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Submerged seed, turion and oospore rain: A trap quantifying propagule deposition under aquatic vegetation

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ABSTRACT

Submerged, free-floating and floating-leaved macrophytes produce a broad variety of specialized propagules to ensure population continuity and enhance dispersal. We quantified macrophyte propagule deposition in shallow ponds using a trap positioned near the sediment, designed to monitor diaspore rain in lentic aquatic environments. Propagule traps were tested under different set-ups, firstly within enclosed mesocosm experiments and secondly in vegetation communities growing in the open field. Mesocosms were installed in ponds containing monospecific stands of *Chara globularis* and *Potamogeton pusillus* under two contrasting conditions, with and without duckweed (*Lemna minor*), to evaluate cover impact on propagule release from the submerged macrophytes. During the studied interval, deposition of *C. globularis* oospores was not affected by *Lemna* cover. In *P. pusillus*, lemnid cover coincided with strong phenotypic alterations, including high turion investment. Traps openly installed in ponds containing *Parvopotamion*- and *Magnopotamion/Hydrocharition*-type associations showed that propagule rain was intensive underneath some macrophyte species and generally mirrored vegetation composition. Certain species were either over- or underrepresented. Generally, macrophyte abundance did not influence propagule deposition. Propagule traps are useful in studies assessing reproductive dynamics and resource allocation, potentially bypassing or complementing sediment propagule bank research, and aiding identification of recruitment bottlenecks.

1. Introduction

Macrophytes propagate by means of a remarkable array of dispersal and survival units, generated sexually (seeds or oospores), vegetatively (turions, tubers, bulbils or rhizomes) or by random fragmentation and thallus regrowth (Grace, 1993; Barrat-Segretain, 1996; Bonis and Grillas, 2002; Bociąg and Rekowska, 2012). Different methods exist to quantify propagule production. Direct measures of abundance and relative weight of reproductive structures on the parent plant or macroalgal thallus (Bonis et al., 1993; Casanova, 1994; Calero et al., 2015; Wan et al., 2016) can help to infer phenology and resource allocation in response to a particular environmental situation, but might over- or underestimate real propagule output (since biomass is sampled discontinuously) and generally are not applicable for correct derivation of ripe propagule dimensions. A second strategy, explored in the current study, is the collection of released seeds or abscised propagules.

Propagule trapping in aquatic habitats has traditionally been employed along streams or river networks, in order to study hydrochorous dispersal, dispersal filtering and ecological connectivity (Cellot et al., 1998; Boedeltje et al., 2003a, 2004; Gurnell et al., 2008; Engström et al., 2009; Nilsson et al., 2010; Fraaije et al., 2015). Generally, these studies focus on the dispersal aspect of reproductive structures and the ecological consequences for the recipient habitat. Propagule traps could, however, likewise be convenient to relate macrophyte growth conditions with reproductive output. This way, it is possible to identify the effect of natural, anthropogenic or experimental changes on reproductive effort and success, which in turn can complement observations regarding macrophyte plasticity.

To our knowledge, using submerged traps would represent a novel way to evaluate reproductive phenology in the relatively stagnant environment of shallow lakes or ponds. Previously employed trapping devices would not be suitable under these conditions, since (1) in streams, overflows or tidal zones, organism retention is aided by water flow, active sweeping or tidal action (Cellot et al., 1998; Boedeltje et al., 2003a, 2004; Wolters et al., 2004; Riis, 2008; Vanschoenwinkel et al., 2008); (2) astroturf mats (Wolters et al., 2004; Sarneel et al., 2014; Fraaije et al., 2015) are best suited to catch drifting material; (3) traps originally assembled for assessment of (in)organic sediment flux or composition are often expensive or automated (Håkanson et al., 1989; Muzzi and Eadie, 2002; Kerfoot et al., 2004; Dubovskaya et al., 2015;

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Makabe et al., 2016; but see Bloesch and Burns, 1980); and (4) propagule traps designed for terrestrial habitats (Chabrerie and Alard, 2005; Stevenson and Vargas, 2008; Berg et al., 2016) require adaptations for use in submerged environments.

We evaluated the applicability of a macrophyte propagule trap installed on top of the sediment to assess propagule rain in function of vegetation characteristics and potential stress. Data on propagule rain can be highly informative, as for many macrophyte species occurring in stagnant waterbodies the fate of their propagules, features of the reproductive strategy and its response to stress gradients remain largely unsolved (Titus and Hoover, 1991; Eckert et al., 2016). To test our design, we conducted two mesocosm experiments and an open-field trial in two pond sets with contrasting macrophyte communities:

1. Firstly, the mesocosm studies involved duckweed (*L. minor*) cover stress (inducing reduced light penetration or gas exchange) on an angiosperm (*Potamogeton pusillus* L.) and a charophycean (*Chara globularis* Thuillier) submerged macrophyte. In *C. globularis*, oospore release was expected to be stimulated by favourable temperature and light conditions (Calero et al., 2015). In *P. pusillus*, we anticipated a divergent response in reproductive effort (trade-off between sexual and clonal reproduction; Eckert et al., 2016), with investment in seed production under low-stress (open) conditions, and increased turion release as a result of *L. minor* cover (Kaplan and Štěpánek, 2003).
2. Secondly, we analysed propagule rain under *Parvopotamion*-like as well as *Magnopotamion/Hydrocharition*-type vegetation associations (Schaminée et al., 1995; European Commission, 2013), respectively in a peri-urban, eutrophied pond system and a network of fishless, isolated pools, in order to relate species abundance with representation in the settled propagule pool.

In addition, we hypothesized that greater macrophyte abundance allows increased propagule production (Samson and Werk, 1986; Watkinson and White, 1986; Bonis et al., 1993).

2. Materials and methods

2.1. Design of the propagule trap

The body of the propagule trap consisted of a circular, commercially available plastic basket fabricated for the potting of aquatic plants (Fig. 1). Dimensions of the basket were 11.8 cm diameter at the opening (surface area: 0.011 m^2), 9.0 cm diameter at the bottom and a height of 10.2 cm, resulting in a volume of 0.87 L. Edges and bottom side of the collectors were delicately meshed (pore size of around 2 × 2 mm), aiding the expulsion of water during lifting. The inside of the pot was coated with 180 µm polyester fabric, sealed to the plastic with a water-resistant glue. The fine mesh size of the inner gauze allowed for retention of smaller seeds and oospores, which are typically above 200 µm in diameter (Haas, 1994; Kleyer et al., 2008).

Underneath the basket, we attached a square, concrete tile (dimensions: 95 mm × 95 mm × 35 mm; weight: 0.84 kg) – wrapped with nylon string (thickness 2 mm) – with a plastic cable tie. We ensured that basket and tile were closely fused, in order to limit underwater movement of the basket. The tile functioned as an anchor, keeping the trap steady but sufficiently lightweight to allow retrieval. Combined height of the anchor and collector was around 150 mm.

At one edge of the basket's opening, we attached a nylon chord (length variable in function of water depth; thickness: 2.5 mm). The chord was stuck through a hollow piece of grey or coloured foam pipe insulation (diameter: 40 mm; thickness: 20 mm) and fastened at the opposite side of the basket. The insulation piece served as a submerged or floating float, which allowed finding back and retrieving the propagule trap.

In very shallow water (< 0.50 m deep), we pinned the basket directly in the sediment using 24 cm-long tent pegs fitted on opposite sides of the opening. This set-up likely works best in mesocosm experiments (as was the case), or when positions of the propagule traps are clearly marked. Compared to the anchored version, plugging the trap in the sediment reduces total height to 100 mm. Alternatively, the trap can be partly inserted in the sediment, although this might result in contamination of deposited material.

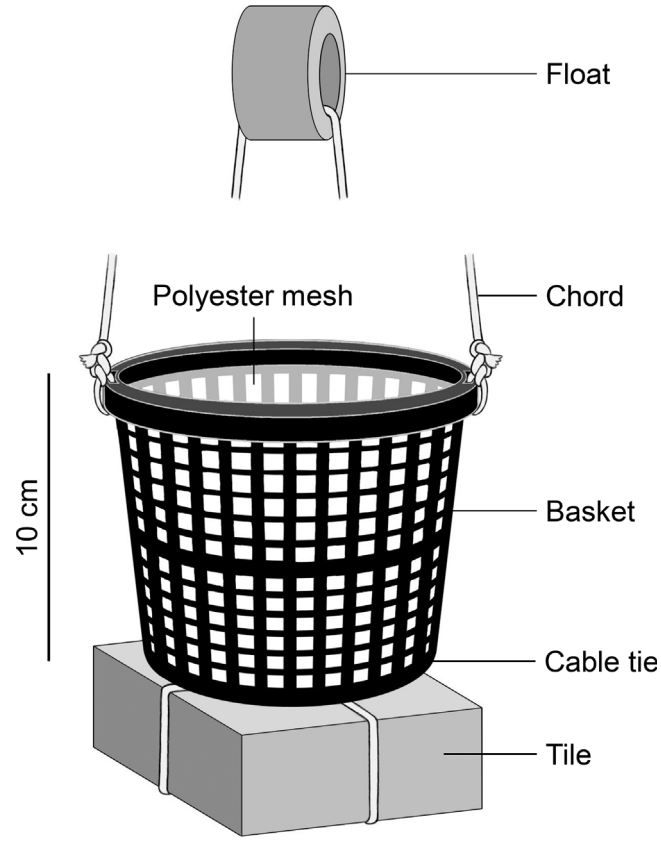

Fig. 1. Macrophyte propagule trap design. Float may be submerged or floating at water surface. Diameter of trap opening is 11.8 cm. The polyester coating attached on the inner side of the collector has a mesh size of 180 µm.

2.2. Field trials and study area

We evaluated the propagule traps under field conditions in two distinct settings (Table 1): (1) two mesocosm experiments were used to monitor the evolution of oospore settlement under *Chara globularis* and turion and seed release under *Potamogeton pusillus* in response to *L. minor* cover; and (2) an unprotected, non-manipulated open-water study on reproduction of submerged aquatic vegetation was conducted in ponds. During field visits, observations of inflorescences or macrophyte-attached propagules were registered.

2.2.1. Mesocosm experiment on Lemna cover stress

The first experiment, conducted in a eutrophic peri-urban pond in the Brussels-Capital Region, Belgium (Table 1), included 16 circular mesocosms with diameter 0.48 m (depth 0.4 m; surface area 0.18 m^2). Plots consisted of bottomless plastic bins with a modified, crown-shaped lower half. Mesocosms were gently installed on top of a *C. globularis* meadow, in a linear fashion. In the middle of each plot, one propagule trap was carefully pinned in the sediment underneath the macroalgae using tent pegs. A floating plant cover treatment was initiated by alternating *L. minor*-covered plots (100% cover) with open controls. Fronds of *L. minor* were spread by hand to establish a single floating layer, which autonomously maintained good status and full

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