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Growth of a native versus an invasive submerged aquatic macrophyte differs in relation to mud and organic matter concentrations in sediment

Márcio José Silveira*, Sidinei Magela Thomaz

Universidade Estadual de Maringá, Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura – Nupelia, Av. Colombo 5790, Maringá, PR, 87020-900, Brazil

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ABSTRACT

Eutrophication has reduced the colonization of submerged plants in some freshwater ecosystems, and organic matter (OM) together with grain size in sediment may mediate such decreases. We tested the isolated and combined effects of sediment mud and OM concentrations on the early growth of two species of submerged macrophytes, *Egeria najas* (native) and *Hydrilla verticillata* (invasive). We hypothesized that the sediment OM concentration has more important effects than the mud concentration on plant growth and that *E. najas* is more successful than *H. verticillata* in highly organic sediment. We tested these hypotheses using mesocosms with several combinations of mud and OM concentrations in the sediment. We used plant length, the number of lateral branches, root dry mass and total plant dry mass as response variables. Both OM and mud were found to be important determinants of the growth of both species, but the former had a stronger influence than the latter. However, the responses of all plant attributes differed between the species. For example, the growth of *E. najas* increased linearly with increasing OM concentration, but *H. verticillata* responded to this variable with a quadratic tendency. The decrease in the growth of the invasive species at high OM concentrations may be associated with its lower tolerance to phytotoxic compounds released by the decomposition that occurs in more organic sediment. In conclusion, our experimental data support the importance of the sediment OM in the growth of the native *E. najas* and invasive *H. verticillata*. However, future studies should investigate the adaptation mechanisms that allow both plants to colonise such distinct sediment types.

1. Introduction

Eutrophication has reduced the presence of submerged macrophytes in some freshwater ecosystems over the last 100 years (Sand-Jensen et al., 2000; Seddon et al., 2000). Sediment organic matter (OM), which usually increases with eutrophication, is one of the factors used to explain this tendency (Irfanullah and Moss, 2004; Liu et al., 2004). Nutrients typically increase with the OM concentration in the sediment (Barko and Smart, 1986; Newbolt et al., 2008), which could account for higher plant growth in more organic sediment (Pulido et al., 2011). However, after a threshold, OM may hinder plant growth through the release of phytotoxins (Barko and Smart, 1986; Wu et al., 2009). Because of its importance for macrophytes growth, sediment OM, along with other environmental factors, can influence entire macrophyte communities by determining the patterns of species distribution (Chappuis et al., 2014).

Several studies have indicated that an increase in sediment OM may inhibit the growth and survival of some submerged plant species (Barko and Smart, 1986; Terrados et al., 1999). Thus, sediment OM could be a filter preventing invasion by non-native macrophytes, such as the extremely invasive submerged macrophyte *Hydrilla verticillata* (L.f.) Royle, which is highly productive in its introduced ranges (Bianchini Jr. et al., 2010) but is sensitive to phytotoxins released by organic sediment (Barko and Smart, 1986; Wu et al., 2009). This species has successfully invaded ecosystems and caused ecological and economic impacts worldwide (Cook and Lüönd, 1982; Sousa, 2011); thus, studies of its ecology are of great interest. It has recently appeared in and colonised the Upper Paraná River (Brazil), but it grows poorly in sites with highly organic sediment (Sousa et al., 2009, 2010). The decline of *H. verticillata* in its native range (Asia) is also attributed to eutrophication and the consequent increase in sediment OM (Yan et al., 1997; Qiu and Wu, 1998). However, the OM concentration in sediment does not seem

* Corresponding author. Tel.: +55 443011 5952; fax: +55 443011 4625.
E-mail address: s.marciojs@gmail.com (S.M. Thomaz).

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to compromise the success of several Neotropical macrophytes, such as *Egeria najas* (Planch), *Cabomba furcata* Schult. & Schult. f. and *Myriophyllum aquaticum* (Vell.) Verdcourt, which are found in habitats with high OM concentrations, such as floodplain lakes (Sousa et al., 2009; Sousa et al., 2009).

In addition to OM, other sediment features, such as grain size, are also determinants of submerged macrophyte success. Increased plant growth in fine sediment appears to be a response to nutrient availability (Boeger, 1992). Most aquatic macrophytes grow poorly in coarse sediment compared with fine sediment because the latter increases nutrient diffusion and exchange between the roots and the sediment (Barko and Smart, 1986).

Sub-tropical lakes in the Upper Paraná River floodplain accumulate sediment with a high mud concentration (grain size <0.062 mm) together with high quantities of OM (Rosin et al., 2010; Ragonha et al., 2013). Some of these lakes are colonized by the native submerged species *E. najas*, but they are apparently less prone to colonization by the non-native *H. verticillata* (Sousa et al., 2009; Sousa et al., 2009). Although OM and mud may explain the distribution of these and other species of macrophytes, it is difficult to distinguish the effects of both variables on plant success because they are positively correlated in natural ecosystems. Thus, experimental manipulations of these two important sediment features are necessary to determine their individual and interactive roles in plant growth.

In this study, we assessed both isolated and interaction effects between OM and mud on the success of *E. najas* and *H. verticillata* in mesocosms. We chose these two species because the former is very common in several natural and man-made ecosystems in the Neotropical region, while the latter has a great invasive potential. We asked the following questions: (i) which sediment feature (OM or mud) is the most important determinant of plant establishment and growth? (ii) How do these species respond to increases in OM and mud in sediment? We hypothesized that (i) sediment OM is the variable that best explains plant performance compared with mud and that (ii) *E. najas* growth will be less affected than *H. verticillata* growth in OM and mud-rich sediment. We predicted that dry mass, plant length and the number of lateral branches, which are surrogates of plant success, are not limited by high OM and mud concentrations for *E. najas*, but that these factors are negatively affected in *H. verticillata*.

2. Materials and methods

Our experiments were conducted on the campus of the University of Maringá (South Brazil). Apical portions of healthy macrophytes (15 cm long), sediment and riparian forest litter were collected from the Upper Paraná River floodplain (22°45′S, 53°15′W and 22°45′S, 53°30′W). Fragments of both species of macrophytes were collected from a site at the main river channel where the two species co-existed. Litter was dried at 60 °C to a constant weight and ground in a mill to obtain a homogeneous powder, which was used to manipulate the sediment OM concentrations. All natural sediment was incinerated at 560 °C for four hours to eliminate OM, and it was then sieved according to the method described by Wentworth (1922) and Suguio (1973) to remove all mud (silt + clay; grain size <0.062 mm). The two fractions of OM-free sediment (one with particle sizes of <0.062 mm and the other with particle sizes of >0.062 mm) were saved for later use in the experiment. This procedure produced mud-free and OM-free sediment.

To assess the independent effect of OM, litter powder was added to the OM-free sediment >0.062 mm to produce a gradient of 0, 2, 4, 7, 12 and 22% g DW OM. Then, these different sediments were mixed with OM-free mud sediment (<0.062 mm particle size, collected by sieving as described above) to obtain a gradient of 0, 5, 15, 25, 40 and 55% g DW mud. This procedure allowed for all possible mixtures of mud and OM, producing a total of 36 combinations, which are (the procedure and all combinations) shown in Fig. 1. These percentages were chosen to simulate the range found in the field in the Paraná River floodplain (Sousa et al., 2009, 2010 Rosin et al., 2010; Ragonha et al., 2013). The treatment with 2% g DW mud and 5% g DW OM can be considered to be a control because it is similar to the condition found at the site where both macrophyte species co-existed (Sousa et al., 2010).

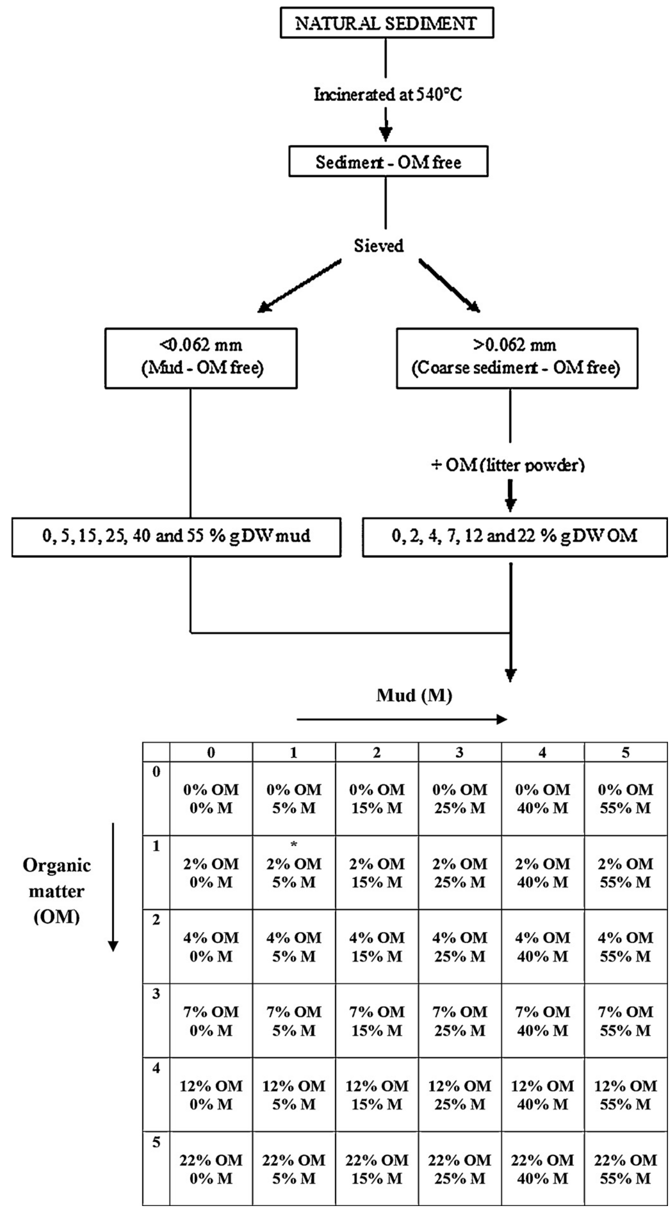

Fig. 1. Experimental procedures and addition matrix, showing the percentages of organic matter (OM) and mud (M) added to the sediment of the sampling units. *The approximate levels of OM and mud found in the sediment where both species of macrophytes co-existed in situ. Note that comparisons between six levels of both mud and OM produced the 36 treatments.

The apical portions of *E. najas* and *H. verticillata* without adventitious roots or branches were planted in pots (8 × 8 × 10 cm) with the sediment treatments shown in Fig. 1. Each pot contained one apical portion. We used three replicates for the treatment pots (a total of 108 pots for each species). Although the number of replicates can be considered to be low, our procedure produced a gradient of sediment OM and mud that permitted the use of