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N, P, K profiling, and stoichiometric ratios of some Usneoid lichens of Kumaun Himalaya

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Abstract: Usneoid lichens are important components of forest ecosystems, contributing to nutrient cycling, ecosystem functioning, and environmental monitoring. However, information on their nutrient composition and stoichiometric relationships in the Himalaya remains limited. This study investigated the physicochemical properties, macronutrient concentrations, and ecological stoichiometry of three Usneoid lichens: *Usnea aciculifera*, *U. florida*, and *U. orientalis*, collected from three altitudinal zones (1000-2200 m) in the Kumaun Himalaya.Thallus pH, electrical conductivity (EC), and macronutrient concentrations (N, P, and K) were analyzed using standard aqueous extraction and wet digestion methods. Nutrient allocation patterns, elemental percentages, and stoichiometric ratios were also assessed. Significant interspecific variation was observed among the studied taxa. Thallus pH ranged from 3.56 ± 0.20 in *U. florida* to 6.46 ± 0.20 in *U. aciculifera*, while EC varied between 0.10 ± 0.09 and 0.53 ± 0.00 dS m^{-1}. Nitrogen concentration was highest in *U. orientalis* (1.52 ± 0.20%), phosphorus in *U. aciculifera* (0.60 ± 0.00%), and potassium in *U. florida* (0.14 ± 0.33%).Stoichiometric ratios showed considerable variation, with N ranging from 2.00 to 5.08, N from 8.35 to 19.00, and P from 1.64 to 5.00. Correlation analysis revealed strong positive relationships among nutrient concentrations, pH, and EC, indicating coordinated nutrient accumulation and species-specific allocation strategies. The findings highlight distinct nutritional adaptations among Usneoid lichens and demonstrate their potential as bioindicators of nutrient dynamics and environmental conditions in Himalayan forest ecosystems.
Keywords: Usneoid Lichen • Macronutrients • Stoichiometric Ratios • Ecological Significance • Kumaun Himalaya

Introduction

Usneoid lichens are a unique kind of filamentous, fruticose form of lichens distinguished by their long, hair-like, branched, and shrubby thalli. The genus *Usnea* is primarily represented by species of the Usneoid group belonging to the family Usneaceae. Lichens are developed by a sustained symbiotic relationship between a photosynthetic partner usually a green alga (photobiont) and a non-photosynthetic fungal partner (mycobiont). Morphologically, fruticose lichens grow over the substratum with a single attachment through a holdfast. The thalli are filamentous or pendent, mostly produce long, hair-like, branched, and shrubby structures. These lichens synthesize secondary metabolites, such as usnic acid and are used as antibacterial and antioxidant properties; therefore, such lichens are grouped as Usneoid (Devkota et al 2017). These compounds are essential for antimicrobial defines, stress tolerance, and photoprotection (Kranner et al 2008). Besides, lichens are also playing a significant role as efficient bioindicators of ecosystem integrity. Their poikilohydric physiology and direct reliance on atmospheric inputs for moisture and nutrients make them extremely sensitive to changes in the surroundings. Several forest types of the Himalayas provide a suitable habitat for lichens, which flourish in chilly, damp, and largely undisturbed areas, particularly in *Quercus*, *Abies*, *Pinus*, and *Rhododendron* rich forests (Upreti et al 2015).

Lichens absorbed atmospheric nitrogen and trace elements across their whole thallus surface and contribute to nutrient dynamics. Usneoid lichens are also useful markers of climate change and air quality because they indicate variations in their physiological state, distribution, and abundance (Bajpai et al 2016). Besides, exploration of their N, P, and K status, as well as associated stoichiometric patterns, are still limited. This study focuses on analysing nutrient dynamics, nutrient availability, and adaptation strategies under changing substrate conditions. Thus, the study intends to (i) measure the levels of potassium, phosphorus, and nitrogen in three common Usneoid lichens of the study area, (ii) assess their nutrient stoichiometry ratios, and (iii) interpret species-wise differences in connection to their substrate chemistry and ecological adaptation.

Materials and Methods

The present study was conducted in three altitudinal zones of Almora district, Kumaun Himalaya. Geographically, the region lies between 29°30′ and 30°20′ N latitude and 79°20′ and 80°20′ E longitude. The lower elevation zone is situated between 1000 m-1400 m at Kosi and dominated with *Pinus roxburghii* trees. The middle elevation is located between 1400 m and 1800 m at Katarmal and characterized by oak-pine mixed vegetation. Similarly, the higher region ranges from 1800 m to 2200 m altitude at Syahi Devi-Shitlakhet forest. This high elevation zone is dominated by *Quercus leucotrichophora* and associated with *Rhododendron arboreum*, *Myrica esculenta*, *Alnus nepalensis*, and *Asculus indica* trees.

Data collection

Collection of lichen specimens: The lichen specimens were collected from three selected elevation zones of the study area. Specimens of Usneoid lichens were systematically gathered from multiple substrates, including bark, rocks and soil surfaces (Awasthi 2007). During field visits, preliminary identification of lichen specimens was done using a 10x hand lens to examine thallus morphology. Collected specimens were brought to the laboratory for their taxonomic identification and nutrient analysis.

Identification of lichen taxa: Collected specimens were identified based on their morphology, anatomy, and chemistry in the laboratory using various identification keys (Divakar and Upreti 2005). The voucher specimens were submitted at Department of Botany SSJU Almora (Uttarakhand).

Thallus pH analysis: The aqueous suspension method was used to determine the pH of lichen thallus (Allen, 1974). 1.0 g of finely powdered oven-dried samples were suspended in 10 mL of double-distilled water (1:10 w/v), allowed to equilibrate for 30 minutes, and then measured using a digital pH meter that had been calibrated. Every measurement was made in triplicate and reported using dry weight.

Electrical Conductivity (EC) analysis: A calibrated conductivity (EC) meter was used to equilibrate, filter, and evaluate finely powdered lichen samples suspended in double-distilled water (1:10, w/v). The dry-weight results were presented as dS m^{-1} according to (Muhr et al 2000).

Macro-nutrient NPK analysis: The total N, P, and K contents, 0.5 g of oven-dried lichen samples were wet digested using a H_2SO_4–H_2O_2 digestion combination. Following the filtration and dilution of the digests, nutrient contents were determined. Parkinson and Allen (1975) approximated nitrogen, while (Koenig and Johnson 1942) and (Black and Evans 1965) calculated phosphorus and potassium, respectively.

Evaluation of Stoichiometric Ratios: To evaluate the nutritional balance in lichen thalli, elemental stoichiometric ratios were calculated. The following formulas were used to calculate the ratios on a mass basis (Güsewell 2004).

$$N:P = N/P,$$

$$N:K = N/K,$$
$$P:K = P/K,$$

where N, P, and K stand for the total percentages of potassium, phosphorus, and nitrogen in lichen thalli. Relative nutrient limitation and elemental coupling in lichens were interpreted using these ratios.

Calculation of Stoichiometric Percentages: Stoichiometric percentages of N, P, and K were calculated for ternary plot representation in order to visualize patterns of nutrient allocation. The following formulas were used to standardize each element's relative contribution (Sardans et al 2012; Tessier and Raynal 2003).

$$N\%_{stoich} = \frac{N}{N+P+K} \times 100,$$
$$P\%_{stoich} = \frac{P}{N+P+K} \times 100,$$
$$K\%_{stoich} = \frac{K}{N+P+K} \times 100,$$

In order to compare the patterns of nutrient allocation among lichen taxa, the normalized values, which add up to 100%, were utilized as inputs for stoichiometric ternary plots.

Data analysis: The data were presented as mean ± standard deviation (SD) on a dry weight basis, with each measurement being carried out in triplicate. To assess species variability, descriptive statistics such as mean, SD, and coefficient of variation (CV%) were calculated. Relationships between stoichiometric indices, macronutrient concentrations, and physicochemical properties were investigated using Pearson's correlation analysis. For the graphical representation of the data, R software version 4.5.0 and Microsoft Excel were used.

Result

This study evaluated N, P, K dynamics, stoichiometric ratios, and its percentage found on three selected Usneoid lichens viz. *Usnea aciculifera*, *U. florida*, and *U. orientalis* (Table 1). Considerable variations were observed among species in substrate pH, electrical conductivity (EC), and nutrient concentrations. The data also reveal distinct interspecific differences in substrate chemistry and nutrient accumulation patterns, as reflected by variations in mean values, standard deviations, and coefficients of variation (CV%) (Table 2).

Table 1: Physicochemical properties and macronutrient composition of sampled Usneoid lichens of the study area.

SN	Usneoid lichen	pH	EC (dS/m)	N (%)	P (%)	K (%)
1	*Usnea aciculifera*	6.46	0.1	1.2	0.6	0.12
2	*U. florida*	3.56	0.53	1.17	0.23	0.14
3	*U. orientalis*	5.46	0.39	1.52	0.3	0.08

Table 2: Descriptive statistics (Mean ± SD and CV%) of substrate chemistry and nutrient status in sampled thalli

Usneoid lichen	pH	CV%	EC dS/m	CV%	TN %	CV%	TP %	CV%	TK %	CV%
Usnea aciculifera	6.46 ± 0.20	5.43	0.10 ± 0.09	0.09	1.20 ± 0.25	9.9	0.60 ± 0.00	1.16	0.12 ±0.05	2.26
U. florida	3.56 ± 0.20	9.84	0.53 ± 0.00	0	1.17 ± 0.15	6.15	0.23 ± 0.00	3.2	0.14 ± 0.33	13.15
U. orientalis	5.46 ± 0.20	6.42	0.39 ± 0.07	0.07	1.52 ± 0.20	6.34	0.30 ± 0.00	2.34	0.08 ± 0.04	2.97

Status of pH and Electrical Conductivity of Usneoid lichens: The pH of the lichen thalli varied greatly within the studied *Usnea* species, ranging from highly acidic to almost neutral conditions (Table 2). *U. aciculifera* had the highest pH (6.46 ± 0.20), indicating a mild acidic to nearly neutral thallus habitat. *U. florida* had the lowest pH (3.56 ± 0.20), indicating a highly acidic thallus. *U. orientalis* had an intermediate pH of 5.46 ± 0.20 (Fig. 1). The coefficient of variation (CV%) for pH ranged from 5.43% to 9.84%, indicating relatively low variability between replicates.

U. florida had the most fluctuation (9.84%), whereas *U. aciculifera* showed the least variance (5.43%), suggesting that pH measurements were more consistent. Additionally, the Electrical conductivity (EC) values varied significantly between the species under investigation, ranging from 0.10 to 0.53 dS m^{-1}. *U. florida* has the greatest EC value (0.53 ± 0.00 dS m^{-1}), followed by *U. orientalis* (0.39 ± 0.07 dS m^{-1}) and *U. aciculifera* (0.10 ± 0.09 dS m^{-1}) (Table 2; Fig. 2). The higher EC values indicate a higher concentration of soluble ions in the thallus tissues. The CV% linked to EC showed very little variation between replicates, ranging from zero to 0.09%. Notably, EC of *U. Florida* were remarkably consistent among samples, with no discernible fluctuation (CV = 0%).

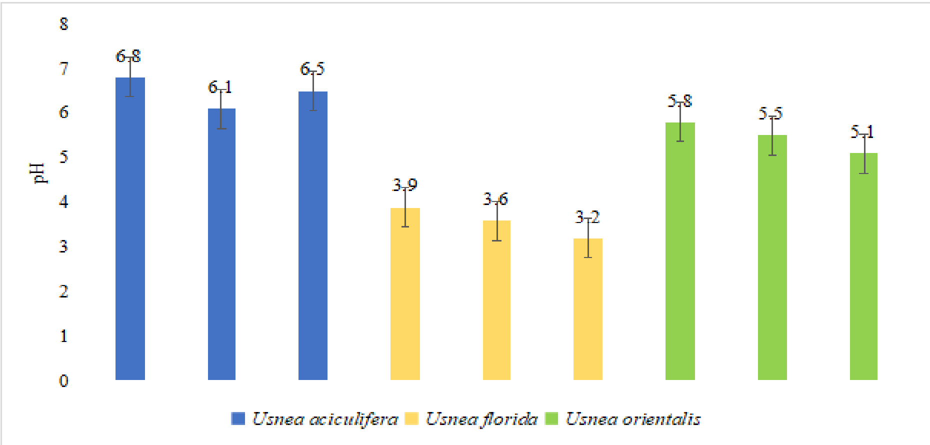


Fig.1: Comparative analysis of pH values of selected *Usnea* species

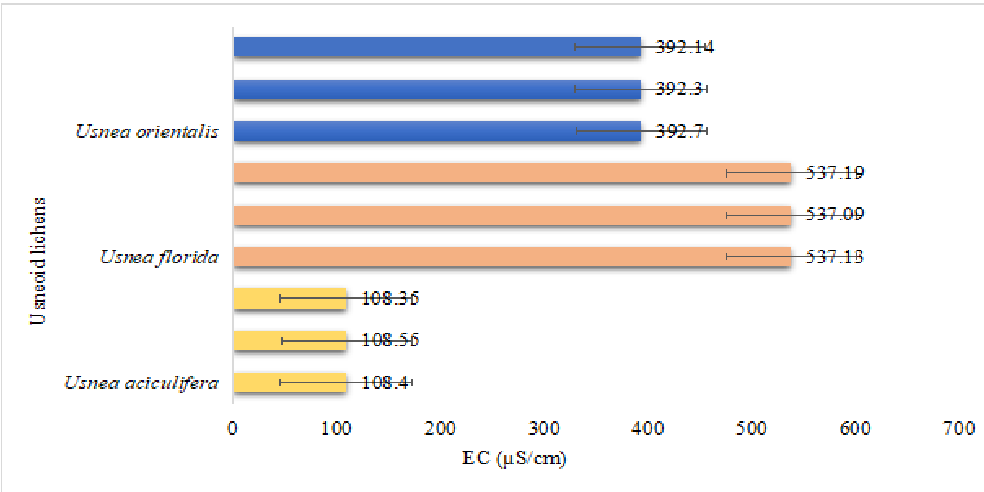


Fig. 2: Illustration of comparative analysis of EC (dS/m) values recorded in selected species of Usneoid lichens

Nitrogen Content of the thallus: The total nitrogen (TN) contents of all the species ranged from 1.17% to 1.52%. *U. florida* has the lowest NT (1.17 ± 0.15%), whereas *U. orientalis* had the highest TN concentration (1.52 ± 0.20%), followed by *U. aciculifera* (1.20 ± 0.25%). The TN CV% showed moderate heterogeneity in nitrogen buildup, ranging from 6.15% to 9.90%. Likewise, *U. florida* had also the lowest variability (6.15%), indicating more consistent nitrogen content among its samples, while *U. aciculifera* had the largest coefficient of variation (9.90%) (Table 2).

Phosphorus Content analysis: The range of total phosphorus (TP) was 0.23% to 0.60%. *U. florida* had also the lowest TP concentration (0.23 ± 0.00%), whereas *U. aciculifera* had the greatest phosphorus content (0.60 ± 0.00%), followed by *U. orientalis* (0.30 ± 0.00%). Low variability among replicates was shown by the TP coefficient of variation, which ranged from 1.16% to 3.20%. Phosphorus values showed a high degree of stability, with *U. florida* showing the most variation (3.20%) and *U. aciculifera* showing the lowest variation (1.16%) (Table 2).

Potassium Content status: The total potassium (TK) concentration ranged from 0.08% to 0.14%, with discernible interspecific variations. *U. florida* had the greatest potassium levels (0.14 ± 0.33%), followed by *U. aciculifera* (0.12 ± 0.05%), and *U. orientalis* (0.08 ± 0.04%). The CV% for TK showed high variability, ranging from 2.26% to 13.15% as compared to the other examined nutrients. While, *U. aciculifera* showed the least variability (2.26%), indicating more stable potassium concentrations, *U. florida* displayed the highest coefficient of variation (13.15%), indicating significant variation in potassium accumulation among replicates.

Stoichiometric Ratios: Among the *Usnea* species under study, the stoichiometric ratios of potassium (K), phosphorus (P), and nitrogen (N) varied significantly (Table 3; Fig. 3). The range of the N:P ratio was 2.00 to 5.08. *U. florida* had the highest N:P ratio (5.08), closely followed by *U. orientalis* (5.06), while *U. aciculifera* had the lowest ratio (2.00). The N:K ratio varied more widely, from 8.35 to 19.00. *U. florida* had the lowest N:K ratio (8.35) (Table 3), whereas *U. orientalis* had the highest (19.00), suggesting a higher relative abundance of nitrogen relative to potassium. The P:K ratio also varied from 1.64 to 5.00, with *U. florida* having the lowest ratio (1.64) and *U. aciculifera* having the highest ratio (5.00).

Table 3: Indicating interspecific variation in nutrient balance in sampled Usneoid lichens

	Stoichiometric ratio			stoichiometric percentage		
Lichen taxa	N/P	N/K	P/K	N%	P%	K%
U. aciculifera	2	10	5	1.72	1.22	0.82
U. florida	5.08	8.35	1.64	1.37	0.566	0.4896
U. orientalis	5.06	19	3.75	1.38	0.577	0.4326

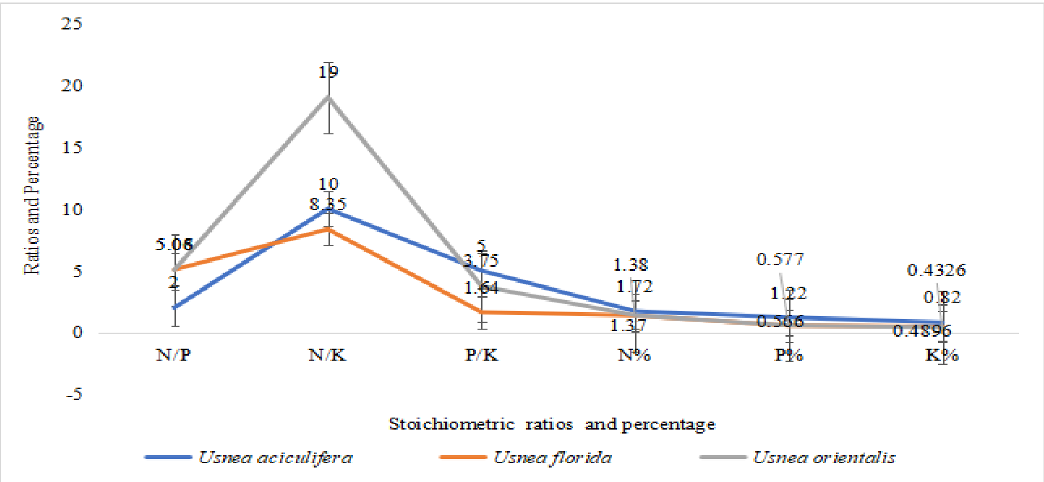


Fig. 3: Comparison of stoichiometric ratios (N/P, N/K, P/K) and elemental percentages (N%, P%, K%) among three *Usnea* spp.

Stoichiometric Percentages (N%, P%, and K%): Significant variation was observed in the nutritional content of among the *Usnea* species (Table 3). With values ranging from 1.37% to 1.72%, nitrogen was the most prevalent nutrient across all species. *U. aciculifera* has the highest nitrogen concentration (1.72%), followed by *U. florida* (1.37%) and *U. orientalis* (1.38%) (Fig 4). While highest phosphorus concentration was recorded in *U. aciculifera* and lowest in *U. florida* ranging from 0.566% to 1.22%. Similarly, potassium concentration was 0.43% in *U. orientalis* to 0.82% in *U. aciculifera*. *U. florida* and *U. orientalis* had relatively lower phosphate and potassium contents, while *U. aciculifera* consistently showed higher concentrations of all three macronutrients, indicating more nutrient accumulation potential. Within the genus *Usnea*, results demonstrate interspecific variations in elemental storage and nutritional content.

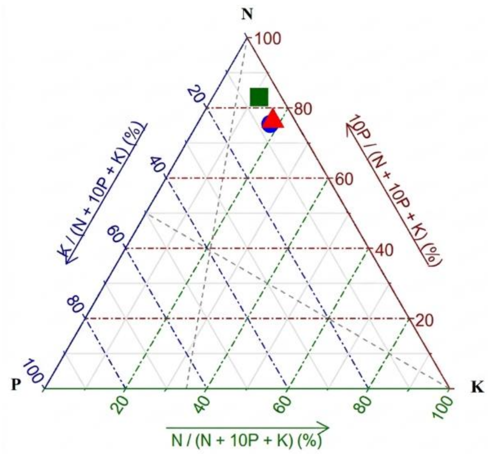
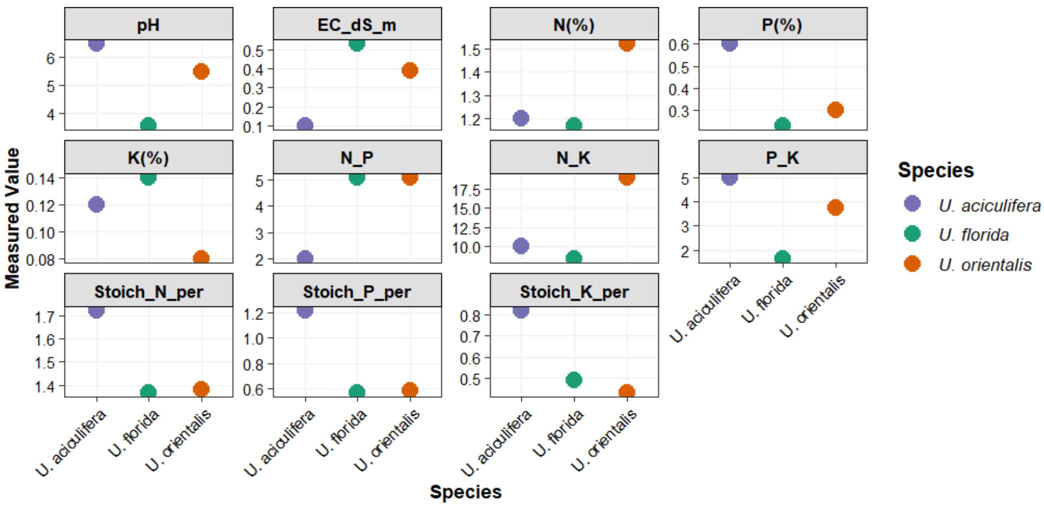


Fig.4: Nitrogen, Phosphorus, and Potassium Elemental Stoichiometric balance in *Usnea*

Fig 5: Physicochemical Properties, Stoichiometric Percentage, and Stoichiometric Ratios of Usneoid Lichens



Integrated nutrient patterns and ecological implications: Different patterns of nutrient buildup were also seen in the *Usnea* species, indicating physiological and ecological adaptations unique to each species. The highest pH and phosphorus levels were found in *U. aciculifera*, suggesting a favorable environment for nutrition retention and increased metabolic potential. While, *U. florida*, possesses the highest potassium concentration, lowest pH, and the best EC, indicating improved ionic control and adaptation to more acidic environments. The highest nitrogen concentration was found in *U. orientalis*, suggesting a higher potential for growth and protein synthesis (Fig 5).

Correlation analysis of physicochemical parameters, macronutrients, and stoichiometric indices: Strongly coordinated nutritional dynamics were shown by the Pearson correlation matrix, which showed significant and highly structured correlations among the three *Usnea* species(Fig 6)

Correlation of thallus pH: Phosphorus content (P%; r = 0.86), P/K ratio (r = 0.99), nitrogen percentage (N Stoich %; r = 0.780), phosphorus percentage (P Stoich %; r = 0.774), and potassium percentage (K Stoich %; r = 0.66) all showed significantly positive associations with thallus pH. However, significant negative associations between pH and the N/P ratio (r = -0.76) and electrical conductivity (EC; r = -0.93) was also recorded. Additionally, a moderately negative connection (r = -0.48) was found between K (%) and pH. It exhibits decreased ionic conductivity and increased phosphorus availability are linked to higher pH levels (Fig 6).

Correlation of Electrical Conductivity (EC): Strong and negative correlations were found in EC and pH (r = -0.93), P/K ratio (r = -0.94), nitrogen % (r = -0.95), phosphorus and potassium percentage represented by (r = -0.95) and (r = -0.89) respectively. Besides, a significant positive connection (r = 0.94) between EC and N/P ratio was also found. These results imply that decreased nutrient percentages and modified elemental stoichiometry are linked to rising ionic concentration within the thallus.

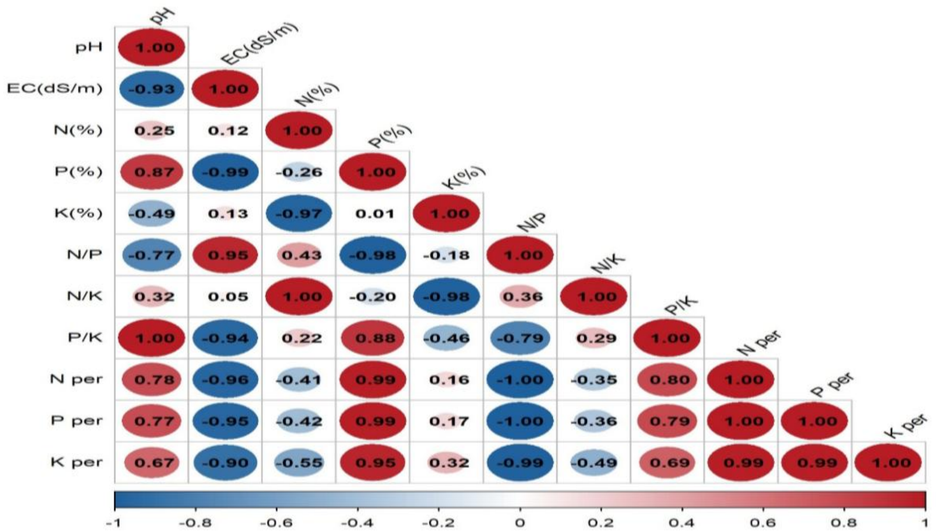


Fig. 6: Correlation matrix of physicochemical attributes and nutrient stoichiometry of Usneoid lichen taxa

Correlation of Electrical Conductivity (EC): Strong and negative correlations were found in EC and pH (r = -0.93), P/K ratio (r = -0.94), nitrogen % (r = -0.95), phosphorus and potassium percentage represented by (r = -0.95) and (r = -0.89) respectively. Besides, a significant positive connection (r = 0.94) between EC and N/P ratio was also found. These results imply that decreased nutrient percentages and modified elemental stoichiometry are linked to rising ionic concentration within the thallus.

Correlation of Nitrogen Content (N%): The N/K ratio and nitrogen content had a very strong positive association (r = 0.99), suggesting that changes in nitrogen had a significant impact on the N/K stoichiometric relationship. Potassium content (r = -0.96),

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nitrogen % (r = -0.40), phosphorus percentage (r = -0.41), and potassium percentage (r = -0.55) all showed significant negative associations with nitrogen. N% and pH (r = 0.25), EC (r = 0.12), and P/K ratio (r = 0.22) showed positive but very minor relationships (Fig 6).

Correlation of Phosphorus Content (P%): Strong positive correlations were analysed for phosphorus content and pH (r = 0.867), P/K ratio (r = 0.88), nitrogen % (r = 0.98), phosphorus percentage (r = 0.98), and potassium percentage (r = 0.95). however, Phosphorus, exhibit a very substantial negative connection with both the N/P ratio (r = -0.98) and EC (r = -0.98). The results suggest that phosphorus is a key factor in the nutritional balancing of the Usneoid taxa under study.

Correlation of Potassium Content (K%): Nitrogen content (r = -0.96) and the N/K ratio (r = -0.98) showed a very strong negative correlation with potassium content. Potassium percentage (r = 0.32), phosphorus percentage (r = 0.17), and nitrogen percentage (r = 0.16) all showed positive correlations, there was virtually no correlation between potassium and phosphorus content (r = 0.01).

Correlation of Stoichiometric Ratios: The N/P ratio had a high positive correlation with EC (r = 0.94) but a negative correlation with pH (r = -0.76), phosphorus content (r = -0.98), P/K ratio (r = -0.78), nitrogen % (r = -0.99), phosphorus percentage (r = -0.99), and potassium percentage (r = -0.99). This suggests that higher N/P ratios were linked to reduced nutrient percentages and phosphorus availability. The N/K ratio had an almost perfect positive association with nitrogen concentration (r = 0.99), but a very high negative correlation with potassium content (r = -0.98). Weak to moderate correlations were found with the other variables.

The P/K ratio showed substantial positive connections with phosphorus content (r = 0.88), nitrogen % (r = 0.79), phosphorus percentage (r = 0.79), and potassium percentage (r = 0.69), as well as nearly perfect positive correlations with pH (r = 0.99). The P/K ratio and EC showed a significant negative connection (r = -0.94).

Correlation of Stoichiometric Percentages: Nitrogen percentage (N Stoich %) showed a very high positive association with potassium percentage (K Stoich %; r =0.98) and an almost perfect positive correlation with phosphorus percentage (P Stoich %; r =0.99). Similar patterns were noted for the proportion of phosphorus, which exhibited a high positive connection (r = 0.98) with the percentage of potassium. These robust positive correlations imply that the lichen thalli experienced coordinated N, P, and K accumulation (Fig 6).

Discussion

A significant heterogeneity was observed in the chemical microenvironment of the Usneoid thalli, as evidenced by the thallus pH ranging from 3.56 in *U. florida* to 6.46 in *U. aciculifera*. However, similar pH level varies between 3.0 and 5.5 was recorded in *U. florida* collected from a coniferous forest of Los Angeles Basin, California by (Jovan et al 2012). These differences are anticipated since lichens obtain nutrients mostly from precipitation, air deposition, and canopy leachates rather than directly from soil, leading to species-specific patterns of nutrient accumulation. (Kranner et al 2008) study reported that *Usnea* species preferred to grow in acidic to slightly acidic habitats, often ranging between pH 3.5 and 6.5. But, higher pH of *U. longissima* (pH 4.0-5.8) and *U. barbata* (pH 3.7-6.2) have also been observed in Himalayan regions (Zhang et al 2023). The pH value of host tree bark (*Quercus*) varied from 4.7 to 6.1 (Öztürk & Oran 2011). This host pH range preferred by several Usneoid lichens. It provides an ideal environment for the growth of epiphytes, especially lichens. In contrast, the comparatively higher pH of *U. aciculifera* suggests a greater buffering capacity and enhanced nutrient retention. The strong negative correlation between pH and EC (r = -0.93) further indicates that increased ionic concentrations within the thallus may contribute to acidification processes.

(Munzi et al 2023) was studied acidity and ion accumulation dynamics in epiphytic lichens exposed to varying atmospheric inputs. Thus, lower coefficients of variation for EC (0.01-0.02%) and pH (0.72-1.11%) also suggest stable microhabitats (Brodo et al 2001). In the present study nitrogen contents in *U. longissima* (2.1-3.8%) and *U. barbata* (2.5-3.4%) were recorded within the range (Wang et al 2019). The value of nitrogen in many temperate fruticose lichens was recorded between 1.0-3.0% (Zhang et al 2023). In the present study this value was within range represented by 1.52% and 1.17% in *U. orientalis* and *U. florida* respectively. However, *U. orientalis* has comparatively high nitrogen concentration indicates effective nitrogen absorption and digestion. Increased nitrogen availability improves thallus development, photobiont production, and protein synthesis (Johansson et al 2011). Nitrogen significantly affects elements stoichiometry in the species under study, as seen by the nearly perfect positive correlation (r = 0.99) between nitrogen content and the N:K ratio. Phosphorus concentrations ranged from 0.23% in *U. florida* to 0.60% in *U. aciculifera*. These values are generally greater than the 0.08-0.30% phosphorus concentrations reported earlier (Marks et al 2015). The high phosphorus level seen in *U. aciculifera* could be a result of both favorable microenvironmental circumstances and effective phosphorus retention. Since phosphorus is essential for ATP, nucleic acids, and membrane phospholipids, its availability is frequently linked to higher growth potential and metabolic activity. This interpretation is supported by the strong positive correlation between phosphorus concentration and pH (r = 0.86) and the strong negative correlation with EC (r = -0.98), suggesting that phosphorus accumulation is favored under less acidic conditions.

The amounts of potassium ranged from 0.08% in *U. orientalis* to 0.14% in *U. florida*, which are within the range as fruticose lichens from temperate forests (Gough et al 1988). Potassium is essential for osmotic regulation, enzyme activation, and stress tolerance. The N:P ratio in both the Usneoid lichens was recorded lower as compared to many vascular plants (Wieder et al 2022). But they play a significant role for nutrient enhancement in temperate ecosystems (Jovan et al 2012). The stoichiometric analysis also revealed distinct nutrient allocation strategies (Johansson et al 2011).

Conclusion

The Usneoid lichens possesses usnic acid and used as secondary metabolites and also responsible for nutrient enrichment particularly in temperate areas. This study evaluated stoichiometric relationships, nutritional composition, and physicochemical characteristics of some temperate fruticose lichens. Significant interspecific variations in elemental balance and nutrient dynamics were observed. *Usnea aciculifera* showed highest phosphorus accumulation and nutrient retention. Similarly, *U. orientalis* exhibited the highest nitrogen concentration, while *U. florida* was characterized as highest electrical conductivity and potassium content under acidic conditions. Variations in N:P, N: K, and P: K ratios, together with strong positive correlations among nutrient percentages, indicated species-specific nutrient allocation strategies and coordinated nutrient accumulation in the Usneoid thalli.

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