenophases, BBCH 95 – senescence period
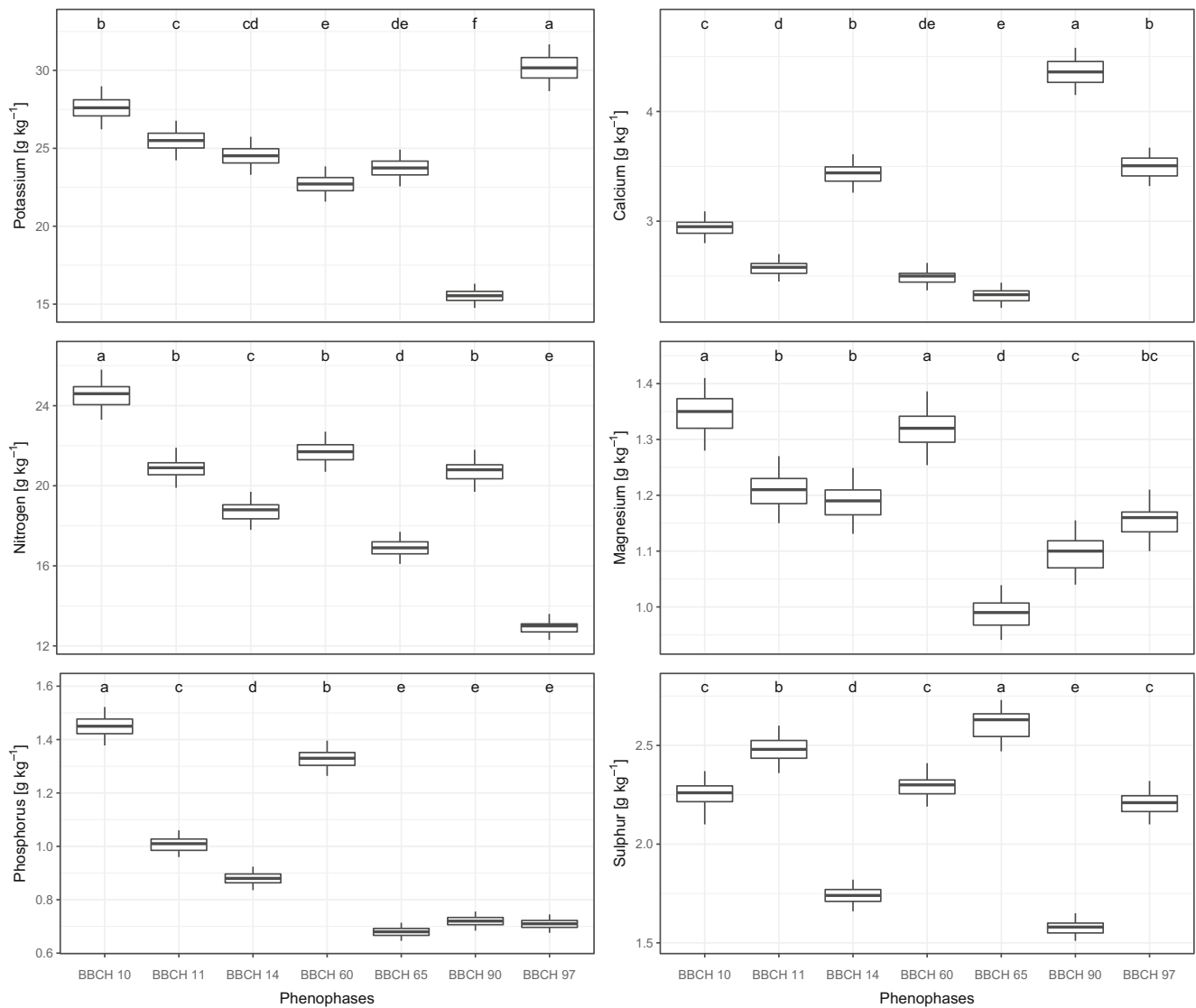
Fig. 2 The content of nutrients in aboveground biomass of *Carex pilosa* during selected phenophases (n = 30). The letters indicate differences in elements contents at the significance level α = 0.05 (one-way ANOVA, Tukey's HSD test). BBCH 10, 11 and 14 – vegetative phenophases, BBCH 60 and 65 – generative phenophases, BBCH 90 and 97 – senescence period

(BBCH 65) phenophase for both species, while the lowest value was recorded in the period preceding the flowering of plants (BBCH 51 and BBCH 60). The [N:S] ratio, changing from 1.7 to 2.9, was relatively stable in *Dentaria bulbifera*, while it was more than four times higher (ranging from 5.9 to 13.1) in *Carex pilosa*. This ratio rose from spring to the senescence period for both species. A clear downward trend for the [N:K] ratio was observed only in *Dentaria bulbifera* –the highest value (1.5) was recorded during BBCH 11, while the lowest value (0.4) occurred in BBCH 95. The [K:Mg] ratio reached values above 10 in both species. Maximum values were attained during the end of the life cycles (BBCH 95 and BBCH 97). For *Dentaria bulbifera,* we found [K:Ca] ratios ranging from 2.6 (BBCH 95) to 5.0 (BBCH 51), while relatively higher values were recorded for *Carex pilosa*,

ranging from 3.6 (BBCH 90) to 10.2 (BBCH 65). The [Ca:P] ratio changed from 1.9 (BBCH 60) to 6.1 (BBCH 95) for *Carex pilosa*, while for *Dentaria bulbifera,* the ratio changed from 3.2 (BBCH 51) to 27.7 (BBCH 95). These changes were significant ($P < 0.05$). The [Ca:Mg] ratio was always higher than 1 for both species, with increasing values from the beginning of the life cycle to plant senescence.

Discussion

In the comparison of the content of macronutrients in the examined Cambisol, we detected that nitrogen showed the highest values, as was also reported by Michopoulos et al. (2008) in mountain beech forest. On the other hand, we found

Table 2 Transfer coefficients (nutrient content in plant/content of available nutrient in soil) throughout the phenophases of the studied species

Species	Stage	BBCH code	P	K	N	Mg	S	Ca
Dentaria bulbifera	vegetative	BBCH 11	201.96	175.33	17.42	14.35	12.41	6.38
	generative	BBCH 51	237.72	227.94	18.25	14.25	13.41	5.39
	generative	BBCH 65	95.64	164.04	11.43	9.57	12.58	4.89
	senescence	BBCH 95	43.22	181.76	4.88	10.22	3.07	8.34
Carex pilosa	vegetative	BBCH 10	143.09	161.69	9.71	6.77	1.63	2.06
	vegetative	BBCH 11	99.48	149.37	8.27	6.08	1.79	1.80
	vegetative	BBCH 14	86.86	143.64	7.42	5.98	1.26	2.40
	generative	BBCH 60	131.13	133.02	8.59	6.63	1.66	1.74
	generative	BBCH 65	67.09	139.07	6.69	4.97	1.89	1.62
	senescence	BBCH 90	71.06	90.99	8.21	5.51	1.14	3.05
	senescence	BBCH 97	70.06	176.74	5.12	5.80	1.60	2.44

a relatively low calcium content, in accordance with Hölscher et al. (2002). When evaluating both *Tilia-Fagus-Fraxinus-Acer-Ulmus* forest and mono-specific beech forest, they found significantly lower concentrations of exchangeable nutrients (K, Ca, Mg) in the beech forest. Kooijman (2010) stated that beech may acidify its surroundings and reduce soil moisture by the eluviation of clay particles in calcium-poor soil (decalcified marl), which is sensitive to acidification and clay migration. On the other hand, in calcium-rich limestone soil, the pH is well buffered, and clay dispersion is prohibited. Both Mg and Ca have similar effects and enter the soil together, but the content of Ca is usually higher than that of Mg. Our results confirm this fact because the Ca content was 86.7% higher than the Mg content. Podrázský and Remeš (2010) analysed the mineral layer of soil under mixed forest and found that it contained 0.24 g kg^{-1} of Mg, which is also comparable to our records. In general, the content of S in soils varies considerably (1–10 g kg^{-1}) depending on many factors, but one of the most important seems to be the type of soil. Humus-rich soils contain more S, especially in organic form, compared to those with a low humus supply (Hanousek et al. 2017). The content of S in our findings was at the lower end of this range, which was likely caused by the low humus level in this poor-quality forest soil. The phosphorus content depends on both the mechanical composition and humus content of soils, where humus-rich soils usually contain higher levels of P compared to low-humus soils (Foster and Bhatti 2006). The past management of the land may have a persistent impact on the present-day soil P state. The soil P after pasture-to-forest conversion is generally higher compared to that in ancient forest (Falkengren-Grerup et al. 2006; Baeten et al. 2011). Talkner et al. (2009) found that the soils of mixed species stands contained more organically bound P (0.25 g kg^{-1}) than those of pure beech stands (0.15 g kg^{-1}). Additionally, Zavišić et al. (2018) reported that the soil P content increased significantly from 0.02 g kg^{-1} in P-poor sandy-loam soil to 0.50 g kg^{-1} in P-rich soil on basalt

within old beech forest stands in Germany. Our findings revealed that the P content in the Cambisol was at the lower limit of the range reported by the other authors.

Nutrient requirements can differ among plant species throughout the growing season (Golay et al. 2016). During the initial phenological phases of *Dentaria bulbifera,* we found a relatively high content of nutrients needed for the development of vegetative and generative organs. Later, a significant decrease in their content was found, likely caused by reversed transport into the root system. Therefore, we detected lower contents of some nutrients (N, S, P) during leaf colouring compared to those during the spring period. The only exception was the content of Ca, which showed the highest value at the time of plant senescence. This finding corresponds with the reports of some authors of increasing accumulation of Ca in older plant tissues (Marschner 2012). Slight differences in the accumulation of nutrients was found for *Carex pilosa*. Surprisingly, the highest content was not observed for N but for K. The observation of the highest content for K is consistent with results published by Kuklová et al. (2015). These findings contradict the generally accepted model considering nitrogen as the element with the highest values of content in plant biomass (Knecht and Göransson 2004). We suppose that our finding is related to the life form of *Carex pilosa*, which is sempervirent. Considerable protection against freezing is required for successful survival during the harsh winter and the early-spring period. This may be the reason for the sufficient supply of K in the aboveground biomass. Similarly, as was the case for *Dentaria bulbifera*, the nitrogen content in *Carex pilosa* decreased over time, but a less dramatic drop was observed. This phenomenon may be related to the fact that sempervirent graminoids, which are capable of growing slowly under favourable conditions during the winter period (see Schieber 2000), require a permanent minimum level of content.

Table 3 Nutrient ratios in aboveground biomass of herbs during selected phenological phases

Species	Stage	BBCH code	N/P	N/S	N/K	K/Mg	K/Ca	Ca/P	Ca/Mg
Dentaria bulbifera	vegetative	BBCH 11	21.50	2.56	1.47	10.49	3.28	4.47	3.19
	generative	BBCH 51	19.14	2.49	1.18	13.75	5.04	3.21	2.72
	generative	BBCH 65	29.80	1.66	1.03	14.74	4.00	7.28	3.68
	senescence	BBCH 95	28.16	2.91	0.39	15.28	2.60	27.74	5.87
Carex pilosa	vegetative	BBCH 10	17.03	11.13	0.89	20.29	9.38	2.04	2.16
	vegetative	BBCH 11	20.87	8.66	0.82	21.24	9.92	2.57	2.14
	vegetative	BBCH 14	21.28	11.00	0.76	20.77	7.15	3.89	2.91
	generative	BBCH 60	16.43	9.82	0.96	17.33	9.12	1.89	1.90
	generative	BBCH 65	25.22	6.49	0.71	24.21	10.23	3.46	2.35
	senescence	BBCH 90	28.79	13.14	1.33	14.25	3.56	6.06	3.98
	senescence	BBCH 97	18.47	5.86	0.43	26.23	8.64	4.99	3.03

Relatively high values of the TC were reached for our selected macroelements in comparison to the trace elements and heavy metals referred to by Jamnická et al. (2007, 2013) and Huang et al. (2018). In the context of the nutritional demands of plants, we expected these results. Nevertheless, some TC values were unexpected, e.g., the transfer ability of P or K was more than 40–80 times higher in comparison to the transfer of Ca in both species. Despite the fact that these two elements were the least present in a soil, it is obvious that they are necessary for plants, as was evident through the occurrence of the highest TC values. For the other three elements, the coefficients were more than 10 times lower for both species. The ability to accumulate nutrients was higher in *Dentaria bulbifera* than in *Carex pilosa*. It is possible that the belowground organs of *Dentaria bulbifera* store more nutrients during the relatively short life of its aboveground parts.

A significant excess of some nutrients can cause a deficiency in another nutrient. Nitrogen is a typical example of this phenomenon, as plants can effectively use this element only if the P content is sufficient at the same time. Thus, P indirectly affects growth and is considered to be a limiting nutrient in plant biomass production (Huang et al. 2013). If the value of [N:P] is higher than 16, the limiting factor is P. On the other hand, a value smaller than 14 means that the limiting nutrient is N (Koerselman and Meuleman 1996). Güsewell (2004) stated that the [N:P] ratio depends on the plant development stage. Lower values are usually observed in flowering plants in comparison to those in the vegetative phase. Our findings do not support this statement; the highest or nearly highest [N:P] ratio was detected in the full flowering phase, indicating P deficiency in plants because the ratio was always higher than 16. This was likely caused by the low P supply in the Cambisol we examined, which was also reflected in the relatively low P content in the biomass (P limitation). Lambert and Turner (1998) suggested that a [N:S] ratio smaller than 14 indicates S sufficiency in plant tissues, while a ratio greater than 14 indicates S deficiency. The [N:S] ratio changed from 1.7 to 2.9 and was relatively stable in *Dentaria bulbifera*. Significantly higher values of the ratio (from 6.5 to 13.1) were observed in *Carex pilosa*. Based on this finding, we can state that sulphur deficiency was not observed. On the other hand, it is possible that the lower content of this element, despite a sufficient supply in the Cambisol, indicates less demand for sulphur in these two forest plants. The most common [N:K] ratios mentioned range from 1 to 4 (Fiedler and Höhne 1987), which is consistent with our results. The relatively high [N:K] ratio in the phase of leaf yellowing was likely caused by the partial transfer of K into the creeping rhizome before the dormancy period in *Carex pilosa*. The uptake of K may be impaired by other nutrients, such as Na, Ca or Mg. For this reason, we analysed the relationship between K and Mg, which are antagonists. Redundancy of Ca and Mg may cause deficiency of K and vice versa. Therefore, the [K:Ca] or [K:Mg] ratios should range between 2 and 10 for proper plant development. Our findings show that the [K:Mg] ratio was higher than 10 in both species, which can indicate Mg insufficiency in the species. Grzegorczyk et al. (2017) found that the [Ca:P] ratio ranged from 3.9 (in *Taraxacum officinale*) to 15.3 (in *Cirsium oleraceum*). This ratio, ranging from 1.9 to 27.7 in our investigations, showed the most variability among all ratios, especially for *Dentaria bulbifera*. This change was likely caused by the transport of P into belowground parts of the biomass during the senescence period of the species to store this nutrient for the following spring period. For the healthy growth of plants, the [Ca:Mg] ratio should exceed 1, as reported by Schulte and Kelling (2004). In our case, this ratio was always higher than the suggested value, so we can state that both species were in the appropriate physiological state.

In conclusion, this paper represents the first insight into the nutrient dynamics of two dominant understory plant species in a beech forest. We confirmed that the nutrient content, nutrient

ratio and transfer of macronutrients from the soil to plant biomass are not static values but vary throughout the growing season in relation to the phenological phases of the plants. Similarly, the dynamics of both nutrient content and the accumulation of macronutrients in plant biomass are related to the life form of the plant. The ability to accumulate nutrients was higher in *Dentaria bulbifera* than in *Carex pilosa*. Our findings also show that some nutrients were present in sufficient quantity, while others were not. Currently, we do not know whether this insufficiency affects the vitality or survival of these herb-layer species. We think that it is necessary to sample both the belowground and aboveground biomass multiple times during the whole growing season for the accurate analysis of nutrient dynamics in ecological studies. Near-future research should focus on the populations of the associated plant species within the investigated site to obtain comprehensive insight into the nutrient limitations in the examined communities. Additionally, biotopes with different moisture or temperature regimes should be taken into account to better understand the processes of the nutrient supply in the framework of the biogeochemical cycle and the response of plants to changing environmental conditions.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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