Theses of the PhD dissertation

PROPAGATION AND GROWTH OF SUBMERGED MACROPHYTES IN LAKE BALATON

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1 Introduction

Aquatic macrophytes are important for the life of a lake from several aspects. Apart from constituting a food source by themselves for many species, they also provide shelter against predation as well as surfaces for epiphytes, sessile invertebrates and egg deposition for some fishes and amphibians. Macrophytes influence not only certain groups of biota, but the complete food-web structure of a lake. They play also an important role in regulating whole-lake processes such as dampening waves and stabilizing the sediment, thereby enhancing sedimentation and decreasing resuspension by wave-upwelling. By reducing resuspension, they influence the light climate in the whole lake, through decreasing turbidity and impeding the development of large phytoplankton masses.

While mass occurrences of some macrophytes affecting a whole lake happen under certain circumstances up to such an extent, that plants have to be controlled, often a rather patchy pattern is characteristic with temporally and spatially highly unpredictable presence in different areas within a lake. Several attempts have been made to clarify why macrophytes occur in or re-colonise one place but not the other, however in most cases no conclusive results could be reached and often established models had to be revisited and modified.

In lake restoration, after regulating external nutrient input, sustaining the presence of macrophytes is crucial for stabilizing clear water conditions. In order to achieve this, macrophyte colonisation has to be encouraged and supported by all available knowledge on macrophyte propagation.

Macrophyte population dynamics, colonisation processes and also macrophyte community composition, depend on both environmental conditions and dispersal ability of the species. Therefore, one needs to understand the influence of environmental forces on growth as well as to get to know the process of propagation and establishment in depth, if conservation and management is to be successful.

Macrophytes have several ways of propagation, which often occur in combination. Nevertheless, vegetative propagation dominates in most cases, while sexual reproduction is often limited. Vegetative reproduction – including clonal growth as well as propagation by several asexual propagules – is an especially effective way of propagation in aquatic environments as the dispersal of vegetative propagules is facilitated by water convection.

Clonal growth – spreading by growth of rhizomes – is for example one of the most common strategies of reproduction for macrophytes. The characteristic shape (e.g. circular polycormons of *Potamogeton perfoliatus* or round patches of *Typha*) in which we find macrophytes often indicates this process. The availability of resources and their patchy or unpredictable distribution has been shown to have an effect on clonal architecture of some species. Fragmentation is a further means of vegetative propagation, which involves unspecialized vegetative parts of the plants. By re-rooting, there is a good possibility that from a fragment a new plant will get established. At last, there is also propagation by sexually generated seeds. Even though for most macrophytes vegetative propagation dominates the usual yearly cycle, they are nevertheless important for re-establishing populations as well as for the maintenance of genetic diversity. All these possible ways of propagation vary, depending on the species, the populations and the environment. None of them have been researched on macrophyte populations in Lake Balaton and only for a few species do we have data on their requirements for growth and propagation.

In my thesis, I therefore concentrated on investigating the different means of macrophyte propagation and colonisation while taking environmental effects into account constituted a subordinate part of my work.

2 Aims

Changes in macrophyte abundance still occur in Lake Balaton – not only at the whole lake level, but more pronounced in the local patchiness. The reasons for such a great variability in abundance are however still obscure. The mechanisms of propagation and outer environmental influences on macrophyte populations are expected to be the main explanatory factors. The aim of this work was firstly to enlighten some of the propagation mechanisms of macrophytes in Lake Balaton (A-D), but also to take some of the effects of environmental conditions on the plants into account (E).

A. I wanted to assess how far shoot fragments can contribute to the propagation of different macrophyte species in Lake Balaton. In order to examine species-specific effects as well as other (ecological-environmental) factors influencing rooting success I set up an experimental series, to decide whether species differ in their abilities of colonising by fragment rooting and whether their rooting rate and fragment growth depend on the part of the shoot from which the fragments originate from (apical or mid-shoot parts).

B. I investigated the clonal architecture of *Potamogeton perfoliatus* in Lake Balaton, how it reflects clonal growth and how it is affected by different environmental conditions. For evaluating clonal growth in a variety of habitat conditions, I assumed a foraging strategy according to which certain features should be more pronounced on more agreeable sites, which were assumed to have more nitrate, more phosphorus, less organic matter content in the sediment and/or smaller fetch lengths (less mechanical stress).

C. I aimed at assessing the possibilities of macrophytes for sexual reproduction in Lake Balaton and investigated to this end what the most favourable conditions for macrophyte seed germination are. I wanted to ascertain whether seed germination is influenced by temperature, by a previous cold-treatment or by light conditions.

D. I wanted to know which mechanisms use the different macrophyte species in Lake Balaton for colonisation and how they occupy cleared patches. Further, I tried to find out whether there are species-specific strategies and whether there are seasonal differences in gap colonisation.

E. In contrast to the diverse colonisation and receding processes, which result in presence/absence, reactions on a smaller scale, like changes in morphology can be considered as well in order to assess environmental effects on plants and possibly on population dynamics. For this, I chose a dominant macrophyte of Lake Balaton, *P. perfoliatus* and investigated how the different environmental conditions in Lake Balaton are reflected in the morphology of my model plant. More precisely, I assessed whether wave exposure, sediment nutrient content and light have an effect on leaf and shoot growth.

3 Material and Methods

A. The possible re-rooting (colonisation) of shoot fragments of 6 species (*Potamogeton perfoliatus, Potamogeton pectinatus, Myriophyllum spicatum, Najas marina, Ceratophyllum demersum, Egeria densa*) was studied in an experimental series under semi-controlled conditions. 15 cm long fragments – either including the shoot apex or only stem parts – were placed in water pans filled with 2 cm sediment and 7 cm water. Three repetitions, with 23 fragments per species on average were performed. Data analysis was performed in R 2.10.0, using logistic regression analysis for colonisation probability and ANOVA for the effect of shoot parts.

B. Clonal growth was investigated on *P. perfoliatus*, one of the main macrophytes of Lake Balaton. Plants together with their rhizomes were removed from the sediment as completely as possible. 7 features of clonal architecture were measured (rhizome internode length (reflecting spacer lengths, generally two rhizome internodes for *P.*

perfoliatus), shoot length, number of rhizome branchings; shoot, rhizome and root dry weight and shoot : root ratio calculated) and together with environmental data of the sampling sites (sediment nutrient and organic matter content and wave exposure, approximated by fetch length) analyzed by PCA and multiple linear regressions. For testing hypotheses, a number of interrelations mainly based on foraging theory were assumed, regarding the growth of the above listed architectural variables and sampling site attributes.

C. A series of germination experiments were conducted in order to examine the germination requirements of Lake Balaton macrophytes. Seeds were collected during the late-summer months. *P. perfoliatus*, *P. pectinatus* and *N. marina* seeds were used. Previous cold-treatments were applied for 1-2.5 weeks at 1-2°C. Seeds were put into petri-dishes (7-15 seeds in each) on thoroughly wetted filter paper. For examining the effect of light, 1/3 of *P. perfoliatus*-dishes were wrapped in aluminium foil. White fluorescent tubes or low-energy light bulbs provided light in a 12 hour light/dark cycle. Seeds were checked at least weekly, for 3 months. Data on germination time was analysed with ANOVA or Kruskal-Wallis test. Numbers of germinated seeds were compared by Chi-square-tests.

D. The combination and application of a certain set of means of spreading under field conditions were examined in a field experiment. Ten patches (1 m^2) within vegetated areas were cleared by hand, removing also subterranean plant parts. Monthly, newly colonised plants were removed from the squares. Species and probable way of colonisation were noted, as well as plant biomass. Seasonal effects were also examined. Chi-square tests and t-tests were applied for testing the different strategies.

E. Morphological differences on *P. perfoliatus* shoots were examined along environmental gradients. From 17 sampling sites, 4-6 shoots were collected and 11 morphological features measured (shoot length, internode length, mean leaf area, leaf length:width ratio, standard leaf area, number of leaves, stem diameter at the base, stem mass density, stem dry weight, leaf dry weight and total plant dry weight). Morphological data were analysed together with environmental data (wave exposure, nutrient content of the sediment and light conditions, resulting from a water depth gradient) by PCA and General Linear Model.

4 Results

A. Fragments of all examined species (*C. demersum, E. densa, M. spicatum, N. marina, P. pectinatus, P. perfoliatus*) showed good survival (> 83%) for the first 6 weeks. *E. densa, P. perfoliatus* and *M. spicatum* fragments re-rooted to 93%, 90% and 83%, respectively. Rooting of *P. pectinatus* was much less successful (60%), while *N. marina* rooted hardly (10%). Rooting started for all species between the 2nd and the 3rd week, the process was on average quickest for *E. densa* and *M. spicatum* (2.4 weeks), a bit slower for *P. perfoliatus* (2.8 weeks) and slowest for *P. pectinatus* (3.7 weeks). Fragments including shoot apices rooted at a better rate (*P. perfoliatus* and *M. spicatum*) and shoot length growth was significantly increased for *M. spicatum*, *P. perfoliatus* and *E. densa*.

B. Maximum length of the *P. perfoliatus* rhizomes retrieved from the sediment as a whole was more than 2 m in mid-summer, based on which a growth rate of 67 cm per month was calculated. Typical ontogenetic patterns in spacer lengths were found, first increasing with age and later decreasing. Fetch length and organic matter content of the sediment had a significant negative effect on rhizome branching frequency, and a positive effect on spacer length and root biomass. The effect of nitrate concentration in the sediment was negative on spacer length, shoot and root biomass. Plants on sites with better conditions (more nutrients, less hydraulic stress, less organic matter in sediment) built an altogether more compact clone.

C. *P. perfoliatus* seeds from Lake Balaton germinated to 14.7% on average, while the mean germination time was 47 days. Previous cold treatment (stratification) had a significant positive, while dark treatment had a negative effect on germination. *P. pectinatus* seeds germinated to 7.5% on average, mean germination time was 34 days.

D. Investigating the colonisation of gaps, certain species specific strategies were found. Among the rooting macrophytes, *M. spicatum* colonised preferentially by fragment rooting (80% of all colonisation events), while *P. pectinatus* and *P. perfoliatus* used mostly rhizomatic growth for colonisation (58% and 40%, respectively). Latter achieved the highest biomass on the newly colonised patches (2 g dry weight on average per m^2), while mean dry weight of all newly established plants was between 0.9 and 1.8 g. Colonisation was most intense in August.

E. Shoot morphology of *P. perfoliatus* did not outline any clear groups in Lake Balaton, shoots from the northern and the southern shores of the Lake were not substantially different. However, several of the morphological features examined complied with gradients in the environment, i.e. in sediment nutrient conditions, wave exposure and light conditions. Light deficiency (greater water depth) generally had a negative effect which had to be compensated by shoot elongation, while a surplus in nutrients increased the size of several other morphological features (e.g. stem and leaf biomass, leaf area, internode length). Higher hydraulic stress resulted in greater stem diameter, stem density and greater leaf biomass, while in leaf area there were no differences present.

5 Conclusions

A. Rooting from fragments was very successful in the laboratory experiment, thus it could be assumed that it is also a relevant strategy for plants in the field. Indeed, the high rooting activity of *M. spicatum* shown in the laboratory corresponds to its behaviour observed in the field, but for *P. perfoliatus* and *P. pectinatus* colonisation by re-rooting in the field was less intense than expected. Better rooting of apical fragments is probably related to the phyto-hormonal activity of the apical meristems.

B. The rhizomes of *P. perfoliatus* extended to more than 2 m, showing a considerable spreading potential from already established plants or from winter-buds. Clonal architecture (spacer length, rhizome ramification, ramet placement) corresponded in most features to the hypothesized effects of environmental forces and proved thereby a certain foraging potential of *P. perfoliatus*.

C. Sexual propagation is a very important feature for most clonal plant populations under certain circumstances, and should not be neglected. Consistent results were mainly achieved for *P. perfoliatus* which proved the importance of cold temperatures prior to germination (stratification), light and the preference of warmer temperatures. For *P. pectinatus* only the significance of stratification could be shown. From this we can assume, that seeds mostly germinate in spring, after the winter-cold in Lake Balaton.

D. Species-specific colonisation strategies could be established and quantified. *M. spicatum* colonised gaps predominantly by re-rooting of shoot fragments, while *P. perfoliatus* and *P. pectinatus* colonised mainly by rhizomatic (clonal) growth. Due to the observed features, *P. perfoliatus* is more successful in sustaining and expanding already existing patches (mostly by rhizomatic growth) than newly establishing by any means. *M. spicatum* is probably best capable of establishing on new sites further away from already existing patches. An increase in colonisation rates towards the end of summer/autumn seems to be a general pattern, as it has been described for some other species in other habitats, too.

E. Morphological features of *P. perfoliatus* could be linked rather well to certain environmental gradients existing in Lake Balaton, such as trophic state, wave exposure and water depth. Some of the observed responses in morphology could be interpreted as actually induced by environmental forces and furthermore also as being adaptive.

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