



# Assessing the efficiencies and challenges for nutrient uptake by aquatic plants



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## ABSTRACT

Aquatic plant meadows are valuable components to the ‘coastal filter’ and it is important to understand the processes that drive their ability to cycle nutrients. However, at present, the field-based evidence for understanding the drivers of nutrient uptake by plants is lacking. This study aimed to investigate how well individual shoots of aquatic plants could meet their nitrogen demands using the sediment nutrient pool (porewater ammonium) and to explore which traits helped to facilitate such uptake. Several species were investigated in shallow, submerged (2–4 m) mixed-species communities in the northern Baltic Sea using incubation experiments with enriched ammonium. After a 3.5 h incubation time, individuals were collected and analysed for nitrogen ( $\delta^{15}\text{N}$  DW) and  $^{15}\text{N}$  (at-%) concentrations. Uptake by plants was calculated per unit nitrogen in response to the  $^{15}\text{N}$ -labelled source and to overall nitrogen availability. Background porewater ammonium availability was highly variable between individual plants. Species identity did not significantly affect uptake metrics and the effect of ambient porewater availability was weak. As biomass increased there were significant logarithmic declines in the 95th quantiles of nutrient uptake rates, ambient porewater nutrient availability and aboveground nitrogen tissue concentrations (% DW). Such findings suggested that uptake rates of plants were significantly demand-driven and the nutrient conditions of the porewater were significantly driven by the demands of the plant. Findings parameterised the unfulfilled potential for some aquatic plants to cycle nutrients more efficiently and highlighted the potential importance of access to new nutrient sources as a way of enhancing nutrient cycling by aquatic plants. Plant traits and community properties such as the activity of infauna could facilitate such an access and are likely important for nutrient uptake.

## 1. Introduction

Aquatic plant meadows are valuable for cycling nutrients in coastal zones (McGlathery et al., 2007). They absorb dissolved nutrients and store them as biomass, which is then available for further processes such as burial or grazing by consumers, and it ultimately slows the re-release of inorganic nutrients into the surrounding environment (McGlathery et al., 2007). Understanding uptake processes is particularly important in the Baltic Sea because many of its ecosystems are threatened by eutrophication (see Andersen et al., 2009; Gustafsson et al., 2012) which has been accelerated by an increase in nutrient concentrations from anthropogenic nutrient loading to coastal zones (Gustafsson et al., 2012). It is hence imperative to investigate how well aquatic plants can access and utilise nutrient pools in the surrounding environment and understand what enhances their ability to cycle nutrients.

Aquatic plants absorb dissolved organic and inorganic nutrients from the water column and, mainly, the sediment porewater (Ertfemeijer and Middelburg, 1995; Touchette and Burkholder, 2000). Nutrient availability in the sediment is increased by processes such as excretion by fauna (Peterson and Heck, 2001; Peterson and Heck, 1999) as well as the decomposition of organic matter (Kenworthy and Thayer, 1984), including vegetation and fauna, phytodetritus (Evrard et al., 2005) and other particles entrained from the water column (Kennedy et al., 2010). Such factors are highly spatiotemporally variable (e.g. Hemminga, 1998; Wirachwong and Holmer, 2010; Fourqurean et al., 1992). Nutrients can be depleted to the extent that aquatic plant growth is nutrient-limited (Pérez et al., 1991; Ferdie and Fourqurean, 2004; Armitage et al., 2011); which is not always the case (as observed by Olsen and Valiela, 2010; Mutchler and Hoffman, 2017; Campbell and Fourqurean, 2014), but nutrient availability can drive spatial differences in plant patch development (Furman et al., 2017). Such a large-

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scale response to nutrient availability is owing to the responsive foraging and growth strategies by roots and clonal ramets to nutrient availability (Furman et al., 2017; Kembel et al., 2008; Campbell et al., 1991; de Kroon and Mommer, 2006). Thus, nutrient variability is highly influential to the development of aquatic plant meadows and their ability to cycle nutrients.

If an individual plant had a greater capacity to meet its nutrient demands using the resources that were available (e.g. Comas and Eissenstat, 2004), it would cycle nutrients more efficiently in the place that it grows, be more robust to temporal change in nutrient availability and in turn the meadow structure would be more robust to changes in nutrient availability. The growth of the root network of a plant is coordinated by its hormonal cues in response to nutrient demands. In terrestrial environments, the growth responses and root architectural strategies to meet nutrient demands change between species (Kembel et al., 2008; Campbell et al., 1991). These strategies can enhance uptake to different levels of success depending on the environment. For instance, having a higher root length per unit root mass (Specific Root Length, SRL) reduces the distance that nutrients must diffuse to reach the roots, and this benefits plants in nutrient poor environments because it catalyses nutrient supply (Aerts, 1999). However, in nutrient-rich zones the nutrient supply is no longer the limiting factor; instead it is the rate at which plants can absorb the available nutrients and so their physiological nutrient uptake kinetics become more important for enhancing nutrient uptake (Aerts, 1999). In the context of aquatic plant communities, we do not know which strategies are valuable for uptake and thus, what the nutrient microenvironment is like for an individual plant. While the physiology of different aquatic plant species can vary (e.g. Gustafsson and Norkko, 2016), coarser-scale morphological variations which affect uptake rates are still yet to be explored. For instance, seagrasses and other aquatic plants often develop a network of ramets which can share nutrients (Marbà et al., 2002); a strategy which enhances nutrient uptake in terrestrial environments with heterogeneous nutrient availability (Roiloa and Hutchings, 2013). Yet for any single shoot in natural conditions, we do not understand which conditions are most important for uptake success. For seagrass, root traits are likely to represent extremely poor nutrient conditions because the spatiotemporal variability of nutrients can be so influential on meadow growth (Furman et al., 2017) that the variability of traits which enhance uptake kinetics are likely to be redundant compared to the ability for plants to increase their reach to access new nutrient sources. In this case, growing longer roots would likely be the most important attribute for nutrient uptake rather than the amount of absorptive surfaces (i.e. Root biomass). However, without evidence we do not know whether nutrient uptake by each seagrass shoot is dictated by the abundance of nutrients available to be absorbed, whether plants benefit from investing more in extracting nutrients from their immediate environment (e.g. High SRL) or the ability for roots to access new nutrient pools (e.g. Maximum root length) is the most important trait in the natural environment.

As nitrogen is hypothesised to be the main nutrient which limits growth at higher latitudes (Hemminga, 1998; Short, 1987), and sediment porewater ammonium the main nitrogen source, porewater ammonium was the focal nutrient of this study. Our aim was to quantify nitrogen uptake rates by several aquatic plant species from the sediment porewater environment. We hypothesised that species would have significantly different nutrient uptake rates, and these differences would be owing to the variation in morphological root traits between species. It would be highly difficult to conduct such an investigation in typical seagrass meadows because they are often monocultures (Hemminga and Duarte, 2000), which means that there would not likely be enough variability in uptake strategies to find insightful trends. In the northern Baltic Sea, the brackish-water conditions allow for a unique assembly of marine, estuarine and limnic species to coincide within the same meadow (Kautsky, 1988; Gustafsson and Norkko, 2016), therefore these communities were ideal for capturing a variety

of uptake strategies facilitated by interspecific differences, while environmental conditions in the experiment remained relatively consistent. In this experiment, we examined how efficiently individual shoots could fulfil their nitrogen demand in response to a nutrient enrichment, and by comparing uptake rates between several species, we explored which uptake strategies were most beneficial to uptake rates. It is important to investigate which strategies enhance uptake in aquatic plants because it allows us to identify which mechanisms might otherwise be limiting nutrient uptake, thus nutrient cycling, in aquatic plant communities in the northern Baltic Sea.

## 2. Methods

### 2.1. Study site and vegetation

The experiment was conducted in the shallow, submerged (2–4 m) mixed species vegetative communities around Tvärminne Zoological Station, Finland. Tvärminne is situated on the Hanko Peninsula of the Finnish archipelago, Baltic Sea (59° 50' 400" N, 23° 14' 56" E WGS84). The species measured have both a limnic and marine origin; the freshwater species *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Stuckenia pectinata*, *Potamogeton perfoliatus* and *Zannichellia major*, and the marine/brackish species *Zostera marina* and *Ruppia cirrhosa*. We incubated independent ramets of a clone to prevent translocation during incubation. Individuals with a single shoot were selected, however for small species with a trailing growth (*R. cirrhosa* and *Z. major*), incubating multiple shoots was unavoidable. To prevent multiple species from being in the same incubation, we focussed on sparse stands. While sparse stands may not facilitate optimal conditions for aquatic plants, there is also less competition for nutrients and it is possible to investigate the nutrient uptake drivers of a single plant shoot without the influence of other shoots around. All incubations were at least 1 m apart from each other and individuals did not have noticeable grazer marks nor biofouling. Species-averaged canopy heights can range from 10 to 70 cm in this area and season (Gustafsson and Norkko, 2016), but individuals in this study did not exceed 20 cm in height.

The sediment of the study site had approximately 0.5–0.8% OM content and 1.2–7.3% silt fraction (< 0.063 mm) (Gustafsson and Norkko, 2018).

### 2.2. Field work

Short term nutrient enrichment incubations were conducted in situ using SCUBA (Fig. 1). <sup>15</sup>N - enriched ammonium sulfate solution (40 ml, 47 μM, 99 at-%) was used as an immediate-release sediment fertiliser followed by incubations (Fig. 1). 36 incubations were conducted on 4 days, 9 incubations on each day, during the late growth season (August–September) 2015 and 10 further incubations were conducted in September 2016 (Table 2). A minimum of 3 replicates of each species were incubated on each day and a further 3 specimens were collected intact from the surrounding meadow as ambient samples to obtain the background <sup>15</sup>N in plant tissue. Not all incubations were successful due to insufficient root or belowground biomass available for the analysis, but this remained unknown until harvest (see Table 2). Rooting depths can vary between species (approx. 5–20 cm, pers. obs.) and within species (length can change by a magnitude of 10, Gustafsson and Norkko, 2018), which meant that selecting a standardised depth for enriching the sediment porewater and for measuring the ambient porewater nutrient availability to plants required due consideration. For instance, injecting the liquid fertiliser too shallow into the sediment would likely lead to an immediate re-release of the majority of fertiliser into the water column. Likewise, too deep an enrichment and the fertiliser would be out of reach of roots for some of the individuals. The sediment porewater was enriched at 7–8 cm deep; approximately half way down the depth of the core and close to the maximum lengths that the roots of aquatic plants in the study area typically reached

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