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Do invasive exotic and native freshwater plant species respond similarly to low additional nitrate doses?



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ABSTRACT

Nutrient status of freshwater ecosystems has a significant influence on biological invasions, species richness and community structure. The role of phosphorus in driving these effects has been widely reported while its colimitation with nitrogen and other elements has received more recent attention. In a greenhouse experiment, we investigated the growth responses of two invasive exotic (*Egeria densa* and *Salvinia molesta*) and one native (*Vallisneria spiralis*) freshwater plant species to additional low concentrations of nitrate nitrogen (N-NO₃). The species were grown at five nitrate concentrations (0.02, 0.05, 0.1, 0.5, and 0.9 mg N-NO₃ L⁻¹). We found that the growth of *E. densa* and *V. spiralis* increased with increasing nitrate concentration. Surprisingly, *S. molesta* had the fastest growth rate at the midrange nitrate concentration of 0.1 mg N-NO₃ L⁻¹ and its leaf production was not affected by nitrate treatment. Irrespective of nitrate concentration, the invasive exotic species, particularly *S. molesta*, showed much greater growth responses than the native *V. spiralis*. We conclude that freshwater plant growth responses to low nitrate concentrations will be species specific but the faster growth rates of *S. molesta* provide an example of how differences between co-occurring invasive exotic species and native species could have profound effects on the structure and function of freshwater ecosystems under changed environmental conditions.

1. Introduction

Nutrients from anthropogenic sources are increasingly finding their way into water bodies worldwide (Wersal and Madsen, 2011). This is mainly due to the accelerated conversion of natural areas to grazing, cropping and urban uses resulting in nutrient-enriched runoff (Brodie and Mitchell, 2005). For example, waterways in urban areas often contain higher nutrient concentrations than natural freshwater ecosystems (Moss et al., 2013) and eutrophication has become one of the most frequently observed threats to freshwater ecosystems (Sand-Jensen et al., 2000). The nutrient elements regarded as the most important for primary production in freshwater ecosystems are phosphorus (P) and nitrogen (N) (Bornette and Puijalon, 2011; Bracken et al., 2015). However, their relative importance has been subject to intense debate (Moss et al., 2013) that is still unresolved (Penuelas et al., 2013).

Both P and N directly affect growth and development of freshwater plants (Bornette and Puijalon, 2011). P is often considered the most limiting and at the same time the most detrimental nutrient element since excessive P loading has been implicated in dramatic declines in freshwater species diversity and abundance (Sand-Jensen et al., 2000; Hilt et al., 2006). In contrast, N limitation is deemed only transient due to the pervasive occurrence of N-fixers in the environment (Schindler et al., 2008). Moreover, atmospheric reactive N can be distributed by precipitation into areas that are otherwise not directly affected by human mediated eutrophication (Elser et al., 2009). However, effects of increased N input into habitats that are normally nutrient-poor can be quite profound as it may lead to reduced freshwater plant diversity and altered community structure and function (Moss et al., 2013).

A direct consequence of eutrophication in freshwater systems is the promotion of exotic plant invasions since invasive species tend to respond more strongly to increased nutrient availability than their native counterparts (Van et al., 1999; Flores-Moreno et al., 2016). This has been shown to be the case across a range of invasive plant species (Funk and Vitousek, 2007; Hastwell et al., 2008; Madsen and Wersal, 2008; Hussner, 2009). Under eutrophic conditions invasive exotic species may partially or wholly displace native species from habitats because of their superior competitive ability, resulting in altered community structure (Njambuya et al., 2011; Gérard et al., 2014; Ceschin et al., 2017). For example, high nitrate concentrations may lead to

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proliferation of more competitive free-floating species (including invasive exotic ones) at the expense of native submerged freshwater plants (Barker et al., 2008).

In addition to having enhanced growth in high nutrient conditions, some studies have shown that invasive species may also have greater growth rates in low nutrient habitats due to their high resource use efficiency (Funk and Vitousek, 2007). For instance, the invasive species, *Hydrilla verticillata*, had faster growth rates than the confamilial native species *Vallisneria americana* at low nitrate concentrations of 0.2 mg N-NO₃ L⁻¹ (Kennedy et al., 2009). Most studies of freshwater plant responses to eutrophication (e.g. Cary and Weerts, 1983; Al-Hamdani and Sirna, 2008; Yu et al., 2015) have focused on high levels of nutrient additions. Relatively less is known about freshwater plant responses to small increases in nutrient levels in oligotrophic systems, which presents a knowledge gap that needs to be addressed.

The aim of this study was to assess the growth responses of two invasive exotic (Egeria densa and Salvinia molesta) and one native (Vallisneria spiralis) freshwater plant species to low levels of nitrate addition. Egeria densa (Hydrocharitaceae) is a rooted perennial, submerged species native to parts of South America (Uruguay-Paraguay-Brazil) that has been introduced into several water bodies around the world due to its popularity as an aquaculture species (Thiébaut et al., 2016). It has become a nuisance in its introduced range because of its rapid growth and is regarded as one of the most invasive freshwater plant species (Curt et al., 2010). Vallisneria spiralis (Hydrocharitaceae) is a widespread rooted submerged Australian native perennial that also occurs in Africa, southern Europe, and southern and eastern Asia (Aston, 1973). Salvinia molesta (Salviniaceae) on the other hand, is a free-floating fern native to South America that is one of the most destructive invasive species in the lake and river systems of tropical and subtropical habitats (Schooler et al., 2011). The submerged species are capable of taking up nutrients using their leaves as well as roots (Madsen and Cedergreen, 2002). Salvinia molesta, in contrast, lacks true roots and utilises its highly dissected submerged leaves and the underside of its floating leaves for nutrient uptake (Julien and Bourne, 1986). Egeria densa and other congeners of V. spiralis utilise both dissolved CO₂ and bicarbonate ions (HCO₃-) for photosynthesis (Pierini and Thomaz, 2004; Yin et al., 2017). However, E. densa is a C₄ species while V. spiralis is a C3 species that also fixes carbon via crassulacean acid metabolism (CAM)-like pathway (Webb et al., 1988; Casati et al., 2000). Like most free-floating species, S. molesta has a C₃ carbon fixation pathway (Longstreth, 1989).

These species have a wide distribution in the lowland freshwater systems of eastern Australia (Roberts et al., 1999). They commonly cooccur in the Hawkesbury-Nepean River system which is a major waterway in the greater Sydney region of New South Wales (NSW), Australia (Rahman and Salbe, 1995; Roberts et al., 1999). The health of this river system is vitally important as it provides 90% of Sydney's drinking water (Rahman and Salbe, 1995) and has a significant conservation and recreation value (Howell and Benson, 2000). Understanding the invasion risk of exotic species into the uninvaded sections of this system at relevant nitrate concentrations should be a high priority in order to inform future management decisions. We therefore grew the plant species in monocultures in a controlled greenhouse experiment across a range of low nitrate treatments ($0.02-0.9 \text{ mg N-NO}_3 \text{ L}^{-1}$). We hypothesise that:

- 1) all species will have greater growth rates and lower foliar C:N ratios in the higher nitrate concentrations due to nitrates benefiting the growth of freshwater plants.
- the invasive exotics growth response will be relatively greater than that of the native V. *spiralis*, particularly at the higher levels of the nitrate concentrations.

2. Methods

2.1. Greenhouse conditions

The experiment was conducted in greenhouses at the Plant Growth Facility of Macquarie University (NSW, Australia; 33.7745 °S, 151.1169 °E). The ambient temperature of the greenhouses was maintained at 27 °C/22 °C day/night producing water temperatures of 24 °C/ 19°C day/night. This temperature range is consistent with the mean lower Hawkesbury River summer water temperatures (Sydney Water, unpublished data). The temperature, humidity and photosynthetically active radiation (PAR) of the greenhouses were continuously monitored using a Multi-grow Controller System (Autogrow Systems, Auckland, New Zealand). The average midday PAR at the water surface was 550 $(\pm 320) \mu$ mol m⁻² s⁻¹. Underwater PAR was not measured due to logistical challenges. The greenhouses received $150 \,\mu mol \, m^{-2} \, s^{-1}$ supplemental lighting using LED red and blue Grow lights (Philips, Eindhoven, Netherlands) for two hours per day to ensure a photoperiod of 13/11 day/night hours. The average humidity at midday ranged between 65-75%.

2.2. Plant preparation

Egeria densa plants were obtained from Manly Dam (Warringah, NSW, Australia; 33.7818 °S, 151.2556 °E), whereas *V. spiralis* were obtained from a commercial supplier (Austral Watergardens, Cowan, NSW, Australia; 33.5772 °S, 151.1857 °E). *Salvinia molesta* plants were collected from Lake Munmorah (Wyong, NSW, Australia; 33.1923 °S, 151.5749 °E). The plants were collected on various dates between 27th June and 15th July 2016 and maintained in tap water until propagation.

Before planting, E. densa and V. spiralis plants were gently washed under running tap water and a fine paint brush was used to remove periphytes and herbivores. The plants were then trimmed to the following dimensions: 10 cm leaf length for V. spiralis (method adopted from Blanch et al., 1998; Kennedy et al., 2009; Yu et al., 2015), 5 cm stem length with an axillary shoot for E. densa and a rhizome section $(0.023 \pm 0.009 \text{ g} \text{ dry weight})$ consisting of two fully grown healthy leaves without an apical bud for S. molesta. Once prepared, each plant was drained for two minutes on a paper towel and the wet weight measured using an analytical electronic balance (Mettler Toledo, Port Melbourne, VIC, Australia). The number of leaves of each V. spiralis plant was also recorded. In order to obtain the initial dry weights of the experimental plants, we determined the relationship between wet and dry weights of a sub-sample of 20 individual plants of each species. The wet weights of the experimental plants were then used to calculate their initial dry weights using the regression equation calculated from the wet and dry weights of the sub-sample of plants. The sub-sample plants were also used to obtain the initial mean foliar C and N content of each freshwater plant species. This was done by grinding 0.5 g of dry leaf biomass from each plant using a cross beater mill (Glen Creston, Stanmore, UK) and then analysing these samples using combustion with a TruSpec CHN analyser (LECO, St Joseph, MI, USA).

A sub-sample of ten plants from each submerged freshwater plant species (*E. densa* and *V. spiralis*), prepared in the same manner as the experimental plants, were used to obtain chlorophyll-*a* levels as a proxy for the initial periphytic algal load. This was done by shaking each plant by hand in a beaker containing 300 mL tap water for 90 s (Zimba and Hopson, 1997; Jones et al., 2002). Chlorophyll-*a* analysis of the wash water from each plant was then conducted by a commercial laboratory following APHA 10200H method (APHA, 1998). This process was repeated for each of the plants harvested at the end of the experiment (after 6 weeks) to determine the amount of periphytic algae accumulated over the growth period. At the end of the experiment samples of the water column were collected and sent to a commercial laboratory for determination of chlorophyll-*a* concentration as a proxy for phytoplankton load. We assumed phytoplankton load was zero at the start of

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