

ORIGINAL PAPER

C/N/P stoichiometry of forest soil in relation to the tree species and slope position in the Carpathian Mountains

Karolina Staszczel-Szlachta^{(1)✉}, Ewa Błońska⁽¹⁾, Andrzej Szlachta⁽²⁾, Jarosław Lasota⁽¹⁾

⁽¹⁾ Department of Ecology and Silviculture, Faculty of Forestry, University of Agriculture in Krakow, 29 Listopada 46, 31-425 Kraków, Poland

⁽²⁾ Świerklaniec Forest District, Oświęcimska 19, 42-622 Świerklaniec, Poland

ABSTRACT

The aim of our study was to determine the C/N/P stoichiometry of forest soils in relation to the tree species and slope position in the Carpathian Mountains. Ecological stoichiometry is used as an effective approach to the analysis of feedback and relation between the different components of an ecosystem. Knowledge about the distribution of C, N and P as well as their stoichiometry allows for a better understanding of ecosystem function and stability. C/N/P ratio reflects natural changes in ecosystems as well as those resulting from the management methods or caused by human activity. We assume that tree species and altitude influence the quantity and quality of soil organic matter in forest soils and in turn the C/N/P stoichiometry. The study was carried out in the Jałowiec Massif in Beskid Żywiecki of southern Poland (49°39'64"N; 19°28'67"E). Study plots were located along altitudes at 600, 800 and 1000 m a.s.l. in a beech stand *Fagus sylvatica* and fir stand *Abies alba*. The enzymatic activity, content of C, N and P were recorded in testing soil samples. The C/N/P stoichiometry was calculated for reflecting the nutrient availability in soil along altitude gradient. Our study confirmed the role of climatic condition and tree species in shaping the stoichiometry C/N/P of mountain soils. Soils under influence of fir stands are characterized by a wider C/N/P ratio compared to soils under influence of beech stand. The higher content of soil organic matter that is less decomposed was noted in higher locations as a result of the impact of fir stand. The activity of four out of six tested enzymes decreased with height, which confirms the limitation of biological activity of soils in higher positions. We found that the enzymatic stoichiometry depend on the altitude. The type of tree species had no effect on enzymatic ratios. The altitude influenced the temperature and moisture which are related to microorganisms activity, which results in differences in the stoichiometry of soil enzymes. Our study support the use of enzymatic stoichiometry for reflecting the nutrient cycle in mountain forest ecosystem.

KEY WORDS

altitude, enzyme activity, forest ecosystem, nutrients, temperate climate

✉e-mail: karolina.staszczel@student.urk.edu.pl

Received: 8 August 2023; Revised: 9 October 2023; Accepted: 10 October 2023; Available online: 14 November 2023

 Open access

©2023 The Author(s). <http://creativecommons.org/licenses/by/4.0>

Introduction

Stoichiometry is the study of energy and chemical elements balance in biological systems (Sterner and Elser, 2002). Ecological stoichiometry is used as an effective approach to the analysis of feedback and relation between the different components of an ecosystem (Cleveland and Liptzin, 2007). Knowledge about the distribution of C, N and P as well as their stoichiometry allows for a better understanding of ecosystem function and stability (Liu *et al.*, 2020a). C/N/P ratio reflects natural changes in ecosystems as well as those resulting from the management methods or caused by human activity (Lasota *et al.*, 2022). The current study provides evidence that altitudinal gradients can cause change in C/N/P stoichiometry in soil (Cleveland and Liptzin, 2007; Zhang *et al.*, 2019). Exploring the diversity of soil C/N/P stoichiometry will improve our knowledge of forest ecosystem dynamics and soil carbon accumulation in climate change (Feng *et al.*, 2017).

In mountainous area with increasing altitude a.s.l. climatic factors change, the temperature drops, the sum of rainfall increases, the period of snow cover lingering extends and the vegetation period is shortened. As a result of climate conditions the plant cover changes which determines the soil properties (Staszek *et al.*, 2021). Cool and humid conditions of the mountain climate weaken the processes of microbiological decomposition of organic matter.

The altitude and species composition were major factors controlling the quality and amount of soil organic matter (Łabaz *et al.*, 2014; Bayranvand *et al.*, 2017). According to Zanella *et al.* (2011) humus forms depends on environmental factors and biological factors such as forest stand species composition. Previous research confirms the role of tree species in shaping soil characteristics, especially surface horizons (Błońska *et al.*, 2021). Trees, through fallout of litter and root systems have the strongest impact on soil properties, especially quality and quantity of soil organic matter (Baldrian and Šnajdr, 2011). Deciduous and coniferous species differ in the amount and quality of detritus supplied to the soil (Błońska *et al.*, 2017, 2021). Deciduous tree species release larger amounts of alkaline cations into the soil, and a faster decomposition rate of the litter of these species favours the release of more mineral nitrogen. Previous study confirms the role of the species composition and planting method in shaping the C/N/P ratios of soils and plants (Lasota *et al.*, 2021). Measurement of the enzymes activity involved in the C, N, P and S cycles provide knowledge about the biogeochemical circulation that occurs in soil (Yavitt *et al.*, 2004). Soil microorganisms produce enzymes to acquire carbon and nutrients from soil organic matter, which allows for maintain a relatively stable biomass element composition under various resource conditions (Sinsabaugh and Shah, 2012). Soil enzyme stoichiometry has been used to reflect microbial resource limitation (Wang *et al.*, 2020).

The aim of our study was to determine the C/N/P stoichiometry of forest soils in relation to the tree species and slope position in the Carpathian Mountains. We assumed that the deciduous and coniferous species deliver different amounts and quality of detritus to the soil resulting in differences in C/N/P ratio. We tried to explain how varied altitude affects the processes associated with the transformation and accumulation of C, N and P in forest ecosystem. In our research, we hypothesize that soil enzyme stoichiometry reflects changes caused by different species composition and location condition in altitude gradient.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN. The research was carried out in the Jałowiec Massif in Beskid Żywiecki in southern Poland (49°39'64"N; 19°28'67"E). The study took place in Magurska

Nappe on the sandstone and shales, Cambisols (WRB, 2014) dominated the chosen study plots, which were established at three different altitudes at 600, 800 and 1000 m a.s.l. Study plots were located along the slope with an inclination of 15°. The tested soils were characterized by the similar texture of sandy loam (average sand content was 54%, silt 42% and clay 3%). The average temperature of the growing season for the study plots at 600 m a.s.l. was 12.4°C. for the study plots of 800 m a.s.l. was 11.3°C and at an altitude of 1000 m a.s.l. was 10.2°C. Average soil moisture at 600, 800 and 1000 m a.s.l differed and amounted to 22.74%, 29.60% and 34.10 respectively. The research plots were located in a beech stand *Fagus sylvatica* L. and fir stand *Abies alba* Mill. The average age of both tree stands was about 60 years. In each variant of the altitude, 3 research plots (10 ares) with beech and fir were designated. Three soil samples from different location were collected on each plot. The samples were taken after removing the litter from a depth of 0-15 cm.

LABORATORY ANALYSIS. The total nitrogen (N) and organic carbon (C) were analysed by the LECO CNS True Mac Analyzer (Leco, St. Joseph, MI, USA). The P content were measured using a ICP-OES ThermoCAP 6500 DUO (Thermo Fisher Scientific, Cambridge, U.K.) after mineralisation of the mixture with concentrated nitric and perchloric acids at ratio of 3:1. The C/N, C/P and N/P ratios on a molecular level were calculated.

The enzymatic activity was determined in fresh soil samples of natural moisture, which were passed through a sieve with a diameter of 2 mm. Soil samples for the determination of enzymatic activity were stored at 4°C. The activity of six extracellular enzyme (β -glucosidase (BG), β -D-cellobiosidase (CB), β -xylosidase (XYL), N-acetyl- β -D-glucosaminidase (NAG), phosphatase (PH) and arylsulphatase (SP)) was determined (Pritsch *et al.*, 2004; Turner, 2010; Sannaullah *et al.*, 2016). Enzymatic stoichiometry were calculated using BG/NAG, BG/PH and NAG/PH for the soil C/N, C/P and N/P ratios (Lasota *et al.*, 2021).

STATISTICAL ANALYSIS. ANOVA test was used to assess differences between soil characteristics. General linear model (GLM) was used to investigate the effects of the tree species and altitude on the C, N and P ratios. Principal component analysis (PCA) was used in order to interpret factors in certain data sets. The Statistica 12 software (StatSoft, 2012) was used for data analysis and differences with $p < 0.05$ were considered statistically significant.

Results

At 600 m a.s.l., soils were characterized by significantly higher pH compared to other altitudes, in addition, the pH of fir stands differs significantly from beech stands at an altitude of 1000 m a.s.l. The examined soils differed in the content of C, N and P (Table 1). In the soils of beech stands, a significantly higher C content was recorded at the altitude of 1000 m a.s.l. and in the case of fir stands at the altitude of 800 and 1000 m a.s.l. The soils of fir stands in the higher positions (800 and 1000 m a.s.l.) were characterized by significantly higher C contents compared to the soils of beech stands. In the case of N, significantly higher contents were recorded in soils of higher positions, and in the soils of beech stands on altitude 1000 m a.s.l. and for the soils of fir stands of 800 and 1000 m a.s.l. The soils of fir and beech stands differed significantly in the content of N (Table 1). The content of P increases with the altitude in the soils of the studied stands. In the case of soils with beech stands, significantly higher P content was recorded in soils at the altitude of 1000 m a.s.l., and in the case of soils with fir stands at the height of 800 and 1000 m a.s.l. In soils at the height of 1000 m a.s.l. differences in the content of P between the studied stands were noted (Table 1). In the case of beech stand soils, the C/N ratio increases

Table 1. C, N, P content and enzymes activity (nmol MUB.g⁻¹.d.s.h⁻¹) in soil under influence of different tree species in altitude gradient (a.s.l.)

| Species | Altitude | pH | C | N | P | CB | BG | NAG | XYL | SP | PH |
|---------|----------|-------------|--------------|--------------|-----------------|-------------|----------------|----------------|---------------|--------------|-----------------|
| Beech | 600 | 4.84±1.04ax | 5.23±0.91bx | 0.37±0.05bx | 536.77±109.84bx | 8.18±4.09ax | 53.74±21.06ax | 32.21±15.57ax | 1.98±1.51ax | 10.35±4.30ax | 461.23±80.26ax |
| | 800 | 4.09±0.19bx | 6.72±1.65aby | 0.42±0.08abx | 640.32±119.98bx | 1.72±1.36bx | 32.41±13.23abx | 24.15±10.24abx | 2.00±2.41ax | 5.67±6.32abx | 503.69±22.12ax |
| | 1000 | 4.04±0.25bx | 8.80±2.02ay | 0.49±0.09ay | 859.73±68.13ax | 1.22±1.10bx | 19.97±11.98bx | 11.75±8.14bx | 8.83±12.15ay | 2.04±2.76bx | 501.89±105.52ax |
| Fir | 600 | 4.91±0.20ax | 4.51±0.62bx | 0.32±0.04by | 458.72±56.84bx | 4.67±4.23ay | 42.36±15.06ax | 33.01±14.75ax | 1.99±1.52bx | 11.52±7.10ax | 498.58±98.76ax |
| | 800 | 3.94±0.15bx | 10.44±2.92ax | 0.55±0.10ax | 627.43±89.45ax | 2.37±3.05ax | 45.72±14.79ax | 25.16±11.80ax | 3.91±3.02bx | 4.61±3.46abx | 569.52±200.51ax |
| | 1000 | 3.65±0.08by | 14.81±5.60ax | 0.74±0.23ax | 689.51±52.15ay | 1.48±0.62ax | 33.01±12.93ax | 17.82±9.05ax | 35.76±27.04ax | 0.51±0.43bx | 728.16±330.13ax |

Mean ± standard deviation; pH in H₂O; C₀ – organic carbon [%], N – total nitrogen [%], P content [mg.kg⁻¹]; CB – β-D-cellobiosidase, XYL – β-xylosidase, NAG – N-acetyl-β-D-glucosaminidase, BG – β-glucosidase, PH – phosphatase and SP – arylsulphatase; small superscript letters: a, b – significant differences between altitude; x, y – significant differences between tree species

Table 2. GLM analysis for C/N/P stoichiometry in soil under influence of different tree species in altitude gradient (a.s.l.)

| Species | C/N | | C/P | | N/P | | BG/NAG | | BG/PH | | NAG/PH | |
|--------------------|-------|---------|-------|---------|-------|---------|--------|--------|-------|---------|--------|---------|
| | F | p | F | p | F | p | F | p | F | p | F | p |
| Species | 16.81 | 0.0002* | 24.98 | 0.0000* | 24.08 | 0.0000* | 0.01 | 0.9305 | 0.01 | 0.9433 | 0.01 | 0.9754 |
| Altitude | 53.04 | 0.0000* | 8.96 | 0.0005* | 2.19 | 0.1229 | 0.78 | 0.4600 | 16.08 | 0.0000* | 11.57 | 0.0000* |
| Species x altitude | 5.76 | 0.0057* | 7.82 | 0.0011* | 8.43 | 0.0007* | 1.66 | 0.2045 | 3.37 | 0.0425* | 0.09 | 0.9176 |

*Significance effect (P<0.05)

with the altitude (Fig. 1). At the altitude of 600 m a.s.l. is 16.5 at the altitude of 800 m a.s.l. is 18.2 and at the altitude of 1000 m a.s.l. it amounts to 29. The C/N ratio in the soils of beech stands at the altitude of 1000 m a.s.l. was statistically significantly higher than the others. C/N ratio in the soils of fir stands at the altitude of 800 and 1000 m a.s.l. was statistically significantly higher than the others. There were no significant differences in the C/P and N/P ratios in the soils of the beech stands. In the soils of fir stands at the altitude of 800 and 1000 m a.s.l. a significantly higher C/P ratio was noted compared to soils at a height of 600 m a.s.l. In the case of the soils of with fir, an increase in the N/P ratio was recorded with altitude. A significantly higher N/P ratio was found in the highest positions (Fig. 1). The conducted GLM analysis confirmed the statistically significant importance of the species in shaping the C/N, C/P and N/P ratios (Table 2). Altitude played a role in shaping the C/N and C/P ratios. The combined effect of species and altitude was reported for the C/N ratio (Table 2).

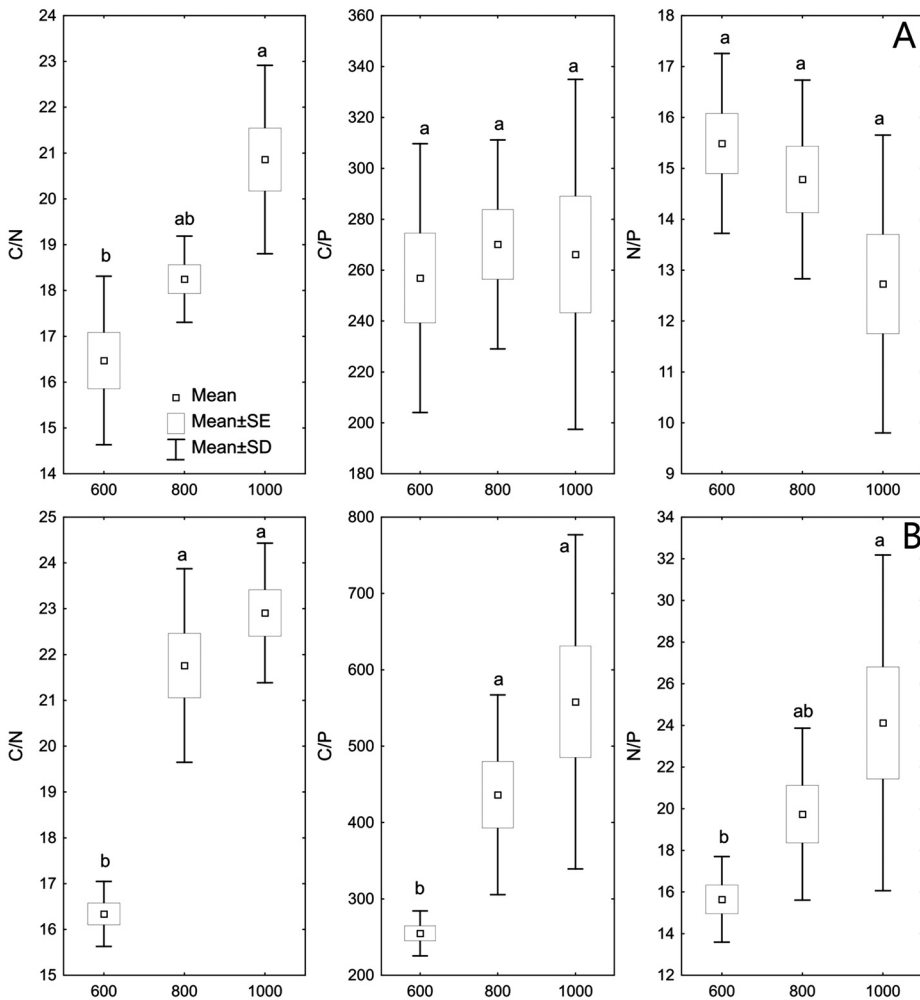


Fig. 1.

C/N/P stoichiometry in soil under different tree species in altitude gradient
 A – soil under influence of beech, B – soil under influence of fir; 600, 800 and 1000 – altitude a.s.l.

In the studied soils, diversification of enzymatic activity was noted (Table 1). In the case of CB, BG, NAG and SP, there was a decrease in activity with altitude, regardless of the tree species studied. For XYL and PH, activity increased with altitude. In the case of the soils of beech stands, the activity of CB, BG and SP was significantly higher in the soils of the lowest positions (600 m a.s.l.). In the case of the soils of fir stands, the activity of SP was significantly higher in the soils of the lowest positions (600 m a.s.l.) and the activity of XYL was significantly higher in the soils of the highest positions (1000 m a.s.l.) (Table 1). Our analysis of the BG, NAG and PH activity stoichiometry demonstrated that the studied soil samples do not differ statistically significantly in the ratio of BG/NAG (Fig. 2). Significantly lower BG/PH and NAG/PH ratios were recorded in soils with beech and fir in the highest position (1000 m a.s.l.). The conducted GLM analysis did not confirm the significant importance of the species in shaping the enzymatic stoichiometry (Table 2). Altitude was statistically significant in shaping the BG/PH and NAG/PH ratios (Table 2).

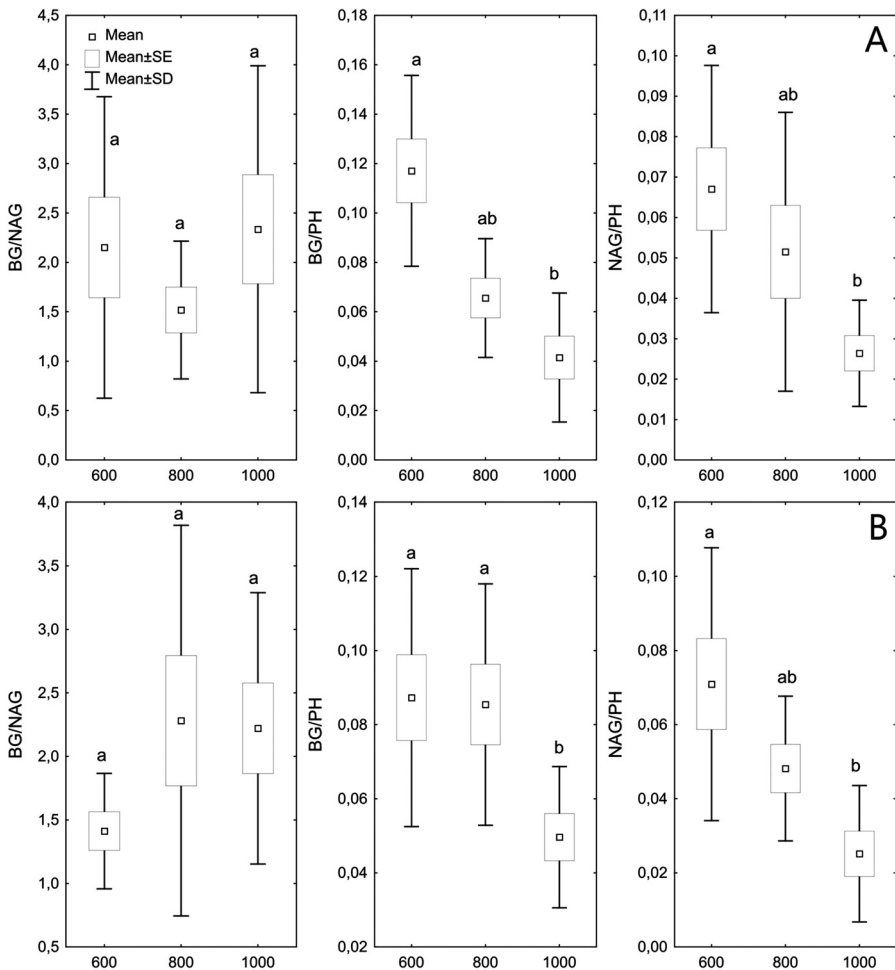


Fig. 2.

Stoichiometry of BG, NAG, and PH activities in soils

BG – β -glucosidase, NAG – N-acetyl- β -D-glucosaminidase, PH – phosphatase; A – soil under influence of beech, B – soil under influence of fir; 600, 800 and 1000 – altitude a.s.l.

Our PCA analysis accounts for 56.1% of the variability we found in the properties we examined (Fig. 3). Factor 1 is related to the altitude while factor 2 is related to the tree species. The performed PCA analysis confirmed the importance of the position in the height gradient in shaping the C, N and P stoichiometry. The soils of the highest positions (1000 m a.s.l.) are characterized by the highest C/N, C/P, N/P and BG/NAG ratios. At the same time, the soils of these locations are characterized by the highest content of C, N and P. The soils of the lowest positions (600 m a.s.l.) are characterized by a higher activity of CB, BG, NAG, SP and higher ratios of BG/PH and NAG/PH (Fig. 3).

Discussion

In our research, variability in the C/N/P stoichiometry resulting from location condition in the altitude gradient and different tree species were noted. The C/N/P ration increased with an increase in altitude. The soils under the influence of fir stands were characterised by the higher C/N/P ration compared to soil under influence of beech forest stands. The C/N/P ratio in the soils of fir stands was to times higher than in the soils of beech stands (558/24/1 and 266/13/1 respectively). At the lowest locations, the C/N/P ratio in the soils of beech stands is 257/15/1, and in the soils of fir stands is 255/16/1. The differences in the C/N/P ratio are due to the marked differences in the carbon, nitrogen and phosphorus content of soils along the altitude gradient. A significantly higher C, N and P content was recorded at higher altitudes. The changes in the C/N/P ratio in the altitude gradient is related to the climatic conditions that determine the size of plant biomass and the decomposition rate. Temperature modifies the photosynthesis, respiration, and growth rates of plants (Bohn *et al.*, 2018). Altitudinal gradients in mountains are correlated

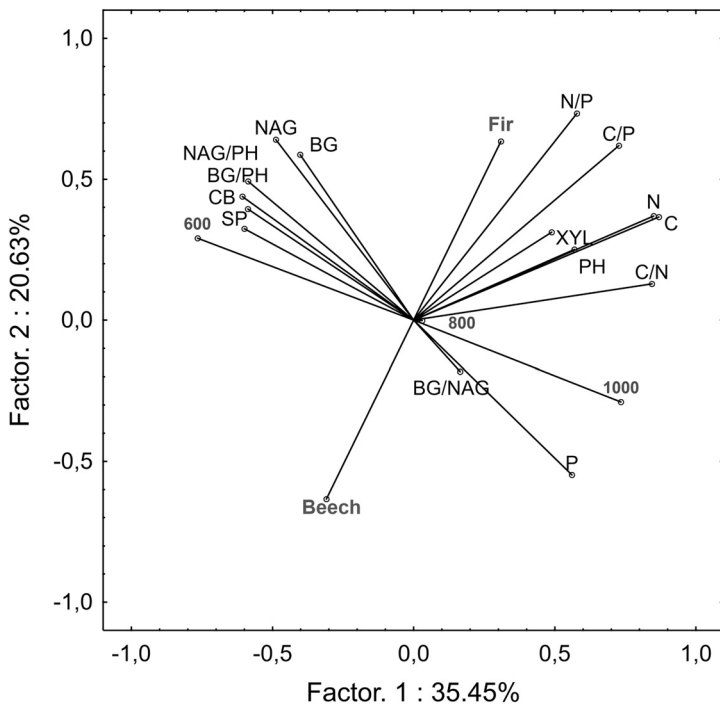


Fig. 3.

Projection of variables on planes of the first and second PCA factors

with climate gradients and changes in vegetation communities (Gutiérrez-Girón *et al.*, 2014). At lower positions, which have favourable climatic conditions with a longer growing season, plants produce more biomass, which feeds the upper soil (Kotas *et al.*, 2018). The characteristic decline in vegetation with increasing altitude results in a low input of organic carbon to soils (Bangroo *et al.*, 2017) accompanied by a slower rate of decomposition. The temperature and precipitation are regarded as key drivers of soil organic carbon turnover time and increased temperature has been shown to accelerate the microbial decomposition of soil organic carbon, resulting in a shorter turnover time (Zhang *et al.*, 2017; Staszal *et al.*, 2021; Zhao *et al.*, 2021a). According to Zhao *et al.* (2021b) the climatic factors had greater influences on soil microorganisms than soil physical and chemical properties, and 53% of the total variance was explained by the climatic condition (annual temperature and precipitation). In our study, the activity of four out of six tested enzymes (CB, BG, NAG and SP) decreased with height, which confirms the limitation of biological activity of soils in higher positions. In forest soils the microorganisms are limited by soil nitrogen and phosphorous levels as seen in the enzyme stoichiometry (Lasota *et al.*, 2022). The N/P and C/P enzyme ratios indicate N and P limitation in the soil (Liu *et al.*, 2020b; Lasota *et al.*, 2021). In the studied soils we recorded a high carbon content with a small share of nitrogen. In the presented experiment, a significant decrease in the enzymatic N/P ratio with altitude was noticed for both species. NAG activity can be treated as a measure of the intensity of nitrogen mineralization (Ekenler and Tabatabai, 2004). It can be assumed that the decrease in NAG activity with altitude as well as the decrease in the enzymatic N/P ratio indicate a significant decrease in the efficiency of N mineralization in the harsher climate of high mountain locations. Limiting the availability of easily assimilable nitrogen in high mountainous locations reduces the activity of microorganisms while, slowing down the transformation of soil organic matter (Robertson and Groffman, 2015).

The higher content of P at higher altitudes is in line with the previous study conducted by De Feudis *et al.* (2016), who proved that organic phosphorous, bioavailable phosphorous, and alkaline monoesterase activity increased with altitude in subalpine forest soils in Italy. Zhang *et al.* (2019) suggested that higher phosphorous content at higher altitudes is related to lower temperatures that limit microbial diversity and abundance. Ma *et al.* (2004) noted various microorganisms communities in the altitude gradient which was caused by changes in temperature and precipitation as well as vegetation. Kreyling *et al.* (2012) claimed that the organic matter in soil results from microbial degradation and the presence of other nutrients such as N and P. Doolette *et al.* (2017) indicated that temperature and soil moisture affected organic phosphorous composition, in mountains forest soil, 54-66% extractable phosphorus was contributed by organic phosphorus composition. In addition to the increase in phosphorus content with altitude, an increase in nitrogen content was also recorded which is in line with the results of previous research (Niklińska and Klimek, 2007). Large amounts of nitrogen during the initial stages strengthen decomposition, and in the later stages, slow down the decomposition of lignins (Vestgarden, 2001). As precipitation is usually higher at high altitudes than at low mountain altitudes, it can be assumed that a decrease in the rate of organic matter decomposition in higher altitudes is associated with the removal of more mobile chemical elements (K, Ca and Mg) by leaching and acidification of humus horizons. Gesler *et al.* (2002) confirmed that organic phosphorus is associated with Al and Fe compounds in the humus layer.

Our study indicated the role of the tree species in shaping the C/N/P stoichiometry in forest soils in the gradient of altitude. Beech and fir trees provide the soil with different amount and quality of detritus. It is known from previous studies that deciduous and coniferous species have a different effect on soil properties, especially acidification, soil organic matter properties

(Błońska *et al.*, 2021). The impact of tree species specificity on soil properties is the results of aboveground and underground biomass properties (Błońska *et al.*, 2016, 2017, 2018). Deciduous wood litter has a higher pH, higher nutrient content and a faster decomposition rate than that of coniferous litter (Paluch and Gruba, 2012). The soils with fir stands were characterized by a higher C/N/P ratio compared to the soils of stands with beech in higher positions.

Conclusions

Our research confirms that altitude and trees species have an effect on soil C/N/P stoichiometry. The highest C/N/P ratio was noted in the highest locations regardless tree species. The C/N/P ratio in the soil of fir stands in the highest locations was twice higher than in the soils of beech stands. We found that the enzymatic stoichiometry (BG/PH, NAG/PH) depended on the altitude. The type of tree species had no effect on enzymatic ratios. The altitude impacted temperature and moisture condition which are related to microorganisms activity, which results in differences in the enzymatic stoichiometry. We can assume that temperature will be growth in the future and it will result in upward migration of vegetation and an increase in plant cover as well as an increased rate of soil organic matter decomposition. A higher input of organic detritus will change the characteristics of soil organic matter and increased of decomposition rate resulting from the rate of basic nutrient cycle (C, N and P). Our study indicated that change in the forest ecosystem related with climate change can be monitored using the C/N/P stoichiometry.

Authors' contributions

K.S.S, E.B., J.L. – conceived and designed the investigation; analysed and visualised the data; E.B., J.L. – concepts research methodology; K.S.S., A.S. – field work, soil sampling; K.S.S., E.B., J.L., A.S. – preparation of manuscript.

Conflicts of interest

The authors have no competing interests to declare that are relevant to the content of this article.

Funding and acknowledgements

This work was supported by the Ministry of Science and Higher Education of the Republic of Poland (AD11; A463).

References

- Baldrian, P., Šnajdr, J., 2011. Lignocellulose-degrading enzymes in soil. In: G. Shukla, A. Varma, eds. *Soil enzymology*. Berlin: Springer-Verlag, pp. 167-186. DOI: <https://doi.org/10.1007/978-3-642-14225-3>.
- Bangroo, S., Najjar, G.R., Rosool, A., 2017. Effect of altitude and aspect on soil organic carbon and nitrogen stocks in the Himalayan Mawer Forest Range. *Catena*, 158: 63-68. DOI: <https://doi.org/10.1016/j.catena.2017.06.017>.
- Bayranvand, M., Kooch, Y., Hosseini, S.M., Alberti, G., 2017. Humus forms in relation to altitude and forest type in the Northern mountainous regions of Iran. *Forest Ecology and Management*, 385: 78-86. DOI: <https://doi.org/10.1016/j.foreco.2016.11.035>.
- Błońska, E., Klamerus-Iwan, A., Lasota, J., Gruba, P., Pach, M., Pretzsch, H., 2018. What characteristics of soil fertility can improve in mixed stands of Scots pine and European Beech compared with monospecific stands? *Communication in Soil Science and Plant Analysis*, 49: 237-247. DOI: <https://doi.org/10.1080/00103624.2017.1421658>.
- Błońska, E., Lasota, J., Gruba, P., 2016. Effect of temperate forest tree species on soil dehydrogenase and urease activities in relation to other properties of soil derived from loess and glaciofluvial sand. *Ecological Research*, 31 (5): 655-664. DOI: <https://doi.org/10.1007/s11284-016-1375-6>.
- Błońska, E., Lasota, J., Gruba, P., 2017. Enzymatic activity and stabilization of organic matter in soil with different detritus inputs. *Journal of Soil Science and Plant Nutrition*, 63: 242-247. DOI: <https://doi.org/10.1080/00380768.2017.1326281>.

- Błońska, E., Piaszczyk, W., Staszal, K., Lasota, J., 2021. Enzymatic activity of soils and soil organic matter stabilization as an effect of components released from the decomposition of litter. *Applied Soil Ecology*, 157: 103723. DOI: <https://doi.org/10.1016/j.apsoil.2020.103723>.
- Bohn, F.J., May, F., Huth, A., 2018. Species composition and forest structure explain the temperature sensitivity patterns of productivity in temperate forests. *Biogeosciences*, 15: 1795-1813. DOI: <https://doi.org/10.5194/bg-15-1795-2018>.
- Cleveland, C.C., Liptzin, D., 2007. C/N/P stoichiometry in soil: is there a 'Redfield ratio' for the microbial biomass? *Biogeochemistry*, 85: 235-252. DOI: <https://doi.org/10.1007/s10533-007-9132-0>.
- De Feudis, M., Cardelli, V., Massacesi, L., Bol, R., Willbold, S., Cocco, S., Corti, G., Agnelli, A., 2016. Effect of beech (*Fagus sylvatica* L.) rhizosphere on phosphorus availability in soils at different altitudes (Central Italy). *Geoderma*, 276: 53-63. DOI: <https://doi.org/10.1016/j.geoderma.2016.04.028>.
- Doolette, A.L., Smernik, R.J., McLaren, T.I., 2017. The composition of organic phosphorus in soils of the Snowy Mountains region of south-eastern Australia. *Soil Research*, 55: 10-18. DOI: <https://doi.org/10.1071/sr16058>.
- Ekenler, M., Tabatabai, M.A., 2004. β -glucosaminidase activity as an index of nitrogen mineralization in soils. *Communications in Soil Science and Plant Analysis*, 35 (7-8): 1081-1094. DOI: <https://doi.org/10.1081/CSS-120030588>.
- Feng, D., Bao, W., Pang, X., 2017. Consistent profile pattern and spatial variation of soil C/N/P stoichiometric ratios in the subalpine forests. *Journal of Soils and Sediments*, 17: 1-12. DOI: <https://doi.org/10.1007/s11368-017-1665-9>.
- Giesler, R., Petersson, T., Högberg, P., 2002. Phosphorus limitation in boreal forests: effect of aluminium and iron accumulation in the humus layer. *Ecosystems*, 5: 300-314. DOI: <https://doi.org/10.1007/s10021-001-0073-5>.
- Gutiérrez-Girón, A., Díaz-Pinés, E., Rubio, A., Gavilán, R.G., 2014. Both altitude and vegetation affect temperature sensitivity of soil organic matter decomposition in Mediterranean high mountain soils. *Geoderma*, 237-238: 1-8. DOI: <https://doi.org/10.1016/j.geoderma.2014.08.005>.
- Kotas, P., Šantrůčková, H., Elster, J., Kaštovská, E., 2018. Soil microbial biomass, activity and community composition along altitudinal gradients in the high Arctic (Billefjorden, Svalbard). *Biogeosciences*, 15: 1879-1894. DOI: <https://doi.org/10.5194/bg-15-1879-2018>.
- Kreyling, J., Peršoh, D., Werner, S., Benzenberg, M., Wöllecke, J., 2012. Short-term impacts of soil freeze-thaw cycles on roots and root-associated fungi of *Holcus lanatus* and *Calluna vulgaris*. *Plant and Soil*, 353: 19-31. DOI: <https://doi.org/10.1007/s11104-011-0970-0>.
- Lasota, J., Babiak, T., Błońska, E., 2022. C:N:P stoichiometry associated with biochar in forest soils at historical charcoal production sites in Poland. *Geoderma Regional*, 28: e00482 DOI: <https://doi.org/10.1016/j.geodrs.2022.e00482>.
- Lasota, J., Małek, S., Jasik, M., Błońska, E., 2021. Effect of planting method on C:N:P stoichiometry in soils, young silver fir (*Abies alba* Mill.) and stone pine (*Pinus cembra* L.) in the upper mountain zone of Karpaty Mountains. *Ecological Indicators*, 129 (6): 107905. DOI: <https://doi.org/10.1016/j.ecolind.2021.107905>.
- Liu, J., Chen, J., Chen, G., Guo, J., Li, Y., 2020b. Enzyme stoichiometry indicates the variation of microbial nutrient requirements at different soil depths in subtropical forests. *PLoS ONE*, 15: e0220599. DOI: <https://doi.org/10.1371/journal.pone.0220599>.
- Liu, L., Zhang, L., Pan, J., Niu, J., Yuan, X., Hu, S., Liu, C., Shad, N., Huang, J., Deng, B., Deng, W., Liu, X., Zhang, W., Liu, Y., 2020a. Soil C-N-P pools and stoichiometry as affected by intensive management of *Camellia oleifera* plantations. *PLoS ONE*, 15 (9): e0238227. DOI: <https://doi.org/10.1371/journal.pone.0238227>.
- Łabaz, B., Galka, B., Bożacz, A., Waroszewski, J., Kabała, C., 2014. Factors influencing humus forms and forest litter properties in the mid-mountains under temperate climate of southwestern Poland. *Geoderma*, 230: 265-273. DOI: <https://doi.org/10.1016/j.geoderma.2014.04.021>.
- Ma, X., Chen, T., Zhang, G., Wang, R., 2004. Microbial community structure along an altitude gradient in three different localities. *Folia Microbiologica*, 49 (2): 105-111. DOI: <https://doi.org/10.1007/BF02931382>.
- Niklińska, M., Klimek, B., 2007. Effect of temperature on the respiration rate of forest soil organic layer along elevation gradient in the Polish Carpathians. *Biology and Fertility of Soils*, 43: 511-518. DOI: <https://doi.org/10.1007/s00374-006-0129-y>.
- Paluch, J., Gruba, P., 2012. Effect of local species composition on topsoil properties in mixed stands with silver fir (*Abies alba* Mill.). *Forestry*, 85: 413-426. DOI: <https://doi.org/10.1093/forestry/cps040>.
- Pritsch, K., Raidl, S., Marksteiner, E., Blaschke, H., Agerer, R., Schloter, M., Hartmann, A., 2004. A rapid and highly sensitive method for measuring enzyme activities in single mycorrhizal tips using 4-methylumbelliferone-labelled fluorogenic substrates in a microplate system. *Journal of Microbiological Methods*, 58: 233-241. DOI: <https://doi.org/10.1016/j.mimet.2004.04.001>.
- Robertson, G.P., Groffman, P.M., 2015. Nitrogen transformations. In: E.A. Paul, ed. *Soil microbiology, ecology and biochemistry*. Fourth edition. Burlington, Massachusetts: Academic Press, pp. 421-446. DOI: <https://doi.org/10.1016/B978-0-08-047514-1.50017-2>.
- Sanaullah, M., Razavi, B.S., Blagodatskaya, E., Kuzyakov, Y., 2016. Spatial distribution and catalytic mechanisms of β -glucosidase activity at the root-soil interface. *Biology and Fertility of Soils*, 52: 505-514. DOI: <https://doi.org/10.1007/s00374-016-1094-8>.
- Sinsabaugh, R.L., Shah, J.J.F., 2012. Ecoenzymatic stoichiometry and ecological theory. *Annual Review of Ecology and Systematics*, 43: 313-343. DOI: <https://doi.org/10.1146/annurev-ecolsys-071112-124414>.

- Staszcz, K., Błońska, E., Lasota, J., 2021. Slope aspect and altitude effect on selected soil organic matter characteristics in Beskid Mountains forest soils. *Folia Forestalia Polonica, Series A – Forestry*, 63 (3): 214-224. DOI: <https://doi.org/10.2478/ffp-2021-0022>.
- Sterner, R.W., Elser, J.J., 2002. Ecological stoichiometry. The biology of elements from molecules to the biosphere. Princeton: Princeton University Press, 464 pp. DOI: <https://doi.org/10.1515/9781400885695>.
- Turner, B.L., 2010. Variation in pH optima of hydrolytic enzyme activities in tropical rain forest soils. *Applied and Environmental Microbiology*, 76: 6485-6493. DOI: <https://doi.org/10.1128/AEM.00560-10>.
- Vestgard, L.S., 2001. Carbon and nitrogen turnover in the early stage of Scots pine (*Pinus sylvestris* L.) needle litter decomposition: effects of internal and external nitrogen. *Soil Biology and Biochemistry*, 33: 465-474. DOI: [https://doi.org/10.1016/S0038-0717\(00\)00187-5](https://doi.org/10.1016/S0038-0717(00)00187-5).
- Wang, J., Wu, Y., Li, J., He, Q., Bing, H., 2021. Soil enzyme stoichiometry is tightly linked to microbial community composition in successional ecosystems after glacier retreat. *Soil Biology and Biochemistry*, 162: 108429. DOI: <https://doi.org/10.1016/j.soilbio.2021.108429>.
- Yavitt, J.B., Wright, S.J., Wieder, R.K., 2004. Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. *Austral Ecology*, 29: 177-188. DOI: <https://doi.org/10.1111/j.1442-9993.2004.01334.x>.
- Zanella, A., Jabiol, B., Ponge, J.F., Sartori, G., De Waal, R., Van Delft, B., Graefe, U., Cools, V., Katzensteiner, K., Hager, H., Englisch, M., 2011. A European morphofunctional classification of humus forms. *Geoderma*, 164: 138-145. DOI: <https://doi.org/10.1016/j.geoderma.2011.05.016>.
- Zhang, T., Wang, G., Yang, Y., Mao, T., Chen, X., 2017. Grassland types and season dependent response of ecosystem respiration to experimental warming in a permafrost region in the Tibetan Plateau. *Agricultural and Forest Meteorology*, 247: 271-279. DOI: <https://doi.org/10.1016/j.agrformet.2017.08.010>.
- Zhang, Y., Li, C., Wang, M., 2019. Linkages of C: N: P stoichiometry between soil and leaf and their response to climatic factors along altitudinal gradients. *Journal of Soils and Sediments*, 19: 1820-1829. DOI: <https://doi.org/10.1007/s11368-018-2173-2>.
- Zhao, M., Wang, M., Zhao, Y., Wang, G., Xua, Z., Jiang, M., 2021b. Variations in soil microbial communities in the sedge-dominated peatlands along an altitude gradient on the northern slope of Changbai Mountain, China. *Ecological Indicators*, 129: 107964. DOI: <https://doi.org/10.1016/j.ecolind.2021.107964>.
- Zhao, Y.F., Wang, X., Jiang, S.L., Zhou, X.H., Liu, H.Y., Xiao, J.J., Hao, Z.G., Wang, K.C., 2021a. Climate and geochemistry interactions at different altitudes influence soil organic carbon turnover times in alpine grasslands. *Agriculture Ecosystems and Environment*, 320: 107591. DOI: <https://doi.org/10.1016/j.agee.2021.107591>.

STRESZCZENIE

Stechiometria C/N/P gleb leśnych w zależności od gatunku drzew i gradientu wysokości w Karpatach

Celem badań było określenie stechiometrii C/N/P gleb leśnych w zależności od gatunku drzewa i położenia stoku w Karpatach. Stechiometria ekologiczna jest wykorzystywana jako skuteczne podejście do analizy sprzężeń zwrotnych i relacji między różnymi składnikami ekosystemu. Znajomość rozmieszczenia C, N i P oraz ich stechiometrii pozwala na lepsze zrozumienie funkcji i stabilności ekosystemów. Stosunek C/N/P odzwierciedla zarówno naturalne zmiany w ekosystemach, jak i te wynikające ze sposobów gospodarowania lub spowodowane działalnością człowieka. Założono, że gatunek drzewa i wysokość nad poziomem morza wpływają na ilość i jakość materii organicznej w glebach leśnych, a co za tym idzie na stechiometrię C/N/P. Dotychczasowe badania potwierdzają rolę gatunków drzew w kształtowaniu cech gleb, zwłaszcza poziomów powierzchniowych. Drzewa poprzez opad ściółki i systemy korzeniowe wywierają najsilniejszy wpływ na właściwości gleby, a zwłaszcza na jakość i ilość materii organicznej w glebie. Badania przeprowadzono w południowej Polsce, w masywie Jałowca w Beskidzie Żywieckim (49°39'64"N; 19°28'67"E). Powierzchnie badawcze zlokalizowane były na wysokościach 600, 800 i 1000 m n.p.m. w drzewostanie bukowym *Fagus sylvatica* L. i jodłowym *Abies alba* Mill. W próbkach glebowych oznaczono aktywność enzymatyczną oraz zawartość C, N i P. Stechiometrię C/N/P obliczono w celu odzwier-

ciędlenia dostępności składników odżywczych w glebie wzdłuż gradientu wysokości (tab. 1). Wyniki badań potwierdzają, że wysokość nad poziomem morza i gatunki drzew mają wpływ na stechiometrię C/N/P gleby (ryc. 1). Najwyższy stosunek C/N/P odnotowano na najwyższych stanowiskach, niezależnie od gatunku drzew. Stosunek C/N/P w glebie drzewostanów jodłowych na najwyższych stanowiskach był dwukrotnie wyższy niż w glebach drzewostanów bukowych. Stwierdzono, że stechiometria enzymatyczna (BG/PH, NAG/PH) zależała od wysokości (ryc. 2). Gatunek drzew nie miał wpływu na wskaźniki enzymatyczne (tab. 2). Wysokość nad poziomem morza miała wpływ na temperaturę i wilgotność, które są związane z aktywnością mikroorganizmów, co skutkuje różnicami w stechiometrii enzymatycznej. Przeprowadzona analiza PCA potwierdziła znaczenie położenia w gradiencie wysokości w kształtowaniu stechiometrii C, N i P. Gleby położone najwyżej (1000 m n.p.m.) charakteryzują się najwyższymi wskaźnikami C/N, C/P, N/P i BG/NAG oraz najwyższą zawartością C, N i P. Gleby najniższych stanowisk (600 m n.p.m.) cechują się z kolei wyższą aktywnością CB, BG, NAG i SP oraz wyższym stosunkiem BG/PH i NAG/PH (ryc. 3). Można przypuszczać, że w przyszłości temperatura będzie rosła, co spowoduje migrację roślinności w górę i zwiększenie szaty roślinnej oraz przyspieszenie rozkładu materii organicznej w glebie. Większy dopływ detrytusu organicznego zmieni charakterystykę materii organicznej gleby i przyspieszy tempo rozkładu wynikające z tempa obiegu podstawowych składników pokarmowych (C, N i P). Wykonane badania wykazały, że zmiany w ekosystemie leśnym związane ze zmianami klimatycznymi można monitorować za pomocą stechiometrii C/N/P.