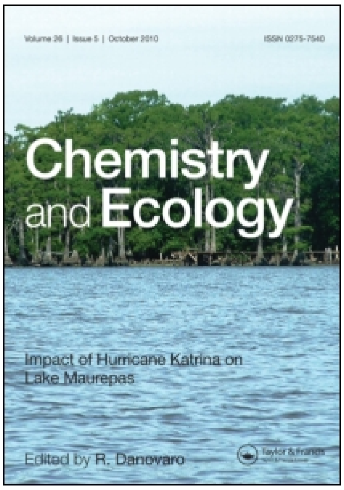

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Tissue nutrient concentrations in aquatic macrophytes: comparison across biophysical zones, surface water habitats and plant life forms

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RESEARCH ARTICLE

Tissue nutrient concentrations in aquatic macrophytes: comparison across biophysical zones, surface water habitats and plant life forms

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Aquatic plant tissue (nitrogen) N and phosphorus (P) concentrations, together with the N:P ratio in general, respond poorly to ambient nutrient supply. The variability in plant tissue nutrient concentrations appears to be highly conditioned by taxonomic (mostly species) effects. The significant role that other attributes of the surrounding environment may have in modifying the degree of taxonomic dependence on plant nutrient concentration is yet to be tested with a broader characterisation of plant life forms (bryophytes, helophytes, hydrophytes), so as to investigate implications for ecosystem processes. Plant samples (378) were collected across 65 sites spanning a wide range of aquatic habitats (lotic and lentic) and biophysical zones (flood-plain, glacial terraces, mountains) located in NE Scotland. Significant differences in plant tissues N, P and the N:P were found after grouping sampling sites by either habitat or biophysical zones; the latter even after removing the largest taxonomic effect. The range in plant tissue N and P was relatively wide within habitats and zones, reflecting the high species diversity of the studied area. As a group, bryophytes had smaller N and P concentrations, and consequently wider biomass C:N and C:P ratios, a situation which may impose constraints on the flow of energy through food-webs of the mountain and bog areas where they dominate.

Keywords: ecoregion; plant stoichiometry; carbon; nitrogen; phosphorus; potassium; aquatic habitats

1. Introduction

In spite of the apparent intimate link that is likely to exist between aquatic plants and the surrounding water/sediment environment, a poor correlation often exists between aquatic plant tissue N and P concentrations and the ambient nutrient supply [1]. This apparent discrepancy may result (apart from methodological issues) from some combination of a lack of elemental (C, N, P) plasticity [2]; taxonomy and/or plant life form differences in nutrient acquisition [3–4]; or other physico-chemical attributes of the wider aquatic environment, such as pH, $p\mathrm{CO}_2$, and current velocity [5–7]. Even when the correlation (or regression) is strong (high r – or r^2 – and highly significant *P* value [8,9]), the tissue nutrient concentration response to nutrient enrichment is generally weak (as indicated by the slope of the regression curve), and above the threshold concentration where growth rate limitation would occur [10,11].

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Hence, there have been various comparative studies where plant tissue nutrient metrics (e.g. N, P and N:P) have been compared using various ways of stratifying the sampling programme in order to reduce variability within the sampled population. These include biotic factors, such as plant life forms, and more physically related factors, such as bio-geographical zones and habitats [12–14]. Separating the role of individual factors can be extremely difficult, as emphasised by the lack of studies that attempt to achieve this separation, particularly in aquatic habitats. Confounding effects occur between purely physical aspects of a particular zone and the likely chemistry. An example of this being that upland streams tend to be flashy (high physical disturbance) while also having low nutrient concentrations, compared to lowland tributaries that are hydrologically more damped and have higher nutrient concentrations. Resource acquisition strategies of the primary biomass would be expected to vary between these differing environments.

While aquatic plant tissue nutrient (C, N, P) concentrations may not be useful as a direct bioindicator of change in water column and sediment N and P concentrations, they provide robust stoichiometric data for studies on ecosystem metabolism and nutrient cycling, particularly when the variability in C, N, P plant tissue concentrations are decomposed into life forms (helophytes, hydrophytes, bryophytes) [11].

Using the River Spey basin where water chemistry varies markedly between surface water habitats and biophysical zones [15], it was hypothesised that surface water habitats and biophysical zones harboured plant communities with different tissue C, N, P concentrations and C:N:P ratios, independently of aquatic plant life forms (helophytes, hydrophytes, bryophytes) and indicators of inorganic N and P supply. Since the lack of nutrient limitation was a major assumption, it was further investigated for the three life forms considered in this study, using N, P, K plant tissue concentrations and their stoichiometric ratios.

2. Material and methods

2.1. *River Spey catchment*

The River Spey rises from the Monadhliath Mountains and flows 157 km north-eastwards to the North Sea. The catchment area (circa 3000 km^2) is underlain by crystalline rocks (schists and gneisses) dating from the Precambrian and Cambrian periods and intruded in places by granitic rocks. Much of the current landscape reflects the action of successive glaciations. The River Spey basin is an area of great conservation value due to its large populations of Atlantic salmon (*Salmo salar* L.), sea lamprey (*Petromyzon marinus* L.), otter (*Lutra lutra* L.) and freshwater pearl mussels (*Margaritifera margaritifera* L.). Further information and maps can be found in previous studies [15–17].

2.2. *Sampling area*

The study area, a 10 × 10 km grid square (Long 3°55'W, lat 57°07'N), has an altitude range between 220 and 980 m. The landscape is characterised by contrasting geology, soil and land cover. The SW–NE floodplain axis of the River Spey separates the Monadhliath Mountains (NW) from the Cairngorm Mountains (SE). The sampling design was a stratified random survey. The 10 × 10 km grid square was divided into 25 tetrads from which a representative number of sites were sampled [15]. Sampling sites covered a wide range of surface water bodies (large rivers, small streams, pools, backwaters and ditches, lochans, lochs and bogs) and were situated in different biophysical zones based on solid geology, soils and land cover (including floodplain, glacial terraces, and mountain areas). The spatial heterogeneity of the surface water chemistry was previously investigated and significant differences were identified among biophysical zones and among surface water habitats [15]. Bryophytes dominate the mountain and piedmont regions, and vascular plants the fluvio-glacial terraces and floodplain water bodies [11].

2.3. *Collection and analysis of samples*

The most frequent/abundant species (3–12 plant species per site) were collected during July and August 2003. Three to 10 samples were collected from different individuals and pooled together for each species of vascular plant surveyed within a site. Samples from emergent species were only collected when growing within the water body. The anchoring system, degenerating leaves and inflorescences were removed, except for the isoetids where rooting material was included. The isoetids have generally, at least during the Summer, the same tissue nutrient (N, P) concentration in their stem/root and foliar tissue [18–20]. All plant material was gently cleaned using nutrient poor water before analysis. Total C and N were determined by combustion of dried, milled samples using a CHN Thermo Finnigan elemental analyser (FlashEA 1112 series). Total P and K were determined by inductively coupled plasma – optical emission spectroscopy after 30 minutes digestion in 50% nitric acid at 120°C. The detection limits were 0.03 and 0.02 % dry weight for N and C respectively, and 6 mg and 10 mg kg^{-1} dry weight for P and K, respectively.

2.4. *Data processing*

The list of taxa was divided into three life forms: bryophytes (e.g. *Fontinalis*, *Sphagnum*), helophytes (e.g. *Carex*, *Menyanthes*, *Equisetum*) and hydrophytes made of floating and submerged forms (e.g. *Elodea*, *Nymphaea*, *Potamogeton*, *Litorella*) – (see list of taxa in [11]). Data were retained for statistical analysis when sites had at least three plant samples (three species). The resulting dataset was made up of 378 plant samples across 65 sites. The dataset consisted of 268 vascular plants, 105 bryophytes and 5 charophytes.

Individual sampling sites were grouped and statistically analysed alternatively on the basis of either their surface water habitat or their surrounding biophysical zone. Flowing water habitats consisted of two groups, the large rivers Feshie and Spey (catchment area $\approx$ 200–1000 km^2) and the remaining small streams (catchment area $\approx$ 0.08–21 km^2). Standing waters were sub-divided into three habitats after consideration of their area and depth relationships. The pool habitat (area $<$10,000 m^2, depth $<$1 m) comprised ditches, isolated pools and river backwaters. Lochans are shallow lakes with an area between 5,000 and 80,000 m^2 and depth $<$2 m, while lochs are larger ($>$40,000 m^2) and deeper ($>$2 m) lakes. Finally, two sites were classified as bogs because of the abundance of *Sphagnum* moss.

Standard one-way analyses of variance (Type III sum of squares) were run to test whether the average N, P concentrations and N:P ratios in plant tissue were all equal among surface water habitats and among biophysical zones. When rejected ($\alpha = 0.05$), the *post hoc* Tukey multiple comparison test, modified for unbalanced design, was performed to identify significant differences between groups [21]. Linear multiple regressions were run with Canoco 4.5 [22] to partial out the effects of habitats, zones and plant life forms on plant tissue characteristics.

2.5. *Nutrient limitation*

Concentrations of ammonium-N, nitrate-N and soluble reactive phosphorus of the column water were extremely small, with 50% of samples falling below 8, 5 and 1 $\mu\mathrm{g}\,\mathrm{l}^{-1}$ respectively during Spring and Summer [15].

Hydrophyte N and P critical nutrient concentrations for species 95% maximum growth rate [23,24] were used as an indicator of nutrient limitation [11]. Hydrophyte tissue nutrient concentrations suggested that N, N + P and P limitation was likely in only 2(0–30)%, 5(0–9)% and 15(0–45)%, respectively, of the plant samples collected. Helophyte biomass production might have been limited by N in only 9% and P in 0–18 % of the samples, as indicated by N:P vegetation critical ratios <10 and >16–20, respectively, combined with the vegetation critical plant N concentration of 1.5 % DW and P 0.05–0.1 % DW [14,25]. Limitation by K in helophytes was unlikely with vegetation concentration K$>$0.8% DW in 99% of samples [26] and vegetation critical ratios N:K$<$2.1 and K:P$>$3.4 in 96% and 100% of the samples, respectively [27]. Bryophytes were likely to be saturated in N with 97% of samples exceeding 1% DW [28].

While there is much debate about the usefulness and validity of these critical N, P, K concentrations and N:P:K ratios [14], the variability in N and P concentrations in wild freshwater aquatic macrophytes of the River Spey basin was in fact poorly related to water and sediment nutrient supply, and resulted essentially from taxonomic (mostly species) effects [11]. The assumption of lack of nutrient limitation is therefore acceptable.

3. Results

There were some significant ($p < 0.001$) differences in plant nutrient tissue characteristics across biophysical zones and habitats. Moderate differences were obvious between biophysical zones (Figure 1). Nitrogen contents were generally lower in the mountain areas (Cairngorms, Monadhliath). The south-east glacial terrace had lower N plant concentrations than the north-west glacial terrace. Plant P concentrations were highest in the floodplain and north-west glacial terraces, and lowest in the mountains (Cairngorms, Monadhliath) and main rivers (Spey, Feshie). The floodplains and glacial terraces had the lowest plant N:P ratio (Figure 1).

Differences among habitats, however, were very weak (Figure 2). Aquatic macrophytes growing within bogs had lower N concentrations. Plant nutrient characteristics showed no marked differences in flowing *versus* standing water, or with the size of surface water systems (Figure 2).

The variability (quartile range) in N and P plant tissue concentrations within habitats or biophysical zones was generally similar, except in the mountains where it tended to be narrower (Figures 1 and 2).

Large differences were observed among the three plant life forms (Figure 3). Bryophytes had lower C, N, P concentrations and higher C:P ratio than helophytes and hydrophytes. The C:N ratio of bryophytes and helophytes was not significantly different. Hydrophytes had higher N, P tissue concentrations and lower C:N:P ratios than helophytes. The largest differences observed in plant tissue elemental composition were with P.

When combined, plant life forms, biophysical zones and surface water habitats explained 43, 40 and 33% of the variability in plant N, P and N:P, respectively (Figure 4). Plant life forms had the best predictive power over biophysical zones and surface water habitats. While some of this explained variance was confounded, the unique effects of biophysical zones for N, P and N:P and surface water habitats for N were still significant (Figure 4).

4. Discussion

While the distribution of bryophytes and vascular plants (helophytes, hydrophytes) is rather disjunctive [11,29], it was still possible to separate some (not all) water habitat and biogeographic zone effects on plant N, P and N:P, respectively, from the effect of plant life forms. There was

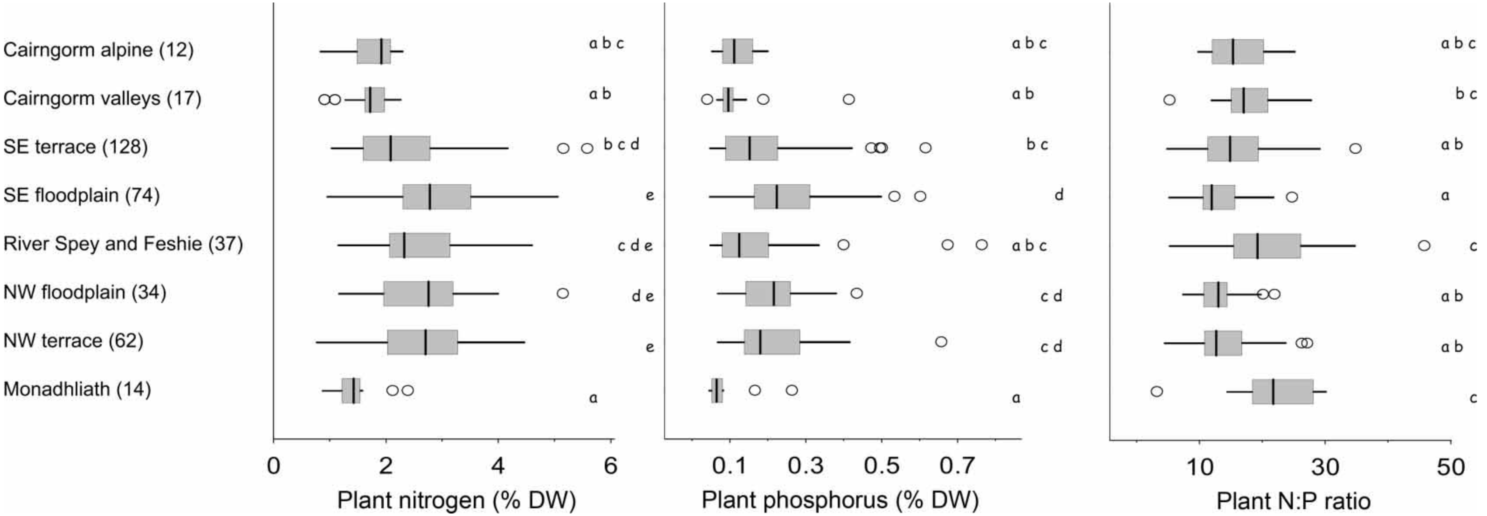

Figure 1. Variability in plant tissue N, P concentrations and N:P ratio across biophysical zones. The boxes represent the quartiles and the median; the whiskers represent the range, with outliers (open circle) when individual data points lay beyond 1.5 times the quartile range. Significant differences are indicated by letters, after running a one-way ANOVA with normal (type III) sums of squares and *post hoc* Tukey multiple comparison test, modified for unbalanced design ($\alpha = 0.05$).

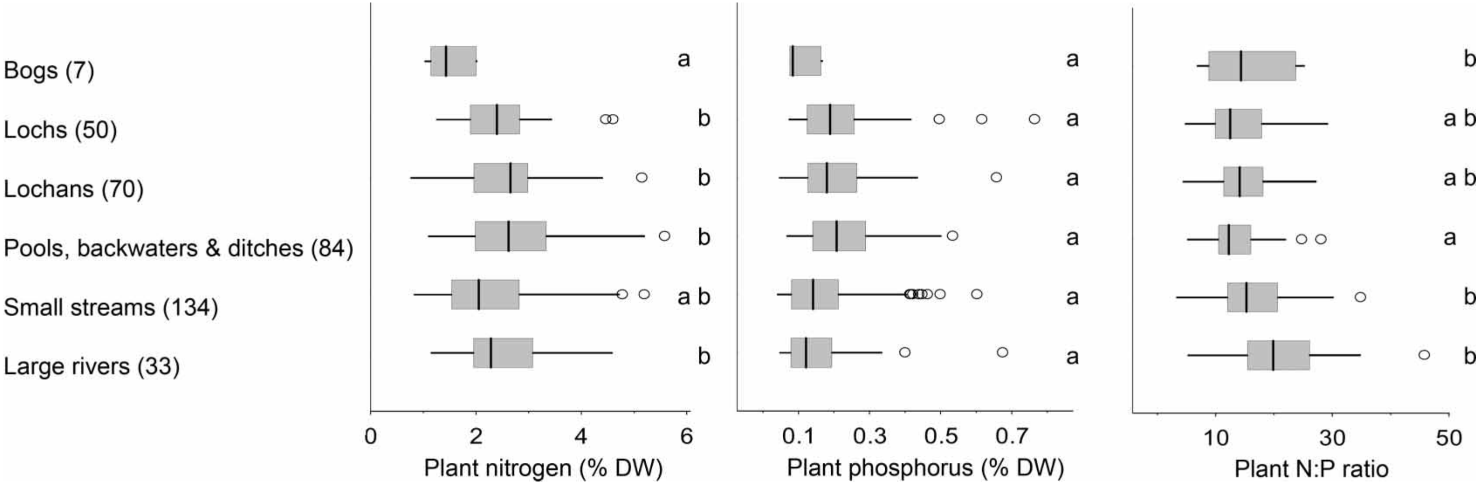

Figure 2. Variability in plant tissue N, P concentrations and N:P ratio across habitats. The boxes represent the quartiles and the median; the whiskers represent the range, with outliers (open circle) when individual data points lay beyond 1.5 times the quartile range. Significant differences are indicated by letters, after running a one-way ANOVA with normal (type III) sums of squares and *post hoc* Tukey multiple comparison test, modified for unbalanced design ($\alpha = 0.05$).

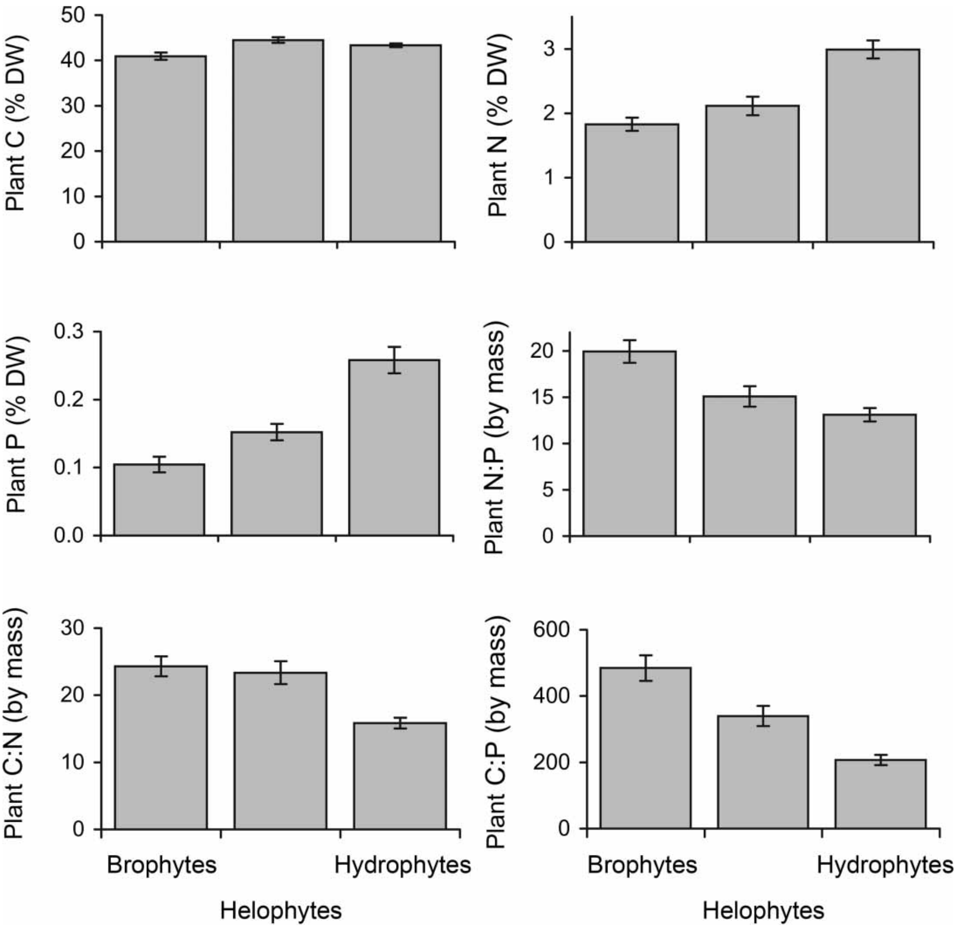

Figure 3. Average (±95% confidence interval of the mean) plant tissue C, N, P concentrations and C:N:P ratios across plant life forms.

overall very little difference between habitats (Figure 2), and more surprisingly perhaps, between running water systems and standing waters, where the renewal of the water (hence nutrient supply) and biological activity (as indicated by oxygen and silica deficiency in pools, backwaters, ditches and lochans; [15]) differed markedly.

In other studies, significant differences have been reported among habitats such as lotic *versus* lentic [30], contrasting sediment composition [31], or stream water velocity [7] for some species only. The streams of the Cairngorm Mountains had SRP concentrations below the analytical detection limit ($<1\,\mu g\,P\,l^{-1}$) but higher Summer NO_3 concentration in the alpine zone ($50\,\mu g\,N\,l^{-1}$) than in the valleys ($<5\,\mu g\,N\,l^{-1}$). This 10 times difference in N supply was not reflected in the plant tissue signature (Figure 1). The lower plant N concentration in bogs (Figure 2) may partly be due to the low pH [5], but the lower plant N concentration in the biophysical zones dominated by bryophytes suggests that it was more likely an effect of plant life form (Figure 1).

This is re-enforced by examining the similarity in plant nutrient signature among the two main mountain areas (Monadhliath and Cairngorms), both mostly colonised by bryophytes, but with contrasting surface water properties (acid neutralising capacity, pH; [15]). This was confirmed by the multiple regression analyses, where most of the variance in plant nutrient signature was explained by the unique effect of plant life forms partly confounded with a biophysical zone effect.

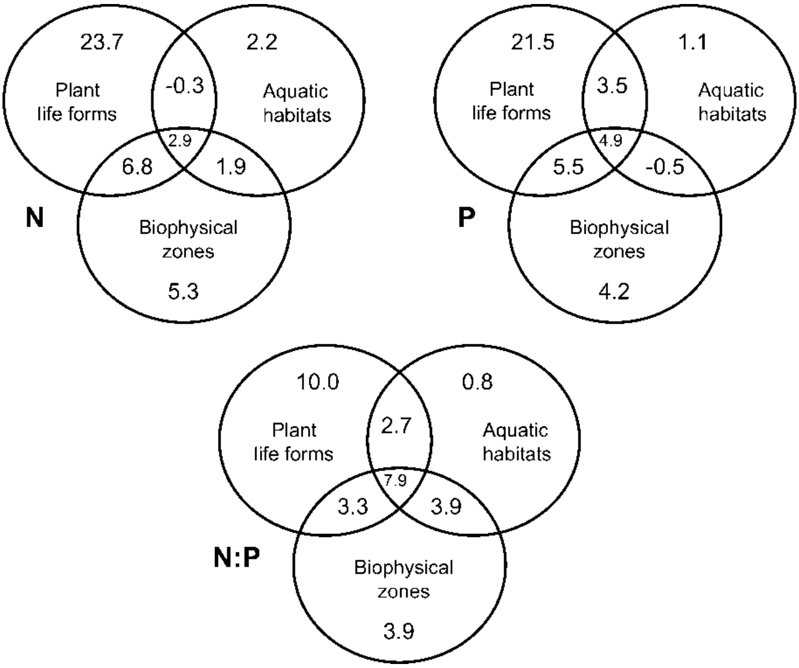

Figure 4. Variance partitioning (expressed as percentage of variance explained) using linear multiple regressions of the effects of aquatic plant life forms, habitats and biophysical zones on N, P and N:P plant tissue stoichiometry.

Despite the very coarsely defined grouping into plant life forms, this still explained a relatively large amount of the variance in plant N and P concentrations (30–35%), as noticed previously [11,32]. There were no additional effects of biophysical zones and surface water habitats, however, on N and P plant tissue concentration, after taking into account the external nutrient supply and species identity [11]. This was expected because species tend to grow in different habitats and biophysical zones [29,33] and therefore the effects were confounded. High species diversity and plant life forms within surface water habitats and biophysical zones will likely reflect functional diversity (the wide range of plant tissue nutrient content available to consumers and decomposers).

The lower N and P concentration in plant tissue in the extreme mountain and bog environments may put additional constraints on the fluxes of energy in the food web [34]. Consumers of plant biomass will have to ingest and digest twice the volume of fresh plant tissue to get an equivalent quantity of N and P compared to those present in floodplain and glacial terrace habitats, and this will be even worse because of lower biomass yields in the mountains (see Figure 2 in [11]). Decomposition processes may also be more driven by fungi than bacteria, especially where pH is low (Cairngorm Mountains, bogs). Changes in nutrient supply may also alter ecosystem processes and food web dynamics in small streams [35]. So far, however, because of the small concentrations involved (e.g. 50% of SRP samples falling below 1 $\mu g\,L^{-1}$ during Winter, Spring and Summer, and below 6 $\mu g\,l^{-1}$ during Autumn), these systems will not be protected by current water quality standards (e.g. SRP <20 and <40 $\mu g\,l^{-1}$ for the implementation of the Water Framework Directive (2000/60/EC) high and good environmental standards respectively in rivers with low alkalinity (<1 meq l^{-1}) and above 80 m altitude [15,36]).

Bryophytes were the first plant to colonise the land 480 million years ago [37] and probably evolved in environments relatively poor in nutrients (particularly when soils were not yet fully formed), hence their lower N and P requirements and lower growth rates than later vascular plants, especially angiosperms that appeared much later in the cretaceous period. Mountain streams are unlikely to be colonised by vascular plants even with increasing nutrient concentrations (such as nitrate due to atmospheric deposition, climate change or recovery from acidification) because of physical constraints (river bed shear stress under high flows), but a shift from diatoms to bryophytes, liverworts to mosses, or slow to fast growing species of bryophytes may be observed in the long term [35]. Surveys and temporal monitoring at key sites are needed to establish the diversity of liverworts and mosses in small mountain streams and relate the species distribution to environmental parameters and ecosystem processes [38].

Finally it was striking to observe such a wide range of nutrient concentrations in plant samples collected during the same season and under similar hydrological conditions within habitats and zones. This perhaps reflects the relatively good to excellent surface water qualities and wide species diversity of the studied area. As nutrient concentrations increase in standing waters, a shift in plant communities can be observed from rooted slow growing to floating fast growing species [39,40], where the range of nutrient concentration in plants may be more restricted towards to the upper values recorded in this study, and may reflect plant growth rates (especially P, as for terrestrial taxa [4]).

5. Conclusion

Aquatic plant N, P and N:P ratios differed among biophysical zones and habitat, but much of the variance was explained by plant life forms (bryophytes, hydrophytes, helophytes). Plant N and P concentrations were lower in mountain areas and bogs, and this may constrain the flow of energy into food webs (decomposers, consumers). The aquatic systems studied here had a wide range of plant nutrient content, reflecting high plant diversity. Further protection and monitoring is required, however, in order to fully appreciate the quality and evolution of these systems against a changing climate and pollutant exposure.

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