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Nutrient content in tissues of *Groenlandia densa*, *Myriophyllum spicatum* and *Zannichellia palustris*: an attempt to understand the intercompartmental relationships in a small stream in the Middle Atlas Mountains of Morocco

by

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Abstract

Research has long focused on the relative importance of leaves and roots as sources of nutrient supply for macrophytes, as well as the function each stream compartment plays in their growth and development. This study aims to expand the debate on aquatic ecology and to better understand the connection between compartments in aquatic systems by highlighting the relationship observed in rivers between nutrients in macrophytes tissues, water, and sediments. We measured the concentrations of P-PO_4, N-NO_3 and N-NH_4 in three different compartments of the Amengous stream in the Middle Atlas of Morocco. *Myriophyllum spicatum* (L.), *Groenlandia densa* (L.) Fourr. and *Zannichellia palustris* (L.) were selected as plant species. Our results show that even if the species coexist in the same habitat, they respond differently to nutrient richness. *G. densa* has a higher nutrient accumulation capacity than *M. spicatum* and *Z. palustris* and prefers the water compartment as a nutrient source. Although *M. spicatum* can accumulate phosphate compounds from water and sediment, ammonium is not its preferred nitrogen source. *Z. palustris* shows a tendency to accumulate nitrogen compounds through the roots, while it prefers the assimilation of phosphorus compounds through the leaves rather than the roots.

Key words: macrophyte, stream, nutrient uptake, intercompartment relationships, autoecology

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1. Introduction

Macrophytes are vitally important to aquatic ecosystems. Depending on the level of submergence in the water, different aquatic forms of macrophytes are distinguished – hydrophytes, amphiphytes and helophytes, which provide habitat for various taxonomic groups such as periphyton, macroinvertebrates, and fish (Carden 2002; Qu et al. 2018). Macrophytes are primary producers that contribute to water chemistry by transferring nutrient compounds between the water column and the sediment. Through the process of photosynthesis, macrophytes integrate the inorganic environment with the biotic environment (Clarke 2002; Haury et al. 2008). Hydrophytes respond to physicochemical changes in hydrosystems (e.g. water level, temperature, salinity, nutrients, turbidity) with high morphological and physiological plasticity, which allows these macrophytes to adapt to the heterogeneity of aquatic environments (Ensminger et al. 2005; Zhu et al. 2015; Zhu et al. 2016).

The bioavailability of nutrients (nitrogen and phosphorus compounds) affects the growth and distribution of macrophyte communities (Cotton et al. 2006; Dong et al. 2014). Thus, the abundance of these compounds in the aquatic environment allows macrophytes to avoid competition and promotes the coexistence of several species (Baattrup-Pedersen et al. 2002; Mebane et al. 2021; Moura Júnior et al. 2019). After being oxidized by microorganisms, nitrogen is directly assimilated by macrophytes in the form of ammonium or nitrate ions. Phosphorus is considered a limiting nutrient in aquatic environments due to its low solubility compared to nitrogen for two reasons: 1) its form, which can be assimilated by macrophytes, is scarce; 2) when passing through the terrestrial ecosystem, it is strongly bound by major soil components and taken up by terrestrial plants (Golterman 1975; Thiébaut 2008).

The response of macrophytes to different concentrations of nitrogen and phosphorus in the aquatic environment makes it possible to distinguish between oligotrophic, mesotrophic, eutrophic, and hypereutrophic communities. Higher specific richness is typically found in oligotrophic and mesotrophic habitats, whereas lower specific richness is found in eutrophic, and hypereutrophic habitats. This view is supported by several studies that have shown that water pollution reduces species richness (Camargo 2018; Steffen 2013). Pollution limits sensitive species, selects resistant species, and can also promote the proliferation of certain species responsible for competition for light and space (Dutartre et al. 2008; Nouri et al. 2022).

Although several studies have shown that nutrient richness in the 'water' compartment of rivers affects the composition and distribution of aquatic plants (Fernández-Aláez et al. 2018; O'Hare et al. 2018; Weekes et al. 2014), the latter can also play an important role in the cycling of nutrients between water and substrate due to their ability to accumulate and/or secrete nutrient concentrations (Gurnell et al. 2006). Nutrient uptake and storage by aquatic plants depends on their type and life form. Free-floating, unrooted plants obtain nutrients exclusively from water, as they do not come into contact with the substrate (Bini et al. 1999; Scheffer et al. 2003), unlike rooted macrophytes, which can access two sources of nutrients (sediment and water). Many studies have revealed that the 'sediment' compartment is the primary source of nutrients for macrophytes, followed by the 'water' compartment (Dutartre et al. 2008).

Studies have been conducted to demonstrate the link between nutrient concentrations in plant tissues and those in river compartments (Carr & Chambers 1998; Korol et al. 2016). Researchers in this field have long discussed the relative importance of leaves and roots as sources of nutrient uptake by rooted macrophytes (Clarke 2002; Li et al. 2018; Robach et al. 1995). Further research is needed to understand the intercompartmental relationship in aquatic systems. Therefore, this study aims to highlight the ability of aquatic species to accumulate nutrients in their tissues, as well as its implications for intercompartmental interactions in lotic waters. We measured the concentrations of three nutrients that are most readily available to aquatic plants ($P\text{-}PO_4$: orthophosphates, $N\text{-}NO_3$: nitrate, and $N\text{-}NH_4$: ammonium) in three different compartments (water, sediment, and macrophytes) of the Amengous stream in the Middle Atlas of Morocco. Three plant species were selected (*Myriophyllum spicatum* (L.), *Groenlandia densa* (L.) Fourr. and *Zannichellia palustris* (L.) that share the same habitat and form a plant association in the Amengous stream. Therefore, they present some spatio-temporal stability in the studied watercourse, which can lead to more reliable results.

Given that most of the research in this field has addressed macrophytes in lakes or those cultured in laboratories (Costa & Henry 2010; De Nardi et al. 2010; Mony et al. 2007; Shilla et al. 2006; Stefanidis & Papastergiadou 2019), and the conditions of these environments are different from those in rivers, and the ecology of macrophytes is reliant on the hydrodynamics of the environment, this study can also be viewed as a precursor to ecophysiological studies of *G. densa*, *M. spicatum* and *Z. palustris* in rivers.

2. Materials and methods

2.1. Study area

The Amengous stream is a tributary of the Fellat River. It originates at an altitude of 2000 m in the Bakrit region of the Middle Atlas in Morocco (Fig. 1). The Department of Water and Forests classifies it as a permanent fishing reserve. Aquatic vegetation is abundant along the banks and covers a large part of the surface area of the watercourse. The riverbed in the upstream reaches is predominantly rocky and calcareous, while sedimentation in the downstream reaches has led to the formation of muddy deposits. Outside the rainy season, the width of the riverbed ranges from 1.5 m to 10 m, and the depth varies from 0.2 m to 0.8 m. The flow velocity generally varies between 0.2 and 0.4 m/s, depending on the nature of the flow facies – lotic or lentic. The lack of riparian vegetation in some sections promotes bank erosion and strong exposure to sunlight. The Amengous stream flows through extensive agricultural land. Excessive water abstraction for irrigation has a substantial impact on the flow of this watercourse, promoting the invasion of hydrophytes.

2.2. Sampling procedure

Sediment, water, and macrophyte sampling was conducted at four sampling sites during the peak of the vegetative season (May and June 2019). The selected plants are *M. spicatum*, *G. densa* and *Z. palustris*. They are widespread in the Amengous stream and form a plant association. At each site, the three investigated species were collected (whole plants) randomly from several stands within a homogeneous hydrological area (with no substantial difference in flow velocity, depth, etc.). Each site was divided into three subzones, one in the center and one on each bank of the watercourse. At least three samples of each macrophyte species were collected within each subzone, for a total of at least nine samples per site. The macrophytes were washed carefully with deionized water to remove epiphytes

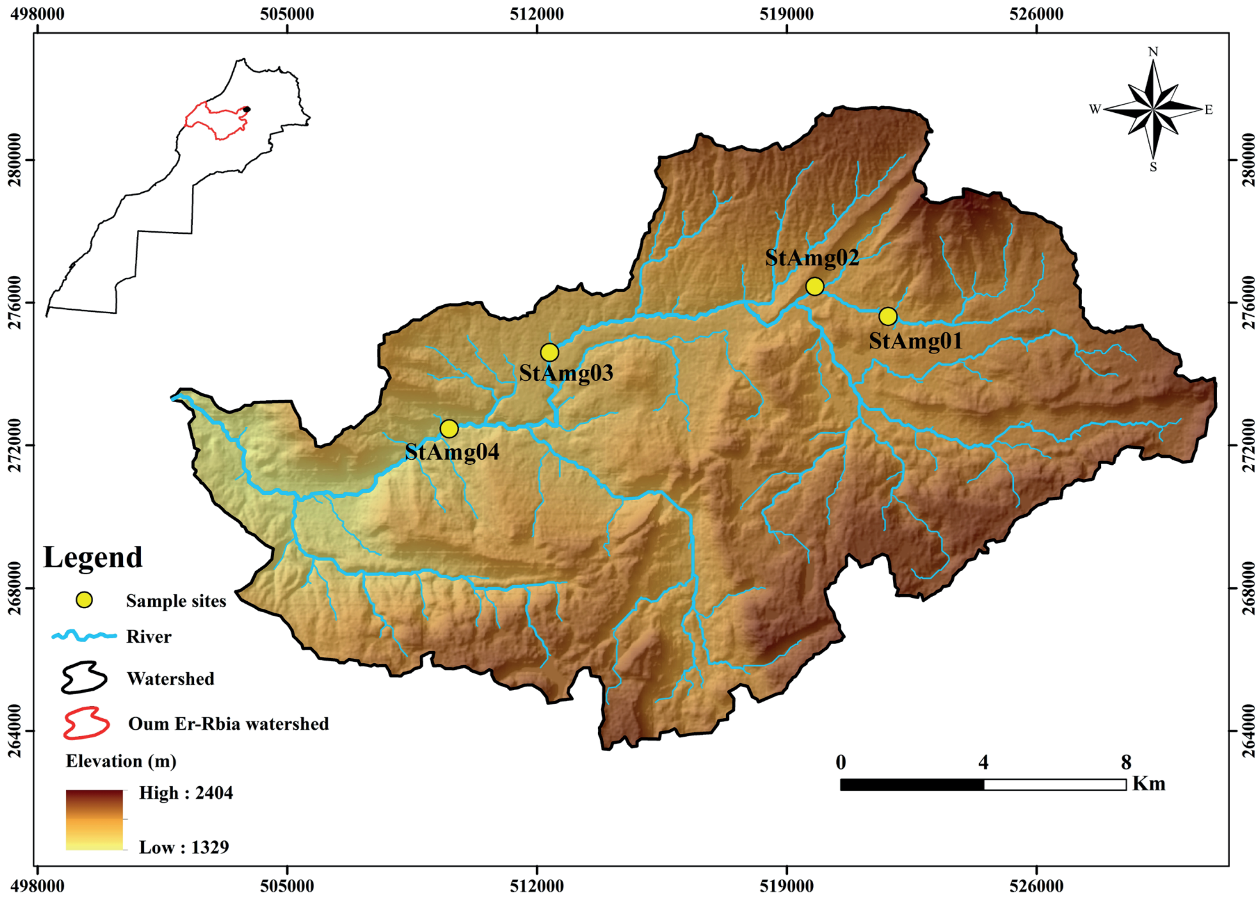

Figure 1

Location of sampling sites in the Amengous stream.

and sediment. They were repeatedly blotted dry with water-absorbing paper. Next, the macrophyte samples were desiccated at 105°C for 30 min and then dried at 60°C to constant weight. The dried samples were ground to a uniform fine powder and stored in sterile plastic flasks.

At each macrophyte sampling site, sediment cores were sampled from the first 10 cm, corresponding to the root layer. Sediment samples were dried at a temperature of 103°C to constant weight, ground and stored in a sterile plastic bag, which was clearly labeled.

Water samples were collected at the same time as sediment and macrophyte samples using clean polyethylene bottles, cooled to a temperature below 4°C in the dark and transported to the laboratory within 12 h to avoid any deterioration problems.

In the laboratory, water samples were analyzed for P-PO$_4$, N-NH$_4$, and N-NO$_3$ concentrations using spectrophotometry (Rodier 2009). Analysis of nutrient content in sediment and plant tissue samples was carried out after acid digestion. N-NH$_4$ concentrations in plant tissues and sediments were determined according to Baethgen and Alley (Baethgen & Alley 1989). P-PO$_4$ concentrations were determined in plant dry matter and sediment by the standard molybdenum blue method after acid digestion (Rodier 2009). N-NO$_3$ concentrations in plant and sediment samples were determined following standard methods detailed in Cataldo et al. (1974).

2.3. Statistical analysis

An analysis of variance (one-way ANOVA) was performed to assess significant spatial differences in nutrient concentrations across the macrophyte species and the two compartments (sediment and water). A linear regression analysis was performed to model the relationship between nutrient content in plant tissues, water and sediment. A preliminary ANOVA and linear regression analysis was performed (Shapiro–Wilk test) to verify the adequacy and normalization of the data.

3. Results

Mean values of nutrient concentrations in macrophyte tissues, water and sediment for all sampling campaigns are presented in Figures 2 and 3.

3.1. Nutrient concentrations in macrophyte tissues

A significant spatial effect on the mean content of orthophosphates (P-PO$_4$), ammonium (N-NH$_4$) and nitrate (N-NO$_3$) in tissues was found for all macrophyte species (ANOVA, $p < 0.001$; Table 1). There were also significant differences in the tissue nutrient content between the analyzed plant species (ANOVA, $p < 0.001$; Fig. 2). *G. densa* showed phosphorus and nitrogen storage capacity, different from *M. spicatum* and *Z. palustris* (Fig. 2, Fig. 3). The average value of P-PO$_4$ in G. *densa* tissues varied between 118 µg g^{-1} (StAmg02) and 226 µg g^{-1} (StAmg03), while the highest values of N-NO$_3$ and N-NH$_4$ concentrations were detected in samples from StAmg03 (1052 µg g^{-1}) and StAmg04 (800 µg g^{-1}) sites, respectively. The concentrations of P-PO$_4$, N-NH$_4$, and N-NO$_3$ in *G. densa* tissues increase at the downstream sites (StAmg03 and StAmg04). *M. spicatum* maintains the same gradient for P-PO$_4$ and N-NO$_3$ concentrations and shows some consistency for N-NH$_4$ concentrations along the sites, with the exception of StAmg03. The tissue P-PO$_4$ concentration for *Z. palustris* was higher than that for *M. spicatum*, while concentrations of N-NO$_3$ and N-NH$_4$ were low compared to *G. densa* and *M. spicatum* (Fig. 3). Figure 2 shows that the lowest concentrations of N-NO$_3$ (114 µg g^{-1}) and N-NH$_4$ (96 µg g^{-1}) were recorded at downstream site StAmg04.

3.2. Nutrient concentrations in sediment

The results show that the average concentrations of P-PO$_4$ and N-NO$_3$ in the sediment compartment show no significant spatial variation (ANOVA, $p > 0.05$; Table 1). Only N-NH$_4$ concentrations vary significantly between the sites, with a minimum average of 312 µg g^{-1} at StAmg04 and a maximum average of 518 µg g^{-1} at StAmg02 (Fig. 2).

Table 1

Summary of the results of ANOVA applied to the spatial variability of nutrient content in sediment, water, and macrophyte species. p – significance level; df – degree of freedom.

	P-PO$_4$			N-NH$_4$			N-NO$_3$		
Groenlandia densa	F-value	df	*p*	F-value	df	*p*	F-value	df	*p*
Myriophyllum spicatum	15.47	3	0.000	116.36	3	0.000	245.92	3	0.000
Zannichellia palustris	17.89	3	0.000	33.29	3	0.000	9.45	3	0.000
Sediment	45.06	3	0.000	315.10	3	0.000	13.51	3	0.000
Water	3.03	3	0.053	21.50	3	0.000	2.52	3	0.087
Groenlandia densa	50.23	3	0.000	59.64	3	0.000	109.62	3	0.000

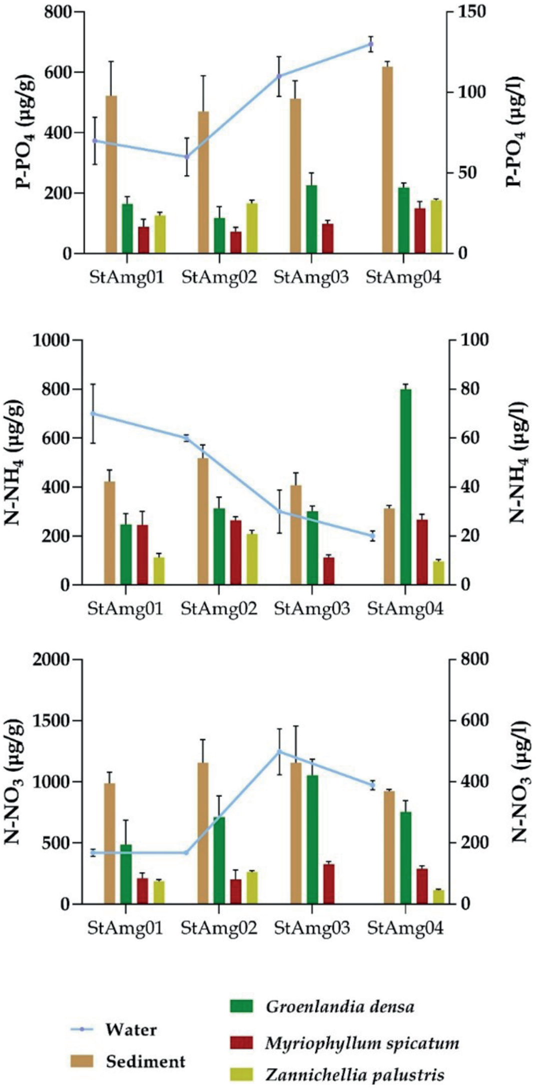

Figure 2

Spatial variation of mean $P\text{-}PO_4$, $N\text{-}NO_3$, and $N\text{-}NH_4$ concentrations in the compartments of the Amengous stream.

3.3. Nutrient concentrations in water

In the water compartment, the average $P\text{-}PO_4$ measurement varies from 70 µg l^{-1} (StAmg01) to 132 µg l^{-1} (StAmg04). Samples from StAmg01 and StAmg02 had low average concentrations of $N\text{-}NO_3$ (172.5 µg l^{-1}), while samples from StAmg03 had a maximum concentration of 498 µg l^{-1}. In contrast to $N\text{-}NH_4$, which progressively decreases downstream, the average concentrations of $P\text{-}PO_4$ and $N\text{-}NO_3$ increase along the upstream–downstream gradient. All of these nutrients showed significant variability among the study sites (ANOVA, $p < 0.001$; Table 1).

3.4. Relationships between nutrient content of water, sediment and aquatic plants

To investigate the relationship between the content of each nutrient and the three stream compartments (plant, water, and sediment), a linear regression was performed (Fig. 4). The results show that the content of $P\text{-}PO_4$ in *G. densa* and *Z. palustris* samples is significantly correlated with their content in water, but not in sediment. In the case of *M. spicatum*, $P\text{-}PO_4$ concentrations show a significant correlation with concentrations in water and sediment. In the case of *G. densa* samples, $N\text{-}NH_4$ content is negatively correlated with both compartments (water and sediment), whereas it is positively correlated with the sediment compartment in the case of *Z. palustris* samples. However, it shows no significant correlation with the two compartments (water and sediment) for *M. spicatum* samples. Nitrate ($N\text{-}NO_3$) concentrations in *G. densa* and *M. spicatum* show only a significant positive correlation with water. On the other hand, nitrate ($N\text{-}NO_3$) concentrations in *Z. palustris* show a significant positive correlation with sediment and a significant negative correlation with water. $P\text{-}PO_4$ and $N\text{-}NH_4$ content in water is positively correlated with $P\text{-}PO_4$ and $N\text{-}NH_4$ content in the sediment compartment (Fig. 4).

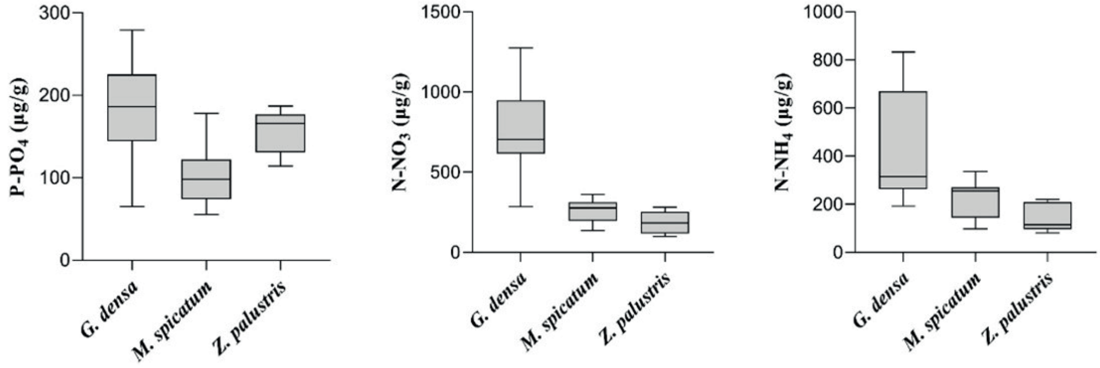

Figure 3

Mean concentrations of $P\text{-}PO_4$, $N\text{-}NO_3$, and $N\text{-}NH_4$ in macrophyte tissues.

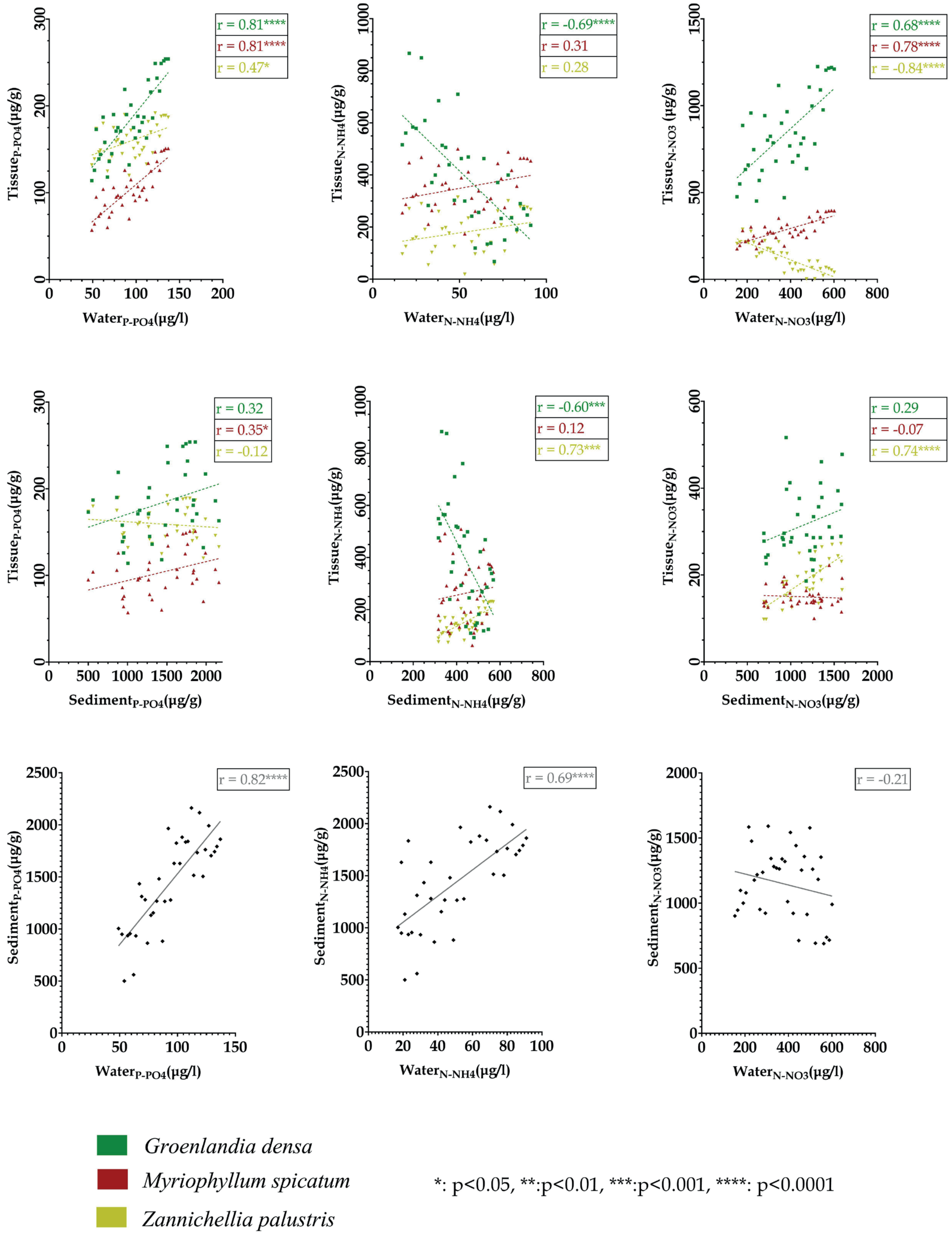

Figure 4

Scatterplot showing the regression of nutrient content in water, sediment, and plant tissues.

4. Discussion

Nutrient availability is one of the key elements in the development of aquatic plants. Although recent studies have shown that the abundance of nutrients in water affects the composition and distribution of aquatic plants, other studies have shown that the substrate is the primary source of nutrients for these plants. According to some studies, *G. densa, M. spicatum and Z. palustris* serve as bioindicators of mesotrophic to eutrophic environments (Muller et al. 1997; Thiébaut 2008), and the specificity of their association in the Amengous stream provides an opportunity to extend previous ecological studies conducted in the same watercourse to better understand the interactions between aquatic plants and their physical environments (Nouri et al. 2022). This opportunity is contrasted with the paucity of research on the ecophysiological responses of each of these species to trophic level changes in rivers, which limits our ability to compare our results with those in the available literature.

Although the linear regression results alone are insufficient to determine which compartment serves as the ideal source for the studied macrophytes, they clearly reflect the complexity of understanding the interactions in aquatic ecosystems and the dynamics of nutrients across different compartments. The above-mentioned results show that *G. densa* tends to accumulate orthophosphates to a greater extend than *M. spicatum* and *Z. palustris*. In addition, *G. densa* is strongly correlated with this nutrient in the water compartment but does not bind to it in the sediment. Although some authors have proposed that the sediment compartment may be the primary source of phosphorus for plants with large root systems (Denny 1972), others have shown that aquatic plants in nutrient-rich streams can compensate for the limited availability of SRP in the surrounding water or sediment through foliar absorption (Madsen & Cedergreen 2002). In terms of anatomy, *G. densa* has a large absorption surface due to the expanded form of its leaves. In addition, G. *densa* has a poorly developed root system, and some of its shoots submerged in the bottom organic sediments lack leaves. The water compartment may play a critical role in the availability and transfer of phosphorus in its dissolved form ($P\text{-}PO_4$), which aquatic plants can absorb directly and rapidly (Benkaddour 2018; Thiebaut & Muller 2003).

Even though *M. spicatum* coexists with *G. densa* in the Amengous stream, it responds differently to the abundance of nutrients in the environment. It has a low tendency to accumulate orthophosphates ($P\text{-}PO_4$) compared to the two other species, *G. densa* and *Z. palustris*. *M. spicatum* shows a significant positive correlation with the two compartments of the watercourse (water and sediment), which can be explained by foliar and root uptake of phosphates, as well as its high competitiveness compared to other aquatic plants (Angelstein et al. 2009; Valley & Newman 1998). A Chinese study of 21 aquatic plants showed that *M. spicatum* can absorb nutrients via roots and shoots, which helps it survive and allows it to be invasive (Huang et al. 2018).

The correlation of the two forms of nitrogen ($N\text{-}NO_3$ et $N\text{-}NH_4$) in different compartments shows that *M. spicatum* does not tend to accumulate ammonium from sediment and/or water, instead preferring nitrates as a nitrogen source. According to the literature, *M. spicatum* is an aquatic plant that is sensitive to ammonium, which is considered a stressor for this species (Tan et al. 2019). *G. densa,* on the other hand, accumulates both forms of nitrogen to a greater extent than *M. spicatum* and *Z. palustris*. The significant negative correlation that *G. densa* shows with ammonium content in the two stream compartments can be explained either by the strong nitrate-to-ammonium reduction in this species, or by a competitive strategy known in some macrophytes that allows *G. densa* to efficiently accumulate nutrients for reuse during periods of depletion (Thiébaut 2005; Xing et al. 2016).

This study shows that in rivers where fluctuations in resources (nutrients) are significant, submerged macrophytes behave differently when assimilating and storing nutrients such as phosphorus, nitrates, and ammonium. Even though *G. densa*, *M. spicatum,* and *Z. palustris* share the same habitat and environmental conditions, they do not have the same capacity to obtain nitrogen and phosphate compounds from water or sediment compartments. *G. densa* exhibited high accumulation of nitrogen and phosphate compounds, making it the most suitable species for removing large amounts of elements responsible for the phenomenon of eutrophication in aquatic ecosystems. This finding supports previous research that showed the tolerance and capacity of *G. densa* to accumulate other substances, such as heavy metals (Podlasińska et al. 2021).

5. Conclusions

This work explored the content of nutrients such as nitrogen, phosphate and ammonium in various compartments of aquatic ecosystems. We investigated the complex interactions between aquatic plant tissues, water and sediment, with a particular focus on nutrients. Species respond differently to nutrient richness, even when they coexist in the same habitat. Given that *G. densa* prefers to obtain nutrients in the water compartment, it may accumulate more nutrients than *M. spicatum* and *Z. palustris*. Ammonium is not a preferred source of nitrogen for *M. spicatum*, despite the fact that it can absorb nutrients such as phosphate compounds from sediment and water. *Z. palustris* tends to assimilate nitrogen compounds through its roots and phosphorus compounds through its leaves. The data obtained indicate the importance of aquatic plants as nutrient regulators in aquatic ecosystems, as well as the mechanisms of nutrient transport and recycling between compartments. These data need to be complemented by more comprehensive research on nutrient kinetics in aquatic ecosystems. The current findings could be a first step toward improved management of aquatic ecosystems and minimizing the negative consequences of pollution and eutrophication.

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