

Nutrient content in biomass of bilberry (*Vaccinium myrtillus* L.) in different habitats of protected areas of Inner Western Carpathians

MARTIN KUBOV^{1,2*}, RASTISLAV JANÍK², JAKUB TOMES¹, BRANISLAV SCHIEBER²

¹Department of Integrated Forest and Landscape Protection, Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia

²Institute of Forest Ecology, Slovak Academy of Sciences, Zvolen, Slovakia

*Corresponding author: kubov@tuzvo.sk

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Abstract: The primary objective of this paper was to compare the nutrient content (N, Ca, S, K, P, Mg) of bilberry biomass, both aboveground and underground, growing in different habitats along the altitudinal gradient. The research was conducted in protected areas of the High Tatras National Park (Slovakia). Two different habitats subjected to study, namely spruce forest stands affected by disturbances (D – disturbed forest stands) and stands unaffected by disturbances (U – undisturbed forest stands), were located at different altitudes: 1 100 m a.s.l., 1 250 m a.s.l., and 1 400 m a.s.l. We found significant differences in the soil nutrient content along the altitudinal gradient. The highest content of nutrients was detected mostly at the highest altitudes in both habitats. The minimum reached 0.01 g·kg⁻¹ (phosphorus), while the maximum was 8.33 g·kg⁻¹ (nitrogen). In the case of the bilberry biomass, we found statistically non-significant differences in the content of nutrients among the altitudes within both habitats (D vs. U). The principal component analysis (PCA) showed that the aboveground biomass of bilberry had a significantly higher nutrient content compared to the underground biomass. Nutrient content in aboveground and underground biomass ranged from 1.00 g·kg⁻¹ (phosphorus) to 13.49 g·kg⁻¹ (nitrogen) and from 0.38 g·kg⁻¹ (magnesium) to 7.55 g·kg⁻¹ (nitrogen), respectively. The biological absorption coefficient (element content in dry biomass/element content in soil) reached the highest values mostly at the lowest altitude for both aboveground and underground biomass.

Keywords: disturbances; High Tatras; soil; spruce forest

European mountain forests represent a unique ecosystem that is generally exposed to a specific climate (such as extreme temperature and precipitation) as well as topography conditions (such as slope aspect, elevation gradient, and topo-

graphic position). One of the most typical coniferous species in European mountains is Norway spruce [*Picea abies* (L.) Karst.], which is perfectly adapted to these specific conditions with many different plant communities. Until the early 1980s,

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these spruce forests were considered a stable element of the mountain areas (Houston Durrant et al. 2016). However, a rapid increase in various types of disturbances in mountain spruce forests throughout Central Europe has been causing a decline in the health conditions of these forests (Senf, Seidl 2018). Mountain spruce forests have been affected by abiotic (wind, snow, and drought), biotic (bark beetles and rot) and anthropogenic (pollution) factors. These factors influenced the vitality and health of the stands at different levels, from the individual to the ecosystem response. On the other hand, the disturbances have a positive effect on the structural and biological diversity of stands – small-scale gap dynamic and variability of micro-climate conditions (Gardiner et al. 2010). The effects of a small-scale disturbance may thus have a significant impact on the ecological stability of spruce mountain forests because of increased resistance and partially also resilience (Brang 2001). However, the situation has been dramatically worsened by climate change, which affects disturbance regimes of mountain spruce forests from small-scale to large-scale disturbances and threatens the ecological stability of forests (Seidl et al. 2017). This could be a problem for the abundance of plant species typical of mountain spruce forests. One of them is also the perennial dwarf shrub bilberry, known as European blueberry (*Vaccinium myrtillus* L.). This relatively short (usually up to 30 cm), upright-growing plant is well adapted to the effect of the climate (low temperature, frost, high snow cover) and topography (slope aspect, elevation gradient, and topographic position) conditions in mountain areas. Several studies reported that bilberry plays a significant role for many other species because it is an important food source for insects, pollinators, and fruit-eating birds and mammals (Hjältén et al. 2004). Furthermore, bilberry abundance has been used as an indicator of biodiversity within forest ecosystems (Nestby et al. 2011). The abundance and biomass of bilberry may be affected by disturbances and forest management (Matějka 2015; Matějka et al. 2016; Eldegard et al. 2019). According to related studies, bilberry abundance, as well as vegetative growth, shoot survival, and fruit production, was reduced after clear-cutting (Uleberg et al. 2012). On the other hand, some studies referred to increased solar radiation, lower humidity, higher air and soil tem-

perature and increased wind speed in disturbed forests in comparison with undisturbed ecosystems (Braithwaite, Mallik 2012). Additionally, the soil of disturbed forests (damaged area) is particularly more nutritious compared to forest stands with close canopy (Fischer 1992). Therefore, more grasses (*Calamagrostis villosa*), dense fern cover (*Athyrium distentifolium* and *Athyrium filix-femina*) and nitrophilic species (*Rubus idaeus*) have been found in the herb layer after disturbance in mountain areas. The above-mentioned factors could affect bilberry phenology, reproduction and nutrient cycles. In general, the life cycle of bilberry is linked to climatic conditions and soil nutrients (Rohloff et al. 2015). It is expected that the increase in air temperature in mountain areas will affect the duration and formation of snow cover, which influences the length of the bilberry growing season. Snow cover is essential for the bilberry population because it protects it against frost damage and provides the plant with the moisture it needs throughout the spring. In contrast, early snowmelt and late frost in disturbed forests can negatively affect the physiological and metabolic processes of bilberry plants and thereby influence phenological development, mainly bud formation and flower initiation (Selås et al. 2015). The nutritional content of bilberry during physiological and phenological development is strongly dependent on soil properties (e.g. soil water content) and climatic conditions. Several studies showed that normally, bilberry grows in acidic soil environments with optimal pH levels between 4 and 5.5 (Caspersen et al. 2016). However, forest disturbances (mainly wind disturbance) affect soil layers so that soil horizons get mixed, which can lead to a slight increase in pH (> 5.5). However, some studies say that bilberry has a relatively high pH tolerance level (Tsuda et al. 2014). Yang et al. (2022a) found that high soil pH can damage the bilberry plant's photosynthetic, antioxidant, and osmotic adjustment systems. According to related studies, soil pH is a key factor in controlling soil nutrient availability and plant growth and development (Wielgus et al. 2022; Yang et al. 2022b). Yet surprisingly little is known about nutrient content and plant nutrient uptake of bilberry along the altitudinal gradient. The importance of studying bilberry populations on natural elevation gradients lies in the fact that it allows the study of ecosystem responses to long-

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er-term climate trends over short-term monitoring (Ørbæk 2022). Some abiotic factors, like air temperature or nutrient availability, decrease with increasing altitude (Körner 2003). On the other hand, precipitation, snow cover height, and duration or frequency of frosts increase with increasing altitude (Heegaard 2002). The content of nutrients and phenolic compounds in bilberry was studied by several authors (Vaneková et al. 2020). However, only a few works were devoted to the investigation of the seasonal dynamic of macronutrients along the altitudinal gradient (Pato, Obeso 2012). While this relationship has been studied in other wood species, e.g. Norway spruce (Jamnická et al. 2020), this relationship is, to our knowledge, not known for bilberry. The aim of our study was to assess whether the nutrient content in bilberry is affected by habitat and altitude. Therefore, we investigated bilberry biomass (aboveground vs. underground) in different habitats (undisturbed forest stands vs. disturbed forest stands) and also at different altitudes, specifically at 1 100 m a.s.l., 1 250 m a.s.l., and 1 400 m a.s.l., in selected protected areas of the High Tatras National Park.

MATERIAL AND METHODS

Study site and sampling design. The research was conducted in the Tatra National Park (TANAP), which is part of the international long-term ecological monitoring and research project (Halada et al. 2014; Barna 2015; Figure 1). The study area

is located on the edge of the 2004 windstorm area (Fleischer, Homolová 2011) at the altitudes between 1 100 m a.s.l. and 1 400 m a.s.l. and is affected by bark beetle outbreaks (Table 1). The area represents a type of larch-spruce forest (*Lariceto-Piceetum* community) affected by repeated windstorm disturbances. The last large-scale windstorm disturbance occurred in 2004, and heavily affected forest stands between 900–1 500 m a.s.l. Subsequently, in 2007, a large-scale bark beetle outbreak was triggered. In May 2014, a windstorm also affected the forest stands, but not to the extent it was in 2004.

Tree species composition in the study area was dominated by the Norway spruce [*P. abies* (L.) Karst. (Fleischer, Homolová 2011)]. The other co-dominant species are European larch (*Larix decidua* Mill.), European silver fir (*Abies alba* Mill.), Stone pine (*Pinus cembra* L.), and a few broad-leaved tree species (*Sorbus aucuparia* L., *Salix caprea* L., *Betula* sp.). The vegetation is characterised as patches of *Vaccinio myrtilli-Piceetum*, union *Vaccinio-Piceion*, with permanent elements such as *Vaccinium myrtillus*, *Oxalis acetosella*, *Rubus hirtus*, *Prenanthes purpurea*, *Polygonatum verticillatum*, and *Dryopteris dilatata*. The geological substrate (parent rock) consists of granodiorites and quartz diorites. The dominant soil type is acid Dystric Cambisol in mountain foothills formed by moraines (Gáfríková et al. 2020). The mor humus is present in the study plots. Soil depth, the thickness of horizons, bulk density,

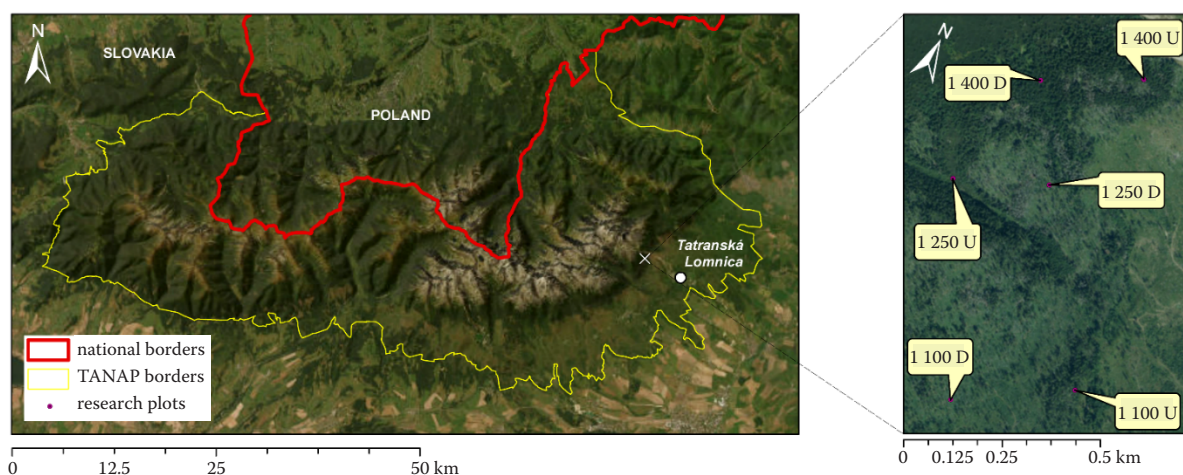


Figure 1. Location of the study area in the Slovak Republic

TANAP – Tatra National Park; 1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed forest stand; U – undisturbed forest stand

Table 1. Basic characteristics of the research plots in the High Tatra Mountains

Habitat	Research plots	GPS	Altitude (m a.s.l.)	Slope (°)	Exposure	Age (years)	Stocking
Undisturbed spruce forest	1 100 U	49°10'29.33'N, 20°14'45.12'E	1 100	10	SE	100	0.8
	1 250 U	49°10'36.91'N, 20°14'32.59'E	1 250	35	SE	165	0.4
	1 400 U	49°10'51.03'N, 20°14'24.14'E	1 400	35	SE	165	0.4
Disturbed spruce forest	1 100 D	49°10'28.03'N, 20°14'43.08'E	1 100	10	SE	–	–
	1 250 D	49°10'34.59'N, 20°14'31.05'E	1 250	35	SE	–	–
	1 400 D	49°10'52.82'N, 20°14'26.67'E	1 400	35	SE	–	–

D – disturbed spruce forest; U – undisturbed spruce forest

as well as the content of coarse rock fragments in soil horizons, are similar in all plots (Gömörýová et al. 2011). The forest type was classified according to geobiocenosis in the sense of Zlatník (1976), and the names of plant taxa were given according to Dostál (1989).

Climate data. Air temperature and precipitation during the analysed year (2019) were measured in openings located at three different altitudes (1 100 m a.s.l., 1 250 m a.s.l., and 1 400 m a.s.l.) using a meteorological station with Minikin T_{ie} and

Eri sensors (EMS, Czech Republic) and a built-in datalogger. However, some of them were broken during the period of the study. For this reason, the interpolation method was used to complete the missing data (Figure 2). Therefore, we used the data from two closest professional meteorological stations in Tatranská Lomnica (830 m a.s.l.) and Skalnaté Pleso (1 754 m a.s.l.). Both stations, managed by the Slovak Hydrometeorological Institute (SHMI), were located less than 1 km from our study area.

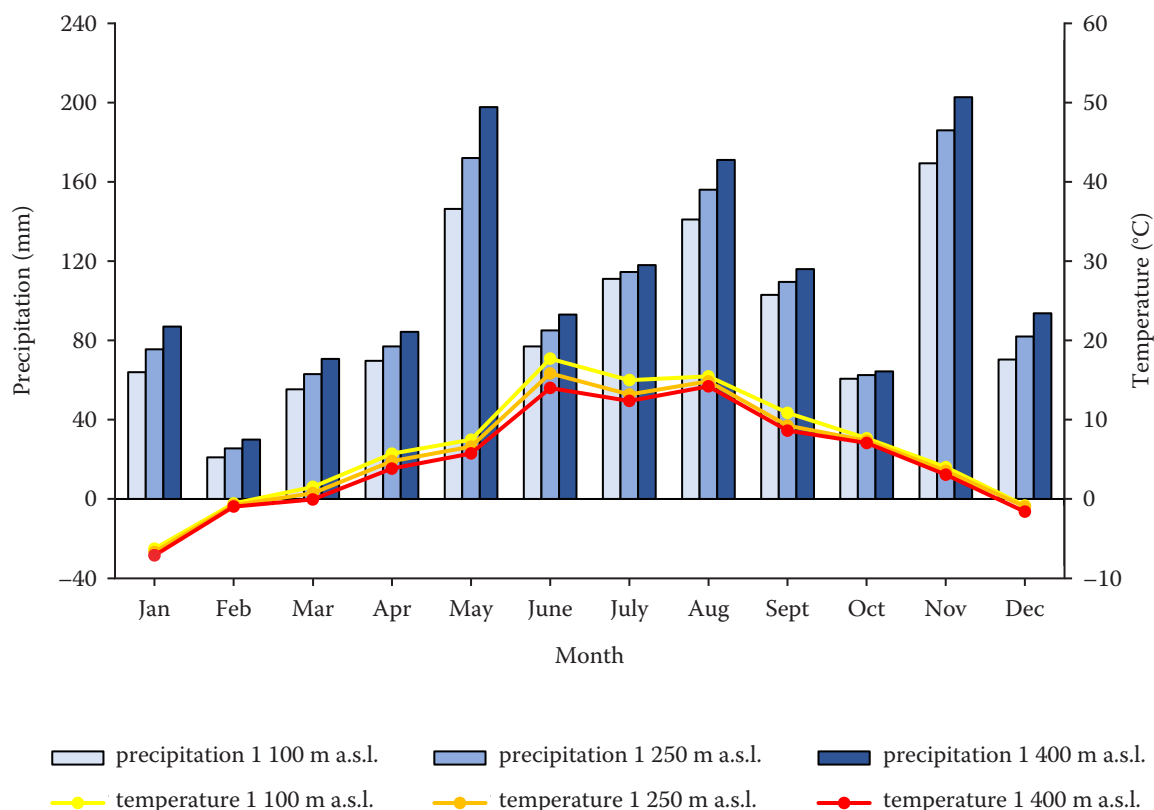


Figure 2. Climate diagram for the three study sites in 2019

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Plant species characteristics and phenological observations. The bilberry is classified within the *Myrtillus* section of the *Ericaceae* family. The leaves have very short petioles and are deciduous, alternate, spherical-oval, finely serrated, and dark green at maturity. The flowers grow in the axils of the leaves, and they are not obviously evident because they droop to the ground on the 3 to 5 mm long peduncle and are hidden under the leaves (Hájková et al. 2012). The ramets of bilberry in our study have the following parameters: the length was 40.3 (32–63) cm, and the weight reached 11.6 g of dry matter per ramet on average. We focused on five phenological phases – two vegetative (BBCH 07 – shoot expansion, BBCH 92 – autumn leaf colouring), and three generative (BBCH 65 – full bloom, BBCH 72 – petal fall, and BBCH 86 – blue fruit) during the sampling. Their determination was performed according to the international BBCH scale (Meier 2018).

Content of nutrients in the plant and soil. Individual bilberry ramets were randomly harvested in 5 selected phenophases during the growing season in 2019. Biomass samples (aboveground and underground) consisting of approximately 30 ramets were collected, put in a plastic bag and labelled. At the same time, the exact point near the soil surface was marked on each ramet. Then, the samples were separated using scissors into the aboveground and underground parts in a laboratory. The aboveground biomass represents the green part (annual shoots and leaves) of the ramet, while the underground part consists of thin, branched rhizomes with numerous adventitious roots. The roots were excavated carefully from the soil horizon to preserve most of them. They were carefully cleaned in a laboratory using clean water. Cleaning of roots is one of the most important parts of the task because just a few grains of sand bound to roots can lead to erroneous estimates of nutrient content in underground biomass. Subsequently, the biomass samples were dried for 48 h in a drying oven at a temperature of 105 °C until reaching constant weight. The dry matter was pre-prepared by a rotary mixer and pulverised by Fritsch Planetary Micro Mill (Fritsch, Germany). The total N and S content was determined with a FLASH 1112 Nitrogen, Carbon, and Sulphur Analyser (Thermo Fisher Scientific Inc., Germany). The Ca, Mg, K, and P contents were determined after the mineralisation

of the samples in concentrated HNO₃ using microwave decomposition (UniClever type – Plazmatronika, Poland). The content of P was measured with an atomic emission spectrometer (AES-ICP, type LECO ICP-3000; LECO, USA), while the Ca, Mg, and K contents were analysed using a SensAA atomic absorption spectrometer (GBC, Australia). Sampling of soil samples was carried out over an area of 900 m² in the middle of the growing season 2019 (July). Six samples of topsoil (5–15 cm) were taken along two line transects (contour and fall line with lengths of 10 and 15 m, respectively) at a regular distance of 5 m. Soil samples were kept in a plastic bag, brought to the laboratory and air-dried. Subsequently, the samples were sieved through a 2-mm sieve to remove the coarse fraction. The remaining fine-earth fraction was homogenised before chemical analysis. The samples were dried at 105 °C until reaching constant weight and 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 the Mehlich II method (Mehlich 1984), and then the samples were analysed using an atomic emission spectrometer (AES-ICP), type LECO ICP-3000. The soils were classified according to ISSS-ISRIC-FAO, i.e. the World Reference Base for Soil Resources presented in Bedrna et al. (2000).

Biological absorption coefficient. The biological absorption coefficient (*BAC*), defined by Kovalevsky (1983), was calculated as the ratio between the nutrient content in the plants and the same nutrient in the soil. Lugwisha and Othman (2016) state that *BAC* explains the transfer of elements from soil to plants, helping to explain the bioavailability and bioconcentration of the selected elements. The *BAC* > 1 indicates that the element is taken up more readily by the plant than by the soil, whereas the *BAC* < 1 indicates more element concentration in soil than those taken up by plants. We used this relationship to determine the bilberry capacity to accumulate nutrients from a soil subsystem into the biomass during the growing season. In this study, we used *BAC* to assess the accumulation of nutrients specifically for aboveground biomass and also underground biomass of bilberry.

Data analysis. Statistical analyses were performed in R (Version 4.1.2, 2021; R Core Team 2021). The sig-

nificance of the differences was assessed by the analysis of variance (ANOVA) followed by a post hoc Tukey's Honestly Significant Difference (HSD) test, with significance level $\alpha = 0.05$. We used the principal component analysis (PCA; Wilks 2019) to reveal the features in the nutrient content along the altitudinal gradient and different habitats (undisturbed/disturbed spruce stands) for soil samples, aboveground and underground biomass of bilberry. The Monte-Carlo test was used to estimate the relationship between PCA results and altitude and habitat. The degree of correlation of the two variables, soil versus aboveground or underground biomass, was expressed by a Pearson correlation coefficient (Evans 1996). The homogeneity of variance was evaluated using Bartlett's test.

RESULTS

Nutrient content in the soil. Analyses of the topsoil (0–15 cm) at each study site showed a low base saturation ($\text{pH} < 6.0$). The mean values of potentially accessible contents of macronutrients in the soil in each study site are summarised in Table 2. The content of N showed the highest value among all nutrients in all the study sites. Significantly lower content was found for S and Ca. The content of other nutrients (K, Mg, and P) did not exceed $0.08 \text{ g}\cdot\text{kg}^{-1}$ (except for the locality 1 400 D: Mg $0.25 \text{ g}\cdot\text{kg}^{-1}$ and K $0.17 \text{ g}\cdot\text{kg}^{-1}$). The analysis showed higher values in the content on all the sites disturbed by bark beetles (localities D) in comparison with undamaged plots. We found significant differences ($P < 0.05$) in the content of N and S between undisturbed spruce forests (localities U) and forests disturbed by bark beetles (localities D) in sites located

at 1 100 m a.s.l. Significant differences in the content of S and Ca were found in a higher elevation (1 250 m a.s.l.). On the other hand, we revealed significant differences in the content of all nutrients, except P, at the highest sites (1 400 m a.s.l.). Significant differences in the mean nutrient content were also found along the vertical gradient 1 100–1 250–1 400 m a.s.l.

The results of the principal component analysis (PCA) are presented in Figure 3. This principal component analysis based on a correlation matrix indicated that the two principal components explained up to almost 92.5% of variation in the data. The plotting of component scores showed a tendency to form two groups. The first group comprised disturbed forest stands at different altitudes characterised by high values of selected nutrients. The second group consisted of undisturbed forest stands at different altitudes, with lower values of selected nutrients. The existence of two distinct groups underlines different nutrient concentrations in disturbed and undisturbed forest stands. The Monte-Carlo test with 10 000 permutations was used to examine the statistical significance of the correlations between PCA ordination results and stand type along an altitudinal gradient in disturbed/undisturbed spruce forest. Our analysis shows a very low negative correlation ($r = -0.097$) without statistical significance for soils in altitudinal gradient and a high negative correlation ($r = -0.977$) with statistical significance $P < 0.0001$ for soils in different stand types.

Nutrient analysis on the vertical gradient. The PCA showed variations of the nutrient content in the aboveground biomass of bilberry and identified component 1 (Dim1) and component 2 (Dim2) which explained about 43.9%

Table 2. The content of nutrients ($\text{g}\cdot\text{kg}^{-1}$) in the soil (depth 0–15 cm) on research plots

Research plots	N	S	Ca	K	Mg	P
1 100 D	3.42 ± 1.65^a	1.41 ± 1.35^a	0.18 ± 0.08^a	0.06 ± 0.01^a	0.04 ± 0.01^a	0.02 ± 0.001^{ab}
1 250 D	3.26 ± 0.34^a	0.59 ± 0.03^a	0.24 ± 0.16^a	0.08 ± 0.01^a	0.04 ± 0.01^a	0.01 ± 0.001^b
1 400 D	8.33 ± 1.80^b	1.63 ± 0.53^a	1.04 ± 0.65^b	0.17 ± 0.09^b	0.25 ± 0.15^b	0.03 ± 0.001^a
1 100 U	2.01 ± 0.27^a	0.38 ± 0.04^a	0.13 ± 0.11^a	0.05 ± 0.01^a	0.05 ± 0.04^a	0.02 ± 0.003^a
1 250 U	2.93 ± 0.23^b	0.48 ± 0.06^b	0.09 ± 0.04^a	0.05 ± 0.01^a	0.02 ± 0.01^a	0.01 ± 0.001^b
1 400 U	6.66 ± 0.69^c	0.72 ± 0.10^c	0.30 ± 0.11^b	0.07 ± 0.02^a	0.03 ± 0.01^a	0.01 ± 0.001^b

^{a-c} Statistical significance in vertical gradient at the level of $P = 0.05$ (one-way ANOVA, Tukey's HSD test, $n = 7$); 1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed spruce forest; U – undisturbed spruce forest; mean $\pm$ standard deviations are displayed

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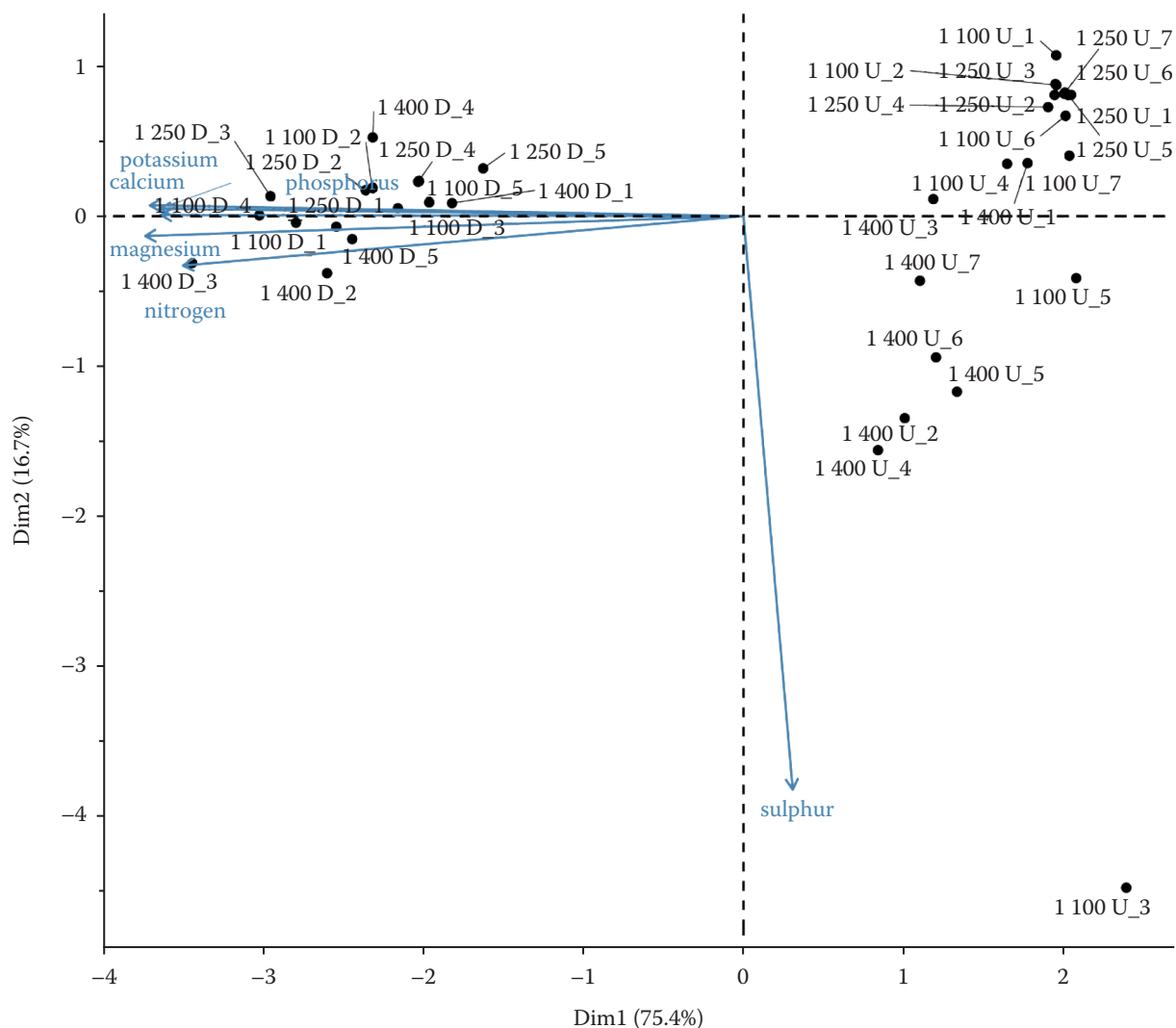


Figure 3. Principal component analysis (PCA) – Biplot of the nutrient content in the soil on the vertical gradient in different habitats

1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed forest stand; U – undisturbed forest stand; 1–7 – numbers of soil samples

and 26.3% of the variation, respectively (Figure 4). The plotting of nutrition scores showed a tendency to form two groups in different positions with a large distance between them. The first group represents Ca and Mg, while the second group represents other nutrients. Ca is positively correlated with Mg. Nutrients from the second group (P, N, S, and K) were correlated positively with each other. However, the first group (Ca and Mg) was not correlated with the second group. This suggests that these two groups have different patterns of variation in the aboveground biomass of bilberry. The Monte-Carlo test between the PCA ordination results and stand type along an altitudinal

gradient showed medium correlations ($r = 0.418$) with significance ($P < 0.05$) for aboveground biomass of bilberry grows in altitudinal gradient and very low correlations ($r = 0.028$) for aboveground biomass of bilberry grows in different stand types, without statistical significance.

Figure 5 shows the PCA of the underground biomass of bilberry. Component 1 (Dim1) explains 46.5% of the total variances, and component 2 (Dim2) explains 27.4% of the total variances in PCA.

Dim1, which explained the dominant portion of variance, had a significant positive effect on all the selected nutrients (S, N, P, Mg, K, and Ca)

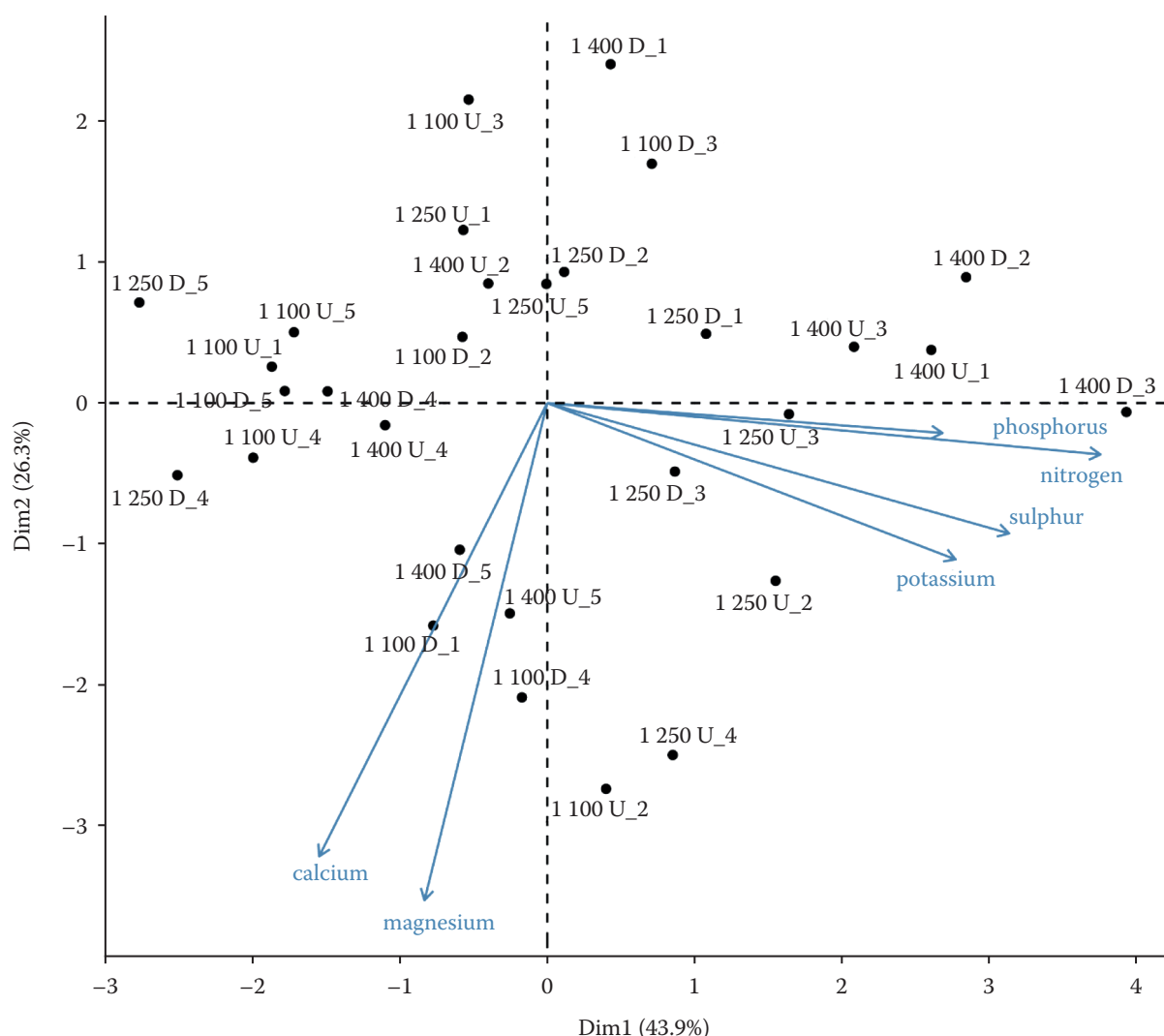


Figure 4. Principal component analysis (PCA) – Biplot of the nutrient content in the aboveground biomass of bilberry on the vertical gradient in different habitats

1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed forest stand; U – undisturbed forest stand; 1–5 – numbers of aboveground biomass samples

in the underground biomass of bilberry. Nutrients were distributed very close to each other and positively correlated with each other. The results of the Monte-Carlo test between PCA ordination results and stand type along the altitudinal gradient revealed low correlations ($r = 0.226$ and $r = 0.149$, respectively) for underground biomass of bilberry grows in altitudinal gradient and also for underground biomass of bilberry grows in different stand types, in both cases without statistical significance.

The analysis of the aboveground and underground biomass of bilberry on the vertical gradient showed a higher content of nutrients in forests

disturbed by bark beetles. The only exception was the aboveground biomass of bilberry at 1 250 U (the average content of nutrients was about 8.5% higher than at 1 250 D). The content of nutrients in aboveground biomass decreased in this order: N > Ca > K > P > Mg > S (found at 1 100 D, 1 100 U, and 1 250 D). A slightly different order was found at 1 400 D (N > Ca > K > P > S > Mg) and 1 250 U or 1 400 U (N > Ca > K > S > Mg > P). In these cases, we found significant differences between some nutrients (for example N, Ca, K) on each plot in the vertical gradient. On the other hand, the analysis of the underground biomass of bilberry showed the same order (N > K > Ca > S > P > Mg)

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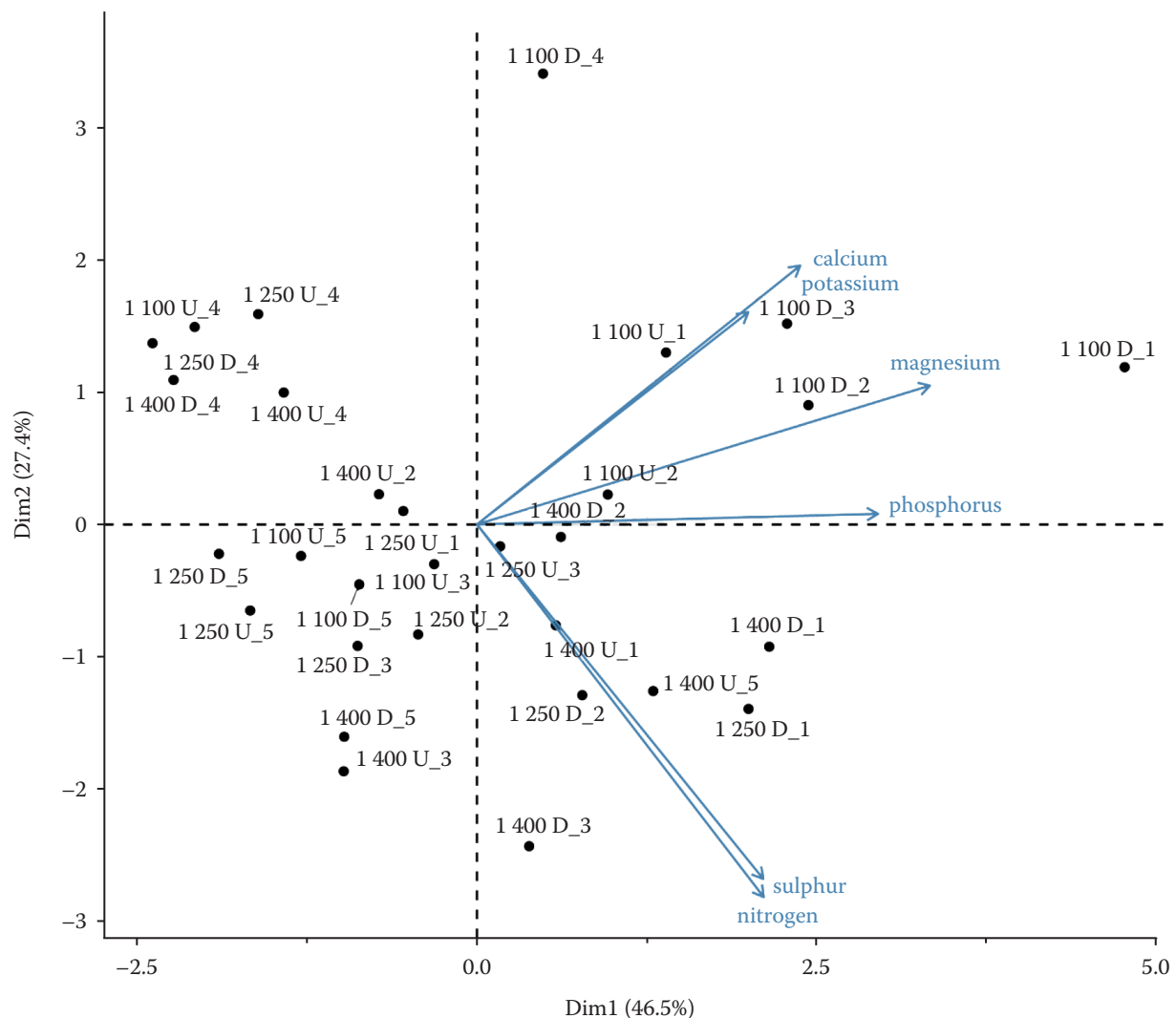


Figure 5. Principal component analysis (PCA) – Biplot of the nutrient content in the underground biomass of bilberry on the vertical gradient in different habitats

1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed forest stand; U – undisturbed forest stand; 1–5 – numbers of underground biomass samples

on all plots. Significantly higher content of nutrients was found for N, Ca, and K (Table 3).

Regarding the participation of bilberry in the biogeochemical cycles of nutrients, we analysed the *BAC*, which reflects temporal accumulation of nutrients during the growing season. Some significant differences in nutrient accumulation between the aboveground and underground biomass of bilberry were found (Table 4). The highest *BAC* values were achieved for P, K, and Ca, while S had the lowest accumulation in the aboveground biomass of bilberry. The underground biomass of bilberry showed almost the same nutrient order but with lower values. By comparing the abil-

ity of bilberry biomass to accumulate nutrients on the vertical gradient, we found lower values (significant differences) of the coefficients mostly on sites in 1 400 m a.s.l. We assume that the values of the coefficients reflect the bioaccumulation potential of bilberry on the vertical gradient (1 100–1 400 m a.s.l.) and their interaction with the different habitats (localities D vs. localities U).

The relationships between the content of nutrients in the aboveground/underground biomass of bilberry and nutrients in the soil are presented in Table 5. The rule does not apply that the higher content of selected nutrients in the soil (e.g. N and S) also means the higher content

Table 3. The content of nutrients ($\text{g}\cdot\text{kg}^{-1}$) in the biomass of bilberry on research plots

Research plots	N	S	Ca	K	Mg	P
aboveground biomass						
1 100 D	11.79 ± 1.27^a	1.01 ± 0.05^a	7.22 ± 1.87^a	3.72 ± 0.91^a	1.17 ± 0.15^a	1.15 ± 0.23^a
1 250 D	11.82 ± 2.17^a	0.94 ± 0.08^a	6.73 ± 0.74^b	3.84 ± 0.96^a	1.11 ± 0.15^a	1.07 ± 0.27^a
1 400 D	13.44 ± 2.00^a	1.08 ± 0.25^a	6.02 ± 1.40^b	4.77 ± 0.94^a	1.02 ± 0.21^a	1.14 ± 0.47^a
1 100 U	11.31 ± 1.48^a	0.92 ± 0.12^b	7.19 ± 1.98^a	3.58 ± 0.45^a	1.16 ± 0.18^a	1.07 ± 0.22^a
1 250 U	13.49 ± 0.88^a	1.20 ± 0.11^a	6.92 ± 1.34^a	4.38 ± 0.88^a	1.13 ± 0.22^a	1.00 ± 0.23^a
1 400 U	13.10 ± 2.14^a	1.16 ± 0.22^{ab}	6.31 ± 0.56^a	4.26 ± 0.36^a	1.13 ± 0.22^a	1.05 ± 0.17^a
underground biomass						
1 100 D	6.81 ± 1.27^a	0.71 ± 0.22^a	2.13 ± 0.46^a	2.33 ± 0.49^a	0.48 ± 0.08^a	0.71 ± 0.14^a
1 250 D	6.95 ± 2.16^a	0.77 ± 0.26^a	1.50 ± 0.06^b	1.84 ± 0.08^a	0.38 ± 0.05^a	0.63 ± 0.14^a
1 400 D	7.55 ± 1.84^a	0.94 ± 0.30^a	1.49 ± 0.26^b	2.10 ± 0.41^a	0.40 ± 0.05^a	0.56 ± 0.10^a
1 100 U	5.99 ± 1.14^a	0.66 ± 0.21^a	1.67 ± 0.26^a	1.95 ± 0.19^a	0.41 ± 0.05^a	0.65 ± 0.10^a
1 250 U	6.34 ± 1.38^a	0.70 ± 0.12^a	1.61 ± 0.19^a	1.84 ± 0.13^a	0.39 ± 0.02^a	0.57 ± 0.08^a
1 400 U	7.29 ± 1.47^a	0.85 ± 0.32^a	1.46 ± 0.33^a	2.10 ± 0.40^a	0.40 ± 0.04^a	0.56 ± 0.06^a

^{a,b} Statistical significance in vertical gradient at the level of $P = 0.05$ (one-way ANOVA, Tukey's HSD test, $n = 5$); 1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed spruce forest; U – undisturbed spruce forest; mean $\pm$ standard deviations are displayed

of the same nutrient in the aboveground or underground biomass of bilberry. Our correlation analysis shows a low correlation between the content

of the selected nutrients in the soil and the biomass of bilberry from both habitats (undisturbed and disturbed).

Table 4. Biological absorption coefficient (BAC – element concentration in dry matter/element concentration in soil dry matter) in the biomass of bilberry on research plots along the vertical gradient

Research plots	N	S	Ca	K	Mg	P
aboveground biomass						
1 100 D	4.66 ± 3.84^a	1.30 ± 0.97^a	43.48 ± 15.87^a	56.55 ± 6.42^a	30.22 ± 5.45^a	67.51 ± 22.85^a
1 250 D	3.62 ± 0.94^{ab}	1.58 ± 0.18^a	36.26 ± 18.10^a	52.83 ± 15.19^a	32.73 ± 11.25^a	77.01 ± 23.87^a
1 400 D	1.79 ± 0.47^b	0.77 ± 0.39^a	10.40 ± 11.35^b	31.69 ± 20.50^b	7.07 ± 6.75^b	48.06 ± 27.43^b
1 100 U	5.70 ± 1.42^a	2.47 ± 0.43^a	114.40 ± 111.18^a	67.59 ± 13.12^a	51.95 ± 9.67^a	53.71 ± 16.69^a
1 250 U	4.69 ± 0.28^a	2.49 ± 0.58^a	109.52 ± 94.15^a	85.63 ± 10.73^a	47.28 ± 8.07^a	81.11 ± 21.59^{ab}
1 400 U	2.00 ± 0.57^b	1.67 ± 0.44^a	33.13 ± 31.11^b	69.06 ± 17.84^a	37.46 ± 15.07^a	83.37 ± 12.65^a
underground biomass						
1 100 D	2.83 ± 2.36^a	1.01 ± 0.96^a	12.80 ± 3.79^a	36.64 ± 11.13^a	12.54 ± 3.24^a	43.06 ± 19.02^a
1 250 D	2.13 ± 0.78^a	1.30 ± 0.45^a	8.39 ± 4.60^{ab}	25.75 ± 7.09^{ab}	11.45 ± 4.52^a	44.78 ± 10.66^a
1 400 D	0.89 ± 0.57^b	0.70 ± 0.43^a	2.95 ± 3.85^b	14.95 ± 13.50^b	4.37 ± 3.48^b	24.37 ± 12.07^b
1 100 U	3.03 ± 0.91^a	1.80 ± 0.65^a	26.75 ± 22.63^a	36.60 ± 5.28^a	18.38 ± 3.96^a	32.35 ± 6.10^b
1 250 U	2.21 ± 0.48^a	1.45 ± 0.34^a	23.24 ± 13.79^a	36.82 ± 7.72^a	16.69 ± 4.72^a	46.27 ± 7.32^a
1 400 U	1.10 ± 0.28^b	1.25 ± 0.54^a	6.90 ± 4.91^b	35.40 ± 14.12^a	13.39 ± 5.09^a	44.55 ± 9.08^{ab}

^{a,b} Statistical significance in vertical gradient at the level of $P = 0.05$ (one-way ANOVA, Tukey's HSD test, $n = 5$); 1 100, 1 250, 1 400 – altitude of research plots (m a.s.l.); D – disturbed spruce forest; U – undisturbed spruce forest; mean $\pm$ standard deviations are displayed

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Table 5. The relationships (Pearson's r) between the content of nutrients in biomass and soil in different habitats ($n = 15$); non-significant relationships were found in all cases

Research plot	N	S	Ca	K	Mg	P
aboveground biomass						
D	0.36	0.05	−0.08	0.42	0.04	0.11
U	0.16	0.28	−0.27	0.44	0.11	0.07
underground biomass						
D	−0.12	−0.20	−0.28	−0.07	−0.35	−0.28
U	0.36	0.19	−0.14	−0.20	−0.16	0.46

D – disturbed spruce forest; U – undisturbed spruce forest

DISCUSSION

Previous studies have focused mainly on the relationships between nutrient content in the aboveground biomass and the structure of the stands, but the content of nutrients in the underground biomass of bilberry has rarely been reported (Nybakken et al. 2013). Other field studies compared the growth and concentrations of nutrients in various sorts of plant tissue of bilberry (e.g. leaves, stems, roots) in differently polluted areas (Kukla, Kuklová 2008; Taulavuori et al. 2013; Kandzioara-Ciupa et al. 2021). The study from protected areas, such as national parks, conducted by Parzych (2016) showed a higher concentration of nutrients in leaves and shoots than in roots. This finding corresponds with our study, which found significantly higher concentrations of nutrients in the aboveground biomass. The content of nutrients in aboveground bilberry biomass shows that N is the most abundant nutrient in bilberry (followed by Ca and K). We noted this order on each site, regardless of altitude and different habitats. This finding is a generally accepted model considering N as the element with the highest values of content in plant biomass (Knecht, Göransson 2004). Kuklová and Kukla (2003) stated that the surplus of N supports the longitudinal growth of bilberry shoots that lose their resistance against early frosts. We cannot confirm this argument at present. However, we agree that bilberry shoots lack outer bark and are sensitive to frost (Hertel et al. 2018). In mountain spruce forests (e.g. the Tatra Mts.), a thick insulating layer of snow favours bilberry survival during the winter. The order of other analysed nutrients (P, Mg, and S) was different, and unambiguous interpretation was difficult. As we can see, the content of P and S was low (less than

1.15 g·kg^{−1}) and usually occurred at the end of the order. The content of N, Ca, and K was significantly higher than the content of P, Mg, and S. A similar finding was reported by Parzych (2016). The author analysed the content of macro- and microelements in bilberry and lingonberry and found the same order of selected nutrients (N > Ca > K) in bilberry leaves. However, the mean content of nutrients found in the shoots was different and decreased in the following order: Ca > N > Mg. Korcak (1988) states that different organs of bilberry plants generally display different element composition. For example, the content of Ca in leaves during most of the growing season is lower than the content of N (Retamales, Hancock 2012). However, it could be substantially variable across different *Vaccinium* species. Kuklová and Kukla (2003) analysed some herb species (and also bilberry) in two spruce stands (undamaged vs. damaged by acidic atmospheric pollutants) situated in the region of Middle Spiš (Slovakia). As in our case, they found that the content of some nutrients (N, K) was relatively high, while the values of other nutrients (Ca, Mg, P, and S) were low. They reported the following order of nutrients in aboveground biomass: N > K > Ca > Mg > S > P. Moreover, the values of the selected nutrients were similar to ours. Some other authors (Johansson 1993) who also analysed the nutrient content in aboveground biomass of bilberry found a slightly different order of nutrients: N > K > Ca > P > Mg. In addition, with the exception of P and Mg, the content of the selected nutrients in bilberry in our study corresponded with those reported from the mentioned areas. The present results, although based on a limited number of samples, clearly point to minimal differences in the nutrient content of bilberry along the altitudinal gradient. Our study shows non-significant

differences along the altitudinal gradient within the same type of habitat. The only exception was sulphur – significant differences were found between the sites in 1 100 m a.s.l. and 1 250 m a.s.l. in the undisturbed habitat. In addition, in the disturbed stands, we revealed a significant difference for Ca between the sites in 1 100 m a.s.l. and 1 250 m a.s.l., as well as 1 100 m a.s.l. and 1 400 m a.s.l. This does not correspond entirely with Fernández-Calvo and Obeso (2004), who found a significant effect of habitat and altitude on the growth, the content of N and fruit production of bilberry along the altitudinal gradient in three temperate habitats (oak forest, birch forest and heath). In general, the plants receive nutrients in quantities proportional to their concentration in the soil (Parzych et al. 2012). For this reason, we also analysed the *BAC*. This coefficient permitted the evaluation of the nutritional demands of bilberry in different habitats. The highest *BAC* in both habitats were found for K and Ca. Although these two elements were the least present in the soil, it is obvious that they are necessary for bilberry. In this study, we found that the mean content of accumulated nutrients (*BAC*) from soil into the aboveground and underground biomass of bilberry decreased in the following order: $K > Ca > Mg > P > N > S$ in both types of habitats. The least accumulated nutrients by bilberry were N and S. The low *BAC* values for these elements indicate their potential to stabilise in the soil (because they have the highest content in the soil). Generally, the values of *BAC* decreased with increasing altitude. Overall, this might indicate that the bilberry population in the high part of the hill (over 1 400 m a.s.l.) saves energy, and the accumulation of nutrients starts just before reproduction. On the other hand, we assume that these factors (high temperature and late frost) negatively affected the production of berries on the sites in 1 250 m a.s.l. and 1 400 m a.s.l. in disturbed (damaged) forests. Nestby et al. (2014) pointed out that the accumulation of these elements is mainly due to the symbiosis with ericoid mycorrhiza, which provides access to nutrient (e.g. N, S, P) sources that would not be available to bilberry roots alone because bilberry roots lack root hairs (Kuklová, Kukla 2003). We assume that lower values of *BAC* in damaged forests indicate difficulties with nutrient accumulation of bilberry in sites with changed environmental conditions (disturbed sites). On the other hand, we did not find major differences in the nutrient

order in the underground biomass of bilberry between habitats and the altitude. The underground biomass shows the same nutrient order ($N > K > Ca > S > P > Mg$) in each habitat and altitude. These results could indicate that the underground biomass is more stable from the aspect of bilberry morphology and physiology in the accumulation of nutrients than the aboveground biomass. All these data provide relevant information that could help to ascertain the nutritional status of the bilberry population in mountain spruce forests. Nevertheless, no statistically significant correlations were found between the content of nutrients in biomass and soil in this survey.

CONCLUSION

We focused on comparing the nutrient content of bilberry biomass growing in different habitats at different altitudes (1 100 m a.s.l., 1 250 m a.s.l., and 1 400 m a.s.l.). The research was conducted in protected areas of the High Tatras National Park (Slovakia) within two different habitats: spruce forest stands affected by disturbances (D – disturbed forest stands) and unaffected by disturbances (U – undisturbed forest stands). The selected macronutrients (N, Ca, S, K, P, Mg) in the biomass of bilberry (aboveground and underground) and also in the mineral layer of the soil were statistically compared for both types of habitats along the altitudinal gradient. We found that the content of nutrients in the soil was higher in disturbed forests compared to undisturbed stands, which is a manifestation of faster decomposition and a subsequent better nutrient supply. The highest nutrient content in soil was detected at the highest sites (1 400 m a.s.l.). This finding was similar also in the case of the highest content of N, S, and K in both aboveground and underground biomass of bilberry. However, we found statistically nonsignificant differences in the content of the nutrients in the biomass among the altitudes for both habitats (D vs. U). The nutrient stocks followed the sequence $N > Ca > K > Mg > P > S$ and $N > K > Ca > S > P > Mg$ for aboveground and underground biomass, respectively. PCA analysis showed that the nutrients in the soil are closely correlated to one another, sulphur being the only exception. Two orthogonal groups (P, N, S, and K vs. Ca and Mg) were observed in the aboveground biomass. In the case of underground biomass, the situation is simi-

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lar, but the two groups of elements are different: the second group consists of sulphur and nitrogen, which are highly mobile in the soil. Interestingly, sulphur has a similar position against other elements in both PCA for soil and underground biomass. The biological absorption coefficient, reflecting the transfer of nutrients from the soil to the plant, was the lowest at the highest sites, but statistically significant only for N and Ca for both types of the biomass. These significant differences in the highest locality, compared to lower sites, could be caused by the limited ability of bilberry, as an oligotrophic mesophyte species, to utilise these nutrients. Our results confirm that bilberry is a species which utilises nutrients appropriately; it seems that it is not a 'nutrient eater'. This strategy probably helps this species to survive relatively successfully in competition with other species, especially at the edge of its ecological occurrence.

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