Tropical Terrestrial And Epiphytic Ferns Have Different Leaf Stoichiometry With Ecological Implications.

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Abstract

Terrestrial and epiphytic herbaceous forest species have different ecology and leaf stoichiometry. In tropical regions, a great component of herbaceous forest species is represented by ferns with different lifeforms. However, little is known about the differences in leaf stoichiometry between the lifeforms. We account for the concentrations of leaf elements (N, P, K, Ca and Mg) between terrestrial and epiphyte lifeforms and evolutionary clades. The fern species were sampled from the forest of Brunei Darussalam. Five leaves were collected from 5 individuals from 16 terrestrial and 4 epiphytic ferns. The leaves were then acid-digested and analyzed. Epiphytic species had higher concentration of most of the leaf elements. The N:P ratio showed that the epiphytic species being much more nutrient-limited, relying on stochastic events, compared to the terrestrial species which have a constant availability of soil elements. Epiphytes showed a higher concentration of P, which could be explained by their luxury consumption. Epiphytes accumulate elements in a higher concentration than is needed by their normal metabolic activity. Furthermore, epiphyte species have a significantly higher concentration of Ca which could be interpreted as necessity of coping with severe habitat conditions with sclerophyll leaves. The results bring in more information on the poorly studied stoichiometry of tropical Asian fern species. Important in understanding the eco-physiology of terrestrial and epiphytic ferns and determining which species are sensitive to the different forest management and the effect of climate change. This, is in addition to the associated mechanisms.

Introduction

Leaf stoichiometry – the relative abundance and concentration of leaf elements – is a useful tool for understanding the fitness of a species in a particular environment (Ågren and Weih 2012). It therefore determines the distribution of the plant species across different habitats and the biome as a whole (Sun et al. 2017; Tong et al. 2019). The differences in element concentration and their allometric relationship is important for the terrestrial species with a constant supply of nutrients from the soil and the epiphytes that rely on an irregular supply of nutrients (Zotz and Hietz 2001; Cardelús and Mack 2010).

Plant functioning requires up to 17 essential elements of varying concentrations, with nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) often required in large quantities. These are referred to as macronutrients (White and Brown 2010). Among these 5 macronutrients, N and P play a major role in plant growth (root morphology) and metabolic functioning (chlorophyll content) (Razaq et al. 2017). Both N and P are tightly linked and, as such, their ratio (N:P) has been suggested to be a major ecological driver. It is used to indicate the nutrient limitations of N and/or P (Koerselman and Meuleman 1996; Güsewell 2004). The crucial function of K, often the second highest element concentration in leaves (Winkler and Zotz 2010), is in the maintenance of the plant's water status through the regulation of the stomatal aperture (Oddo et al. 2011). Ca has a broad concentration in the leaves (Richardson and Walker 2010) as well as in differing lifeforms (Huang et al. 2019). It is a secondary messenger that transmits environmental change signals to trigger adaptive processes (Ranty et al. 2016). It is also involved in the regulation of transpiration (Song et al. 2008). Mg is an integral component of

leaf photosynthesis (Hermans and Verbruggen 2005) and limits plant growth, productivity and metabolism (Baribault et al. 2012).

These elements are important and plant species exhibit differential concentrations in their leaves (Zheng and Shangguan 2007) as a consequence of the differences in their metabolic requirements (Sardans and Peñuelas 2014) and lifeform (Cardelús and Mack 2010). For instance, species from a hotter-drier environment exhibit lower N and P concentrations compared to species from a colder-humid environment, implying a differential nutrient use strategy (Sardans and Peñuelas 2014). Furthermore, epiphytic species often have to rely on a stochastic source of nutrients while terrestrial species have a much more constant supply (Cardelús and Mack 2010). This discrepancy in growth environment has led to the development of distinct leaf stoichiometric profiles between the two lifeforms (Huang et al. 2019). Epiphytes, due to the irregular supply of nutrients, employ what has been proposed as luxury consumption (Winkler and Zotz 2010). The plants accumulate a high concentration of N (Winkler Zotz 2010), and P (Winkler Zotz 2009) in their vacuoles for use beyond the immediate metabolism needs in terms of protein synthesis, enzyme reactions or stomatal regulations.

Despite the overlap in terrestrial and canopy habitat between ferns and angiosperms as well as their distinctive physiological properties (Brodribb and Holbrook 2004; Brodribb et al. 2009), the relative importance of leaf stoichiometry is poorly known, particularly in the tropics. Ecologically, ferns play a range of crucial roles in the regulation of water and in the nutrient balance in the forest ecosystem (Umana and Wanek 2010; Hargis et al. 2019), controlling the regeneration potential of a forest (Coomes et al. 2005) as well as the phytoremediation of soil (Praveen and Pandey 2019). In tropical regions, ferns can be the dominant species in an ecosystem and contribute significantly to nutrient cycling and other ecosystem processes (Amatangelo and Vitousek 2008, 2009).

However, fern phylogenies distinguish the clade called 'Polypod' ferns, consisting of the order Polypodiales, which has radiated during the Angiosperm's early evolution (Schneider et al. 2004; Testo and Sundue 2016). All the other leptosporangiate ferns are grouped into 'non-polypod' ferns, diversified over tens of millions of years before the angiosperms (Schneider et al. 2004). The non-polypod ferns include the tree ferns, filmy ferns, water ferns, gleichnenioid, osmundaceous and schizeoid ferns. The non-polypod are archaic compared with the modern polyopod. Therefore, it is relevant to know whether the leaf stoichiometry differs from the phylogenetic different clades of species.

In this study, we aim to elucidate the stoichiometric relationship between terrestrial and epiphytic tropical fern species. Our analyses were based on the hypothesis that there would be optimal concentrations of the leaf elements distinct to each fern lifeform because of their optimal adaptation and ecological traits as part of maximizing fitness in their respective growth environments. As such, we addressed 3 questions, i) Are there differences in the leaf stoichiometric profile between terrestrial and epiphytic fern species? ii) Which element has a limiting effect, based on the allometric relationship, in the species life form? and iii) Do differences in the leaf element concentrations explain the ecological adaptations between the lifeforms and phylogeny?

Materials And Methods

This study considered 20 fern species belonging to 12 families and 16 genera (Table S1). The species were collected in 3 localities of mixed dipterocarp forest within Brunei Darussalam: Bukit Teraja Forest Reserve (4°18'N, 114°26'E), Kuala Belalong Field Studies Centre (4°32'N, 115°09'E) and Bukit Shahbandar Forest Recreation Park (4°57'N, 114°51'E). The climate in Brunei Darussalam is categorized as tropical equatorial with a mean annual temperature of 27.9°C ranging from 23.8°C – 32.1°C under a humidity of approximately 82% and mean annual rainfall of c. 2722 mm throughout the year (Islam et al. 2019). The first 2 sites were primary forest with minimum or no direct human disturbance, therefore we can consider the species as being in their natural ecological niche. The third site (Bukit Shahbandar), where only the species *Platyserium coronarium* was sampled, was a disturbed forest with the individuals at the forest margin. However, considering the ecology of the species as an epiphyte exposed to full sun throughout the day, we were confident that there was little alteration and that it did not compromise the species physiology. Moreover, the leaves collected were from mature large individuals. For each species, we collected 5 leaves from 5 individuals to give a total of 25 leaves per species. In 3 species, we had only 4 individuals, *Schizaea dichotoma*, *Asplenium tenerum* and *Lindsaea borneensis*. Only mature leaves were chosen with minimal to no damage and no sign of senescence. The nutritional status of the epiphytic species can rely on the host tree. However, we did not assess the trees where the epiphytes were collected. The fresh leaf samples were placed in sealed plastic bags and later transported, within 4 hours, to the laboratory of the University of Brunei Darussalam. The leaf samples were washed with distilled water prior to oven-drying at 60°C for 24h. The dried leaf samples were milled using a ball mill (Retsch MM400) before proceeding to the chemical analysis. The terrestrial species were collected from the forest floor, whereas the epiphytic species were sampled from the tree trunks belonging to different tree species and rock surfaces in the case of lithophytic *Dipteris lobbiana*. The lithophytic species was considered to be terrestrial due to the relative similarity in growth habitat to the terrestrial species (Zotz 2016). Following the fern classification, the species were classified as either polypods or non-polypods, totaling 12 and 8 species respectively (Smith et al. 2006; Table S1).

Chemical analysis

Total leaf Nitrogen (N) and Phosphorus (P)

The leaf element analysis for both the total N and total P was conducted following a modified procedure from (Allen et al. 1989) in the user manual for the FIA star 5000. Leaf samples of 0.1g were digested using sulfuric acid and a kjeldahl tablet (CQ-AA18 Thompson and Capper Ltd. Batch 140052) for 2 hours using a block digester at 360°C (BD-46, Lachat instruments, Colorado, USA). The acid-digested solutions were then cooled, filtered with filter paper (Sartorius grade 393), and diluted by adding 50 ml of distilled water in a 50 ml volumetric flask. The leaf N and P concentrations were determined colorimetrically using Flow Injection Auto-analyzers (FIA star 5000, Höganäs, Sweden). The concentration values obtained from the FIA were used to calculate the total leaf N and P concentrations.

Total leaf Potassium (K), Calcium (Ca) and Magnesium (Mg)

Leaf samples of 0.2g were digested using a mixture of acid reagents (4.8% H_2SO_4 and H_2O_2) and a LiSO_4 catalyst for 2 hours using a block digester at 360°C (BD-46, Lachat instruments, Colorado, USA; Allen et al., 1989). The mixture contents were then filtered with filter paper (Sartorius grade 393) and diluted by adding 50 ml distilled water in a 50 ml volumetric flask. The total leaf K, Ca and Mg were measured using atomic absorption spectrophotometry (Thermo Scientific ICE 3000) after diluting the acid-digested samples with LaCl_3 for K, Ca and Mg (acid: LaCl_3 in the ratio of 1:1).

Statistical analysis

All element concentrations and ratios were calculated on the basis of mass (mg g^{-1}). We assessed the leaf element concentrations between terrestrial and epiphytic fern species as well as between polypod and non-polypod fern species at a 5% significance level. Prior to the analysis, all of the data was checked for homogeneity of variance and normality using the Levene and Shapiro-wilk tests respectively. Assumptions for normality were violated. However, we proceeded to conduct the analyses using the ANOVA test as it is robust in relation to violations of the normality assumption (Blanca et al. 2017). The data that violates the homogeneity of variance assumption was analyzed using the adjusted Welch-ANOVA test. Subsequently, the pairwise correlations between each leaf element in terrestrial and epiphytic species were analyzed by Spearman correlation. Finally, the association between the different leaf element concentrations with the categories of species' ecological traits and the phylogeny classification were performed using principal component analysis (PCA) using $\log_{10}$ -transformed values. The statistical analyses were performed using RStudio Team (2020).

Results

The leaf element concentrations varied across the species (Table S2; Fig. S1). The magnitude of the variations among all of the studied species considered ranged, according to N (10-fold) P (2-fold), K (7-fold), Ca (18-fold), and Mg (13-fold). The variations in the leaf element concentrations between terrestrial and epiphytic species were significantly different for N, P, K, and Ca while no significant difference was detected for Mg. The epiphytic species had a lower leaf N concentration but a higher P, K, and Ca concentration compared to the terrestrial species (Fig. 1). The concentration of leaf Mg between the two lifeforms was similar (2.30 vs 2.40 mg g^{-1} for terrestrial and epiphytic respectively). The first axis of the PCA explained 41.5% of the variation in leaf element concentrations, which corresponds to the K, Ca and Mg elements. The positive side of the first axis loaded the epiphytic species together with the majority of terrestrial species. The second axis of the PCA explained 26.3% of the variation, representing the N and P elements. However, no clear pattern was observed between the two lifeforms (Fig. S2).

The concentrations of the leaf element ratios between the two lifeforms, with the exception of P:K and P:Mg, were all significantly different (Table 1). The terrestrial species constantly had higher values than

the epiphytes. The pairwise correlations among the concentrations of N, P, K, Ca and Mg exhibited significant relationships within the terrestrial and epiphytic species (Fig. 2). However, the epiphytic species had four unique correlations which was absent in the terrestrial species and three of them correlated with the availability of phosphorous.

Table 1

Probability value (P) testing between terrestrial and epiphytic fern species regarding the variations in the foliar element ratio of nitrogen: phosphorus (N:P); potassium (N:K); calcium (N:Ca); magnesium (N:Mg) and phosphorus: potassium (P:K); calcium (P:Ca); magnesium (P:Mg). The mean ($\pm$ SE) foliar element concentrations (mg g^{-1} dry mass) and the F values compared between terrestrial and epiphytic fern species are also presented. The P values in bold suggest significant differences ($P \leq 0.05$).

Leaf element ratio	F	P	Terrestrial mean leaf element concentrations	Epiphytic mean leaf element concentrations
N:P	18.41	< 0.001	13.57 ± 1.42	6.48 ± 0.84
N:K	31.68	< 0.001	18.73 ± 1.83	7.28 ± 0.88
N:Ca	36.96	< 0.001	11.00 ± 1.44	2.10 ± 0.24
N:Mg	11.26	0.001	8.99 ± 1.14	4.78 ± 0.52
P:K	0.13	0.72	1.35 ± 0.07	1.30 ± 0.13
P:Ca	26.37	< 0.001	0.97 ± 0.08	0.44 ± 0.06
P:Mg	1.82	0.18	0.75 ± 0.05	0.90 ± 0.09

The concentrations of the leaf elements between the polypod and non-polypod species resulted in a significant difference only for the K concentration, with the polypods displaying a double magnitude concentration (Table S3). The leaf element ratios showed a significant difference in N:P with nearly a double value for polypods, whereas the significant difference in the value of N:K was higher in non-polypods with a difference of 10 units between the fern groups (Table 2). The ratios of P:K, P:Ca and P:Mg were all significantly different with a higher value in the non-polypods. The first axis of the PCA variation in leaf element concentrations corresponds to the K, Ca and Mg elements, whereas the second axis represents the N and P elements. The ordination analysis does not show a clear cluster between the two groups, however the non-polypod species cover the negative quadrant for first and second axes, showing unique traits that polypod species do not have (Fig. S2b).

Table 2

Probability value (P) testing between polypod and non-polypod fern species regarding the variations in the foliar element ratio of nitrogen: phosphorus (N:P); potassium (N:K); calcium (N:Ca); magnesium (N:Mg) and phosphorus: potassium (P:K); calcium (P:Ca); magnesium (P:Mg). The mean ($\pm$ SE) foliar element concentrations (mg g^{-1} dry mass) and the F values compared between polypod and non-polypod fern species are also presented. The P values in bold suggest significant differences ($P \leq 0.05$).

Leaf element ratio	F	P	Polypod mean leaf element concentrations	Non-polypod mean leaf element concentrations
N:P	8.49	0.005	16.64 ± 2.34	9.08 ± 1.13
N:K	6.00	0.02	14.24 ± 1.63	23.24 ± 3.30
N:Ca	1.18	0.28	7.82 ± 1.07	10.21 ± 1.92
N:Mg	3.13	0.08	9.25 ± 1.49	16.28 ± 3.68
P:K	22.90	< 0.001	1.10 ± 0.07	2.66 ± 0.32
P:Ca	10.77	0.002	0.76 ± 0.07	1.47 ± 0.21
P:Mg	10.29	0.003	0.69 ± 0.05	1.49 ± 0.25

Discussion

The leaf element concentration in tropical terrestrial and epiphytic fern species had a high level of variability in relation to both the lifeform and species (Table S2; Fig. S1). This high variability among species, in relation to lifeform and species evolution, has also been confirmed for tropical ferns (Watkins, Philip and Cardelús, 2007) orchids and bromeliads (Cardelús and Mack, 2010) as well as subtropical species of bryophytes, lichens and spermatophytes (Huang et al., 2019). The discrepancies between the terrestrial and epiphyte species are due to the differences in habitat, where terrestrial species have access to a larger resource pool in the soil floor whereas epiphytic species have to rely on more stochastic sources of nutrients (Zotz and Hietz 2001; Cardelús and Mack 2010; Chen et al. 2019). This also sometimes depends on the host tree (Cardelús and Mack 2010). Among these elements, N and Ca have the greatest difference with the mean difference between terrestrials and epiphytes being 7.8 mg g^{-1} for N and 3.3 mg g^{-1} for Ca. The high variability of the element concentration among the different species and lifeforms shows that certain elements are a limiting factor for some species. The use of an element ratio is important to show the relationship between the important elements and to indicate the contribution of the limiting factor. The N:P ratio in the two lifeforms ($13.57\text{--}6.48 \text{ mg g}^{-1}$) shows that the N-P nutrition status is significantly different between terrestrial and epiphytes tropical ferns. According to the previous studies, the N:P ratio is rather inconsistent with averages ranging from 12.1 ± 10.5 (Zotz and Hietz 2001) to 16.1 ± 5.8 (Zotz 2004). The values of 14 and 16 are considered to be the threshold used to indicate the limitation of the allometric relationship between N and P (Koerselman and Meuleman 1996). In epiphytic species, an N:P ratio > 12 indicates a P-limitation (Wanek & Zotz 2011). In this study, terrestrial ferns with

a value of 13.57 mg g^{-1} can have a limitation of N and P or a co-limitation of both elements; epiphytic fern with a much lower value at 6.48 mg g^{-1} are most certainly under the limitations of both elements in their biological development. The allometric relationship between terrestrial and epiphytic species shows that for terrestrial ferns, there is a mean average of N at 19.2 mg g^{-1} and P at 1.6 mg g^{-1} and a mean average of N at 11.4 mg g^{-1} and P at 1.9 mg g^{-1} for epiphytes. Therefore, the disproportion between the two elements is higher for terrestrial and lower for epiphytic ferns respectively. This is also confirmed by the much stronger statistically significant P values for N (< 0.001) compared to P (0.02) between the terrestrial and epiphytic species.

In contrast, epiphytic ferns exhibit a slightly significant ($P = 0.02$) higher P concentration relative to terrestrial ferns (Fig. 1). This pattern contradicts the studies where the P is scarce in other epiphytic species such as bromeliaceae (Zotz and Richter 2006; Winkler and Zotz 2009), orchidaceae (Zotz 2004), cyanolichens (Benner et al. 2007), ferns (Huang and Lin 2016) and lichens (Benner and Vitousek 2007). Epiphytic plants have evolved mechanisms to cope with this predicament such as the provision of a luxury consumption of P and storing more P in the form of phytin than metabolically required in the case of P scarcity (Winkler and Zotz 2009). Moreover, P is readily resorbed into green leaves from senescing leaves in epiphytic species (Zotz 2004). We can predict that the higher leaf P concentration in epiphytic ferns, relative to their terrestrial counterpart, is related to their ability to store and resorb P in their leaves. The allometric relationship between N and P can be perceived as the plants resorbing more N (or P) when they are N (or P) starved in terms of a state of nutrient scarcity and imbalance (Han et al. 2013) (Table 1). In other words, plants actively resorb more of the limited nutrient. This justifies the P differences between terrestrial and epiphyte ferns. However, the correlation between P and K, Ca, and Mg shows a negative trend which has important metabolic implications for the species (Fig. 2).

The epiphytes had the highest values for K and Ca (Fig. 1) while not significant for Mg. This study shows that the Ca concentration was significantly different between the fern lifeforms, whereby epiphytic ferns maintain a greater Ca concentration than terrestrial ferns. Important to notice that two epiphytic species have an exceptional high concentration of Ca (Fig. S1) whereas the rest are within the interval of the terrestrial species. However, the difference in Ca concentration in epiphytic ferns is double the amount found in terrestrial species (5.70 mg g^{-1} vs 2.36 mg g^{-1}). The precedent study has reported that the Ca concentration in ferns is consistently lower when compared to woody angiosperms (Amatangelo and Vitousek 2008). Similarly, the Ca concentration was higher in terrestrial angiosperm species from sites close to the study area (soil total Ca = 0.15 mg g^{-1}). This has been related to the thicker and more sclerophylleous leaves found in forests with drier climatic conditions, compared with the thinner leaves in forests with more humid climatic conditions (Metali et al. 2015). The epiphytes considered in this study, except for *Asplenium tenerum*, have thick leaf tissues, specifically *Antrophyum callifolium* and *Platyserium coronarium*. The investment in the higher Ca acts as form of structural reinforcement in the cell walls and membrane of thick sclerophylleous leaves (White and Broadley 2003), with elaborate traits used to acquire nutrients in a dry and nutrient poor environment (Watkins and Cardelús 2012). The greater Ca concentration in epiphytic ferns likely relates to their structural requirement in terms of their

cell walls and membrane regarding the sclerophyll adaptation in dry and nutrient poor environments. Secondly, the exchangeable Ca in the soil of mixed dipterocarp forests is very low (0.01 mg g^{-1} ; Metali et al. 2015) which suggests the possibility of epiphytic ferns obtaining Ca from their hosts. Ca acts as an intracellular messenger that transmits signals to detect changes in the environment, triggering the necessary adaptive responses (Ranty et al. 2016). Epiphytic ferns are exposed to frequent changes in the environmental factors, therefore the higher leaf Ca in epiphytic ferns could promote adaptations in a stressful habitat. This was confirmed by the lower ratios of N:Ca and P:Ca used to promote adaptive growth (Table 1).

One of the crucial roles of potassium in terrestrial plants is the maintenance of leaf water content through the regulation of the stomatal aperture (Oddo et al. 2011). Plants retain a higher K concentration and low N:K ratio in their leaves to alleviate the inhibition of growth under water stress (Sardans et al. 2016). In addition, a higher leaf thickness and better water storage capacity has been linked to a higher K concentration (Lin and Yeh 2008). In this study, epiphytic ferns maintain a greater K concentration in their leaves as well as exhibiting a significantly lower N:K ratio compared with terrestrial ferns (Table 1, Fig. 1). Furthermore, the higher leaf K concentration in epiphytic ferns might relate to their ability to efficiently resorb K more than terrestrial ferns (Suriyagoda et al. 2018). Epiphytic bromeliaceae efficiently absorb K and maintain it in their green leaves through the means of foliar trichomes. They retain in their leaves as a form of luxury consumption storage (Winkler and Zotz 2010). In other epiphytes such as lichens and bryophytes, they retain lower K concentrations and a high N:K ratio because they can survive under more extreme conditions (Huang et al. 2019). It is likely that epiphytic species experience frequent and long periods of drought in an epiphytic habitat which promotes the activation of mechanisms to effectively take up K and conserve it in the green leaves through efficient resorption in order to sustain growth under water-stress conditions.

At the phylogenetic level, element concentration showed no great difference with the exception of K (polypod 1.59 mg g^{-1} and non-polypod 0.88 mg g^{-1} ; $P < 0.001$; Table S3). The two clades showed a significant allometric difference regarding the N:P and N:K relationship (Table 2). The older non-polypod ferns, despite having a similar concentration of P, tend to have a much more limited allometric relationship compared with N. At the same time, non-polypods have a consistently higher ratio for K, Ca and Mg, indicating the different metabolic utilization of P compared with the more evolved polypods. The high ratio values of the elements in non-polypod ferns suggests that they have a better capacity to accumulate the elements in high proportions. They could also have a lower metabolic capability which results in a higher ratio of accumulation compared with polypod ferns. From the ordination analysis despite a clear difference between the two groups we can observe that the negative quadrant is represented only by non-polypod therefore they show to have some physiological capability to cope with low level concentration of elements in their leaves.

In conclusion, we investigated the leaf element concentration of tropical ferns and revealed that there are different concentrations between the terrestrial and epiphyte fern species. The Ca concentration in epiphytic species and the potential relation with sclerophylleous leaf ecology and the transpiration aspect

could be used to develop more implications in the understanding of epiphytic species in a tropical habitat. The epiphytic species with a high variability in element concentration and potential luxury consumption have adapted to an environment with a much more variable and severe condition compared to the terrestrial species. Archaic ferns use the elements in different proportions compared with more evolved ferns. This shows that they can have important implications for their ecology as they often occur in restricted habitats with more specific micro-climatic conditions. These results can be used as basis to assess the potential risk to the performance of epiphytic species in forested habitat under different management styles and due to the changing climate. Moreover, despite this range of adaptation to rough conditions, climate change scenario reports (Gómez González et al. 2017) that there will be areas with an increase in drought conditions. This has clearly relevant implications for conservation for species that have a small population size, that contribute in terms of richness and that provide a habitat and symbiosis for other species.

Declarations

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Figures

Figure 1

Leaf element concentrations for a) nitrogen (N), b) phosphorus (P), c) potassium (K) and d) calcium (Ca) between terrestrial and epiphytic ferns. The two bounds of the box are the 25th and 75th percentiles, the two extreme lines (whiskers) are the 10th and 90th percentiles as error bars and the center line is the median at the 50th percentile. Outliers are shown as individual points. For each leaf element, the results from the ANOVA analysis, with the F and P values between terrestrial and epiphytic fern species, are also presented.

Figure 2

Correlations among the leaf element concentrations (N, P, K, Ca and Mg) in terrestrial and epiphytic ferns. Above the diagonal are the scatterplots within the epiphytic fern species and below the diagonal are the scatterplots within the terrestrial fern species. The values in each scatterplot are the Spearman correlation coefficients (R_s), with asterisks indicating the significance level (* $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$), and ns when not significant.

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