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Quantifying macrophyte colonisation strategies—A field experiment in a shallow lake (Lake Balaton, Hungary)

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ABSTRACT

Life-history traits like dominance of certain reproductive modes (e.g. vegetative, specialized, unspecialized or sexual propagules) and overwintering strategies (evergreen or re-sprouting) determine the success and timing of the ability of aquatic plants to colonize new areas. In the present experiment the distribution of these reproductive modes was examined in-situ, where new gaps were experimentally formed and establishment of new vegetation observed on a monthly bases in ten plots. During a period of 126 days, altogether 73% of all established plants (n = 1822) colonized by rhizomatic growth and 11% by rooting of vegetative fragments. *Myriophyllum spicatum* was observed to use mostly fragment rooting (81%), while *Potamogeton perfoliatus* followed a more mixed strategy combining re-rooting fragments and rhizomatic growth (31% and 41%, respectively). *Stuckenia pectinata* also preferred colonisation by rhizomes (84%). No colonisation by specialized vegetative units (tubers or turions) was observed during the study period The importance of surrounding vegetation was shown by comparing colonisation on inner and marginal sections of the plots (30% vs.70%). Three different patterns of timing of peak colonisation intensities were observed, related to species' life-history traits. While several experimental works have been done on the regeneration and colonisation abilities of different species under laboratory conditions, information on the in-situ application of the different strategies is scarce. Insights on the modes by which plants succeed in colonising gaps helps us understand how (re)establishment of aquatic vegetation might function in lake ecosystems recovering after eutrophication.

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1. Introduction

Plants, thus submerged aquatic macrophytes too, can propagate by both vegetative and sexual means. Macrophytes usually use a wider range of possible modes for establishing in new areas and in newly emerging patches than terrestrial plants do, thereby being able to colonize a diversity of habitats (Barrat-Segretain, 1996; Sculthorpe, 1967). This multiplicity of colonisation modes makes it possible to investigate the relationship between life-history traits (like different ways of reproduction) and colonisation success.

Re-colonisation can occur on different spatial scales: locally, following either minor disturbance (such as strong currents or waves, which can dislocate bundles of plants, or feeding, trampling, boat movements), or major disturbance events, which eradicate greater areas of aquatic vegetation (such as ice-scouring, drought or floods (Barrat-Segretain and Amoros, 1996; Kautsky, 1988), or at the whole lake-level, when a lake returns (through re-oligotrophication) from algae-dominated turbid state that resulted from previous eutrophication (Scheffer, 1990; Scheffer and Van Nes, 2007). Re-establishment of macrophytic vegetation after return from high eutrophication levels is a common issue, especially in shallow lakes world-wide (excellent review by Bakker et al., 2012; Galanti et al., 1990; Hilt et al., 2010; Hobbs et al., 2012; Jeppesen et al., 2005; Lauridsen et al., 2003, 1994; Ozimek, 2006), as it is also in the study area Lake Balaton (Herodek et al., 1988; Istvánovics et al., 2007). This article argues that looking into details at the small scale might elucidate the potentials and limitations of processes on the large scale, whole-lake level.

Colonisation by plants can be regarded as conquering new areas, establishing from propagules which arrived from other areas to that patch. Regeneration is seen as the process by which plants re-grow from some part of the whole plant, which might be below-ground or not (e.g. Barrat-Segretain et al., 1998; Umetsu et al., 2012). For the purpose of this study we defined (similarly to Capers, 2003

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and to Henry et al., 1996) all mechanisms of establishing new, aboveground canopy as colonisation, as they are all ways by which previously non-visible plants appear in the standing vegetation and can participate in further life-history events.

Life history is composed of survival probabilities and rates of reproduction (Partridge and Harvey, 1988), including patterns of development, growth, reproduction and lifespan (Fabian and Flatt, 2012). The development of both vegetative and generative reproductive structures is determined by different life history traits and phenology, which in turn act on potential speed and timing of colonisation. Within the diversity of reproductive options open to a macrophyte, there are two major ways of reproduction, depending on whether a species overwinters solely as sexual propagules (as annuals do) or in some vegetative shape (like perennials). Overwintering in perennials can take place by receding to underground plant parts, while some aquatic perennials remain partly green above-ground. The latter start in spring with a head start in developing biomass.

Colonisation of newly available areas depends, apart from patch suitability, also on the surrounding vegetation within the waterbody, the effect of which is mostly detectable at the boundaries of gaps (e.g. Capers, 2003; Henry et al., 1996). Testing the effect of gap edges throws light on the importance of already existant macrophytic vegetation as kernels of (re)establishment.

The set of reproductive options a species can resort to is delimited and timed by its life-history, whereas the relative importance with which the different colonisation modes are used also depends on the local environment (Capers, 2003; Wiegleb and Brux, 1991). However, it is expected that there are species-specific propagation strategies combining the available options in a characteristic way, but in lake ecosystems this has never before been quantified in-situ. Differences in the preference of colonisation modes might explain spatial as well as temporal patterns of macrophyte occurrence. Therefore, we wanted to investigate, a) whether different macrophyte species use different strategies in colonising and to quantify the propagation modes in relation to each other. In order to test the source of colonisation, we hypothesized that b) edge-effects would be strong, and c) there would be differences between the months in summer and autumn in colonisation intensities, relatable to the species life history traits.

2. Material and methods

Ten plots of 1 m × 1 m were randomly designated in 0.6–1.0 m deep water in Lake Balaton (coordinates: 46°54′50.26″N 17°53′36.38″) on 4th June 2009. Plots were arranged on four points (sub-sites), within a range of 5–70 m apart.

The site represented the typical submerged vegetation of Lake Balaton with *Potamogeton perfoliatus* L., *Stuckenia pectinata* (L.) Böerner, *Myriophyllum spicatum* L., *Ceratophyllum demersum* L. and *Najas marina* L., belonging to the category of "Euhydrophyte vegetation of naturally eutrophic and mesotrophic still waters" in the national vegetation catalogue (Bölöni et al., 2011).

At the start of the experiment, all vegetation was removed from the plots by hand, equipped with scuba diving gear, while care was taken to remove attached subterranean parts of the existent plants as completely as possible. We did not sift through the sediment in order to remove detached propagules, following the approach of Capers (2003).

Plots, divided into a margin (outer 15 cm within the plot) and an inner section, were treated every 3–4 weeks (on 07/07, 03/08, 10/09 and 08/10) until the end of the vegetation period. Each time, all newly grown vegetation was carefully removed while checking whether it had established by one of the following colonisation modes suggested by Capers (2003) and own observations:

1 by re-rooting of vegetative fragments (detectable by the blackened, slightly decomposing endings of a (half-buried) shoot)
2 by clonal (rhizomatic, lateral) growth from neighbouring plants (physical attachment to plants through their rhizomes outside the plot)
3 by re-sprouting of specialized vegetative propagules (turions or tubers) (recognizable by the remnants of the vegetative propagule that sprouted)

Germination of seeds was not included in the assessment of the different colonisation modes as this probably mostly occurs during spring-time, which was not covered by the present study.

If the colonisation event did not fall into any of the above categories, it was noted as "unknown". *C. demersum* and *N. marina* fragments were often found on the plots without rooting, but as fragmentation and being unrooted belongs to their normal lifecycle, these events were counted as colonisation by fragments.

In order to calculate colonisation potentials for the different species, plants were counted and species determined. In compliance with our definition of colonisation, each plant, possibly with several shoots or ramets that appeared on the treated plots was regarded as one colonisation event. This means that for *C. demersum*, which roots only with some minor rhizoids or not at all, colonisation was counted as such if any shoots were found lying on the sediment surface. The same applied for *N. marina*, which is also often found towards the end of the summer unrooted, seemingly without losing vitality.

In order to take into account the correlated observations, generalized estimating equations (GEE) were applied with an assumed Poisson-distribution, implemented in SAS SAS University Edition, Version 2.2 (SAS/STAT). In order to control for potentially confounding effects, the GEE model included apart from species, plot-section (inner and outer) and date of sampling, also time since last vegetation removal (in days), interaction between species and plot-section as fixed effects and sampling site (A, B, C and D), as random effect. First order auto regressive covariance structure was used to describe the within plot error distribution. Fixed effects were tested at alpha level of 0.05 by means of Wald-test. Least squares mean estimations of abundancies in inner and outer plot sections and their geometric means ratios (GMRs, inner/outer) with corresponding Tukey – type 95% confidence intervals were derived. Differences between species in the distribution of colonisation modes were tested with G-test of independence in R version 3.2.2 for all months and for separate month too, in order to check results independently from date (R Developement Core Team, 2016).

3. Results

A total of 1822 plants established during the whole research period from 7th June till 8th October (126 days), resulting in an overall colonisation rate of 1.4 plants per day per m². Most intense colonisation took place during August (peak value from harvesting on 7th September) with 85.1 ± 15.7 colonisation events per m² on average ($\pm$ SE), while it was lowest during the following month, harvested at the beginning of October (19.8 events ± 2.8).

First it was *M. spicatum* and *C. demersum* which colonized most actively, during June (resulting in peak value sampled on 7th July), both declining steadily throughout the study period, with *M. spicatum* slightly increasing again in October (Fig. 1, Table 1). *N. marina* colonisation rates peaked next, in early August. In *S. pectinata* and *P. perfoliatus* most plants established during August, giving a maximum at the sampling on 10th September, exceeding plant densities of *M. spicatum*.

Almost three quarters of all noted colonisation events (73%) could be assigned to rhizomatic growth from surrounding plants,