

Stoichiometry of peatlands and plants: Mutual interactions in biogeochemical cycles

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ABSTRACT

Although peatlands cover only a small fraction of the Earth's surface, they store large amounts of carbon and play a key role in global biogeochemical cycles. A joint assessment of the stoichiometry of biogenic elements (C, N and P) and nutrients ratios may improve our understanding of soil–plant interactions across different types of Histosol. The aim of this study was to analyse the stoichiometry of C:N:P and nutrients ratios in peat soils and conifer needles (*Picea abies* and *Pinus sylvestris*) across three different histosol types: fibric, hemic and sapric. Particular emphasis was placed on soil–plant relationships and evaluating the potential of stoichiometric indicators to diagnose peatland condition. Samples were collected from 255 sites across Poland. Composite soil samples (0–15 cm depth) and conifer needles were analysed for C and N using an elemental analyser, and for Ca, Mg, K, Al and P using ICP-OES. Ratios (C/N, C/P, N/P, Ca/Mg, Ca/Al and Ca-K-Mg/Al) were then calculated. Statistical procedures included descriptive statistics (median and quartile deviation), a Kruskal–Wallis test ($p < 0.05$), a principal component analysis (PCA), generalised linear models (GLM), Spearman's rank correlations and simple linear regressions. Soil carbon content, as well as the C/N, C/P and N/P ratios, decreased systematically from fibric to sapric histosols. Meanwhile, the contents of Ca, Mg, K and Al were significantly higher in sapric soils. In plants, the contents of C, N and P, as well as the C/N, C/P and N/P ratios, did not differ between histosol types. However, the ratios (particularly Ca/Al and Ca-K-Mg/Al) were highest in sapric histosols. Soil–plant correlations were weak for C/N, C/P, and N/P, but slightly stronger for Ca/Al and Ca-K-Mg/Al. PCA (PC1 = 35.52 %; PC2 = 19.41 %) revealed a clear separation, with plants associated with phosphorus and nutrients ratios and soils grouped with C/N and C/P. GLM confirmed the significant effects of both sample and histosol types, with an interaction observed for most indices (except Ca/Mg). Both classical ratios (C/N, C/P and N/P) and ratios (Ca/Al, Ca/Mg and Ca-K-Mg/Al) provide complementary insights into peatland functioning. The decline of C/N and C/P ratios with increasing humification, combined with higher nutrient ratios, indicates their potential for diagnosing peatland degradation and monitoring nutrient cycling dynamics.

1. Introduction

Although peatlands cover only around 3 % of the Earth's surface, they store a significant proportion of its soil carbon, estimated at 500–700 Pg C. This is comparable to, or even greater than, the amount of carbon contained in global plant biomass and equivalent to almost half of the atmospheric reserves (Yu et al., 2010; Page and Baird, 2016). Their ability to accumulate organic matter stems from anaerobic conditions that slow down decomposition processes, enabling peatlands to act as long-term carbon sinks for thousands of years (Frolking et al.,

2011; Wu, 2012). This unique role in the global carbon cycle means that peatlands are a key ecosystem for climate regulation; even minor disturbances can alter their greenhouse gas balance, causing them to transition from being a carbon sink to becoming a significant source of CO₂, CH₄ or N₂O emissions (Frolking et al., 2011; Minayeva and Sirin, 2012). In addition to their climatic importance, peatlands are biodiversity hotspots that provide many ecosystem services (Joosten, 2015). These include regulating water relations, participating in nutrient cycling and preserving palaeoecological archives that document past environmental and climatic conditions (Page and Baird, 2016; Minayeva

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and Sirin, 2012). The latest soil classification systems, such as the World Reference Base for Soil Resources (WRB), include peatlands in the histosol group, emphasising their global importance as a distinct soil category shaped by the accumulation of organic matter (IUSS Working Group WRB, 2022).

The stoichiometry of biogenic elements, particularly the carbon (C), nitrogen (N), and phosphorus (P) ratio, is a key indicator of ecosystem function. It determines the balance between mineralisation processes, the accumulation of organic matter, and the nutrient limitations experienced by plants and microorganisms (Cleveland and Liptzin, 2007; Sardans et al., 2012). Numerous studies have demonstrated the significant influence of both environmental factors, such as climate and soil type, and biotic factors, including plant species composition, on the stoichiometry and availability of nutrients (Wang et al., 2014). In forests, for example, different tree species provide varying qualities of organic litter and root exudates that shape the soil microbiome and the rate of elemental cycling (Prescott and Grayston, 2013; Błońska et al., 2025). Recent studies have emphasised the importance of considering peat-specific stoichiometric trajectories during the formation and degradation of peat. Wang et al. (2015) demonstrated that the accumulation of organic matter in peatlands is coupled with the progressive decoupling of the C, N and P cycles. This process is driven by hydrological and microbial constraints. They found that N and P are retained more efficiently than C during the initial stages of peat accumulation, resulting in elevated C/N and C/P ratios that change predictably along peat profiles. Similarly, Moore et al. (2018) proposed that redox conditions in peat regulate the balance of C, hydrogen and oxygen elements, emphasising stoichiometric constraints that evolve with humification. In early studies it has been demonstrated that deciduous species promote higher-quality organic matter and improved nutrient availability compared to conifers, which tend to acidify the soil and impede mineralisation (Błońska et al., 2025; Lasota et al., 2021). At a broader spatial scale, distinct geographical patterns in C:N:P stoichiometry have been observed in plants and soils, depending on climate, latitude, longitude and habitat characteristics. Notably, C:N:P values in plants tend to be higher than in soils, with positive correlations between the two components of the ecosystem. However, the strength of these correlations depends on the type of vegetation (Feng et al., 2024). A global meta-analysis has also shown that human activity, particularly the drainage of peatlands, significantly alters the stoichiometry of peat soils (Idoko et al., 2025). Drainage leads to a significant decrease in C content (−20.95 %) and an increase in N content (+426.6 %), as well as changes in P availability, which depend on the type of habitat. Consequently, the C/N and C/P ratios decrease, while the N/P ratio can increase by up to fivefold, significantly altering nutrient limitations and ecosystem functioning (Idoko et al., 2025).

In addition to classic C:N:P ratios, the ratio of nutrient to aluminium is a key indicator of soil ecosystem function (Cronan and Grigal, 1995). The calcium (Ca), potassium (K), and magnesium (Mg) to aluminium (Al) ratio (Ca-K-Mg/Al) is of particular importance, as it has been proposed as a criterion for assessing the risk of acidification and the fertility of forest soils (Sverdrup and Warfvinge, 1993). This indicator's critical value (approximately 1.0) establishes the threshold below which the risk of physiological disorders in plants increases due to aluminium toxicity and limited base cation availability. Studies confirm that cation indices reflect environmental pressure well and can serve as early markers of changes in the trophic status of ecosystems (Göransson and Eldhuset, 2001). More recent analyses also suggest that the Ca/Al and Ca-K-Mg/Al ratios are affected by human activities, such as pollution, that impact plant nutrition (Lasota et al., 2024).

Histosols are a distinctive and highly vulnerable category of organic soil. They are formed in environments of prolonged water saturation and are characterised by the accumulation of undecomposed or partially decomposed organic matter exceeding 40 cm in thickness (IUSS Working Group WRB, 2022). Not only are they important C reservoirs, they are also fragile ecosystems that are increasingly threatened by climate

change, drainage and land-use transformation. Within this group, the fibric, hemic and sapric subtypes reflect the successive stages of peat decomposition that fundamentally determine their chemical and ecological properties. Fibric histosols, which are dominated by poorly decomposed plant remains, are acidic and rich in organic C, with high C/N ratios. In contrast, sapric histosols, in which decomposition has advanced the furthest, have lower C content and reduced C/N ratios, as well as higher concentrations of base cations (Ca^{2+} , Mg^{2+} and K^+). Hemic histosols occupy an intermediate position. These differences not only illustrate the internal gradient of humification, but also the close links between vegetation composition, water regime and soil chemistry. Despite their ecological significance, histosols have rarely been comprehensively investigated in an integrated soil–plant system, particularly with regard to stoichiometric relationships combining biogenic elements (C, N, P). Closing this research gap is essential for understanding how peatlands function and are vulnerable to current environmental pressures (Page and Baird, 2016). Lasota and Błońska (2021) previously noted this gap in research, showing that C:N:P stoichiometry responds sensitively to peat drainage across lowland and mountain forest histosols in Poland. Their findings emphasise that dehydration causes a pronounced narrowing of stoichiometric ratios, primarily due to the rapid loss of organic C. Incorporating this dynamic into monitoring protocols enables more accurate assessments of peatland degradation.

Previous studies of peatlands have primarily centred on traditional stoichiometric indicators based on C, N and P. Ratios, such as Ca/Al, Ca/Mg and Ca-K-Mg/Al, which play a key role in assessing soil fertility and plant resistance to environmental stress, have been included much less frequently in parallel analyses. Additionally, there is a lack of comprehensive studies that compare the stoichiometry of biogenic elements in soil and plants in relation to the degree of histosols decomposition (fibric, hemic or sapric). Taking this approach could significantly improve our understanding of plant–soil interactions and their role in peatland biogeochemical cycles.

This study aimed to analyse the stoichiometry of biogenic elements (C, N and P) and nutrients (Ca, Mg and K), as well as aluminium, in soils and plant material of various histosols types. Particular attention was paid to examining the relationships between indices based on biogenic elements (C/N, C/P and N/P) and ratios (Ca/Al, Ca/Mg and Ca-K-Mg/Al), as well as assessing the extent to which these relationships are shaped by the degree of peat decomposition and the dominant vegetation. The following research hypotheses were formulated: 1) The C/N, C/P and N/P indices show systematic differences between histosol types, reflecting the degree of organic matter decomposition and changes in nutrient availability; 2) Ratios (Ca/Al, Ca/Mg and Ca-K-Mg/Al) differentiate between soils and plants depending on histosol type; 3) Significant correlations exist between biogenic and nutrients stoichiometry, indicating linkages between the biogenic element cycle and soil trophic regulation; 4) Stoichiometric plant–soil interactions are crucial for interpreting differences between histosol types and may provide a basis for a better understanding of peatland functioning in biogeochemical cycles.

2. Materials and methods

2.1. Study sites and soil sampling

The research was conducted across Poland, a Central European country characterised by a temperate climate with both oceanic and continental influences. Its geological landscape varies significantly, ranging from glacial plains in the north to more structurally diverse mountainous regions in the south. Peatlands account for around 4.7 % of the country's total land area, primarily in lowland areas (Áskelsdóttir and Pawlaczzyk, 2024). For this study, 255 locations were selected to ensure representative coverage. In lowland and upland zones, sites were spaced using a regular grid of 30 km × 30 km, whereas a denser grid of

10 km × 10 km was applied to the mountainous terrain to better capture environmental heterogeneity. Our sampling design covers the entire territory of Poland and this broad spatial coverage ensures that the full range of nationally occurring Histosol types is represented in the dataset.

The three categories of organic material most commonly found in histosols – fibric, hemic and sapric – were examined (Fig. 1). Fibric histosols correspond to ombrotrophic, oligotrophic peatlands; hemic histosols represent intermediate, mesotrophic mire conditions; and sapric histosols are characteristic of minerotrophic, eutrophic peatlands. Fibric material is characterised by the presence of more than two-thirds (by volume) of identifiable plant remains following manual disintegration. By contrast, hemic material contains between one-sixth and two-thirds of such remains, while sapric material contains less than one-sixth of identifiable plant tissues after rubbing (IUSS Working Group WRB, 2022). The peat-forming processes at the sites studied varied according to these material types and were largely influenced by the dominant vegetation.

Sapric histosols typically developed in areas dominated by sedges (*Carex* spp.) and grasses, while hemic histosols supported mixed communities of sedges and mosses. Fibric Histosols were largely composed of organic matter from *Sphagnum* mosses. Fibric Histosols were represented by species such as *Sphagnum capillifolium*, *Sphagnum palustre*, *Sphagnum fuscum*, *Sphagnum rubellum*, *Sphagnum magellanicum*, *Oxycoccus palustris*, *Eriophorum vaginatum*, and *Polytrichum strictum*. Hemic Histosols were indicated by species including *Eriophorum angustifolium*, *Carex nigra*, *Carex cinerea*, *Thelypteris palustris*, *Comarum palustre*, *Sphagnum girgensohnii*, and *Sphagnum fallax*. Sapric Histosols were reflected by species such as *Carex elongata*, *Carex acutiformis*, *Carex pseudocyperus*, *Scirpus sylvaticus*, *Iris pseudacorus*, *Lycopus europaeus*, *Solanum dulcamara*, and *Calliergonella cuspidata*.

The type of peatland was identified based on the vegetation observed in the field and the morphological features of the peat. Our field diagnoses were subsequently verified and confirmed using the results of chemical analyses of the collected samples. Sapric histosols were the most alkaline (mean pH 5.7), hemic histosols were more acidic (mean pH 4.4), and fibric histosols were the most acidic (mean pH 3.8). Similarly, the C/N ratio, which reflects the degree of peat decomposition and nutrient availability, increased along this gradient, with mean values of 21.2, 33.5 and 38.9, respectively, for sapric, hemic, and fibric histosols. The mean values of electrical conductivity were 267.5 $\mu\text{S}/\text{cm}$ for sapric, 200.5 $\mu\text{S}/\text{cm}$ for hemic, and 195.1 $\mu\text{S}/\text{cm}$ for fibric histosols.

All study plots were located on peatlands with no evident anthropogenic influence, and no signs of drainage or land-use modification were observed in the field. The sites retained natural or near-natural hydrological conditions, with stable water levels and undisturbed surface morphology. The available data revealed no signs of drainage, such

as lowered groundwater tables, the presence of drainage ditches, or advanced surface-peat degradation. In selecting the sampling sites, we applied strict criteria to ensure that all locations represented genuine peat-forming environments, and each plot was confirmed to have a peat layer exceeding 40 cm in thickness. Before collecting the samples, we checked the depth of the peat layer using a peat probe to ensure that it met the diagnostic criteria for Histosols. A total of 255 sampling sites were distributed across Histosol types: 85 on fibric soils, 115 on hemic soils and 55 on sapric soils. Five subsamples were collected at each sampling point from the upper 0–15 cm of the peat layer. The surface litter or moss layer was first removed to ensure that the material originated exclusively from the peat itself. The subsamples were taken at short distances from one another within a homogeneous patch, allowing local variability to be captured and representativeness to be ensured. They were then combined into a composite sample used for subsequent analyses. The collected materials were labelled according to site code and stored in sealed polyethylene bags. In the laboratory, the soils were air-dried, homogenised by manual fragmentation, and processed for chemical analysis. In addition to soil sampling, conifer needles were collected to assess plant elemental stoichiometry. A total of 156 samples of Norway spruce (*Picea abies*) needles and 99 samples of Scots pine (*Pinus sylvestris*) needles were collected. The needle sample was always taken from the tree closest to the corresponding soil sampling point. Only the youngest annual needle growth was used for analysis, ensuring consistency across samples and minimising age-related variability.

2.2. Chemical properties

The C and N content of the soil and plant samples collected was measured using an elemental analyser (TrueMac CNS Analyser, LECO Corporation, St. Joseph, Michigan, USA). The concentrations of Ca, Mg, K, Al and P were determined using an inductively coupled plasma (ICP) spectrometer (ICP-OES Thermo iCAP 6500 DUO, Thermo Fisher Scientific, Cambridge, UK). The P content was determined following mineralisation in a mixture of concentrated nitric and perchloric acids at a ratio of 2:1. Mineralisation was performed using an ETHOS UP microwave digestion system (Milestone). This instrument is equipped with a process monitoring system that displays real-time digestion parameters on a touchscreen and records the full operational history for quality assurance purposes. To verify the efficiency and reliability of the digestion process, a certified reference material (CRM) – a soil matrix with a known lead content – was included in each batch of analysed samples. The CRM used was Metals in Soil QC, Cat. No. D106-540 (ERA), which is accredited in accordance with the ISO/IEC 17025 and ISO 17034 standards, as required by the Polish Centre for Accreditation (PCA). Spectrally pure nitric and perchloric acids were used and all the volumetric flasks were Class A. We then calculated the C/N, C/P, N/P, Ca/Mg, Ca/Al, and Ca-K-Mg/Al molecular ratios. All analyses were performed at the Laboratory of Geochemistry of the Forest Environment and Areas Designated for Reclamation. This laboratory has a well-developed programme for testing and calibrating equipment.

2.3. Statistical analysis

All statistical analyses were performed using the R (R Core Team, 2020) and Python (Python Software Foundation, 2024) software packages. Descriptive statistics for the studied variables were calculated separately for soils and plants, and are expressed as medians with quartile deviation. Differences between histosol types (fibric, hemic and sapric) were tested using the non-parametric Kruskal–Wallis test ($p < 0.05$). Post-hoc comparisons between groups were evaluated by assigning letter-based significance groups. Principal component analysis (PCA) was applied to explore the multivariate relationships among the chemical variables (C, N, P, stoichiometric ratios). The first two principal components were then used to visualise the distribution of the samples and the group centroids (plants, soils and histosol types). Prior

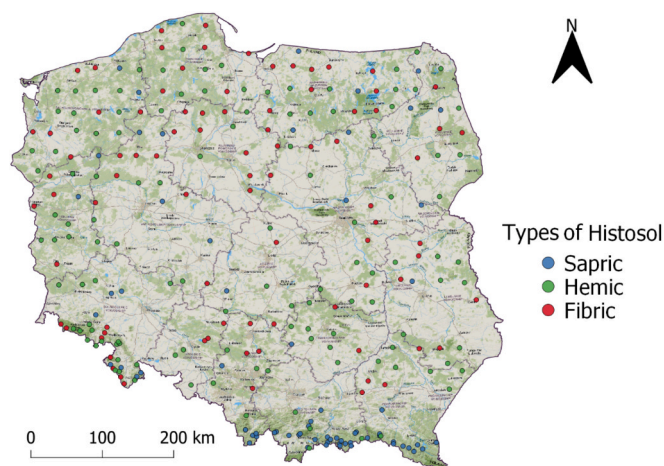


Fig. 1. Geographic location of the study plots, categorised by peatland type.

to PCA, the variables were standardised (z-scores). Generalised linear models (GLM) were fitted to test the effects of sample type (plant vs soil), histosol type (fibric, hemic and sapric) and their interaction on stoichiometric ratios. Model significance was assessed at $p < 0.05$. Spearman's rank correlation coefficients were calculated to examine the relationship between soil and plant stoichiometry. The correlation matrices were visualised as heatmaps, with statistically significant correlations ($p < 0.05$) indicated by asterisks. Simple linear regression models were used to describe the relationships between elemental concentrations (C, N and P) and stoichiometric ratios (C/N, C/P and N/P). Regression curves were fitted separately for plant and soil samples, with an additional subdivision into histosol types. Model performance was evaluated using the coefficient of determination (R^2).

3. Results

Analysis of the chemical composition of soils revealed significant differences between histosol types. The highest C content was recorded in fibric histosols (42.4 ± 2.3 %), followed by hemic histosols (40.5 ± 4.3 %), with sapric histosols having a content more than twice as low (20.4 ± 14.1 %) ($p < 0.05$). There were no significant differences in N content between histosol types, which ranged from 1.2 ± 0.45 % in sapric soils to 1.4 ± 0.33 % in hemic soils. Phosphorus (P) content also showed no significant differences between groups, ranging from 561 ± 163 mg·kg⁻¹ in fibric soils to 712 ± 175 mg·kg⁻¹ in sapric soils.

Clear differences were found between histosol types in the case of basic elements and Al. The content of Ca, Mg, K and Al was significantly higher in sapric histosols, with values several times higher than in fibric and hemic soils. For instance, the average Ca content was 8070 ± 5590 in sapric histosols, whereas in fibric soils it was over four times lower at 1920 ± 762 . Similar trends were observed for Mg and K. The Mg content was significantly higher in sapric histosols (2380 ± 1940) than in fibric (358 ± 85.1), and the K content was also significantly higher in sapric histosols (3520 ± 3270) than in fibric (484 ± 169) and hemic soils (589 ± 269). Similarly, the Al content increased from 3290 ± 2400 in fibric soils to 19300 ± 13300 in sapric soils. In plants, the variability of these elements was lower, but significant differences were also evident.

The C/N ratio was highest in fibric histosols (34.0 ± 9.5), lower in hemic histosols (29.8 ± 6.1) and lowest in sapric histosols (18.8 ± 3.9) ($p < 0.05$). A similar decreasing trend from fibric to sapric histosols was observed for the C/P and N/P ratios. The Ca/Mg ratio was significantly higher in fibric and hemic histosols (3.0 ± 1.4 and 3.3 ± 1.7 , respectively) than in sapric histosols (1.8 ± 3.9). No significant differences were found between histosol types for the Ca/Al and Ca/K/Mg/Al ratios.

No significant differences were found between histosol types for

plant material in terms of C, N and P content, or C/N, C/P and N/P ratios. The Ca/Mg ratio was significantly higher in sapric histosols (2.4 ± 0.6) than in fibric (1.7 ± 0.38) and hemic (1.8 ± 0.52) histosols. Similarly, the Ca/Al and Ca-K-Mg/Al ratios were highest in plants from sapric histosols (56.9 ± 21.6 and 198 ± 94.6 , respectively), with values that significantly exceeded those in fibric and hemic histosols (Table 1).

median $\pm$ quartile deviation, C content (%), N content (%), P content (mg·kg⁻¹), Ca content (mg·kg⁻¹), Mg content (mg·kg⁻¹), K content (mg·kg⁻¹), Al content (mg·kg⁻¹). Small letters in the upper index of the median values mean significant differences between histosols types: a, b, c – different letters indicate significant differences between groups ($p < 0.05$); a, a, a – no significant differences between groups ($p > 0.05$); a, a, b – one group is significantly different from the other two; a, a, ab – the group labelled 'ab' is partly similar to one of the groups but different from the other.

Spearman's correlation analysis of soil and plant stoichiometric ratios revealed generally weak and inconsistent relationships. No significant correlations were found between soil and plant values for the main ratios (C/N, C/P and N/P). Slightly stronger relationships were observed for indicators related to basic elements, particularly Ca/Al and Ca-K-Mg/Al, but these rarely exceeded a moderate level. Correlations for the content of individual elements (Ca, Mg, K and Al) also showed no consistent trends between soil and plants (Fig. 2).

PCA analysis showed that the first two principal components together explained 54.9 % of the total variance (PC1: 35.5 %; PC2: 19.4 %) (Fig. 3). PC1 mainly differentiated between sapric histosol samples, which were located on the positive side, and fibric and hemic histosol samples and soil samples, which were located on the negative side. The sapric variable was strongly positively correlated with PC1. Variables with the highest positive loadings on PC1 included elements ratios (Ca/Al and Ca-K-Mg/Al) and P, while stoichiometric ratios (C/N and C/P) showed strong negative correlations with PC1. PC2 was positively correlated with N and the Ca/Mg ratio, and negatively correlated with the C/N and C/P ratios. Plant samples were located in the positive PC1 area close to zero PC2, while soil samples were grouped on the negative PC1 side. Fibric histosols were close to the beginning of the system, hemic soils were slightly shifted towards negative PC1 and PC2 values and sapric soils were clearly separated along the positive PC1 axis. This indicates a strong influence of P and basic elements. The variable vectors formed two opposing groups: C/N and C/P ratios (negative PC1 and PC2 values) on the one hand, and P and elements indicators (positive PC1 values) on the other. N and the Ca/Mg ratio, in turn, were mainly associated with PC2, differentiating the samples independently of the main stoichiometric gradient (Fig. 3).

Regression analyses of the C/N, C/P and N/P ratios showed only

Table 1
Descriptive statistics of chemical properties of soils and plants across histosol types.

Type of samples	Histosol type	C	N	P	Ca	Mg	K	Al	C/N	C/P	N/P	Ca/Mg	Ca/Al	Ca-K-Mg/Al
Soil	Fibric	42.4 $\pm$ 2.3 ^a	1.4 $\pm$ 0.3 ^a	561 $\pm$ 163 ^a	1920 $\pm$ 762 ^a	358 $\pm$ 85.1 ^a	484 $\pm$ 169 ^a	3290 $\pm$ 2400 ^a	34.0 $\pm$ 9.5 ^a	1910 $\pm$ 565 ^a	51.3 $\pm$ 9.8 ^a	3.0 $\pm$ 1.4 ^a	0.46 $\pm$ 0.45 ^a	0.71 $\pm$ 0.55 ^a
	Hemic	40.5 $\pm$ 4.3 ^b	1.4 $\pm$ 0.33 ^a	658 $\pm$ 182 ^a	3120 $\pm$ 1350 ^b	546 $\pm$ 162 ^b	589 $\pm$ 269 ^a	4590 $\pm$ 4050 ^a	29.8 $\pm$ 6.1 ^b	1430 $\pm$ 561 ^b	46.8 $\pm$ 8.1 ^a	3.3 $\pm$ 1.7 ^a	0.72 $\pm$ 0.77 ^a	0.96 $\pm$ 0.99 ^a
	Sapric	20.4 $\pm$ 14.1 ^c	1.2 $\pm$ 0.45 ^a	712 $\pm$ 175 ^a	8070 $\pm$ 5590 ^c	2380 $\pm$ 1940 ^c	3520 $\pm$ 3270 ^b	19300 $\pm$ 13300 ^b	18.8 $\pm$ 3.9 ^c	777 $\pm$ 409 ^c	36.3 $\pm$ 13.4 ^b	1.8 $\pm$ 3.9 ^b	0.25 $\pm$ 0.83 ^a	0.6 $\pm$ 0.78 ^a
Plant	Fibric	46.8 $\pm$ 0.46 ^a	1.3 $\pm$ 0.18 ^a	1310 $\pm$ 232 ^a	2090 $\pm$ 417 ^a	730 $\pm$ 93.6 ^a	5630 $\pm$ 988 ^a	42.5 $\pm$ 28.7 ^a	43.2 $\pm$ 6.8 ^a	926 $\pm$ 157 ^a	20.7 $\pm$ 4.4 ^a	1.7 $\pm$ 0.38 ^a	32.1 $\pm$ 22.2 ^a	154.0 $\pm$ 84.9 ^a
	Hemic	46.9 $\pm$ 0.41 ^a	1.2 $\pm$ 0.18 ^a	1210 $\pm$ 269 ^a	2050 $\pm$ 534 ^a	728 $\pm$ 106 ^a	4950 $\pm$ 1040 ^b	47.1 $\pm$ 26.4 ^a	46.9 $\pm$ 6.6 ^a	1010 $\pm$ 234 ^a	21.1 $\pm$ 3.5 ^a	1.8 $\pm$ 0.52 ^a	30.1 $\pm$ 21.5 ^a	125.0 $\pm$ 69.3 ^a
	Sapric	46.6 $\pm$ 0.43 ^a	1.2 $\pm$ 0.17 ^a	1310 $\pm$ 269 ^a	2490 $\pm$ 468 ^b	669 $\pm$ 96.4 ^a	4980 $\pm$ 1180 ^{ab}	30.1 $\pm$ 10.5 ^b	44.8 $\pm$ 6.4 ^a	923 $\pm$ 197 ^a	20.3 $\pm$ 2.3 ^a	2.4 $\pm$ 0.6 ^b	56.9 $\pm$ 21.6 ^b	198.0 $\pm$ 94.6 ^b

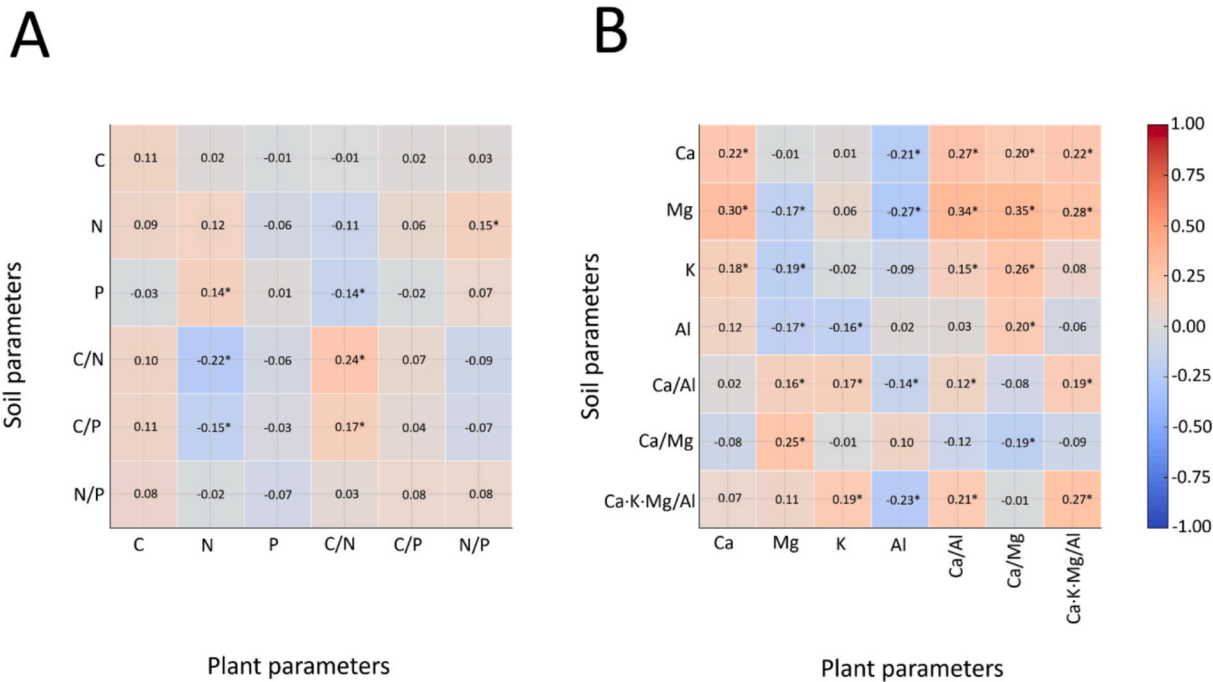


Fig. 2. Spearman's correlation heatmaps between soil and plant stoichiometric parameters. **(A)** Relationships among C, N, P contents and their ratios (C/N, C/P, N/P). **(B)** Relationships among elemental contents (Ca, Mg, K, Al) and derived ratios (Ca/Al, Ca/Mg, Ca-K-Mg/Al). Asterisks (*) denote statistically significant correlations ($p < 0.05$).

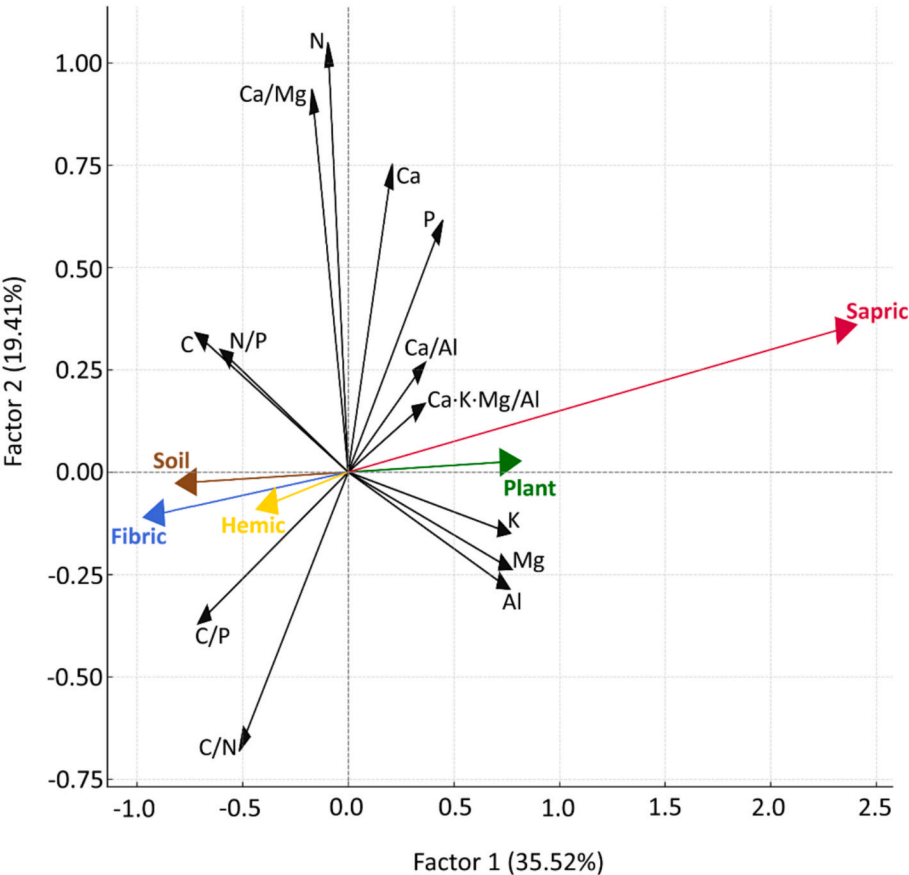


Fig. 3. Principal Component Analysis (PCA) biplot of stoichiometric and elemental variables.

weak to moderate correlations for the C content of plants and soils, with no consistent trends across histosol types (Fig. 4). At the same time,

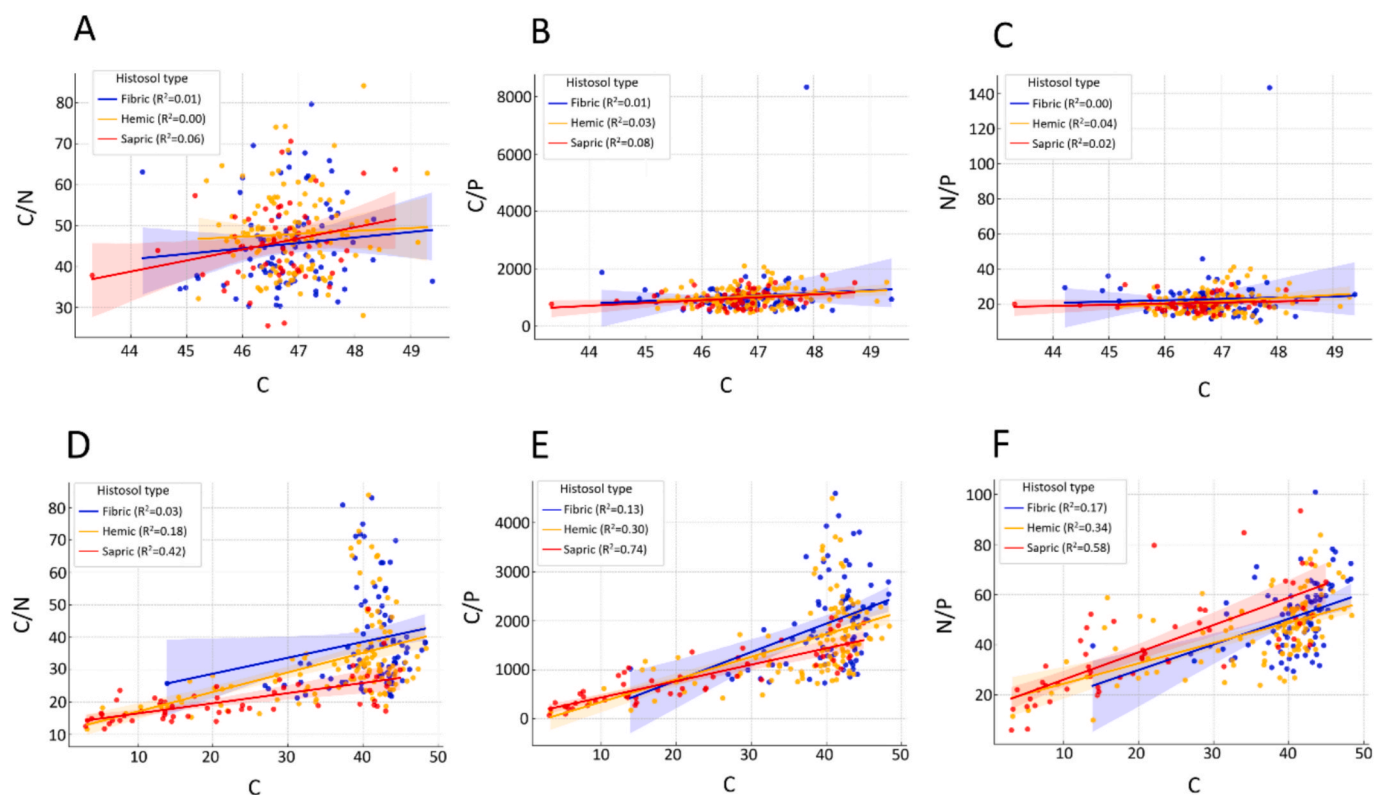


Fig. 4. Relationships between stoichiometric ratios and carbon (C) content in plant and soil samples. (A–C) Relationships between C/N, C/P, and N/P ratios and C content in plant samples. (D–F) Corresponding relationships for soil samples. Data are shown separately for fibric, hemic, and sapric Histosol types. Solid lines indicate linear regression fits with shaded areas representing 95% confidence intervals. Coefficients of determination (R^2) are provided in the legends.

regression analysis showed negative correlations between C/N and N, and between C/P and P (Figs. 5 and 6), confirming the mathematical

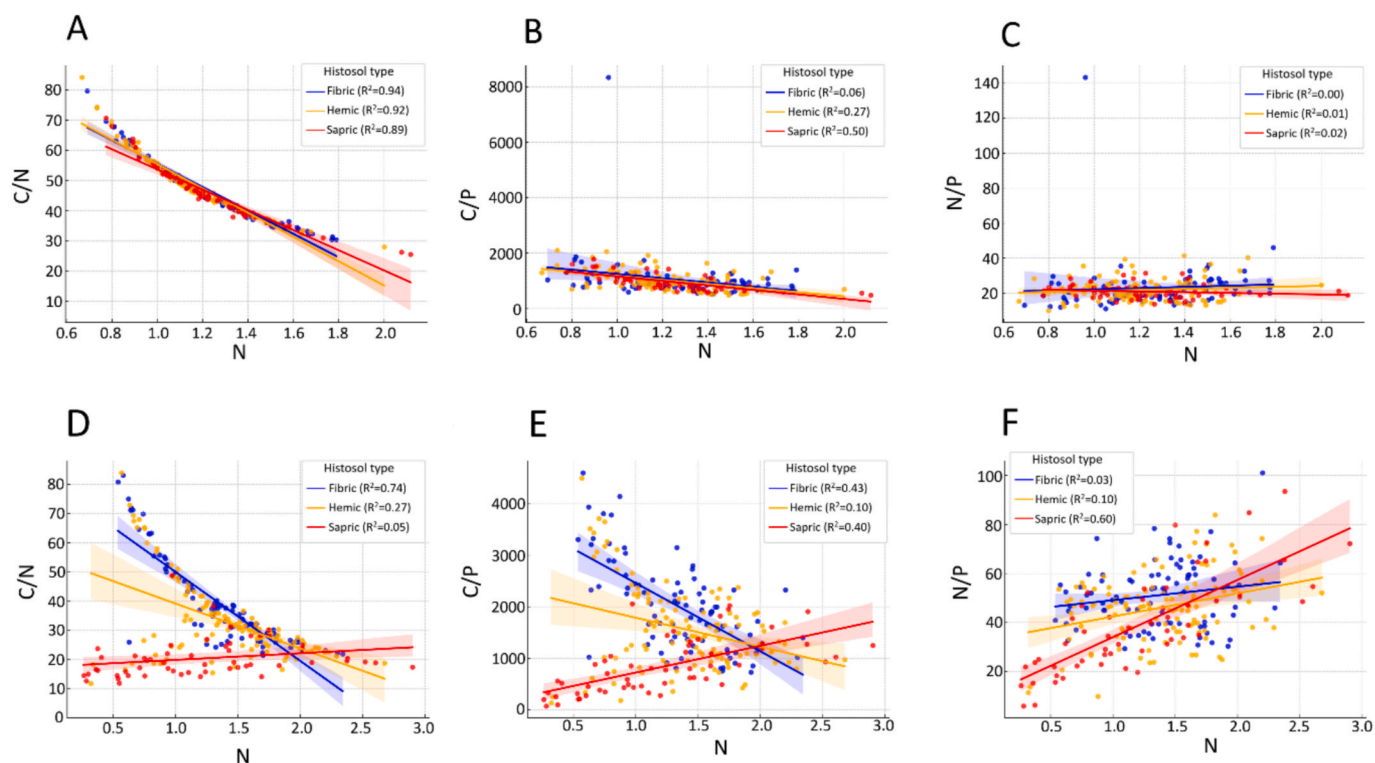


Fig. 5. Relationships between stoichiometric ratios and nitrogen (N) content in plant and soil samples. (A–C) Relationships between C/N, C/P, and N/P ratios and N content in plant samples. (D–F) Corresponding relationships for soil samples. Data are shown separately for fibric, hemic, and sapric Histosol types. Solid lines indicate linear regression fits with shaded areas representing 95% confidence intervals. Coefficients of determination (R^2) are provided in the legends.

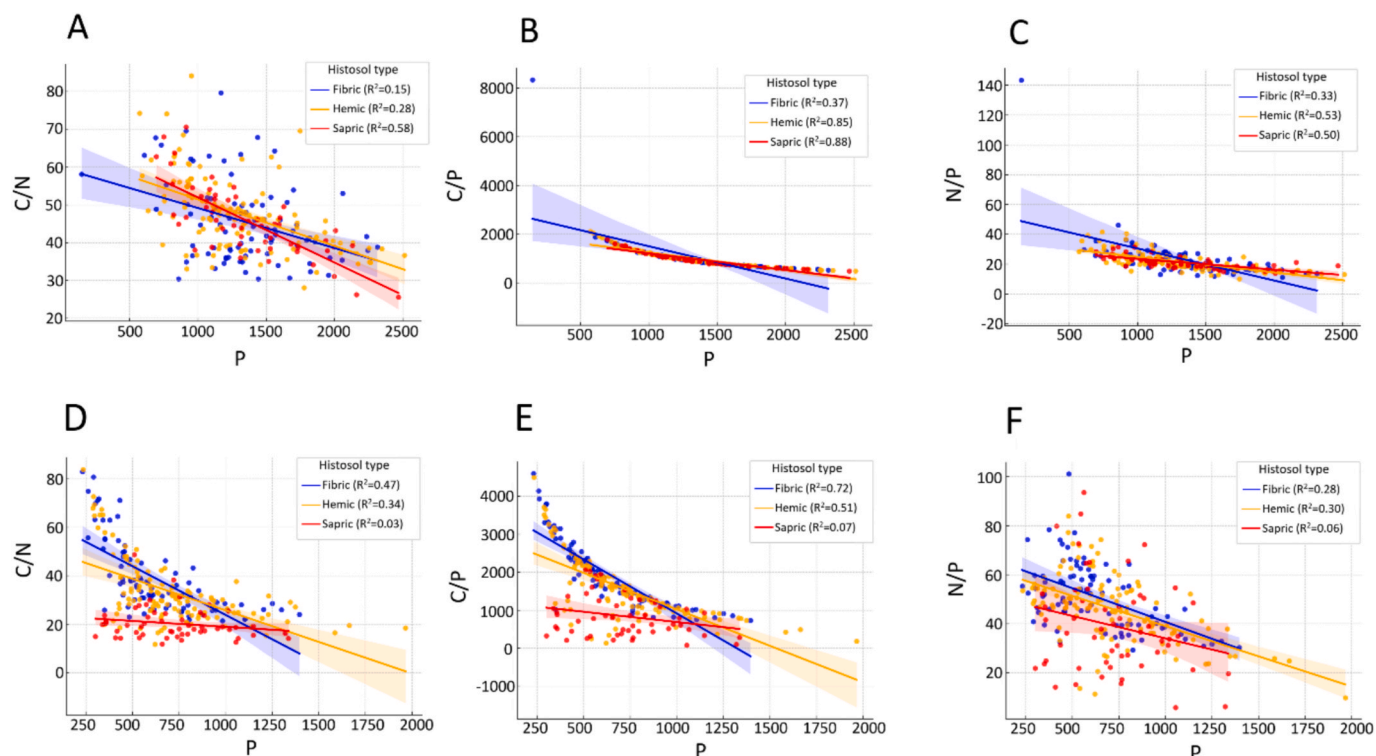


Fig. 6. Relationships between stoichiometric ratios and phosphorus (P) content in plant and soil samples. (A–C) Relationships between C/N, C/P, and N/P ratios and P content in plant samples. (D–F) Corresponding relationships for soil samples. Data are shown separately for fibric, hemic, and sapric Histosol types. Solid lines indicate linear regression fits with shaded areas representing 95% confidence intervals. Coefficients of determination (R^2) are provided in the legends.

nature of these relationships as predicted.

For plants, N/P molar ratios exhibited significant, negative

correlations with P content. The strongest model fit was obtained for hemic and sapric histosols ($R^2 = 0.53$ and 0.50 , respectively) (Fig. 6). C/

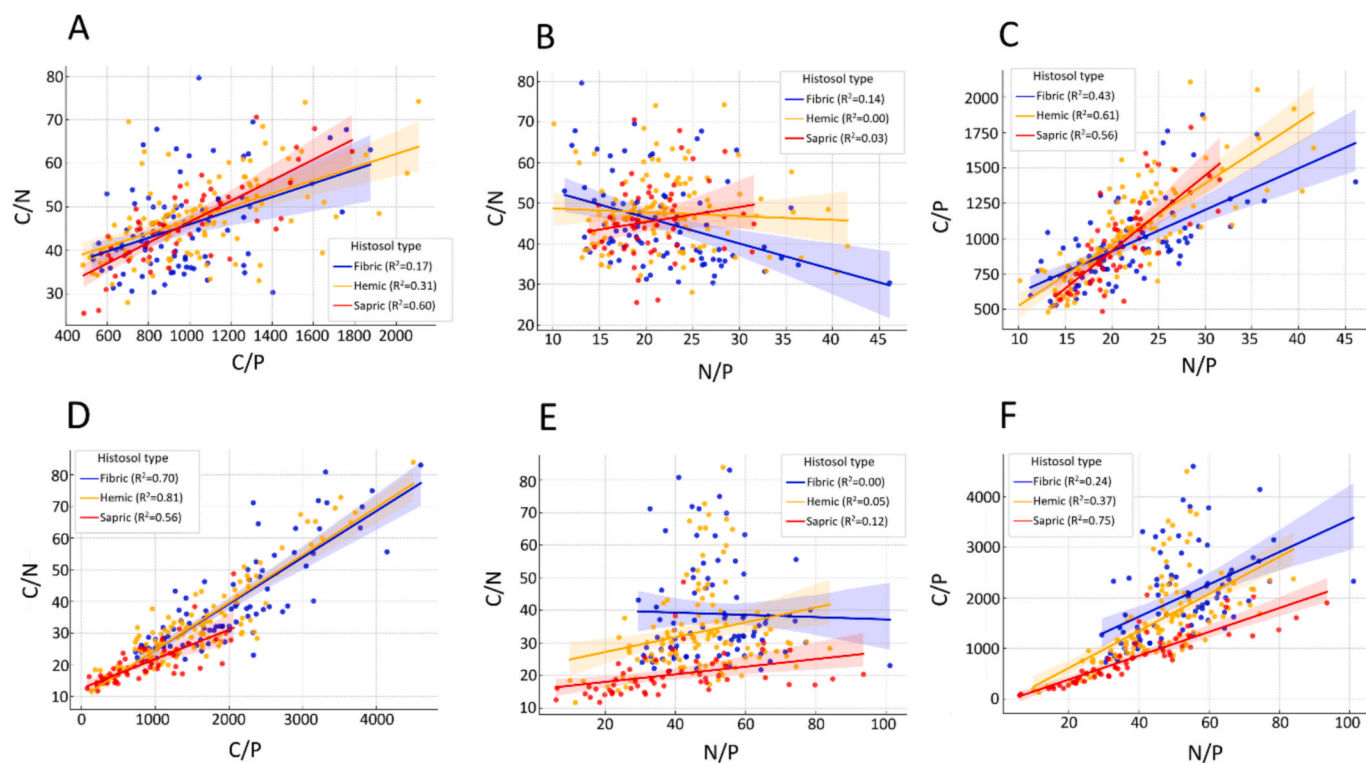


Fig. 7. Relationships among stoichiometric ratios in plant and soil samples. (A–C) Relationships between C/N and C/P, C/N and N/P, and C/P and N/P ratios in plant samples. (D–F) Corresponding relationships for soil samples. Data are shown separately for fibric, hemic, and sapric Histosol types. Solid lines indicate linear regression fits with shaded areas representing 95% confidence intervals. Coefficients of determination (R^2) are provided in the legends.

P ratios in plants also decreased sharply with increasing P content, particularly in hemic and sapric histosols ($R^2 = 0.85$ and 0.88 , respectively) (Fig. 6). In soils, the relationships between N/P and P were weaker than in plants but remained negative, particularly in hemic histosols ($R^2 = 0.30$). The C/P ratio in soil decreased significantly with increasing P in fibric and hemic histosols ($R^2 = 0.72$ and 0.51 , respectively) (Fig. 6).

Analysis of the interrelationships between stoichiometric ratios revealed that C/N and C/P were strongly positively correlated in both plants and soils, especially in hemic histosol soils ($R^2 = 0.81$) (Fig. 7). The strongest positive correlations for C/P and N/P were found in plants on hemic histosols ($R^2 = 0.61$) and in sapric histosol soils ($R^2 = 0.75$) (Fig. 7).

The strongest correlation was found between C and N in sapric soils ($R^2 = 0.76$). Clear positive correlations were also obtained for N vs P in plants growing on sapric histosols ($R^2 = 0.60$) and N vs P in fibric soils ($R^2 = 0.50$). The N vs P relationship was moderately strong in plants growing on hemic histosols ($R^2 = 0.29$) and hemic soils ($R^2 = 0.28$). The remaining trait pairs showed weak or ambiguous correlations in most groups, including C vs. P in both plants and soils, and C vs. N in plants (with R^2 close to zero) (Fig. 8).

GLM analysis revealed that the type of sample (plant vs. soil) and the type of histosol (fibric, hemic or sapric) significantly affected all analysed stoichiometric ratios. A significant interaction between these factors was also found in most cases. The only exception was the Ca/Mg ratio, for which the interaction was not significant ($p = 0.3789$) (Table 2).

The graphical results clearly show differences between plants and soils. The C/N ratio was significantly higher in plants than in soils, with

these contrasts being particularly evident in hemic and sapric histosols. A similar pattern was observed for the C/P ratio, which decreased systematically from fibric to sapric histosols in soil samples, while remaining relatively stable in plant samples. The N/P ratios showed the greatest differences between sample sources; the values were significantly higher in soils than in plants, particularly in fibric and hemic histosols. For elements indices (Ca/Al, Ca/Mg and Ca-K-Mg/Al), however, the pattern was reversed, with significantly higher values recorded in plants, particularly in sapric histosols. Despite the preservation of clear plant–soil differences, the magnitude of the Ca/Mg ratio was similar across all histosol types, confirming the lack of interaction in the GLM analysis (Fig. 9).

4. Discussion

Chemical analysis revealed significant differences in C content and basic stoichiometric indicators between different types of histosol. The highest C content and C/N ratio values were found in fibric histosols, while the lowest values were found in sapric histosols. This is consistent with the gradient of organic matter decomposition, ranging from poorly decomposed to highly degraded peat. Similar trends were reported by Wu (2012) and Page and Baird (2016), suggesting that the extent of humification results in a decrease in the proportion of organic C and a reduction in the C/N and C/P ratios. The values obtained in this study are also consistent with global averages for peat soils, which have significantly higher C/N ratios than mineral soils (Cleveland and Liptzin, 2007; Yu et al., 2010). He et al. (2019) came to similar conclusions when analysing the transformation of wetlands into grassland communities in northern China: habitat degradation led to a decrease in C, N and P

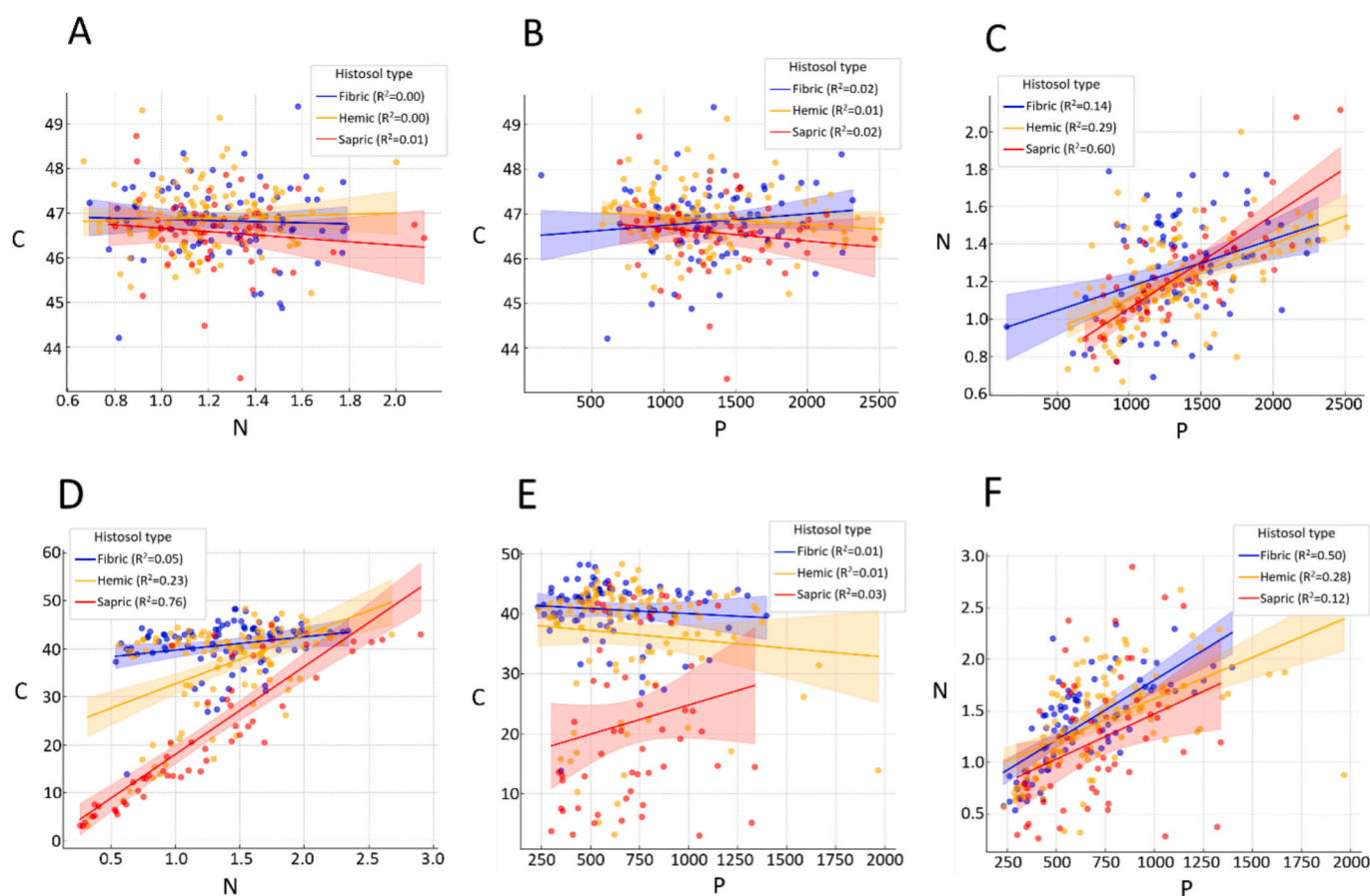
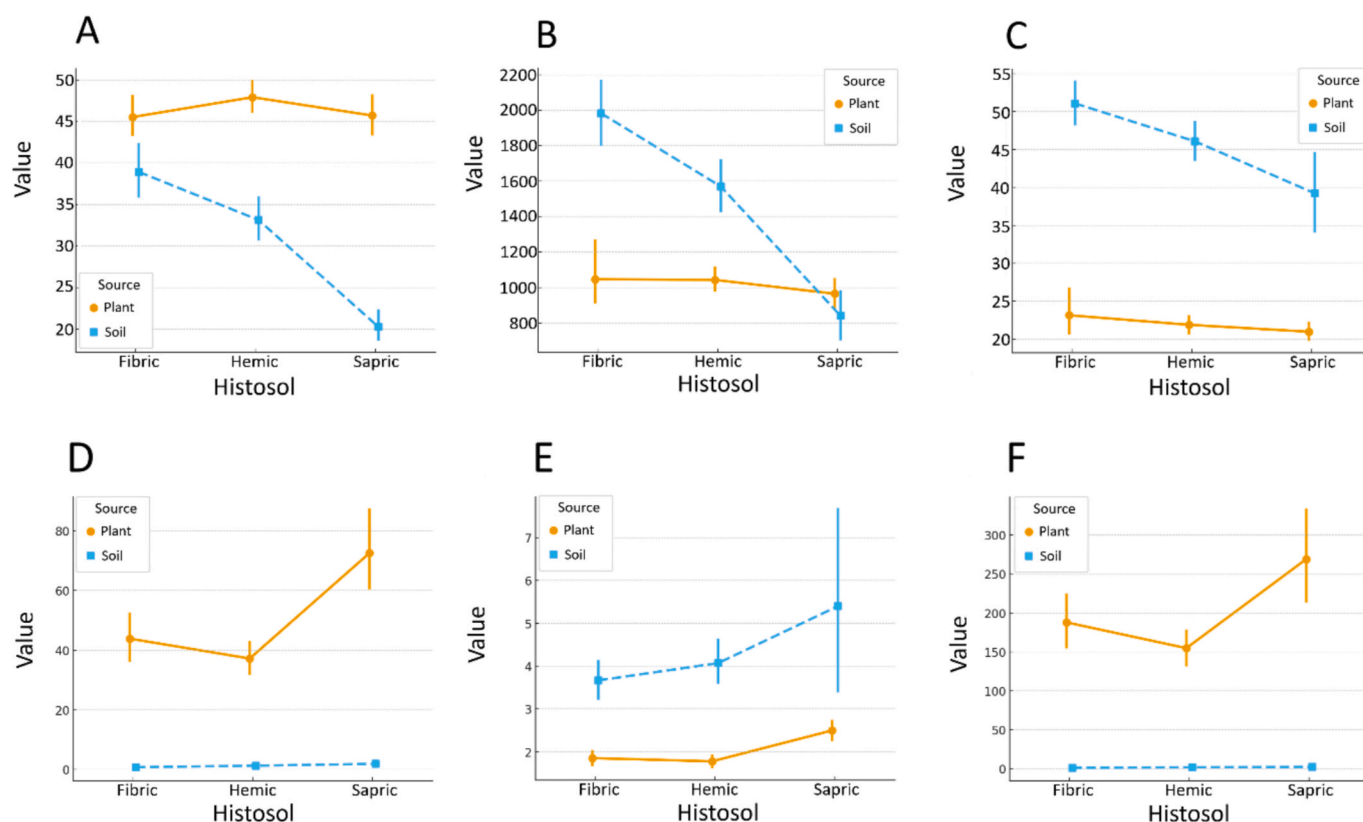


Fig. 8. Relationships between elemental contents in plant and soil samples. (A–C) Relationships between C and N, C and P, and N and P contents in plant samples. (D–F) Corresponding relationships for soil samples. Data are shown separately for fibric, hemic, and sapric Histosol types. Solid lines indicate linear regression fits with shaded areas representing 95% confidence intervals. Coefficients of determination (R^2) are provided in the legends.

Table 2

Summary of the GLM analysis for stoichiometric ratios.

	C/N		C/P		N/P		Ca/Al		Ca/Mg		Ca-K-Mg/Al	
	F	p	F	p	F	p	F	p	F	p	F	p
Source (S)	192.27	0.0000	75.00	0.0000	468.09	0.0000	368.37	0.0000	64.07	0.0000	352.74	0.0000
Histosol (H)	22.57	0.0000	27.13	0.0000	10.39	0.0000	17.21	0.0000	5.19	0.0059	9.57	0.0001
S*H	21.75	0.0000	20.25	0.0000	4.92	0.0076	15.79	0.0000	0.97	0.3789	9.35	0.0001

**Fig. 9.** Interaction plots showing the effects of sample source (plant vs. soil) and Histosol type on stoichiometric ratios. (A–C) C/N, C/P, and N/P ratios. (D–F) Ca/Al, Ca/Mg, and Ca-K-Mg/Al ratios.

content, as well as a marked reduction in C/N and C/P ratios. This indicates that the cycling of elements in organic soils is particularly sensitive to hydrological changes.

Our results, which show a consistent decrease in the C/N and C/P ratios from fibric to sapric histosols, are consistent with broader ecological evidence. Wang et al. (2020) reported that soil stoichiometry shifts significantly in response to climatic stress, with aridity reducing the C/P and N:P ratios. Their earlier work (Wang et al., 2015) also demonstrated that the stoichiometric relationships that occur during peat formation are strictly controlled by the degree of decomposition and the extent to which the peat is saturated with water. The upper horizons exhibit wider C/N/P ratios due to lower rates of microbial immobilisation. This stratification provides a framework for diagnosing the degree of peat development and nutrient availability in histosols. Similarly, Fan et al. (2025) demonstrated that the intensity of forest thinning directly affects the stoichiometric balance of soils, plants, and microbes. Together, these findings suggest that the decomposition of peat in histosols acts as an internal ecological gradient, comparable to large-scale climatic or management-driven processes, resulting in a similar decoupling of the C, N and P cycles.

N and P content did not differ significantly between fibric, hemic, and sapric histosols; however, the observed values were lower than in many studies of Western European peatlands (Sjögersten and Wookey,

2002; Limpens et al., 2008). This may be due to the climatic conditions in Central Europe and the dominance of coniferous species, which influence nutrient cycling through acidic organic precipitation and slower mineralisation rates (Prescott and Grayston, 2013). These findings suggest that the peatlands in Poland exhibit a more restricted N and P cycle compared to many boreal and oceanic peatlands.

Analysis of Ca/Al, Ca/Mg, and Ca-K-Mg/Al ratios revealed distinct differences between soils and plants, as well as among histosol types. This confirms earlier observations that the stoichiometry of conifer needles, such as those of *Picea abies* and *Pinus sylvestris*, only reflects the chemistry of peat soils to a limited extent (Aerts and Chapin, 1999). This influence is further reduced by the low nutritional requirements of these species and their capacity to thrive in nutrient-poor environments (Prescott and Grayston, 2013). Li et al. (2023) emphasise that global patterns of plant and soil stoichiometry depend largely on vegetation type and climate. However, plant–soil correlations often weaken in ecosystems dominated by species that are tolerant of environmental stress. This is confirmed by our results.

In contrast, the relationships between soil and plants were slightly stronger for ratios, especially Ca/Al and Ca-K-Mg/Al, although still moderate. This finding aligns with studies suggesting that the presence of Ca, K and Mg in soil has a more significant impact on the nutritional status of needles than N or P do (Sverdrup and Warfvinge, 1993; Błońska

et al., 2025). Furthermore, Vanguelova et al. (2007) demonstrated that the Ca/Al ratio in fine roots serves as a sensitive bioindicator of acid stress and Al toxicity, with a decrease leading to disturbances in the root systems of trees.

PCA analysis further confirmed the separation of soils and plants in chemical space: plants were mainly grouped in areas associated with high Ca, K and Mg and P indices, while soils occupied areas closer to C/N and C/P indices. This distribution suggests that there are significant differences in the mechanisms that regulate soil and plant stoichiometry. In the case of soils, the processes of humification and cation accumulation are of key importance, whereas in plants, the decisive factors are physiological strategies related to nutrient uptake and redistribution (Aerts and Chapin, 1999; Prescott and Grayston, 2013).

Analysis of ratios (Ca/Al, Ca/Mg, and Ca-K-Mg/Al) revealed clear differences in the ratios between soils and plants, as well as between different types of histosol. The highest Ca, Mg and K values were found in sapric histosols, which also had high ratios. These results are consistent with observations indicating that the advanced decomposition of organic matter promotes the accumulation of nutrients, which are retained within the peat structure (Page and Baird, 2016).

In plants, the ratios, particularly Ca/Al and Ca-K-Mg/Al, were higher than those in the soil, suggesting the presence of effective mechanisms for the selective uptake of nutrients by conifers in conditions of soil stress. High Ca-K-Mg/Al values in the needles of trees growing on sapric histosols may reflect physiological adaptations that limit the Al toxicity (Sverdrup and Warfvinge, 1993). Similar conclusions were drawn in experimental studies which indicated that the Ca-K-Mg/Al ratio may serve as an indicator of tree sensitivity to acidification and environmental stress (Göransson and Eldhuset, 2001).

Conversely, the lack of significant differences in the Ca/Mg ratio between soil and plants suggests that this indicator is less sensitive to habitat variability and does not clearly reflect environmental pressure. This is consistent with our GLM results, which showed no interaction between sample type and histosol type for this indicator. Therefore, these results confirm that, the Ca/Al and Ca-K-Mg/Al ratios are the most important for assessing plant nutrition and potential stress.

Stoichiometric ratios, particularly C/N and C/P, exhibited a distinct gradient associated with the extent of peat decomposition. The highest values were observed in fibric histosols, while the lowest values were found in sapric histosols. This reflects changes in the cycling of organic matter. Similar patterns have been reported in other studies. Leifeld et al. (2020) demonstrated that C/N ratios are highly sensitive to changes in land use and can effectively indicate peatland degradation. Similarly, Lasota and Błońska (2021) found that drainage reduces C stocks and narrows the C/N and C/P ratios. A meta-analysis by Idoko et al. (2025) confirmed consistent decreases in C/N and C/P, as well as increases in N/P, under anthropogenic drainage. This indicates a disruption to the biogeochemical balance. Recent results from Turunen et al. (2024) further highlight differences in C/P and N/P ratios between drained and undisturbed peatlands, reflecting altered microbial nutrient demands and phosphorus (P) mobilisation. Together, these findings are consistent with our observations that stoichiometric indices respond systematically to humification stage and disturbance intensity.

Furthermore, the Ca/Mg ratio, and particularly ratios such as Ca-K-Mg/Al, can also serve as indicators of degradation. Changes in these ratios may indicate acidification and remineralisation resulting from drainage or agricultural activity (Pschenyckj et al., 2023). Using classical stoichiometric ratios (C/N, C/P and N/P) alongside cation-based nutrient ratios provides a comprehensive and sensitive set of indicators for detecting peatland degradation. This offers practical value for assessing peatland conditions and planning management strategies.

5. Conclusions

The results of the study indicate that the stoichiometry of peat soils and their associated coniferous plant life in Poland varies greatly

depending on the type of histosol and the extent to which the organic matter has decomposed. The C content and the C/N, C/P and N/P ratios were highest in fibric histosols and lowest in sapric histosols, reflecting the progressive humification gradient. However, the opposite trend was observed for nutrients and aluminium, which were found to be significantly more abundant in sapric histosols, as reflected in the nutrients. Clear differences were found between soils and plants. While plant stoichiometry was characterised by less variability in C, N and P, ratios (especially Ca/Al and Ca-K-Mg/Al) were significantly higher in needles than in soils. This suggests the presence of selective nutrient uptake mechanisms that mitigate the Al toxicity and nutrient deficiencies. PCA analysis confirmed the separation of soil and plant samples: soils clustered around the C/N and C/P ratios, while plants were primarily associated with P and nutrients ratios. The weak correlations between soil and plant stoichiometry suggest that the chemistry of the needles of species such as *Picea abies* and *Pinus sylvestris* only partially reflects the nutritional status of the peat substrate. This emphasises the significance of species-specific physiological strategies in determining plant stoichiometry in nutrient-poor and acidic environments. A key finding is that both classical stoichiometric ratios (C/N, C/P and N/P) and nutrient-related ratios (Ca/Al, Ca/Mg, Ca-K-Mg/Al) can serve as sensitive indicators of peatland condition. The systematic decrease in C/N and C/P ratios during humification, coupled with an increase in nutrients ratios, suggests their potential for diagnosing peatland degradation and nutrient cycling dynamics. These results provide a foundation for incorporating stoichiometric analyses into monitoring programmes and protection strategies for peatland ecosystems.

CRedit authorship contribution statement

Wojciech Piaszczyk: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Andrzej Szlachta:** Investigation, Conceptualization. **Stanisław Łyszczarz:** Investigation, Conceptualization. **Norbert Szymański:** Methodology, Investigation, Conceptualization. **Michał Jasik:** Supervision, Project administration, Methodology, Investigation, Conceptualization. **Miroslaw Żelazny:** Methodology, Investigation, Conceptualization. **Stanisław Małek:** Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jarosław Lasota:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Ewa Błońska:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2026.117687>.

Data availability

Data will be made available on request.

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