Clonal architecture and patch formation of *Potamogeton perfoliatus* L. in response to environmental conditions

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Introduction

Chapter 1. INTRODUCTION

Submersed macrophytes usually occur in patches which differ in size, height, shape and shoot density. Also *Potamogeton perfoliatus* L. (perfoliate pondweed), a species common to many Central European Lakes, forms such patches ranging from semi-continuous to widely dispersed stands over a wide range of scales (Lehmann 1997). In many lakes, *Potamogeton* patches change location, size, shape and density in the long run (Schmieder 1997), whereas in other lakes they remain spatially stable in the medium range (Gafny & Gasith 1991, Walser 1996) or disappear and reappear from year to year (Scheffer et al. 1992). Macrophyte patches may be round (Valta-Hulkkonen et al. 2003), elliptical (Gusak 1983), ring-shaped (Wikberg & Svensson 2003) or irregular. They may consist of a few shoots or extend to several kilometres and comprise millions of shoots.

Since *P. perfoliatus* is a modular plant consisting of reiterations of ramets along rhizomes that are anchored in the sediment, the visible spatial patterns provide only a partial picture of the complicated belowground patterns. The proper spatial pattern is hidden to the researcher: neighbouring shoots may stem from two different plants, while one plant might spread over several square meters.

The knowledge about the formation of spatial patterns is important for a variety of reasons and applications. Presence or absence of macrophytes as well as size, shape and density of vegetation patches are important for both biotic and abiotic processes in the ecosystem. Spatial patterns play a vital role in structuring of the littoral zone of lakes (Jeppesen et al. 1997). Macrophytes provide a refuge for herbivores (Timms & Moss 1984), shelter for prey (Dvorak & Best 1982), refuge for young fish (Walser & Löffler 1993), substrate for epiphytes (Dvorak & Best 1982, Wetzel 1983), and food for waterfowl, mammals and invertebrates (Moen & Cohen 1989). Moreover, macrophyte composition and patch characteristics affect the number and diversity of invertebrates (De Vos 1954, Webster et al. 1998) influence the distribution and age-characteristics of littoral fish (Weaver et al. 1997), and modify littoral food webs (Beklioglu & Moss 1996, Lauridsen et al. 1996), as well as host-epiphyte relationships (Levin & Mathieson 1991).

In dependence of their spatial characteristics, aquatic plant patches influence nutrient cycles (Barko & James 1997), reduce current velocity (Madsen & Warmke 1983, Fonseca 1989, Losee & Wetzel 1993) and consequently enhance sediment stability, increase sedimentation of particles (Sand-Jensen 1998), stabilize clear water by preventing resuspension of sediments (Meijer et al. 1999) and reducing nutrient levels (Van Donk et al. 1989, Sand-Jensen 1998), lower sediment pH, raise sediment redox potential, release oxygen through their roots, increase P retention in the sediment (Jaynes & Carpenter 1986), and release organic carbon which might influence the bacterial activity or the microbial biomass in the sediment as well as the denitrification potential within deeper root zones (Karjalainen et al. 2001). The P released by decomposing aquatic plants is an important source of P for pelagic phytoplankton (Barko & Smart 1980, Smith & Adams 1986). Plant patches thus substantially modify their own environment and that of the littoral biocoenosis.

Despite the recognition of the importance of spatial patterns of submersed macrophytes for the littoral ecosystem, the rules of pattern formation are not well understood (Lehmann 1997). Why does a fast growing species like *P. perfoliatus* not cover larger uniform lake areas after a certain number of years, even if competitors are absent? Since seeds are considered as relatively unimportant for propagation (Chambers & Kalff 1985), the knowledge of its architectural programme at the individual plant level is the key to understanding patch patterns and patch dynamics. As in other clonal plants, the growth patterns of *Potamogeton* are assumed to be non-random (Dale 1999). Clonal plant architecture comprises growth rules such as number of ramets, branching patterns (frequency and
angle) of the rhizome, biomass allocation to rhizomes and shoots, and the rhizome spacer length in between consecutive shoots. These rules are thought to be plastic to a certain degree allowing for adaptive responses to a spatially heterogeneous environment (Marbà & Duarte 1998).

Whereas clonal architecture and spatial patterns of terrestrial plant species have received considerable attention (Huber & Stuefer 1997, Klimes et al. 1997), there are less studies on clonal growth of aquatic macrophytes. The aqueous medium requires a completely different physiology of aquatic plants compared to terrestrial forms. Moreover, life cycle, reproduction, morphology, clonal architecture and growth pattern are species-specific and can not simply be transferred to other species. If we want to model clonal aquatic macrophytes, we therefore need more consistent studies. Most existing spatial studies on aquatic macrophytes concern above-sediment patch patterns (Vidondo et al. 1997, Bradley & Stolt 2006). In-situ research on the architecture of rhizomes and roots is rare for difficulties with assessment under water and below the sediment (Ervin & Wetzel 1997). Previous work was mainly published on descriptive architecture of seagrasses (Olesen & Sand-Jensen 1994b, Olesen & Sand-Jensen 1994a, Duarte et al. 1996, Duarte et al. 1998, Marbà & Duarte 1998, Klimes 2000, Molenaar et al. 2000, Nielsen & Pedersen 2000, Pagès et al. 2000, Paling & McComb 2000), and Reusch et al. 1998 excavated some seagrass systems in the context of a genetic study. Freshwater macrophyte clonal morphology included studies on emergent Scirpus (Clevering & Hundscheid 1998), Phragmites australis (Vretare et al. 2001), Potamogeton pectinatus (Idestam-Almquist & Kautsky 1995), and Potamogeton alpinus (Brux et al. 1987). In general, architectural studies are neither spatially concise nor related to patch characteristics, and spatial studies exclude clonal architecture. In both fields, comprehensive studies on P. perfoliatus are lacking.

The aim of this thesis is to describe the spatial patterns of P. perfoliatus, to search for the mechanisms that generated the patterns, and to understand the influence of plants on the patterns. Our hypothesis was that in case of the submersed macrophyte species P. perfoliatus, (1) architectural growth rules pre-determine spatial patterns, and (2) environmental factors influence architecture, i.e. the species shows morphological plasticity. In order to understand the spatial growth patterns, a combination of in-situ observations, aquarium experiments and mesocosm experiments was used at small, medium and landscape-size scales (Fig. 1.1).

![Research at different scales](Fig. 1.1)
The core task of the research project was to assess growth patterns. As a result, the thesis provides a detailed architectural library of clonal architecture including biomass allocation, shoot length, and variation of spacer length, branching frequency and branching angle of *P. perfoliatus* in Lake Constance along with detailed maps of below-sediment rhizome networks (Chapter 3).

A number of environmental factors is thought to be responsible for the variability and plastic growth of aquatic macrophytes (Tab. 1.1). In our study, we investigated the effects of nutrient and light conditions on both architecture and pattern. In order to test for nutrient effects, we fertilized small quadrats *in-situ*, analysed clonal architecture and plant tissue samples at sites with different vegetation growth (Chapter 3), and carried out a mesocosm experiment with different nutrient levels (Chapter 5). In order to test for light effects, we carried out a self-shading experiment with three different stand densities and compared clonal architecture and patch characteristics (Chapter 4). An aquarium experiment focusing on the question of resource transfer between ramets also included a light component (Chapter 6).

Additionally, we were interested in clonal integration, i.e. the support of younger ramets by older ramets (or vice versa) by the transfer of nutrients, signals or photosynthetates. The question was whether clonal integration enhances survival, overall performance, and patch expansion in *P. perfoliatus*, and in which manner it affects clonal architecture (Chapter 6).

**Tab. 1.1** Environmental parameters which influence plant growth and/or clonal architecture of submerged macrophytes

| water depth | Duarte & Kalff 1990b, Rea *et al.* 1998 |
| herbivory | Armellina 1999, Jonzén *et al.* 2002 |
All findings were used to create a clonal model based on the previous non-clonal growth model Charisma (Van Nes 2002, Van Nes et al. 2003), a ramet-based spatially explicit model (Chapter 7). Our model is the first detailed model including architectural, spatial, environmental, physiological and demographic components and simulates both individual clonal plant growth and patch growth. By simulating different clonal growth architecture, we built the bridge between clonal architecture and patch patterns.

In the synthesis and discussion (Chapter 8), the most important results are presented, conclusions are drawn, and different theories of architectural responses to habitat quality are discussed. Ultimately, we hope that the information on clonal growth rules can be used for the understanding and management of recolonization and restoration of littoral biotopes.
Chapter 2. LAKE AND MACROPHYTE CHARACTERISTICS

Lake characteristics

Lake Constance is a large water body in Central Europe shared by Germany, Switzerland and Austria (Figs. 2.1, 2.2). The perialpine lake has been formed by the action of glaciers about 15000 years ago. Some of its characteristics are listed below (Tab. 2.1). The lake consists of two separate basins which are connected by a 4 km stretch of the river Rhine. The larger basin, called ‘Obersee’ (Upper Lake), is deep and monomictic. It has steep banks, a relatively well-mixed epilimnion, a true pelagic zone, and a relatively small littoral zone of 15 % (IGKB 2004). The littoral banks of Lake Überlingen are, for example, about 20-30 m wide. The smaller basin, called ‘Untersee’ (Lower Lake), consists of three individual dimictic basins and has an extensive littoral area (28 %).

Lake Constance is situated in the warm-temperate climate zone with atlantic and continental influences and an average annual air temperature of 8-9 °C. The lake surface has not been frozen since the year 1963.

Fig. 2.1 Location of Lake Constance in Europe and geography of Lake Constance (adapted from Straile & Geller 1998, Pinnel 2007); 1: sampling area near the island of Reichenau, Lower Lake Constance (Chapter 3), 2: experimental area at Upper Lake Constance and location of mesocosm (Chapters 4, 5)
Fig. 2.2 Lake Constance, satellite image *(Landesvermessungsamt Baden-Württemberg)*

Tab. 2.1 Lake Constance in brief *(IGKB 2004)*

<table>
<thead>
<tr>
<th></th>
<th>Lake Constance</th>
<th>Upper Lake</th>
<th>Lower Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>location</td>
<td>47 n. lat., 9° e. long.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>elevation</td>
<td>395 m a.s.l.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>average air temperature</td>
<td>8 - 9 °C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>average air temperature, July</td>
<td>18°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>average air temperature, January</td>
<td>-1°C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>average water temperature</td>
<td>5.7 °C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>average precipitation</td>
<td>805 - 1380 mm/a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>main wind direction</td>
<td>W, S/W</td>
<td></td>
<td></td>
</tr>
<tr>
<td>catchment area</td>
<td>11500 km²</td>
<td></td>
<td></td>
</tr>
<tr>
<td>volume</td>
<td>48.4 km³</td>
<td>47.6 km³</td>
<td>0.8 km³</td>
</tr>
<tr>
<td>surface area</td>
<td>535 km²</td>
<td>472 km²</td>
<td>62 km²</td>
</tr>
<tr>
<td>shore length</td>
<td>273 km</td>
<td>186 km</td>
<td>87 km</td>
</tr>
<tr>
<td>maximum length</td>
<td>63 km</td>
<td></td>
<td></td>
</tr>
<tr>
<td>maximum width</td>
<td>14 km</td>
<td></td>
<td></td>
</tr>
<tr>
<td>maximum depth</td>
<td>253 m</td>
<td>40 m</td>
<td></td>
</tr>
<tr>
<td>mean depth</td>
<td>101 m</td>
<td>13 m</td>
<td></td>
</tr>
</tbody>
</table>

The hydrograph of Lake Constance is characterized by low water in January, high water in June after snow-melt in the Alps and a mean annual water level fluctuation of about 2 m (Fig. 2.3). These fluctuations are very important for biological and chemical processes in the littoral zone. During the last years, the annual fluctuations tended to increase and the absolute water levels tended to fall *(IGKB 2004)*.
After an eutrophication period in the 1970ies and a slow recovery, the Upper Lake is now again meso-oligotrophic, the Lower Lake mesotrophic. In comparison to the Upper Lake, the Lower Lake has warmer water, higher water and sediment nutrient levels, and higher sedimentation rates (IGKB 2004). Most in-situ experiments in the framework of this study were carried out at the Lower Lake. The sediment for the mesocosm experiments was also taken from the Lower Lake, while lake water for the aquaria and mesocosm experiments originated from the Upper Lake.

**Macrophyte characteristics**

The lake has extensive stands of submersed macrophytes which underwent a significant change in abundance, species composition and zonation during the last 50 years. The eutrophication period of the 1970s coincided with an increase of eutraphentic species and a decrease of most other species. During the re-oligotrophication period of the 1980s, most disappeared species returned back to the lake. The present state is similar to the one before eutrophication. For a detailed analysis of species, see Schmieder (1998).

*Potamogeton perfoliatus* - the species investigated in this study - is the second most common submersed vascular plant species in Lake Constance after *Potamogeton pectinatus* (Schmieder 1997). Plants consist of primary ramets (i.e. leafy shoot with root), rhizomes and a varying number of secondary respectively higher order ramets (Fig. 2.4). *P. perfoliatus* has a vegetation period from May until September, vanishes in autumn due to senescence and autumn storms and survives the winter in the form of turions in the sediment (Fig. 2.5). *P. perfoliatus* occupies depths between 2 and 5 meters, develops distinct patches, has shoots up to 4.5 m in length (Fig. 2.6) and develops flowers that may or may not reach the water surface depending on the water level fluctuations. In some years, canopies are formed on the surface. During the phase of eutrophication, *P. perfoliatus* decreased considerably in the Lower Lake, but increased again after re-oligotrophication.
Fig. 2.4 *P. perfoliatus* (a) plant with 17 ramets and 8 branchings (b) turions

Fig. 2.5 Annual growth cycle of *P. perfoliatus* in Lake Constance; left axis/squares: no of shoots/m² (rich growth patch, Chapter 3); right axis/curve: av. daily water temperature at 50 cm depth (°C) at Pegel Bregenz (www.vorarlberg.at)

Fig. 2.6 *P. perfoliatus* patches, Lower Lake Constance (photos: J. van Schie, Rijkswaterstaat Waterdienst)
Typical medium to landscape scale macrophyte composition at the Lower Lake

The main project area was located at the Lower Lake, in a bay W-SW of Niederzell on the island of Reichenau (Fig. 2.1). This bay has an extensive shallow littoral area with relatively strong wind exposure. The main species are Potamogeton perfoliatus, Potamogeton pectinatus, Chara spp. and Najas marina ssp. intermedia. Medium to landscape scale data was collected with permanent grids and airborne multispectral scanners.

In order to gain a first overview, a typical landscape-scale grid (25 x 25 m, squares of 1 m²) was established by fixed lines (average depth: 2.50 m) and plants were mapped by snorkelling along the lines. The area was mapped on 21.07.2000 and on 17.05.2001 respectively 25.07.2001 to analyse patch patterns and to look at seasonal changes (Fig. 2.7).

The remotely sensed data of the sampling area was acquired for the years 2000-2002 by a multispectral sensor onboard an aircraft. The Modular Inversion & Processing System (MIP) was used as a processing tool to account for aerosols, sun glitter correction, atmosphere, water surface and water column corrections with a physically based process chain (Heege et al. 2003). The final results are shown as percentage coverage of bare sediment, tall macrophytes (mainly P. perf. and P. pect.) and low macrophytes (Characeae) up to a depth of 4.5 m by fitting with ground truth (Fig. 2.8). Whereas this earlier automatic classification did not discriminate between P. perfoliatus and P. pectinatus, the improved method now includes species discrimination. This is achieved by implementing data from a hyperspectral scanner and utilizing the optimal wavelengths from a comprehensive spectral library of eight macrophyte species, acquired by a submersible spectroradiometer (Pinnel 2007).

Both methods show that the plants form species-specific patches in this area (Figs. 2.7, 2.8). Chara spec. covers extensive bottom areas, especially in form of near-shore bands. In the examined area, P. perfoliatus has its main distribution at the shoreward side of the shallow zone and forms distinct patches. P. perfoliatus shoots reach 2.5 m (the water surface), density is frequently highest in the centre of the patch (Fig. 2.7b).

The comparison of processed scanner images from three different years shows that medium and high growth forms occur roughly at the same sites each year, but patch size and shoot lengths differ (Fig. 2.8). Short species (Chara ssp.) show more variability in bottom coverage. All differences are partly due to different development states at the assessment day due to different weather conditions during earlier growth phases. The P. perfoliatus patch mapped by snorkelling showed not much spatial expansion during one season (Fig. 2.7c). Although at some places, the plants extended by 3 m during the vegetation period, the net area of P. perfoliatus decreased by 1.9 %. Patch receding occurred mainly at the lakeward side with deeper water and may be partially due to light attenuation after increasing water levels.
Fig. 2.7 (a) 3-D representation of distribution and shoot length and plan view of (b) density (21.07.2000) (c) changes in patch growth of *P. perfoliatus* between 17.05.2001 and 25.07.2001.
Fig. 2.8 Patch patterns and patch dynamics over a period of 3 years, north-west Reichenau. Data acquired by an airborne scanner and processed by a physically based algorithm. The ‘golf club’ is a shallow area connected to the mainland by a man made earth dam (graphic: A. Wolfen, Universität Hohenheim).
Chapter 3. SPATIO-TEMPORAL DYNAMICS AND PLASTICITY OF CLONAL ARCHITECTURE IN POTAMOGETON PERFOLIATUS

Susanne R. Wolfer & Dietmar Straile

Abstract

Aboveground and belowground clonal growth architecture was compared for two neighbouring patches of Potamogeton perfoliatus L. in Lake Constance, representing typical sparse and dense growth types. A detailed map of individual ramets and their corresponding rhizome network was produced and the seasonal development of ramet sprouting and rhizome growth was reconstructed. Rhizomes extended at rates ranging between 40 cm y⁻¹ and 63 cm y⁻¹, and added a new shoot for every 1 cm to 20 cm of rhizome produced. The main rhizome axis grew in a semi-linear fashion, with deviation means of 15° and 24°, and developed 0 to 0.5 branches per plant, with an insertion angle from 15° to 90° degree. Total rhizome length of all plants amounted to 5 m m² and 11 m m² at the two sites. The total biomass produced at the two sites differed ten-fold. The neighbouring patches also showed strikingly different allocation patterns which are interpreted as foraging.

Contrary to the prediction of the foraging hypothesis, there was only a small difference in mean spacer length between sites. On the other hand, the spacer length was surprisingly plastic relatively to total biomass. We propose that spacer length is not an independent part of the foraging strategy, but rather a result of overall productivity and biomass allocation.

Phosphorus content of plant tissue at the more productive site was two-fold higher than that at the less productive site which suggests that the different growth types are due to different nutrient availability in the sediment. In-situ fertilization of a less productive site increased the P content to the levels of the productive site.

In-situ fertilization also resulted in higher ramification, lower root allocation and decreased spacer length and confirmed the foraging capability of Potamogeton perfoliatus.

Keywords: macrophyte; clonal architecture; rhizome; biomass allocation; foraging, spatial growth
Introduction

Macrophytes usually occur in patches which play a vital role in structuring of the littoral zone of lakes (Jeppesen et al. 1997). Potamogeton perfoliatus L. forms such spatial patterns ranging from semi-continuous to widely dispersed patches over a wide range of scales (Walser 1996, Lehmann 1997). In many lakes, Potamogeton patches change location, size, shape and density in the long run (Schmieder 1997) but remain spatially stable in the medium range (Walser 1996, Gafny & Gasith 1991), whereas in other lakes, they disappear and reappear from year to year (Scheffer et al. 1992). Presence or absence of macrophytes, as well as size, shape and density of vegetation patches influence element cycles (Barko & James 1997) and littoral food webs (Lauridsen et al. 1996). Despite the recognition of the importance of spatial patterns for the littoral ecosystem, it is not yet understood how these patterns are generated (Lehmann 1997) and which role can be attributed to architectural growth rules, morphological plasticity in response to spatially heterogeneous environmental factors, and competition between species or genets.

The concept of plant architecture suggests that each plant species has its own growth form (Bell 1984). Compared to non-clonal plants, clonal plant architecture comprises additional growth rules such as number of ramets, branching patterns (frequency and angle) of the rhizome, and the rhizome spacer length in between consecutive shoots (Callaghan et al. 1990, Huber et al. 1999). These rules are plastic to a certain degree allowing for adaptive responses to a spatially heterogeneous environment (Marbà & Duarte 1998).

Since seeds are considered as relatively unimportant for propagation of Potamogeton (Walser 1996), the knowledge of its architectural programme is essential for understanding the different rates and patterns at which this plant occupies space. Information on clonal growth rules is also important for the understanding and management of recolonization and restoration of littoral biotopes. Whereas descriptive mappings of aquatic vegetation patches have a long tradition, the importance of modular structure in studies of macrophyte stands has only recently been acknowledged. Most previous work on aquatic plant architecture has been published for seagrasses (e.g. Marbà & Duarte 1998, Molenaar et al. 2000) and emergent macrophytes (e.g. Clevering & Hundscheid 1998, Klimes 2000), whereas the clonal morphology of submersed freshwater macrophytes has received less attention (but see Idestam-Almquist and Kautsky 1995). In general, architectural studies lack spatial information, and vice versa, furthermore investigations on temporal aspects of clonal architecture and spatial pattern formation are rare. In all above-mentioned fields, comprehensive studies on P. perfoliatus are missing.

Below, we present detailed information on the characteristics of clonal growth architecture (length of rhizome spacers, branching intensity, branching angle) of P. perfoliatus, temporal dynamics, and natural variability of two typical growth types in Lake Constance. One site was characterized by lush patch growth with shoots reaching the water surface (referred to as ‘rich growth’ below) whereas at the other site, the shoots remained low and sparse (referred to as ‘poor growth’ below). The conclusions of the study are supported by an in-situ fertilization experiment and will be discussed in the light of foraging theory.

Materials and methods

Study site and general definitions

The growth architecture of P. perfoliatus was investigated at the ‘Lower Basin’ (‘Untersee’) of Lake Constance (9°18’E, 47°39’N), a large, subalpine lake on the borders of Germany, Switzerland and
Austria. The sub-basin has a surface area of 62 km², a mean depth of 13 m and a maximum depth of 40 m (Wessels 1998) and holds an extensive littoral area. *P. perfoliatus* is the second most common submerged macrophyte species in the area (Schmieder 1997), has a local vegetation period from approximately May to September and survives the winter in the form of subterranean turions. The patches with sampling sites A and B (1 m² each) were located in a bay south of the north-western edge of the island of Reichenau, at a depth of approximately 2.2 m ± 0.2 m throughout the growth period. The distance between the two monospecific stands was 30 m.

For description of patch characteristics, the following terminology will be used: 'Plant' is defined as a complete unit of ramets connected by rhizomes, originating from a single primary shoot. 'Ramet' is a single module of a clonal plant, consisting of shoot, rhizome and roots. Spacer length is the rhizome length between two consecutive shoots of the same plant (Fig. 3.1).

![Fig. 3.1 Apical section of *P. perfoliatus* plant. Rhizome diameter increases in growth direction. Turions are formed at main axis and side branches. The younger ramets are more stout than the older ramets](image)

**In-situ growth monitoring**

On May 01 2000, when the first primary shoots were visible, two square frames with 1 m side length and a 10 x 10 cm grid subdivision were placed on the lake sediment at site A and B. The position of individual shoot bases within the grid and their corresponding lengths were noted on PVC-boards by snorkelers on four occasions in May, June and August 2000. The quadrats represent open systems: plants that had their origin outside could grow into the quadrats and plants from inside were allowed to grow out of the quadrats.

**Architectural analysis**

Final harvest was made by SCUBA divers in August 2000. Each shoot was labelled at the top as well as close to the sediment. A transparent board (1 m²) placed above the sampling quadrat was used to draw a map of shoot positions. The shoots were cut off directly above the sediment and harvested with the upper set of tags before the sediment was removed by hand up to a depth of 15 cm. Rhizome networks were removed as completely as possible with the lower set of tags attached.
In the lab, shoot length, ramifications and number of ramets per plant were recorded. All plants were cleaned and separated into shoots, rhizomes and roots. Turions were discarded because owing to their deep position in the sediment, they could not be harvested quantitatively. Plant fractions were dried at 105 °C until constant weight. After allowing for cooling down to room temperature, dry weights were determined on an analytic scale. Ramet number, branching frequency, branch angle, ramet length, a subset of spacer lengths, total rhizome length, specific rhizome weight, and biomass allocation values were determined for all plant material included in the m². For calculations of plant size, plant rhizome length, and radial angle, only those plants growing completely within the quadrat were considered. Spacer length was calculated as Euclidian distance between the nearest sibling ramets. Calculated spacer lengths compared adequately with a subset of measured spacer lengths ($r = 0.98, p < 0.001$).

The drawings of shoot positions and rhizome networks were scaled down by transformed coordinate systems. The mapping of shoots over the investigation period and the additional information about connections between these shoots made it possible to assign daughter shoots to parent shoots and to reconstruct the spatio-temporal growth of individual rhizome systems. A rough estimate of the temporal dynamics of biomass allocation was based on the number of shoots, mean shoot length and the assumption of constant weight-specific allocation into shoots and ramets. Angles were determined to the nearest degree on the reconstructed map.

**Fertilization experiment and tissue analysis**

On July 02 2001, five typical poor growth areas of 0.25 m² were fertilized (‘fertilized type A’) with 250 g slow-release N-P-K-fertilizer Plantacote Depot 4 M® (14 % N, 9 % P$_2$O$_5$, 15 % K$_2$O), additional three low growth sites were assessed as control (‘type A’). All sites had an initial density of eight shoots per m² and were located in the same lake area as A and B, at a maximum distance of 50 m between each other. On August 15 2001, the complete plants including rhizomes were removed from the sediment and processed in the same way as those from locations A and B. Leaf tissue of the fertilized and poor growth sites as well as additional rich growth sites (‘type B’) was analysed for carbon and nutrient content. C was determined by Autoanalyzer (ThermoQuest NCS-2500) after combustion. P and N values were determined by Autoanalyzer II (Bran & Luebbe) following digestion with potassium persulphate. For the statistical analysis of percentages, data were arcsin transformed. Statistical analyses were performed with SAS software (SAS Institute Inc., Cary, NC, USA 1999-2001).

**Results**

**General growth characteristics**

At the first field visit, ramet numbers were identical, but during the following two months, ramet numbers were always higher at site B than at site A. The sites also showed a strikingly different development in several other aspects (Fig. 3.2). At site A, biomass at harvest was more than ten-fold lower (17 g DW m$^{-2}$) than at site B (200 g DW m$^{-2}$). The maximum density was 90 ramets at site A compared to 210 at site B (Fig. 3.3a). The calculated number of plants was 18 with 5 ± 1 ramets each at site A, compared to 25 plants with 8 ± 3 ramets each at site B. On average, shoots measured 12 cm ± 7 cm at site A compared to 66 cm ± 75 cm at site B (Fig. 3.3b). At site B, many shoots had reached the water surface and formed a canopy (285 cm max. shoot length), whereas at site A the longest shoot measured only 48 cm.
Fig. 3.2 Reconstructed spatio-temporal growth dynamics of *P. perfoliatus* at poor growth (A) and rich growth (B) site. Points represent ramets, lines show rhizome connections, arrows indicate growth direction, double arrows show sites of turion formation.
Growth architecture

Primary *P. perfoliatus* ramets developed plagiotropic stems (lateral rhizomes) initiated at the ramet base which produced further ramets on every second rhizome node and adventitious roots at every node (Fig. 3.1). Overwintering organs, also called turions, were formed at the end of the main rhizome as well as on most branch tips. Rhizome branching was acropetal and occurred only at the base of ramets. The maximum level of branching encountered at the research site was 1st order. Remarkably, there were some primary ramets bearing two rhizome axes at two different vertical nodes. Rhizome branch growth was subordinate to the growth of the main rhizome axis. No true branches were found at site A, whereas at site B every second plant (every 17th ramet) had developed a branch. Initial rhizomatous growth direction appeared to be random. The mean radial angle was $15° ± 12°$ at site A and $24° ± 25°$ at site B, and the mean insertion angle (branch angle) was $68° ± 15°$ at site B ($15°$ to $90°$). Especially at site B, rhizomes of different plants crossed each other frequently.

![Fig. 3.3 (a) Temporal development of ramet numbers and (b) average shoot length ± S.E. of *P. perfoliatus* at poor growth (A) and rich growth (B) site](image)

**Fig. 3.3 (a)** Temporal development of ramet numbers and **(b)** average shoot length ± S.E. of *P. perfoliatus* at poor growth (A) and rich growth (B) site

![Fig. 3.4 (a) Frequency distribution of spacer length, values on x-axis indicate midpoints of intervals (b) spacer length ± S.E. between primary and higher order shoots (main axis only) of *P. perfoliatus* at poor growth (A) and rich growth (B) site](image)

**Fig. 3.4 (a)** Frequency distribution of spacer length, values on x-axis indicate midpoints of intervals **(b)** spacer length ± S.E. between primary and higher order shoots (main axis only) of *P. perfoliatus* at poor growth (A) and rich growth (B) site
The spacer length was highly variable at both sites ranging from 1 cm to 20 cm of rhizome produced between two shoots (Fig. 3.4a). However, average spacer lengths were similar with 8.0 ± 3.2 cm at site A and 7.6 ± 3.4 cm at site B. Part of the spacer length variation can be attributed to the order of shoots (Fig. 3.4b). At site B, spacing increased in the direction of new ramet recruitment. Average distance between ramet 6 and 7 (11 cm) was almost three times the distance between primary and secondary ramets. In contrary, spacer length at site A approached a constant already between the secondary and tertiary ramets. Spacer order (ANOVA: $F_{1,162} = 48.5, p < 0.0001$) and the square of spacer order ($F_{1,162} = 24.1, p < 0.0003$) explained 37% of the variability of spacer length. The significant contribution of the square root of spacer length indicates a nonlinear relationship between the length and order of spacers. After accounting for the effects of spacer order, analysis of covariance shows that the two sites differ significantly in spacer length ($F_{1,160} = 12.3, p < 0.001$) but also in the increase of spacer length with spacer order ($F_{1,160} = 10.4, p < 0.001$). The site effect, however, increases the adjusted $r^2$ of the model by only 4%, showing its secondary importance compared to the effects of spacer order.

Final total rhizome length was 5.4 m at site A compared to 11 m at site B. The lower weight-length relationship of rhizomes at site A (6.9 mg cm$^{-1}$) compared to site B (7.7 mg cm$^{-1}$) was probably due to a smaller rhizome diameter at site A. Mean rhizome growth of individual plants ranged between 40 cm yr$^{-1}$ (site A) and 63 cm yr$^{-1}$ (site B) and determines the maximum extension of the outer perimeter of a patch.

![Shoot production (mg dw d$^{-1}$ plant$^{-1}$)](a)

![Rhizome production (mg dw d$^{-1}$ plant$^{-1}$)](b)

**Fig. 3.5 (a)** Shoot growth rate ± S.E. and **(b)** rhizome growth rate ± S.E. per plant of *P. perfoliatus* at poor growth (A) and rich growth (B) site

**Biomass allocation**

At the time of harvesting, sites A and B differed considerably in biomass allocation. Shoot-, rhizome- and root biomass amounted to 73%, 22% and 5% of total dry weight at site A compared to 95%, 4% and 1% at site B. The estimation of temporal dynamics of biomass allocation (Fig. 3.5a,b) shows that the initial shoot growth rates were similar. At the second field visit, the shoot growth rate at site B was several times higher than at site A (Fig. 3.5a) which implies a higher total photosynthetic capacity. Despite the large difference in photosynthetic tissue, the rhizome growth rates showed no significant difference between the two sites (Fig. 3.5b).
**Chapter 3**

**Fertilization experiment and tissue analysis**

Fertilization of plants resulted in longer shoots, almost three-fold biomass (t-test, \( p < 0.08 \)) and a doubling in shoot number (t-test, \( p < 0.08 \)). Mean rhizome length was shorter in the fertilized treatment (5.1 cm) than in the control (6.4 cm) (t-test, \( p < 0.06 \)). The unfertilized plants had no branches, whereas under fertilization, an average of 3.6 branchings per quadrat was found. Shoot allocation was higher (t-test, \( p < 0.03 \)) and rhizome and root allocation were lower (t-test, \( p > 0.05 \) and \( p < 0.01 \)) in the fertilized quadrats than in the controls (Tab. 3.1).

**Tab. 3.1** Biomass allocation (% dry weight) of *P. perfoliatus* in poor growth (type A, \( n=3 \)) and fertilized poor growth (fertilized type A, \( n=5 \)) quadrats

<table>
<thead>
<tr>
<th></th>
<th>Shoot ± S.D. (%)</th>
<th>Rhizome ± S.D. (%)</th>
<th>Root ± S.D. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type A</td>
<td>64 ± 4</td>
<td>29 ± 1</td>
<td>7 ± 3</td>
</tr>
<tr>
<td>Fertilized type A</td>
<td>80 ± 10</td>
<td>17 ± 9</td>
<td>3 ± 1</td>
</tr>
</tbody>
</table>

N content (% dry weight) was lower in type A plants than in fertilized type A plants (Tukey’s HSD test, \( p < 0.005 \)), P content (% dry weight) was lower in type A plants than in fertilized type A plants and rich growth type B plants (Tukey’s HSD test, \( p < 0.001 \)), and C:N, C:P and N:P weight ratios of leaf tissue were higher in type A plants than in fertilized type A plants and rich growth type B plants (Tukey’s HSD test, all \( p < 0.006 \)) (Tab. 3.2).

**Tab. 3.2** N and P contents (% dry weight), C:N, C:P and N:P weight ratios of *P. perfoliatus* leaf tissue in poor growth (type A, \( n=3 \)), fertilized poor growth (fertilized type A, \( n=5 \)), and rich growth (type B, \( n=5 \)) quadrats

<table>
<thead>
<tr>
<th></th>
<th>% N</th>
<th>% P</th>
<th>C:N</th>
<th>C:P</th>
<th>N:P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type A</td>
<td>1.7 ± 0.4</td>
<td>0.14 ± 0.03</td>
<td>22.4 ± 4.4</td>
<td>268.4 ± 55.3</td>
<td>12.2 ± 2.5</td>
</tr>
<tr>
<td>Fertilized type A</td>
<td>3.1 ± 0.8</td>
<td>0.36 ± 0.11</td>
<td>13.8 ± 3.9</td>
<td>120.5 ± 39.8</td>
<td>8.7 ± 0.9</td>
</tr>
<tr>
<td>Type B</td>
<td>2.5 ± 0.3</td>
<td>0.35 ± 0.11</td>
<td>16.1 ± 1.8</td>
<td>120.7 ± 29.1</td>
<td>7.5 ± 1.6</td>
</tr>
</tbody>
</table>

**Discussion**

The results of our study show a common architectural base-programme at two neighbouring stands of *P. perfoliatus*, but also striking variability in some growth characteristics including ten-fold total biomass, two-fold density, five-fold shoot length, two-fold total rhizome length, higher branching frequency, and higher biomass allocation to shoots and less to roots at site B compared to site A.

The unequal nutrient concentrations of plant tissue at the two sites is a strong indication that growth differences were due to differences in sediment nutrient availability (Langeland *et al.* 1983, Hilbert 1990) which is known to show considerable spatial variability (Downing & Rath 1988). Causes such as water column nutrients, light conditions and currents can be ruled out because the two patches are located close by. Genotypic differences are unlikely because *Potamogeton* propagates vegetatively in Lake Constance (Walser 1996). Also the increase in tissue P in the fertilized quadrats suggests that
type A plants were P limited. In fact, the P content of type A plants (0.14 %) is close to that considered as limiting for aquatic macrophytes (0.13 %) by Gerloff and Krombolz (1966).

Foraging theory considers changes in branching frequency, spacer length, and biomass allocation as mechanisms for the preferential location of modules in favourable microsites, and as means of an improved exploitation of resources such as light or nutrients (Hutchings 1997). Intraspecific clonal variability due to nutrient availability has been described for terrestrial plants (Cheplik 1995) and seagrasses (Pérez et al. 1994). As predicted by foraging theory, we found increased branching intensity at the rich site B as well as in the fertilized quadrats. Branching intensity is positively related to nutrient supply in many terrestrial clonal plants (Hutchings & De Kroon 1994), aquatic freshwater plants (Evans 1988), and seagrasses (Terrados et al. 1997a) and is thought to maximize the number of ramets at a suitable site.

As predicted by foraging theory, plants at the nutrient-deficient site allocated considerably more biomass to roots than plants at the rich site, and plants in the controls of the fertilization experiment allocated more biomass to roots than the fertilized plants. This allocation rule has been confirmed by a variety of experiments with clonal terrestrial plants (review of Hutchings 1997) and submersed macrophytes (Kautsky 1991, Reusch et al. 1994). Recently, it has been proposed that allocation differences under different nutrients budgets are rather a consequence of allometry than of morphological plasticity, as smaller plants frequently show a higher allocation to belowground structures (Gedroc et al. 1996, Müller et al. 2000). Site A ramets, however, have ceased height growth in favour of producing longer rhizomes and additional modules and therefore represent an architectural model different from that of site B. Hence, the observed differences in biomass allocation are apparently not the result of allometric differences, but rather the result of different growth strategies.

Mean spacer length did not differ strongly between the two sites. According to the foraging hypothesis, however, plants in good habitats (B) should have shorter spacers in order to place a maximum amount of shoots in the favourable habitat while plants in less favourable habitats (A) should grow long spacers in order to escape from the bad site. Although some investigations confirm the hypothesis for rhizomatous species, other researchers found indifferent or even longer rhizomes in more favourable habitats (De Kroon & Hutchings 1995). To explain the latter results, Hutchings and De Kroon (1994) proposed the growth hypothesis (see also Stoll et al. 1998), according to which spacer length should increase at favourable sites as they allow a higher productivity. The increase in spacer length with the order of ramets at both stands is, for example, in accordance with the prediction of the ‘growth hypothesis’ and can be interpreted as a result of an increasing overall productivity of a rhizome system with increasing amount of photosynthetically active and clonally integrated ramets. The lack of distinct differences between the mean spacer length at sites A and B, however, can neither be explained by growth hypothesis nor foraging theory alone. We therefore suggest that a synthesis of both theories is necessary for a complete understanding of spacer length in Potamogeton. Despite having only one tenth of photosynthetically active biomass, plants at the poor site produced the same average spacer length and more than sixty percent of the total rhizome length compared to site A plants. Principally, longer rhizomes at inhospitable sites can be achieved by means of two mechanisms: (a) by an increased biomass allocation into rhizome tissue, as seen in our study, and (b) by reducing the tissue-mass density and thereby increasing spacer length. Only in case (b), spacer length can be considered as an independent part of the foraging behaviour of the plant, whereas in our study spacer length is mainly an effect of biomass allocation into rhizomes. Such foraging sensu latu can easily be overseen when biomass is ignored. We therefore emphasize that
studies which investigate the foraging capacity of clonal plants need to include measurements of spacer length, biomass and biomass allocation. In case of the fertilization experiment, foraging was more obvious, because due to comparable biomass, mean spacer length tended to be shorter and biomass allocation into rhizomes was lower in the fertilized plants than in the controls.

Overall, plants must function as a balanced system in terms of resource uptake and use, and resources may not be allocated independently from each other (e.g. Hirose 1986; Ågren & Ingestad 1987). On the assumption of different nutrient regimes at the two sites, the mechanisms for biomass allocation may be interpreted in the light of stoichiometric theory. Under nutrient limitation, increased photosynthesis as a consequence of higher biomass can not increase biomass production because of missing nutrients. Consequently, it would be better for the plant to invest into roots to capture more nutrients, and rhizomes in order to grow faster out of a limiting site. Only if a high nutrient uptake rate makes C the limiting factor, it is beneficial for the plant to produce aboveground photosynthetic tissue instead of belowground biomass. At our study site, the allocation response of *P. perfoliatus* to sediment nutrient limitation allows for a patch expansion of roughly two thirds of that under thriving conditions, although the biomass is only one tenth. However, these patches have much shorter shoots and are less dense due to the lower number of plants per area, lower number of ramets per plant, and specific clonal architecture of the species (marginally longer spacers and less branchings). Hence our study shows how plasticity of clonal architecture in *P. perfoliatus* may result in two patch types that constitute two distinctively different habitats within the littoral biocenosis.
Chapter 3
Chapter 4. DENSITY CONTROL IN POTAMOGETON PERFOLIATUS L. AND POTAMOGETON PECTINATUS L.

Susanne R. Wolfer & Dietmar Straile

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Abstract

The effect of density on the growth, recruitment of new ramets, biomass allocation, rhizome spacer length and rhizome branching of the submersed macrophyte Potamogeton perfoliatus L. was experimentally evaluated in a mesocosm with three different initial shoot densities. The findings suggest that the number of primary shoots available in the beginning of the season can strongly influence patterns of growth and clonal reproduction. In contrast to many studies that found decreasing production parameters with plant density, number of ramets and total biomass of P. perfoliatus plants were highest at medium plant density, and lower at low density and at high density. This is probably due to negative feed-back through crowding at high density and unclear negative effects at low density. Shoot allocation tended to increase with density, rhizome allocation tended to decrease with density and root biomass remained unchanged. At low density P. perfoliatus produced longer rhizome spacers and more branchings than at higher densities. Shorter rhizome spacers at high plant density probably restrict patch expansion and cause discrete patch shapes. A likely mechanism for plastic changes in clonal architecture is increasing competition for light at increasing density, but other density-dependent factors may also contribute.

Investigations on propagule numbers of tubers and turions show that self-regulation of ramet number was associated with self-regulation of propagule number in both P. perfoliatus and Potamogeton pectinatus, with higher densities producing less propagules per plant.

Key words: Potamogeton, submersed macrophyte, density, self-regulation, propagules

Introduction

Potamogeton perfoliatus L. and Potamogeton pectinatus L. are common clonal macrophytes in many parts of the world. Natural stands of P. perfoliatus have densities from one shoot / m² to several hundred shoots / m², Potamogeton pectinatus densities may reach more than 1000 shoots / m² (own observation). Since Potamogeton propagates mainly clonally, shoot density is determined by (a) the number of sprouting propagules (= plant density), (b) the number of ramets per plant, and (c) the rhizome length between shoots. The number of sprouting propagules is a product of shoot growth and biomass allocation into reproductive structures of the previous growth season, and propagule survival during winter. In aquatic macrophytes, morphological characteristics like the number of ramets per plant, spacer length and branching may react plastic on environmental factors such as water depth (Strand & Weisner 2001), light (Barko et al. 1982), nutrient availability (Barko et al. 1991), or wave action (Idestam-Almquist & Kautsky 1995).

The shoot density of macrophytes is important for processes in the littoral ecosystem. Macrophyte density or patchiness determine the distribution and age-characteristics of littoral fish (Weaver et al.)
1997) and can affect macro-invertebrates (Webster et al. 1998). Density determines the competitive ability of aquatic clonal plants in mixed stands (Davis & Fourqurean 2001), and fluctuations in density can facilitate species coexistence by delaying the exclusion phenomenon (Bonis et al. 1995). Density may have intraspecific feedbacks such as light and nutrient modification, or regulation of flowering (Thompson et al. 1990).

Most studies of macrophyte density are confined to shoot numbers but ignore details on larger hierarchical levels, e.g. clone fragments or clones, as well as belowground dynamics. We experimentally evaluated the effect of initial ‘propagule’ density on the growth, recruitment of new ramets, biomass allocation, spacer length and branching of plants of the submersed macrophyte *P. perfoliatus* in a mesocosm with three monospecific primary shoot densities (corresponding to plant number). Turions of *Potamogeton perfoliatus* and tubers of *Potamogeton pectinatus* were also investigated, because the number of propagules determines the initial density in the following year and is therefore crucial for the modelling and prediction of patch dynamics. Furthermore the weight of propagules influences growth and survival of the produced shoots (Idestam-Almquist & Kautsky 1995, Santamaría & Rodríguez-Girones 2002).

The main hypotheses to be tested were:
(1) Ramet production decreases with density in *P. perfoliatus* (self-regulation hypothesis)
(2) Propagule production decreases with density in *P. perfoliatus* and *P. pectinatus*.

Materials and methods

The mesocosm experiments were conducted in a basin of 10 m x 5 m x 1.2 m on the premises of the Limnological Institute (University of Constance), nearby Lake Constance, Germany. The distribution of about 8 m³ of lake sediment originating from the lower lake basin created a sediment layer of approximately 15 cm depth.

On May 31, 2000, *P. perfoliatus* and *P. pectinatus* shoots from nearby natural stands (*P. pectinatus* were collected near Egg, *P. perfoliatus* near Unteruhldingen) were planted in three monocultural densities (5, 15 and 40) per 0.25 m² in three replicates. The terms ‘low’, ‘medium’ and ‘high’ density are used in a relative sense on the potential scale for the number of initial shoots (= plant density). All shoots had a shoot length of 15 – 20 cm, and a maximum rhizome length of 10 cm. The quadrats were located within 3 m distance of each other to avoid interaction. Treatments were randomly located within the mesocosm and plants were randomly rooted within the quadrats.

After planting, the mesocosm was carefully filled with lake water to 1 m depth. A pump of a capacity of 3 l/s maintained a constant flow-through with a renewal time of roughly one day. Since the lake water originated from 15 m depth, excessive heating of the water was avoided. Initial mortality of transplants was < 1 % after 8 days. Shoots grew well and at the end of the experiment, part of the shoots from all treatments topped at the water surface.

During the growth period, average length was estimated by measuring a subsample of ramets. On August 4, the water was drained and the rhizome systems were carefully dug out by hand. Turions were present and showed that the growth phase was already completed. Primary, secondary and higher order ramets were counted, spacer length was measured. Plants were separated into shoots, rhizomes and roots, and dried at 105 °C to constant weight. The fractions were weighed on an analytic scale.
Turions could not be harvested quantitatively, because they were located deeply in the sediment and broke off frequently during digging. Since turions are built at all main axes and nearly all branch tips (Wolfer & Straile 2004b), the number of plants and the number of branchings was used to estimate the number of turions instead.

Since the patch perimeter was extremely irregular with single runner shoots far from the centre, patch size was estimated as \((a + (2 \times r \times b))^2\) where \(a\) is the side length of the quadrat in meters, \(r\) is the average total rhizome length of the plants, and \(b\) is a factor correcting for branching \((b_{\text{low density}} = 2.8, b_{\text{medium density}} = 2.5, b_{\text{high density}} = 1.8)\). ‘Spatial ramet density’ (the number of ramets per square meter) was calculated as final ramet number divided by patch size.

Clones of *Potamogeton pectinatus* were not harvested, but tubers were collected by sieving the sediment through a mesh of width = 1 mm. One replicate of the density 15 treatment had to be omitted because of harvesting problems.

Statistical analyses were performed with SAS software (SAS Institute Inc., Cary, NC, USA 1999-2001). Proportional data were transformed to the arcsine of the square root before analysis.

**Results**

*Length growth dynamics*

The first *P. perfoliatus* plants reached the water surface after 49 days which is an average growth rate of 16 mm per day. In the beginning, shoots at higher density grew faster in length than at low density (results not shown). At harvest, average length per treatment was not density dependent anymore (Anova, \(F_{2,8} = 1.34; p < 0.33\)).

*Production parameters*

*P. perfoliatus* produced between 30 and 343 ramets per site, variability within treatments was considerable (Fig. 4.1a). Ramet recruitment (Fig. 4.1b) was highest at medium plant density (Tukey’s HSD-test, \(F_{1,8} = 8.7, p < 0.02\)). Total biomass production per initial shoot was also highest at medium plant density (Fig. 4.1c). The average specific shoot dry weight of 0.85 g m\(^{-1}\) was not different between treatments (Anova, \(F_{2,8} = 0.5, p < 0.6\)).
Biomass allocation and spacer length

Shoot allocation of *P. perfoliatus* tended to increase with initial shoot density and rhizome allocation tended to decrease with density. The final shoot density can, however, better explain shoot allocation ($r^2 = 0.63$, $n = 9$, $p < 0.01$) and rhizome allocation ($r^2 = 0.74$, $n = 9$, $p < 0.003$) than initial density. Root allocation was not affected by final density ($r^2 = 0.001$, $n = 9$, $p < 0.93$) (Fig. 4.2).

![Fig. 4.2 Average shoot, rhizome and root biomass allocation (%) ± S.E. of *P. perfoliatus* grown in a mesocosm at different densities](image)

The decrease in rhizome allocation with increasing initial density goes along with a non-significant decrease in spacer length (Anova, $F_{2,8} = 1.03$, $p < 0.4$) and a non-linear relationship between shoot number and total rhizome length ($r^2 = 0.98$, $n = 9$, $p < 0.0001$, quadratic term: $p < 0.04$) (Fig. 4.3a,b). Since medium plant density produced more ramets, average rhizome length produced per initial shoot was highest at medium plant density, medium at low plant density and lowest at high plant density, all were significantly different (Anova, $F_{2,8} = 16.5$, $p < 0.004$) (Fig 4.3c). The average specific rhizome dry weight of 0.5 gm$^{-1}$ was not different between treatments (Anova, $F_{2,8} = 0.8$, $p < 0.5$).

![Fig. 4.3 (a) Average rhizome spacer length ± S.E. (b) relationship between total rhizome length and final number of ramets per site (c) average total rhizome length per plant ± S.E. of *P. perfoliatus* grown in a mesocosm at different densities](image)
Density control

Branchings

Rhizome branching probability per ramet and number of rhizome branchings per plant of *P. perfoliatus* were affected by density (Anova, $F_{2,8} = 4.24, p < 0.07$, respectively $F_{2,8} = 7.4, p < 0.02$) (Fig. 4.4). The number of rhizome branchings per plant was significantly lower at high density than at low and medium density (Tukey’s HSD-test, $F_{1,8} = 8.9, p < 0.02$) (Fig. 4.4b).

![Fig. 4.4 Average number of rhizome branchings (a) per ramet ± S.E. (b) per plant ± S.E. of *P. perfoliatus* grown in a mesocosm at different densities](image)

Patch size and spatial density

Patch size of *P. perfoliatus* was higher at medium plant density than at medium and at low plant density (Tukey’s HSD-test, $F_{2,8} = 16.7, p < 0.004$) (Tab. 4.1). Spatial density was higher at high density than at medium and low density (Tukey’s HSD-test, $F_{2,8} = 15.7, p < 0.004$) (Tab. 4.1).

<table>
<thead>
<tr>
<th>plant density of <em>P. perfoliatus</em></th>
<th>patch size (m²) of <em>P. perfoliatus</em></th>
<th>spatial ramet density (m²) of <em>P. perfoliatus</em></th>
<th>turion numbers per <em>P. perfoliatus</em> plant</th>
<th>tuber numbers per <em>P. pectinatus</em> plant</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>2.2</td>
<td>20</td>
<td>2.1 ± 0.75</td>
<td>8.0 ± 3.1</td>
</tr>
<tr>
<td>15</td>
<td>4.8</td>
<td>42</td>
<td>2.0 ± 0.10</td>
<td>4.6 ± 0.2</td>
</tr>
<tr>
<td>40</td>
<td>1.9</td>
<td>138</td>
<td>1.3 ± 0.25</td>
<td>2.0 ± 0.9</td>
</tr>
</tbody>
</table>

Propagules

Turion numbers per plant of *P. perfoliatus* were affected by density (Anova, $F_{1,8} = 5.4, p < 0.05$), and were lowest at high plant density and higher at low and at medium plant density. Tuber production of *P. pectinatus* decreased with density (Fig. 4.5a). Numbers produced at low density were significantly higher than those at high density (Tukey’s HSD-test, $F_{1,7} = 6.51, p < 0.04$). Propagule production per plant was roughly 4-times higher at low density, and 2-times higher at medium and high density in *P.*
pectinatus compared to P. perfoliatus (Tab. 4.1). Average fresh weight per tuber was not significantly different between treatments (Anova, $F_{2,7} = 0.99$, $p < 0.44$). All fresh weight frequency curves were skewed to the right and leptokurtic (Fig. 4.5b).

**Discussion**

The findings suggest that initial density can strongly influence patterns of growth and clonal reproduction of P. perfoliatus, by changing (a) relative ramet recruitment (b) biomass allocation (c) branching and (d) spacer length.

The hypothesis of negatively density-dependent growth was only partly confirmed by the results. In accordance with the hypothesis, ramet production and total biomass production per initial shoot were lower at high density than at medium plant density. Reduced rates of ramet recruitment and growth are the most common effects of increased density in terrestrial plant species (De Kroon & Kwant 1991, De Kroon 1993) and higher aquatic plant species (Moen & Cohen 1989, Groth et al. 1996). Regulation can take place via mortality control (Lovett-Doust 1981) or natality control (Briske & Butler 1989, Thompson et al. 1990). The investigation of rhizome nodes of our experimental plants revealed no loss of ramets, suggesting a predominantly natality-regulated ramet recruitment in P. perfoliatus. Hutchings (1979) proposed intraclonal regulation as underlying reason for self-regulation of ramet density, whereas other authors favour a negative feed-back of deteriorating conditions (e.g. self-shading, nutrient depletion) due to overcrowding (De Kroon & Kwant 1991).

Contrary to the self-regulation hypothesis we found less ramet production and growth at low density than at medium density. Cain et al. (1995) also found highest performance of a terrestrial clonal plant at medium density and Worm and Reusch (2000) report that reduced plant density had negative effects on eelgrass shoot growth during the early stages of recolonization. Reduced fitness at low population size (‘allee effect’) is often caused by genetic deficiencies (Fischer et al. 2000), but low population sizes may also involve growth impairment by edge effects (Gardner 1998), increased levels of epiphytes (Reed 1990), excessive irradiance (Scrasi & Dewreede 1998), or stochastic mortality (Dennis 2002). We propose that relative ramet recruitment and biomass production in P. perfoliatus increases at low ramet densities, reaches an optimum where benefits and disadvantages of density-related factors counterbalance each other, and decreases at high densities.
Density control

Density did not only influence growth but also the clonal architecture of *P. perfoliatus*: Shoot allocation tended to increase with density and rhizome allocation tended to decrease with density. The same results have been reported for terrestrial plants (Bazzaz & Grace 1997). In our study, shoot allocation lay well in the range reported for *P. perfoliatus* in the literature (58-95%, Ozimek et al. 1976) and from *in-situ* investigations in Lake Constance (Wolfer & Straile 2004b). Although researchers often found lower root allocation of *Potamogeton* with increasing density (Moen & Cohen 1989, Sand-Jensen & Vindbaek Madsen 1991), our results show no effect of density on root allocation. Root allocation probably indicates that nutrient supply is adequate, otherwise the plants should react plastic on nutrient shortage (Aerts et al. 1991). The reason for the observed differences in shoot and rhizome allocation can be strategies towards different shading conditions (e.g. Ryser & Eek 2000). In case of increased self-shading due to higher density it would be better for the plant to invest (a) in rhizomes in order to grow faster out of the shaded site (foraging *sensu strictu*) at the cost of shoots or (b) shoots to catch more light (foraging in a wider sense; ‘light foraging’) at the cost of rhizomes. Strategy (a) might be problematic because shoots in high density stands already have to cope with a reduced net photosynthesis as a result of reduced irradiance (Scrosati & Dewreede 1998), and might therefore lack the energy to built longer rhizomes. In fact, the plants in our study showed strategy (b). This is in contradiction to the foraging hypothesis which proposes that plants in ‘good’ habitats (= low density, no shade, nutrients) should have shorter spacers in order to establish a maximum amount of shoots in the favourable habitat while plants in less favourable habitats (= higher density, self shading, possibly nutrient limitation) should grow long spacers in order to escape from the bad site (e.g. Sutherland & Stillman 1988). Field investigations, however, showed that only some plants forage by means of spacer length (Hartnett & Bazzaz 1985, Hutchings & De Kroon 1994), and that foraging might be plastic and depends on the relative levels of resources available (Wolfer & Straile, unpublished data).

Density affected branching, where plants of the low density treatment showed higher branching frequencies per ramet than plants of the medium and high density treatment. Experiments have shown that self-shading reduces branching and light induces branching in terrestrial plant species (Ellison & Niklas 1987, Hutchings & De Kroon 1994) and seagrasses (Vermaat & Verhagen 1996, Marbà et al. 1996). Branching frequency is also interpreted as foraging behaviour, since increased branching maximizes the number of ramets at a suitable site (Sutherland & Stillman 1988). In our experiment, however, reduced biomass production at low density compared to medium density shows that patch quality was not optimal at low density, and nevertheless, branching was higher. As a consequence of different trends in ramet numbers and branching frequencies, low and medium density stands reach similar number of branchings per plant, whereas high density plants had less branchings. This leads to self-regulation of density and has consequences for the production of propagules (see below).

Patch expansion is partly ruled by the density-regulated architecture of clonal growth. Our estimations show lower patch expansion at low plant density (due to increased branching and decreased growth) and at higher density (due to shorter rhizome length and decreased growth), and highest patch expansion at medium density. Also the spatial ramet density was highest at high initial density. High density probably restricts patch expansion and causes compact patch shapes.

Besides self-regulation with regard to ramet production and branching, *P. perfoliatus* also showed self-regulation with regard to propagule formation. Since turions are formed on branches and are therefore a direct consequence of plant architecture, low and medium density plants produced more propagules per plant whereas high density plants produced less propagules. In *P. pectinatus*, the tuber production was negatively density dependent throughout. Since the tuber weight did not differ with density, the self-regulation of tuber numbers will lead to better starting conditions in the following
The higher relative propagule production in *P. pectinatus* compared to *P. perfoliatus* is probably required because *P. pectinatus* tubers are subject to a high mortality due to bird foraging, fungus etc. (e.g. Hangelbroek *et al.* 2002) whereas turions are buried deeper in the sediment at water depths probably not reached by water fowl.

Summarizing, *P. perfoliatus* and *P. pectinatus* plants can lessen low density effects and overcrowding by self-regulation of ramet recruitment, growth and propagule production associated with changes in clonal architecture.
Chapter 5. EFFECT OF SEDIMENT STRUCTURE AND NUTRIENTS ON THE GROWTH OF POTAMOGETON PERFOLIATUS

Abstract

A series of assessments and experiments was carried out to test for effects of sediment nutrients on the growth of Potamogeton perfoliatus:

(1) Bare sediments and sediments with differing vegetation cover at Lower Lake Constance were tested for differences in grain size and nutrients. There was no relationship between sediment composition, nutrient content and macrophyte type. We suggest that this is due to sampling methods, lack of knowledge about the appropriate nutrient fractions to be measured in porewater, and the distinct seasonal characteristics of nutrient cycles.

(2) The growth substrate of P. perfoliatus was nutrient enriched with slow-release fertilizer in a mesocosm. The results were compared with in-situ enrichment results described in Chapter 3. Whereas in-situ fertilization increased ramet recruitment and biomass growth, fertilization of the mesocosm sediments showed no significant effect. As predicted by the foraging theory, ramets allocated less biomass to roots when fertilized and rhizome spacer length was significantly shorter in the fertilized plants. Shoot / rhizome allocation was not significantly different.

(3) P. perfoliatus ramets were planted in areas without previous macrophyte growth at Upper Lake Constance, with or without nutrient addition. Only fertilized stands could establish, showing that the occurrence of P. perfoliatus in parts of the Upper Lake is at least partly limited by nutrient availability.

The different responses of growth to fertilization are attributed to the different sediments used: when sediments were naturally nutrient poor, fertilization was beneficial, whereas on nutrient rich sediment, fertilization was indifferent.

Introduction

P. perfoliatus is a species which is known to react to changes of water quality. In Lake Constance, an originally oligotrophic lake, nutrient loads of macronutrients (N and P) increased until the end of the 1970ies due to agricultural runoff and increasing wastewater discharge. Since the construction of area-wide treatment plants, nutrient levels have been decreasing steadily and are now back to pre-eutrophication levels.

While most parts of Upper Lake Constance show little macrophyte growth, large stands are found at the influents of nutrient-rich rivers such as the Schussen. At Lower Lake Constance, P. perfoliatus has been a typical plant since the beginning of the 20th century. During the phase of eutrophication, the species decreased considerably but increased again after re-oligotrophication. In Upper Lake Constance, there was not much change over the years (Schmieder 1997).

Since macrophytes may take up nutrients from the water column over their surface (Sculthorpe 1967, review of Agami & Waisel 1986), water nutrient concentrations and macrophyte biomass are sometimes correlated (Carbiener et al. 1995, Bini et al. 1999). However, root uptake is dominant (Denny 1980, Barko & Smart 1986a, Barko & Smart 1986b) and suggests predominant relationships between sediment nutrients and biomass. Whereas water chemistry may change quickly, the sediment
nutrient status reflects the recent chemical history of the water body. This means that nutrient concentrations in the interstitial water are commonly a better indicator of macrophyte growth.

Nutrients do not only influence biomass but may also affect the morphological characteristics of aquatic macrophytes. Under varying nutrient conditions, there may be variations in plant size, leaf number, leaf morphology, leaf and root turnover rate and storage capability (Aiken & Picard 1980, Hutchings & De Kroon 1994). Moreover, clonal architecture such as spacer length, rhizome allocation and branching may be affected (Wolfer & Straile 2004b; Chapter 3). These changes may be beneficial when they allow for a better usage of the resources available in the growth environment. The ability of stoloniferous and rhizomatous plant to concentrate ramets in nutrient rich patches or to avoid nutrient deficient patches by preferential placement of modules has been interpreted as ‘foraging’ behaviour analogous to the search path of a foraging animal. Rhizome spacer length is supposed to decrease, and branching is supposed to increase with patch quality (Bell 1984, Schmid 1986, Slade & Hutchings 1987a, Slade & Hutchings 1987b, Slade & Hutchings 1987c, Evans 1988, De Kroon & Schieving 1990, De Kroon & Knops 1990, Kelly 1990, Evans 1991, Oborny 1991, Hutchings & De Kroon 1994, De Kroon & Hutchings 1995).


The aim of the study was to assess the effect of sediment nutrients on presence or absence, growth and architecture of *P. perfoliatus*. The assessments and experiments comprised:

1. grain size and nutrient analysis of bare lake sediments as well as lake sediments with differing vegetation cover;
2. nutrient enrichment of growth substrate with a slow-release fertilizer in a mesocosm; analysis of clonal growth parameters and tissue nutrient concentrations;
3. planting of *P. perfoliatus* ramets in lake areas without significant macrophyte growth, either without or with nutrient addition.

**Materials and methods**

**Sediment analysis**

All sites were situated in a bay W-SW of Niederzell, island of Reichenau, within an area of 50 m x 25 m, at a depth between 2.00 m and 2.50 m (see Fig. 2.1).

Three to five replicates of sediment at growth sites of each of the following 5 vegetation types were taken: (a) *P. perfoliatus* tall and dense (> 2.50 m; > 50 shoots/m²), identical to rich growth sites of Chapter 3, (b) *P. perfoliatus* tall and sparse (>2.50 m; < 50 shoots/m²), (c) *P. perfoliatus* low (< 50 cm max. length), identical to poor growth sites of Chapter 3, (d) *Chara sp.*, and (e) bare sediment.
The top layer of sediment (10 cm) was collected by means of hand-driven corers (diameter 12.5 cm). This depth was chosen to include all roots. Overlying water was immediately removed by the principle of communicating tubes. Porewater was extracted from the sediment by centrifugation at 4500 rpm for 10 minutes. Subsamples of the supernatants were filtered (0.45 μm, prewashed Millipore), filtrated and unfiltrated samples were immediately deep frozen and stored until further analysis.

For particle size analysis of the sediments, all visible plant fragments were removed. The samples were wet-sieved through 63 μm and both fractions were dried until constant weight and weighed. The coarse fraction (> 63 μm) was dry sieved through meshes of different sizes according to DIN 18123 and weighed.

Sediment water content was determined by drying 5 ml samples of known weight at 100 °C for 24-48 h (until constant weight), and weighing of the dried sediment.

Total organic content of the sediment was determined as LOI (loss of ignition) by drying the sample at 100 °C and determining the weight loss after combustion at 500 °C for 12 h in a muffle furnace. The total carbon and total nitrogen content were determined with a CHN analyser (Hereaeus).

Concentrations of nitrate and SRP in interstitial water were determined using ionchromatography (Dionex). Concentration of total P was determined photometrically by flow-injection analysis (Eppendorf) following digestion with K₂S₂O₈.

Proportional data were transformed to the arcsine of the square root before analysis. Statistical analyses were performed with SAS software (SAS Institute Inc., Cary, NC, USA, 1999–2001).

Mesocosm fertilization and tissue analysis

A basin of 5 m width, 10 m length and 1.2 m depth (Fig. 5.1) was filled with a 15 cm layer of lake sediment from Lower Lake Constance. Flow-through of lake water was regulated to about 10-20 l/min, i.e. an approximate retention time of 56 hours. P. perfoliatus shoots of 15-20 cm length were collected near Unteruhldingen on 13.06.2001 and immediately planted at densities of 8 shoots per 0.25 m². The experimental set-up consisted of three treatments and 4 randomly distributed replicates. The test quadrats were left untreated, fertilized with 1 kg m⁻² slow-release N-P-K-fertilizer Plantacote Depot 4M® (14% N, 9% P₂O₅, 15% K₂O) (= 1 g P l⁻¹ sediment), or fertilized with 4 kg m⁻² Plantacote Depot 4M® (= 4 g P l⁻¹ sediment). This is in the range of in-situ fertilization experiments listed in the review by Worms et al. 2000. After 14 weeks, the complete clonal plants were removed from the sediment. Number and biomass of shoots, length, spacer length, biomass and number of branchings of rhizomes, as well as the root biomass were determined. Poor plant growth in the treatment with 4 kg P m⁻² was attributed to overfertilization and results are not presented here.

Tissue samples were taken to test for differences in nutrient contents. Three to five healthy looking apical leaves without any sign of senescence were ground in a mortar. C was determined by Autoanalyzer (ThermoQuest NCS-2500) after combustion. P and N values were determined by AutoanalyzerII (Bran&Luebbe) following digestion with potassium persulfate. Proportional data were transformed to the arcsine of the square root before analysis. Statistical analyses were performed with SAS software (SAS Institute Inc., Cary, NC, USA, 1999–2001).
Fig. 5.1 Mesocosm, Limological Institute, University of Constance

Planting experiment

Shoots of *P. perfoliatus* were collected at the main experimental site near the island of Reichenau (see Chapter 3) on 05.07.2001. On 06.07.2001, the shoots were planted at previously vegetation-free sites of Upper Lake Constance south of the island of Mainau (depth = 4 m), east of Staad (depth = 2.50 m and 4 m) and in the ‘Litoralgarten’ (depth = 4 m) by SCUBA divers. At each location, 6 patches (8 ramets/0.25 m²) were planted, half of them without fertilization, the other half with fertilization of 1 g P l⁻¹ sediment slow release fertilizer Plantacote Depot 4M® (14% N, 9% P₂O₅, 15% K₂O).

After one growth season, on 25.09.2001, ramets were counted and measured, and patch size was determined by SCUBA divers. Since ramet numbers, shoot lengths and patch sizes did not differ between sites under the same treatment, sites were pooled for analysis. Means of the sediment parameters were compared using one-way ANOVA at a level of significance of p < 0.05. One year later, on 06.08.2002, half of the sites were re-visited and re-assessed by Scuba divers according to the same protocol.

Results

Sediment analysis

Grain size, H₂O-content and organic C of sediment were not related to vegetation cover type (Tab. 5.1). Furthermore, no significant relationships were found between vegetation cover and porewater nutrients such as SRP, TN and NO₃-N (Tab. 5.1). P values ranged from oligotrophic conditions (< 10 µg l⁻¹ SRP (*P. perf.* sparse, *P. perf.* poor) to mesotrophic conditions (10 and 30 µg l⁻¹) (*P. perf.* dense, *Chara*).
**Tab. 5.1** Sediment characteristics and nutrient concentrations in porewater of sites with or without vegetation cover

<table>
<thead>
<tr>
<th>Unit</th>
<th>P. perf. dense</th>
<th>P. perf. sparse</th>
<th>P. perf. poor</th>
<th>Chara sp.</th>
<th>Sediment</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>H₂O %</td>
<td>35.64 ± 3.43</td>
<td>34.17 ± 2.03</td>
<td>33.91 ± 4.72</td>
<td>39.10 ± 1.91</td>
<td>31.64 ± 1.61</td>
<td>&lt; 0.43</td>
</tr>
<tr>
<td>organic C %</td>
<td>3.96 ± 0.46</td>
<td>3.84 ± 0.34</td>
<td>4.64 ± 0.14</td>
<td>4.20 ± 0.49</td>
<td>3.76 ± 0.07</td>
<td>&lt; 0.52</td>
</tr>
<tr>
<td>&lt; 63µm %</td>
<td>44.52 ± 6.02</td>
<td>45.67 ± 12.86</td>
<td>54.70 ± 10.47</td>
<td>35.43 ± 14.01</td>
<td>58.81 ± 4.69</td>
<td>&lt; 0.42</td>
</tr>
<tr>
<td>&gt; 63µm %</td>
<td>43.17 ± 5.53</td>
<td>45.83 ± 11.92</td>
<td>16.63 ± 5.62</td>
<td>52.81 ± 16.32</td>
<td>30.94 ± 5.23</td>
<td>&lt; 0.15</td>
</tr>
<tr>
<td>&gt; 63mm %</td>
<td>12.31 ± 4.22</td>
<td>8.50 ± 2.21</td>
<td>28.66 ± 16.09</td>
<td>11.79 ± 5.10</td>
<td>10.25 ± 2.15</td>
<td>&lt; 0.30</td>
</tr>
<tr>
<td>TP µg l⁻¹</td>
<td>82.98 ± 42.36</td>
<td>54.03 ± 14.50</td>
<td>122.73 ± 15.16</td>
<td>116.38 ± 46.74</td>
<td>82.84 ± 27.71</td>
<td>&lt; 0.75</td>
</tr>
<tr>
<td>SRP µg l⁻¹</td>
<td>18.46 ± 6.77</td>
<td>6.57 ± 1.83</td>
<td>9.23 ± 1.60</td>
<td>20.08 ± 8.23</td>
<td>11.20 ± 3.37</td>
<td>&lt; 0.45</td>
</tr>
<tr>
<td>TN mg l⁻¹</td>
<td>2.58 ± 0.90</td>
<td>2.23 ± 0.69</td>
<td>2.16 ± 0.10</td>
<td>2.87 ± 0.64</td>
<td>2.65 ± 0.41</td>
<td>&lt; 0.95</td>
</tr>
<tr>
<td>NO₃-N µg l⁻¹</td>
<td>3.60 ± 1.86</td>
<td>28.00 ± 23.59</td>
<td>95.67 ± 76.21</td>
<td>722.50 ± 722.5</td>
<td>18.80 ± 4.91</td>
<td>&lt; 0.48</td>
</tr>
<tr>
<td>N:P</td>
<td>43.91</td>
<td>39.68</td>
<td>18.10</td>
<td>33.82</td>
<td>42.24</td>
<td></td>
</tr>
</tbody>
</table>

**Mesocosm fertilization and tissue analysis**

In comparison to controls, nutrient addition did not produce significantly different growth results concerning the number of ramets (ANOVA, $F_{1,7} = 2.39$, $p < 0.1734$), average shoot length (ANOVA, $F_{1,7} = 0.05$, $p < 0.8300$) and total biomass (ANOVA, $F_{1,7} = 2.29$, $p < 0.1809$) (Fig. 5.2).

Likewise, plant tissues on fertilized and unfertilized sites showed no significant differences with regard to % N (ANOVA, $p < 0.81$) and % C ($p < 0.62$) (Tab. 5.2).

**Fig. 5.2** Ramet number, shoot length, and total biomass of *P. perfoliatus* in unfertilized and fertilized quadrats in a mesocosm ± S.E.

**Tab. 5.2** Tissue nutrient contents at non-fertilized and fertilized sites

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>% N</th>
<th>% C</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>no fertilizer</td>
<td>19</td>
<td>4.79 ± 0.13</td>
<td>40.01 ± 0.20</td>
<td>8.44 ± 0.19</td>
</tr>
<tr>
<td>fertilizer</td>
<td>15</td>
<td>4.74 ± 0.19</td>
<td>40.22 ± 0.42</td>
<td>8.65 ± 0.29</td>
</tr>
</tbody>
</table>
However, root allocation was significantly lower in the fertilized treatment (ANOVA, $F_{1,7} = 15.64$, $p < 0.008$) while biomass allocation into aboveground ($F_{1,7} = 1.08$, $p < 0.34$) and belowground biomass ($F_{1,7} = 1.08$, $p < 0.34$) was not significantly different between treatments (Fig. 5.3). Rhizome spacer length was significantly shorter in the nutrient treatment (ANOVA, $F_{1,7} = 16.38$, $p < 0.056$). The spacer length differed not only significantly between but also within treatments (Fig. 5.3). Part of this variation can be attributed to the order of shoots (Fig. 5.4). Rhizome length was shortest between primary and secondary ramets (4 cm) and increased in the direction of new ramet recruitment. The average branch spacer was longer than the average main axis spacer (i.e. the axis originating from the primary ramet) and increased the later the branch was initiated.

**Fig. 5.3** Biomass allocation and spacer length of *P. perfoliatus* ± S.E. without and with fertilization

**Fig. 5.4** Average rhizome spacer length of *P. perfoliatus* in relation to position within rhizome ± S.E. (a) rhizome spacer length of main axis, 1 is the oldest, 2 is the youngest spacer (b) spacer length of main axis and branches, b1 is the oldest branch, b4 is the youngest branch
Nutrient experiments

Planting experiment

After termination of the experiment, ramet number and ramet length were significantly larger in the fertilized treatments than in the control (t-test, p < 0.001, Fig. 5.5). At unfertilized sites, there was little growth at all. Moreover, on 33% of unfertilized sites all plants had died.

In 2002, when sites were re-visited, patch extension on fertilized sites had increased at an average of 6.5-fold, whereas on unfertilized sites, patch area had either decreased, or patches had completely disappeared.

![Graph showing ramet number and length for fertilized and control treatments](image)

Fig. 5.5 Ramet number, ramet length and patch size of *P. perfoliatus* planted on unfertilized and fertilized sediment ± S.E.

Discussion

Sediment analysis

Although previous experiments have clearly shown that growth performance and morphology of submersed macrophytes may significantly be related to sediment characteristics such as grain size, density, organic matter, and nutrients (Anderson & Kalff 1986, Barko & Smart 1986a, Walser 1996), we found no differences of sediment composition and nutrient content at sites with different or no vegetation growth in Lake Constance. However, also other authors have failed to relate vegetation distribution and growth to sediment parameters *in-situ* (Barko & Smart 1979, Anderson & Kalff 1986, Lehmann 1997).

We suggest that the lack of correlation could be due to sampling problems: Reproducibility depends on both the precision of the technique and the spatial heterogeneity of the sediments. However, although previous papers have presented replicate porewater profiles (Carignan 1984, Carignan *et al.* 1994), the reproducibility has seldom been quantitatively examined (Urban *et al.* 1997). One reason for our insignificant results was the high variability of values leading to a high standard error. In fact, the average SRP value at poor growth sites was only 50% of the value at rich growth sites and more replicates could possibly have led to a significant result. Furthermore, nutrients were measured based on volume in porewater, Barko & Smart (1986a) report, however, that growth was rather correlated with sediment nutrient concentrations based on sediment volume.

In addition, there is a lack of knowledge which nutrient fraction is most representative for macrophyte growth. For example, N is more easily taken up as NH₄, but more often taken up as NO₃ (Agami & Waisel 1986). Measurements reported in literature include total P, SRP, RP, PO₄-P, o-P,
total N, NO$_3$-N, NH$_4$-N, NH$_3$-N etc. Moreover, these parameters may be assessed either in the sediment or in the porewater. This is problematic because P in the porewater constitutes only a very small fraction of the total P bound in the sediment (Søndergaard 2007), but there is hardly any information about bioavailability of sediment P (Golterman 2004). While most authors found relationships between porewater nutrient concentration and nutrient status of plant tissue (Fourqurean 1992, Agawin et al. 1996, Alcoverro et al. 1997), the results are more inconsistent for relationships between porewater nutrients and biomass, plant growth or vegetation cover. There are reports of positive correlations between biomass and PO$_4$ (Chambers & Fourqurean 1991), NH$_4$ (Chambers & Fourqurean 1991, Cízková 2001), SRP (Fourqurean 1992, Cízková 2001), P, TP and N, (Cízková 2001). In other cases, no relations were found between biomass and P (Chambers & Fourqurean 1991), NH$_4$ (Fourqurean 1992), TN (Chambers & Fourqurean 1991, Cízková 2001), or total dissolved solids (Cízková 2001). Similarly, only poor relations were found between shoot nutrient content and growth (Barko & Smart 1986a).

Furthermore, it has to be taken into account that N and P in the interstitial water are characterized by a high spatial and temporal variability (Carignan 1985) and a pronounced seasonal cycle with a minimum in summer (Madsen 1988, McComb et al. 1998). The same applies to tissue nutrient concentrations (Nichols & Keeney 1976). Therefore, it is likely that more replicates have to be taken throughout the growth season to provide meaningful results.

**Mesocosm fertilization and planting experiment**

**Production parameters and tissue analysis**

In contrary to the expectation that fertilization will increase growth, we found no significant effects of fertilization on biomass in the mesocosm. Nevertheless, tissue nutrient levels were rather high - %N was 92 % higher than in-situ and C:N was 42 % lower than in-situ (Wolfer & Straile 2004b, Chapter 3) - indicating that nitrogen tissue content is not always correlated to growth in macrophytes as proposed by Ågren G.I. (1985). Similarly, there are reports about insignificant effects of fertilization of seagrass meadows, even though raised tissue contents indicate increased uptake of nutrients (Erftemeijer et al. 1994, Worms et al. 2000). In contrary, results presented in Chapter 3 show that in-situ fertilization of *P. perfoliatus* plants resulted in increased shoot numbers, longer shoots, and higher biomass on poor growth sites, and planted ramets grew better when nutrients were added. Also Alcoverro et al. (1997) found different responses at different sites to fertilization. These results may be due to the naturally different sediments. The fact that fertilization showed no increase of growth parameters with regard to ramet and biomass production and the high tissue nutrient concentrations in the mesocosm indicated that the sediment utilized was already rich in nutrients. Since productive sites are dominant in the Lower Lake Constance, we assumed that the poor growth sites were a product of either sediment disturbance or nutrient depletion by previous plant uptake. On the other hand, the establishment of healthy stands of *P. perfoliatus* at fertilized sites at Upper Lake Constance shows that the lack of macrophytes in extensive littoral areas of the Upper Lake Constance might be due to N or P nutrient limitation, whereas sediment grain size, currents, herbivores, other nutrients etc. play a minor role.

**Root allocation, rhizome / shoot allocation and spacer length**

Lower root allocation in fertilized treatment or nutrient rich sites as found in our study is commonly reported (Barko & Smart 1981b, Ervin & Wetzel 1997, Wertz & Weisner 1997, Peralta 2003) and has been experimentally proven to maximize plant growth (Hirose 1987, Mooney et al. 1988). Resource
Nutrient experiments

allocation requires balancing of the competing requirements of photosynthetically productive tissue and the nutrient uptake apparatus (Madsen 1991).

On the other hand, biomass allocation into aboveground and belowground biomass was not significantly different between treatments. This is in contrast to other studies (review of Hutchings 1997) where rhizome allocation decreased with increasing nutrients. The reason is probably due to the fact that in our study, biomass of fertilized and unfertilized sites was equal, whereas in other studies, biomass increased due to fertilization.

As predicted by the foraging theory, rhizome spacer length was significantly shorter in the nutrient treatment. Also in-situ (Chapter 3), mean rhizome spacer length was shorter in the fertilized treatment than in the control. According to the foraging theory the benefit of shorter rhizomes consists of a concentration of shoots in favourable places, whereas longer spacers ‘move’ the ramets away from unfavourable sites (for a more detailed discussion of foraging see Chapter 8). This seems to contradict the recent rejection of the foraging theory by many scientists including the original authors (De Kroon & Hutchings 1995), mainly because in rhizomatous species effects of higher nutrients on rhizome spacer length are less consistent (Granéli et al. 1992, Grace 1993, Cain 1994, Dong & De Kroon 1994, Hutchings & De Kroon 1994) than in stoloniferous species. Our findings are also in contrast to the growth hypothesis which suggests that rhizomatous species increase rather than decrease the length of their rhizomes with increasing resource-availability (De Kroon & Knops 1990, Hutchings & Magie 1990, Hutchings & De Kroon 1994, Slade & Hutchings 1987, Stoll et al. 1998). The fact that rhizome spacer length decreased significantly under fertilization, whereas other growth parameters including rhizome allocation remained the same shows that in this case rhizomes became thinner and longer and that the change in spacer length was an independent part of the foraging behaviour. As another example of the influence of nutrients on the clonal architecture of P. perfoliatus, we could also confirm increased branching at higher nutrient availability in-situ (Chapter 3).

Summarizing,

(a) we found no correlation between sediment characteristics and vegetation cover. On the other hand, in the planting experiment only fertilized ramets could establish, indicating that the plants are nutrient limited.

(b) in contrary to in-situ measurements, we found no correlation between tissue nutrient concentration and fertilization in the mesocosm; this is most likely due to the fact that the original nutrient level was high and plants were not nutrient limited in the mesocosm.

(c) we found shorter rhizomes and increased branching at fertilized sites which is in line with the foraging theory.

The effect of nutrients on P. perfoliatus has implications on its distribution in Lake Constance: We could confirm that P. perfoliatus occurs in meso- and eutrophic water bodies and has a high tolerance against raised phosphate and nitrate concentrations (Pietsch 1982) as fertilization increased growth in-situ, and levels of fertilization in the mesocosm were rather high. Therefore, we assume that the decline of P. perfoliatus during eutrophication was partly due to secondary effects of high nutrient loads, such as shading by 5 to 10-fold higher phytoplankton production (Müller 1977) and periphyton growth.
Chapter 6. TO SHARE OR NOT TO SHARE – CLONAL INTEGRATION IN RAMETS OF *POTAMOGETON PERFOLIATUS*

Abstract

The ability of clonal plant species to share resources has been studied in many experiments. *Potamogeton* produces interconnected ramets within short (time) intervals and hence may or may not share resources with ramets growing in less favourable microhabitats.

From a genet point of view sharing with ramets growing under less favourable conditions might not be an optimal strategy when photosynthates could be used to establish other ramets growing under more favourable conditions.

In order to analyse the plasticity in clonal integration of a submerged macrophyte (*Potamogeton perfoliatus*), we set up a factorial aquaria experiment with unshaded or shaded recipient ramets (offspring) which were connected to or separated from donor ramets (parents).

Increased biomass production of offspring in parent-offspring-systems compared to severed offspring in both light and shade showed that ramets share resources via clonal integration.

The relative translocation to the first and second offspring generation was influenced by habitat quality: if first offspring ramets (i.e. the ramets that develop after the mother ramet) were shaded by nets, second offspring ramets clearly profited. This may be partly due to the fact that resources are shifted from first offspring to second offspring ramets.

This complex sharing behaviour might be relevant when plants produce ramets within a dense patch of macrophytes, where support of a shaded ramet might not pay off.

Introduction

Clonal plants are characterized by the reiteration of potentially independent modules, called ramets which consist of shoots, rhizomes or stolons, and roots. Clonal integration involves resource sharing through rhizomes and plays an important role in the regulation of shoot growth. The transport of water, nutrients and photosynthetates has been shown to increase the capacity of plants to tolerate resource heterogeneity, to colonize different microhabitats, and to recover from herbivory (Ong & Marshall 1979, Schmid et al. 1988, Alpert 1999). The degree of resource sharing of a clonal plant species is under both genetical and environmental control (Alpert 1999, Van Kleunen et al. 2000). The primary motor behind clonal integration might either be the resource export from parents acting as a source (push model), or the demand of offspring acting as a sink (pull model) (Pitelka & Ashmun 1985, Marshall & Price 1997). Hormones such as auxins, or cytokinins have been proposed as regulating mechanisms (Alpert et al. 2002).

Among aquatic plants, clonal integration is known from emergent macrophytes (Hester et al. 1994, Amsberry et al. 2000), floating stoloniferous species (Alpert et al. 1991), submerged macrophytes (Xiao et al. 2007a) and marine seagrasses (Tomasko & Dawes 1989, Marbà et al. 2002). We therefore expected that the submerged rhizomatous freshwater species *Potamogeton perfoliatus* L. is also capable of clonal integration. *In-situ* surveys in Lake Constance revealed that each *P. perfoliatus* plant sprouts from a turion in spring, and produces horizontal rhizomes of up to 1.5 m length, bearing up to
15 and more ramets during one season (Wolfer & Straile 2004a,b). Whereas existing experiments studied overall transfer within a multi-ramet clone or sharing within a 2-ramet system (parent and offspring), we investigated the trade-off between the parental support of two ramet generations growing under different habitat conditions. Optimality modelling suggests that in this case, biomass allocation depends strongly on microhabitat heterogeneity (Gardner & Mangel 1999).

In a 2 x 2 factorial aquarium experiment, we tested for the effects of shading of one offspring on the growth of two offspring generations. The first offspring was either left connected to or severed from the parental ramet. Hence, we analysed the relative performance of two ramets in a 3-ramet system (connected) and in a 2-ramet system (severed). At the start of the experiment, the 2nd of the offspring ramets was not yet established. Therefore, in the 2-ramet system where no support from the parent is possible, the success of the clonal fragment will depend on the photosynthesis of the shaded ramet. In contrast, in the three-ramet system, the shaded ramet is not crucial for the success of the clonal fragment as the parent ramet can share resources with the unshaded offspring. Hence, we tested the following hypotheses:

1) growth of offspring ramets in the 3-ramet (parent-offspring) system is enhanced as compared to growth of offspring ramets in the 2-ramet system (severed offspring system), i.e. there is clonal integration between parent and offspring.

2) growth differences between the two offspring ramets will be different in the 2- versus the 3-ramet system.

3) shading influences the growth differences of the two offspring ramets, i.e., the relative translocation of resources to different offspring generations depends on the habitat quality of the individual ramets.

Materials and methods

Origin and pre-cultivation of plant material

*P. perfoliatus* shoots were collected at the Lower Basin of Lake Constance, a large, meso-oligotrophic lake in central Europe (9°18'E, 47°39'N). All shoots originated from the same patch with a diameter of approximately 15 m and had an intermediate developmental age. Since they were cut off above the sediment, they had no rhizomes and no roots when planted. The shoots were planted across three aquaria (length: 80 cm, width: 40 cm, height: 50 cm), filled with 10 cm of natural sediment from Lake Constance and with 125 l of filtered lake water. The water was exchanged twice a week; light was provided by pairs of white and plant-grow tubes at 14 hours a day.

Experimental design

The experiment was started when all planted shoots (parent ramets) were well established and had produced one offspring ramet (O1), i.e. the first offspring ramet. 50 % of the offspring ramets were left connected to their parent, 50 % were severed from their parent. In addition, habitat heterogeneity was introduced in 50 % of the connected and severed observation units by shading O1 with cylinder-shaped nets (Agroflor, height: 40 cm, diameter: 6 cm, shading effect: 63 %) (Fig. 6.1). Eight replicates of each treatment were distributed randomly across the three aquaria. At the beginning of the experiment, neither shoot lengths of *P* ramets (31 cm ± 8 cm), nor shoot lengths of O1 ramets (12 cm ± 5 cm) differed between treatments.
Clonal integration

The experiment was ended after three weeks, when plants had produced the second offspring ramet (O2). The plants were carefully removed from the sediment with their rhizomes and roots, and thoroughly washed. After the measurement of shoot lengths and lengths of the rhizomes between O1 and O2 - called spacer length (SO1) below - shoot, rhizome and root fractions were dried at 105°C, cooled down and weighed on an analytic scale.

Resource sharing was inferred from increased shoot length and biomass in connected, compared to severed offspring ramets (Tomasko & Dawes 1989, Amsberry et al. 2000), but results are only presented for biomass since analyses based on shoot measurements yielded consistent results. Effects of treatments and their interactions on plant growth were tested by ANOVA. As we were not able to use one aquarium for every replicate, we included the factor ‘aquarium’ in the ANOVA to correct for overall growth differences between the three aquaria. Proportional data were transformed to the arcsine of the square root before analysis. Statistical analyses were performed with SAS software (SAS Institute Inc., Cary, NC, USA 1999-2001).

Results

Clonal integration

After three weeks of growth, severing had reduced total shoot biomass of offspring ramets (O1 + O2) strongly (63 % reduction, ANOVA; $F_{1,28} = 25.9$, $p < 0.0001$, Fig. 6.2), whereas shading of the first offspring (O1) had a smaller effect (30 % reduction, $F_{1,28} = 5.5$, $p < 0.05$). Shading did not influence the response of offspring ramet shoot biomass to being severed (severing x shading interaction: $F_{1,28} = 0.02$, $p < 0.8$).
Offspring ramets were differently affected by severing and by shading (Fig. 6.3). Biomass of O1 was highest in the 3-ramet - light treatment as compared to all other treatments. When shaded, there was no significant biomass difference between the 2- and 3-ramet systems, meaning that O1 performance was not significantly increased by the presence of a parent plant. In contrast, O2 did profit from the 3-ramet system under both light and shade conditions (of O1). Furthermore, its biomass increase due to clonal integration was higher when O1 was shaded than when O1 was unshaded. Shading of O1 did not influence the biomass of O2 in the 3-ramet system. As a consequence, biomass of O2 was similar to the biomass of O1 in the 3-ramet - shade treatment, but was less than O1 in all other treatments (Fig. 6.3).

This complex response pattern is supported when analysing the full data set with an ANOVA and distinguishing the two offspring ramets with the factor ‘ramet order’. Both O1 and O2 were negatively influenced by severing and shading (significant main effects: severing, shading, and ramet order, Tab. 6.1). Severing had a stronger effect on O2 biomass as compared to O1 biomass (significant severing x ramet order interaction, Tab. 6.1), whereas there was no indication that shading of O1 affected O1 and
O2 differently (non-significant shading x ramet order interaction, Tab. 6.1). Finally, offspring ramets differed in their response to shading in the 2- versus 3-ramet system (significant three way interaction: severing * shading * ramet order, Tab. 6.1). There was also a small aquaria effect, but the inclusion or omission of the factor ‘Aquarium’ in the ANOVA neither affected the significance levels nor the effect sizes of the studied main effects or interactions.

Tab. 6.1 ANOVA with shoot biomass (log transformed) as dependent variable and severing, shaded ramet order (first or second offspring) and aquarium as independent variables. The latter was included to account for effects due to different growth conditions in the three aquaria. Model $R^2 = 0.74$, $n = 58$, $F = 15.0$, $p < 0.0001$.

<table>
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<th></th>
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<tr>
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<tr>
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</tr>
<tr>
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</tr>
<tr>
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<td>6.39</td>
<td>0.0148</td>
</tr>
<tr>
<td>Aquarium</td>
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<td>0.77</td>
<td>3.92</td>
<td>0.0264</td>
</tr>
</tbody>
</table>

As a consequence of different responses of O1 and O2 to severing and shading, the growth of O2 relatively to O1 (O2 / O1) was significantly influenced by severing ($F_{1,28} = 22.82$, $p < 0.0001$, Fig. 6.4) and the interaction between severing and shading ($F_{1,28} = 8.73$, $p < 0.01$): Shading of O1 increased the O2 / O1 biomass ratio when O1 was connected to a parent ramet, but decreased it when the connection was severed. Biomass of parent ramets was neither affected by severing nor by shading ($F_{1,28} = 0.33$, $p < 0.6$, and $F_{1,28} = 0.1$, $p < 0.75$).

![Fig. 6.4 Biomass ratio of second offspring and first offspring (O2 / O1) (mean ± S.E.) of P. perfoliatus grown in aquaria. Solid lines indicate 'light', hatched lines indicate 'shade' treatments](image)
**Biomass allocation and spacer length**

Root allocation of O1 was affected by severing ($F_{1,28} = 3.53, p < 0.08$), shading ($F_{1,28} = 3.75, p < 0.07$) as well as the interaction between the two ($F_{1,28} = 7.93, p < 0.009$): Shading increased root allocation of connected O1 but reduced it in severed O1 (Fig. 6.5a). No significant treatment effects were observed for shoot allocation (Fig. 6.5b), and rhizome allocation (Fig. 5c). Shoot biomass was significantly related to shoot ($r = 0.36, p < 0.05$) and rhizome ($r = -0.47, p < 0.006$) allocation but not to root allocation ($r = 0.03, p > 0.5$). Consequently, treatment effects on root allocation were also significant when including shoot biomass as a covariate into the statistical model (shading: $F_{1,27} = 4.67, p < 0.05$, severing: $F_{1,27} = 4.45, p < 0.05$, shading x severing: $F_{1,27} = 6.00, p < 0.03$, shoot biomass: $F_{1,27} = 0.93, p < 0.4$).

**Fig. 6.5** (a) Shoot (b) rhizome and (c) root allocation ± S.E. of 3-ramet system and 2-ramet system in *P. perfoliatus* first offspring (O1). Solid lines indicate ‘light’, hatched lines indicate ‘shade’ treatments

Spacer length between offspring ramets (SO1) was reduced in the 2-ramet system ($F_{1,28} = 6.09, p < 0.03$), whereas shading had no significant effect on SO1 ($F_{1,28} = 0.17, p < 0.7$). There was also no influence of shading on the response of SO1 to severing (severing x light interaction $F_{1,28} = 2.13, p < 0.16$) (Fig. 6.6).

**Fig. 6.6** Spacer length between offspring ramets (SO1) in relation to first offspring (O1) shoot biomass. Filled symbols indicate 3-ramet system treatments, open symbols indicate 2-ramet system treatments
SO1 was positively related to O1 shoot biomass ($r = 0.57$, $p < 0.007$). However, if O1 in the 2-ramet systems was analysed separately, SO1 was negatively related to shoot biomass ($r = -0.51$, $p < 0.05$), whereas in 3-ramet systems, SO1 was positively related to shoot biomass ($r = 0.71$, $p < 0.005$) (Fig. 6.6). This suggests that the 3-ramet system O1 responded to growth conditions - which were at least partially related to shading - by decreasing rhizome length, whereas the 2-ramet system O1 responded to growth conditions by increasing rhizome length.

**Discussion**

**Clonal integration**

The substantially higher biomass of offspring in the 3-ramet systems as compared to the 2-ramet systems shows that parent ramets of *P. perfoliatus* were capable of sharing resources acropetally via clonal integration. However, clonal integration was not uniform, but rather sensitive to the growth conditions of the first offspring ramet: O1 ramets benefited substantially from integration only when in the light but were not supported when shaded. In contrast, many previous studies have found physiological integration especially where recipient ramets experienced stress through resource limitation in heterogeneous environments (Alpert & Stuefer 1997, Hutchings & Wijesinghe 1997, Alpert 1999). For example, connected shaded shoots of the seagrass *Thalassia testudinum* achieved growth rates equal to non-shaded controls (Tomasko & Dawes 1989). Likewise, severely shaded ramets of *Lolium perenne* continued to grow and produced new leaves as a result of physiological integration (Ong & Marshall 1979), and shaded shoots of *Eichhornia crassipes* suffered less when connected to parent shoots growing in the light (Methy *et al.* 1990). However, in our study the proximal offspring (O1) benefited from the 3-ramet system, i.e., from the connection to its parental ramet only under full light, but was not supported when shaded. In the latter situation, the shaded ramet O1 was passed by and resources were directed to the distal offspring O2. Indeed, O2 ramets of *P. perfoliatus* benefited from resource sharing relatively more strongly when O1 ramets were shaded. This shows that clonal integration in *P. perfoliatus* can also occur between non-adjacent shoots (see also (Terrados *et al.* 1997) and that resources are shared with distal offspring depending on the microhabitat, i.e. growth conditions, of the proximate offspring. Likewise, resource sharing has often been observed with ramets suffering from herbivory (Marshall & Sagar 1965, Schmid *et al.* 1988, Olson & Wallander 1999). However, lack of support for damaged ramets of a perennial herb was recently demonstrated and attributed to competition between sibling ramets (Hellström *et al.* 2006). Competition within branches of a plant has also been demonstrated in pine trees (Honkanen & Haukojoa 1994) and pea plants (Novoplansky *et al.* 1989) and has been termed the branch- competition hypothesis (Sachs & Novoplansky 1997). This hypothesis predicts that a plant module which is inferior due to e.g., herbivory damage or microhabitat unsuitability should be left out of support when more viable sinks are available. Our results are in line with this prediction. However, shaded O1 in the 3-ramet system showed even strong signs of chlorosis which was not the result of shading *per se*, as shaded O1 in the 2-ramet system appeared vigorous and retained green leaves. This observation suggests that the branch- competition hypothesis is unlikely to give a complete explanation of our results: At the end of the experiment, shoot biomass of O1 and O2 were similar (Fig. 6.3). Assuming a faster growth rate of unshaded O2 relative to shaded O1 suggests that during most of the experimental time, biomass of O1 was larger than biomass of O2. It is hence difficult to believe that despite these biomass differences, competitive superiority of O2 was large enough to result into chlorosis of O1. Rather, the large differences in performance of O1 suggest controlled senescence of shaded O1 in the 3-ramet
treatment possibly associated with remobilization of resources (Ong & Marshall 1979, Stapel & Hemminga 1997) towards O2. Hence, integration seems to have qualitatively altered the response of shaded O1 by inducing a novel response, i.e. chlorosis (De Kroon et al. 2005).

**Biomass allocation and spacer length**

Shading increased root allocation of connected offspring but reduced root allocation in severed offspring. Our statistical analyses suggest that the differences in biomass allocation are not due to allometric growth rules which predict that smaller plants show a higher biomass allocation to belowground structures (Müller et al. 2000). Despite their small biomass, O1 in 2-ramet - shade systems had the lowest root allocation. This might result from a shortage of carbohydrates and the need to invest in shoot biomass (Alcoverro et al. 1997). The lower root allocation in the severed shaded offspring compared to higher root allocation in connected shaded offspring is also in line with the foraging hypothesis proposing that single plants specialize in the most limiting resource (here: light), and integrated plants specialize in the most abundant resource (here probably nutrients) (Stuefer et al. 1996, Stuefer 1998). In a clonal ramet system with ‘division of labour’ (Hutchings & Wijesinghe 1997) ramets may continue to take-up nutrients by roots even when they are non-photosynthetic (Jónsdottir & Callaghan 1990) and in our experiment, shaded O1 may still contribute to plant growth by supplying nutrients to unshaded O2.

As in some terrestrial plants (Wijesinghe & Handel 1994, Van Kleunen et al. 2000), severing significantly reduced spacer lengths of *P. perfoliatus* offspring. This might be attributed to the stronger effect of severing on offspring shoot biomass, and to the overall positive relationship between shoot biomass and rhizome length. In-situ, spacer length of *P. perfoliatus* strongly increases with distance from the primary ramet, possibly as a consequence of an increasing biomass and production of an interconnected clonal fragment with the number of produced ramets (Wolfer & Straile 2004b). As a result of shading, O1 in the 3-ramet system responded to the unfavourable growth conditions by decreasing rhizome length, whereas O1 the 2-ramet system responded to shade conditions by increasing rhizome length, even though shoot biomass was slightly decreased. This is in line with the predictions of the foraging hypothesis: shaded shoots are expected to produce longer rhizomes in order to ‘escape’ from the unfavourable habitat (Hartnett & Bazzaz 1983, Sutherland & Stillman 1988). Possibly, foraging is only expressed in the growth patterns when growth is strongly impaired by shading, and integration is not possible (but see De Kroon & Hutchings (1995) for a critical discussion of the plant foraging hypothesis).

To conclude, our experiment has shown that (1) *P. perfoliatus* parent ramets support their clonal offspring ramets via translocation of resources, i.e. there is clonal integration within a genet, and (2) the relative translocation of resources to different offspring generations depends on the habitat quality of the individual ramets: ramets in unfavourable microhabitats are not integrated when support of other ramets provides higher benefits for the genet. This behaviour might be highly relevant when plants produce new ramets within dense patches of macrophytes (Wolfer & Straile 2004a, Wolfer & Straile 2004b). In such a case it might not benefit the plant to support a severely shaded ramet, but rather to invest in rhizome growth and new ramets at the outer perimeter of the patch, where microhabitats are more suitable.
Chapter 7. MODELLING THE CLONAL GROWTH OF THE RHIZOMATOUS MACROPHYTE POTAMOGETON PERFOLIATUS

Susanne R. Wolfer, Egbert H. van Nes & Dietmar Straile


Abstract

Macrophytes play a crucial role in the functioning of lake ecosystems. Until now most macrophyte models neglected the fact that the majority of macrophyte species expand clonally during the growing season. Inclusion of a detailed description of clonal growth in models can facilitate our understanding of space occupation and patch expansion and predict future macrophyte development. ‘CLOMO’ is an individual-based model which includes a detailed, spatially explicit description of rhizome formation and clone expansion as well as a realistic description of photosynthesis including light limitation and temperature. The model also accounts for transfers of energy or resources between different parts of the clone (‘clonal integration’).

Although the clonal growth of macrophytes is complex and poorly known, the first model results for the macrophyte species Potamogeton perfoliatus were promising and compared well with the field data. The model can produce growth networks very similar to those found in the field. A Monte-Carlo sensitivity analysis showed systematically which parameters have the largest effect on the architecture and expansion of the clones.

The application of the model provided new insights into growth dynamics and patch development:

(1) The model showed that a lack of branching will lead to the extinction of the clonal fragment after a certain number of years. This is due to the fact that the reproduction organs (turions) are formed at the end of a branch and even a small turion mortality will cause a reduction in surviving plant numbers.

(2) The growth of rhizome axes relative to those in the previous year determines the patch density and patch expansion rate. Reversing rhizomes lead to compact patch growth whereas continuing rhizomes lead to loose aggregates.
Introduction

The majority of submersed macrophytes form clones which are connected by belowground rhizomes. Observed from above, a macrophyte patch appears like a simple collection of shoots, but a closer look into the sediment reveals a complex network of ‘ramets’ (= potentially independent units with leafy shoots and roots) interconnected by ‘rhizomes’ (= horizontal shoots lacking chlorophyll). One plant of *P. perfoliatus* can, for example, consist of more than 15 ramets connected by more than 1 m of rhizome (Wolfer & Straile 2004a). Experiments have shown that ramets exchange energy or resources through these rhizomes (Hartnett & Bazzaz 1983), a process called ‘clonal integration’. Furthermore, rhizomes are mobility units, as a clone can move slowly by creating new rhizomes. The architectural growth of main rhizome axes, rhizome branchings, rhizome angles and rhizome ‘spacers’ (= rhizome connection between two neighbouring shoots) follows species-specific clonal rules (Callaghan et al. 1990, Evans & Cain 1995). Nonetheless, spacer lengths and branch angles also show considerable variation (Cain et al. 1995, Wolfer & Straile 2004a,b), sometimes in response to their growth conditions (De Kroon & Hutchings 1995), aiming at the effective exploitation of local resources such as light and nutrients (Callaghan et al. 1990).

Clonal growth architecture is important for macrophyte fitness because it determines propagation, growth and survival, space occupation and patch expansion. Also the sharing of resources such as carbohydrates or nutrients increases fitness (Wijesinghe & Handel 1994, Stuefer et al. 1996, Hutchings & Wijesinghe 1997).

Our objective was to develop a model which can improve our understanding of mechanisms that could cause the observed field patterns of clonal architecture and patch expansion. It does not aim at replacing existing models of aquatic macrophytes, but rather adds a supplementary application. On the long run, it could be used to predict future macrophyte development and the impact of environmental variation.

Although there are many detailed dynamical models of macrophytes (Collins & Wlosinski 1989, Scheffer et al. 1993, Hootsmans 1994, Chen & Coughenour 1996, Muhammetoglu & Soyupak 2000, Van Nes et al. 2003), the clonal growth of submerged macrophytes has, to our knowledge, never been modelled in detail, including architectural, spatial, environmental, temporal and demographic components. For terrestrial plants, only a few of such detailed models exists (Herben & Suzuki 2002, Oborny & Kun 2002). The facts that photosynthesis in water has fundamentally other restrictions than in air and that light submission in water is far more complex require separate models for submersed species.

Here we present the individual-based model ‘CLOMO’ (‘clonal module’), a spatially explicit model that combines a stochastic description of clonal expansion with a ramet-based calculation of primary production and respiration using physiological rules of the non-clonal model Charisma (Van Nes et al. 2002, 2003). Clonal integration was described as simple as possible, since transport between ramets is a poorly understood process. We applied the model to describe the spatial architecture of *P. perfoliatus* L. in Lake Constance.

Special analyses were performed with regard to branching frequency and rhizome growth direction. Furthermore, a Monte Carlo sensitivity analysis (Klepper et al. 1994) was applied to show systematically which parameters have the largest effect on the architecture and expansion of the clones.
Methods

Model description

Overview

CLOMO is an extension of the model Charisma (Van Nes et al. 2002, 2003). Although CLOMO uses the biomass growth unit of Charisma, its new components make it fundamentally different from the earlier version (see Tab. 7.1). While the biomass model Charisma is non-clonal and uses super-individuals to cope with large numbers of individuals (Scheffer et al. 1995), the current model is truly individual-based and operates on a smaller spatial scale. Clones are modelled as a set of ramets (nodes with shoots) interconnected by rhizomes. The model is explicitly spatial, describing patches of plants growing on a grid.

Tab. 7.1 An overview of the main differences between non-clonal macrophyte models (e.g. Collins & Wlosinski 1989, Scheffer et al. 1993, Hootsmans 1994, Chen & Coughenour 1996, Muhammetoglu & Soyupak 2000, Van Nes et al. 2003) and the clonal growth model CLOMO

<table>
<thead>
<tr>
<th>Non-clonal macrophyte models</th>
<th>Clonal macrophyte model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoots are the basic unit for photosynthesis, (self-) shading is calculated for each shoot</td>
<td>Ramets are the basic unit for photosynthesis</td>
</tr>
<tr>
<td>From each seed or tuber emerges a maximum of one shoot in spring; no further shoot emergence during the growth season</td>
<td>From each tuber emerges one ramet in spring; additional ramets are formed during the growth season if there is enough biomass accumulated</td>
</tr>
<tr>
<td>Individual shoots, no clones</td>
<td>Several ramets form a clone</td>
</tr>
<tr>
<td>(Almost) all shoots are assumed to be of equal age and length</td>
<td>Each ramet has a different age and length</td>
</tr>
<tr>
<td>Spacer lengths and number of ramets per clone are ignored</td>
<td>Spacer lengths and number of ramets per clone are important components</td>
</tr>
<tr>
<td>No patch expansion within a season</td>
<td>Position of new ramets is determined stochastically and leads to patch expansion within a season</td>
</tr>
<tr>
<td>Transfer of energy between shoots and roots/reproductive organs only</td>
<td>Additional transfer of energy between ramets</td>
</tr>
</tbody>
</table>

The basic units of the calculations are the ramets. Each ramet has an exact x and y coordinate and is associated with one grid cell. A clone can expand over more than one grid cell. The biomass growth of each ramet is calculated with time steps of 1 day and depends on photosynthesis and local environmental conditions. During their growth, the shoots reserve an increasing part of their net production for creating rhizomes and new ramets. The positioning of new ramets is determined by the length of the rhizome and a stochastic component. Above a certain shoot length, part of the production will be transferred to neighbouring ramets (clonal integration). During one season, apical growth of rhizomes and ramets and branching lead to the origin of a large clonal system (‘plant’). At the end of the growth season, part of the biomass is redirected to overwintering organs (‘turions’) in the sediment, and the rest of the aboveground biomass dies. The turions will develop new sprouts at a preset day in spring. Many of the default parameters have been derived from Lake Constance field data (Tab. 7.2).
Each grid cell has environmental variables associated with it (vertical light attenuation, water level and nutrients). The grid dimensions can be defined by the user.

In the following, we will describe the model focusing on the new features and summarizing the parts that are taken from the earlier version of the model (Van Nes et al. 2002, 2003). The model is implemented in Delphi 5.5, an object oriented version of Pascal. It is freely available on: http://www.dow.wau.nl/aew/charisma/.

Tab. 7.2 Default parameters for the clonal model of *P. perfoliatus*. Source: a - calibrated, b - estimated from field observations (Wolfer, unpublished results), c - assumed to be the same as *P. pectinatus* (Scheffer et al. 1993, Van Nes et al. 2003), d - Wolfer & Straile 2004b, e - Wolfer & Straile 2004a

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>HAge</td>
<td>Half saturation for senescence</td>
<td>d</td>
<td>100 b</td>
</tr>
<tr>
<td>PAge</td>
<td>Exponent in Hill function for senescence</td>
<td></td>
<td>2 b</td>
</tr>
<tr>
<td>pMax</td>
<td>Maximal gross photosynthesis</td>
<td>hr⁻¹</td>
<td>0.006 a</td>
</tr>
<tr>
<td>Q10</td>
<td>Q10 for maintenance respiration</td>
<td></td>
<td>2 c</td>
</tr>
<tr>
<td>Resp20</td>
<td>Respiration at 20 °C</td>
<td>day⁻¹</td>
<td>0.00206 c</td>
</tr>
<tr>
<td>MaxLength</td>
<td>Maximum shoot length</td>
<td>m</td>
<td>5 b</td>
</tr>
<tr>
<td>MaxWeightLenRatio</td>
<td>Mean weight of 1 m young shoot</td>
<td>g m⁻¹</td>
<td>0.8 e</td>
</tr>
<tr>
<td>RootShootRatio</td>
<td>Proportion of shoot allocated to the roots</td>
<td>fraction</td>
<td>0.06 b</td>
</tr>
<tr>
<td>FracPeriphyton</td>
<td>Fraction of light reduced by periphyton</td>
<td>fraction</td>
<td>0.2 c</td>
</tr>
<tr>
<td>hPhotoLight</td>
<td>Half-saturation light intensity (PAR) for photosynthesis</td>
<td>µE m² s⁻¹</td>
<td>30 c</td>
</tr>
<tr>
<td>hPhotoTemp</td>
<td>Half-saturation temperature for photosynthesis</td>
<td>°C</td>
<td>14 c</td>
</tr>
<tr>
<td>pPhotoTemp</td>
<td>Exponent in temperature effect (Hill function) for photosynthesis</td>
<td></td>
<td>3 c</td>
</tr>
<tr>
<td>sPhotoTemp</td>
<td>Scaling of temperature effect for photosynthesis</td>
<td></td>
<td>1.35 c</td>
</tr>
<tr>
<td>HTurbReduction</td>
<td>Half saturation biomass of light attenuation reduction</td>
<td>g m⁻²</td>
<td>100 c</td>
</tr>
<tr>
<td>pTurbReduction</td>
<td>Power in Hill function of light attenuation reduction</td>
<td></td>
<td>1 c</td>
</tr>
<tr>
<td>PlantK</td>
<td>Light attenuation of plant tissue</td>
<td>m² g⁻¹</td>
<td>0.02 c</td>
</tr>
<tr>
<td>cTuber</td>
<td>Fraction of turion weight lost daily when sprouts start growing</td>
<td>fraction</td>
<td>0.1 c</td>
</tr>
<tr>
<td>MaxTurionWeight</td>
<td>Maximum weight of turions</td>
<td>g</td>
<td>0.2 b</td>
</tr>
<tr>
<td>MeanTurionWeight</td>
<td>Mean (initial) weight of turions</td>
<td>g</td>
<td>0.2 b</td>
</tr>
<tr>
<td>MinTurionWeight</td>
<td>Minimum weight of turions</td>
<td>g</td>
<td>0.1 b</td>
</tr>
<tr>
<td>TurionFraction</td>
<td>Fraction of biomass allocated to turions</td>
<td>fraction</td>
<td>0.05 a</td>
</tr>
<tr>
<td>TurionGerminationDay</td>
<td>Day of turion sprouting</td>
<td></td>
<td>114 b</td>
</tr>
<tr>
<td>TurionMortality</td>
<td>Annual mortality of turions</td>
<td>yr⁻¹</td>
<td>0.1 b</td>
</tr>
<tr>
<td>TurionReproDay</td>
<td>Formation day of turions</td>
<td></td>
<td>250 b</td>
</tr>
<tr>
<td>Alpha</td>
<td>Parameter that determines the biomass allocation to subsequent rhizomes and ramets</td>
<td></td>
<td>0.6 a</td>
</tr>
<tr>
<td>MeanRhiAngle</td>
<td>Mean rhizome angle</td>
<td>rad</td>
<td>0 d</td>
</tr>
<tr>
<td>NewRamiLength</td>
<td>Length of the ramet at which it creates a new rhizome and ramet</td>
<td>m</td>
<td>0.15 a</td>
</tr>
<tr>
<td>PBranchingLong</td>
<td>Branching probability of rhizomes</td>
<td>fraction</td>
<td>0.1 d</td>
</tr>
<tr>
<td>RhizomeWeightPerM</td>
<td>Average weight of 1 m rhizome</td>
<td>g m⁻¹</td>
<td>0.5 e</td>
</tr>
<tr>
<td>SDRhiAngle</td>
<td>Standard deviation of rhizome angle</td>
<td>rad</td>
<td>π/9 d</td>
</tr>
<tr>
<td>TurionAngle</td>
<td>Angle of the turion with the parent rhizome</td>
<td>rad</td>
<td>π d</td>
</tr>
<tr>
<td>TurionAngleRange</td>
<td>Range in the angle of the turion with the parent rhizome</td>
<td>rad</td>
<td>0 d</td>
</tr>
</tbody>
</table>


Production and respiration

Most rules for production and respiration are taken from the Charisma model (Van Nes et al. 2003), but bicarbonate is not assumed to be limiting, and senescence is described in a more detailed way.

The daily growth of each shoot ($\Delta W$) depends on the photosynthesis ($P$), the maintenance respiration ($R_m$), the import from previous ramets ($T_1$) and export to subsequent ramets ($T_2$) (Fig. 7.1):

$$\Delta W = W_p - W - R_m + T_1 - T_2$$  \hspace{1cm} (1)

![Fig. 7.1 Schematic overview of the factors that determine the growth of each shoot](image)

Maintenance respiration ($R_m$) is arbitrarily taken in the middle of the range of values published by Madsen and Adams (1989) and Ikusima (1970) for miscellaneous submerged plants ($r_{20} = 0.024 \text{ g g}^{-1}\text{ d}^{-1}$ at 20°C). Temperature dependence of the respiration is formulated using a $Q_{10}$ formulation (default value 2):

$$R_m = r_{20} Q_{10}^{T_{-20}}$$  \hspace{1cm} (2)

Only the shoots take part in the primary production ($P$). The maximum photosynthesis ($P_{\text{max}}$) is limited by the in-situ light intensity at plant leaves ($I$), temperature ($T$), and the age of the ramet ($A$):

$$P = P_{\text{max}} \frac{I}{I + H_i} \frac{1.35T^3}{T^3 + 14} \frac{H_i^2}{H_i^2 + A^2}$$  \hspace{1cm} (3)

The parameter $P_{\text{max}}$ represents the specific daily production of the plant top at 20 °C not having light limitation. Light limitation is described by a Monod function, $H_i$ is the half-saturation constant. Irradiance follows a daily as well as a yearly cycle and light is attenuated in the water column both by the water and the vegetation (Van Nes et al. 2003).

Temperature dependence of photosynthesis was fitted to values of *Potamogeton pectinatus* (Scheffer et al. 1993). As field observations indicate that older ramets are often covered with
periphyton that reduces irradiance and consequently production, a factor for aging was added as a Hill function \( H_A \) is the half-saturation constant of aging).

In the present analyses we assumed that the plants are not limited by phosphorus, nitrogen or carbon in the water, but the model can optionally account for such limitations.

As light varies during the day and with water depth, we integrated photosynthesis over the day and over the length of each shoot by three-point Gaussian integration (Goudriaan 1986). The in-situ light conditions were averaged for each grid cell taking self-shading into account (see below). As accounting for self-shading can be very computer intensive and as the biomass changes are relatively slow, we calculated the light attenuation in each grid cell once in 7 days (at 15 depths distributed evenly over the water column) and interpolated linearly between the calculated points.

For vertical light attenuation, temperature and water level we used 10 years of interpolated data from Lake Constance. For more theoretical questions we averaged these years to avoid stochastic differences between years.

We also included water clarification by macrophytes (Scheffer 1998, Van Nes et al. 2003). In Lake Constance this effect is probably not important as the water is usually rather clear, but this effect is essential for the existence of alternative stable states (Scheffer 1998; Van Nes et al. 2002).

In most simulations we used a grid of 10 x 10 cells of 0.2 m x 0.2 m. To avoid edge effects, ramets that grew beyond the border of the grid were coupled to the opposite grid cells.

**Biomass allocation, clonal growth and clonal integration (transfer)**

The produced biomass is allocated to shoots, rhizomes and roots. The root is a fixed proportion of the shoot that does not take part in photosynthesis. The height of the young shoots increases proportionally with their biomass until the water surface or a predefined maximum height has been reached. If the net production of a shoot is positive, a part is allocated to the rhizomes. The proportion of the production that is allocated depends on the height of the plant: very small shoots do not attribute, fully-grown shoots add all their production to the rhizomes. Between these extremes, the allocated proportion increases linearly with shoot height. The biomass is assumed to be transported acropetally from older to younger ramets (Evans & Whitney 1992, Marbà et al. 2002). Each younger shoot adds a part \( \alpha \) of the transferred biomass to its net production. The remainder goes to the next shoot (Fig. 7.2). Thus, the transport to the shoot of ramet \( i (T_i) \) sums up to:

\[
T_i = \sum_{k=1}^{i} S_{i-k} \alpha (\alpha - 1)^{i-k} \quad i > 1
\]

in which \( S_i \) is the surplus production of shoot \( i \) (\( i = 1 \) is the oldest shoot). For simplicity we assume that there is no cost for transport. Biomass that is transferred to full-grown shoots, will not be used but immediately be transferred further to the next ramet. If there is a branch, the transported biomass is divided equally over both branches. The surplus production of the last ramet goes into the growth of the new rhizome which has a fixed weight-length ratio. If the last shoot reaches a certain fixed height, the growth of the rhizome is ceased and a new daughter ramet is created.

The main rhizome may have an (usually small) angle with the previous rhizome which is drawn from a normal distribution. Each ramet has a certain probability of branching which is drawn from a Bernoulli distribution. The angle of the branch with the main rhizome is also drawn from a predefined normal distribution.
Fig. 7.2 Scheme of the clonal growth of *P. perfoliatus*. $S_i$ is the surplus production of shoot $i$, $T_i$ is the transfer to shoot $i$, $\alpha$ is a parameter that determines which part of the transfer ($T_i$) goes to the next shoot

**Mortality**

The model accounts for (a) a fixed background mortality and (b) mortality at the end of the season. Background mortality results either in a weight loss or in a stochastic loss of the complete shoot depending on whether it has already reached the surface or not (Van Nes *et al.* 2003). At a pre-set day in autumn, all shoots die, and their biomass is reallocated to the rhizomes. At the last (youngest) ramet of each branch of the clone, a turion is created (Wolfer & Straile 2004b). Since it has been shown that turion production often depends on plant biomass (Spencer *et al.* 1993), the turion receives a proportional part of the accumulated energy in each ramet (Fig. 7.3). The amount of energy (biomass) that is transported to each turion is a fixed part of the rhizome biomass up to a fixed maximum. The turion is only created if the rhizome biomass exceeds a certain minimum weight. The growth direction of the clone can be continuing, reversed or stochastic in the next season.

Fig. 7.3 Schematic representation of a clone and the transport of energy from the ramets (circles) to the turions (triangles). At the end of the season the turions get a proportional part (same color) of the accumulated biomass in the rhizomes and shoots. If enough biomass is accumulated, the turion produces a new clone in the next season in which the growth direction is optionally reversed
Scanning of asymptotic regimes

In the previous version of the model we showed that there can be two alternative stable states in the model due to a feedback of vegetation on their light climate (Van Nes et al. 2002, Van Nes et al. 2003). In the current more detailed model, we show whether the model still has alternative stable states, by analysing the effect of increasing and decreasing light attenuation on the equilibrium biomass of *P. perfoliatus*. Vertical light attenuation was slowly increased in small steps while the model was not reset. After a period of stabilising, the biomass at the end of the growth season was plotted for 5 years. When the water had reached maximum vertical light attenuation and the vegetation had disappeared, the same procedure was repeated backwards (i.e. vertical light attenuation was reduced). A small import of turions prevented total extinction of the plants. If the model has alternative stable states it will show a hysteresis in the response, i.e. the vegetation will recolonize at a lower turbidity than the turbidity at which they disappeared.

Monte Carlo sensitivity analysis

We applied a Monte Carlo sensitivity analysis to select the parameters which have the strongest impact on clonal architecture. We generated 20 000 sets of parameters, drawing all parameters randomly and independently from uniform probability distributions within ranges of ±10% around the default values. Three years were simulated with each parameter setting, and the model results (mean shoot length, mean spacer length, fraction belowground biomass, mean number of ramets per clone, approximate expansion area, mean expansion per clone) were stored at three dates per year (at day 189, 219 and 249) of each year. At the end of each simulation, the model was reset to the starting number of turions per grid cell (5 m$^{-2}$). Sensitivity coefficients were defined by linear regression between the parameter values and each model output value, scaled by the ranges used for each parameter (Klepper 1989). Cluster analysis (average linkage) was used to form groups of parameters that had the same or opposite effect on the qualitative model results. As similarity measure the absolute sine of the angle between the vectors of sensitivity coefficients was used. As measure of the total sensitivity the length of this vector was used (Klepper 1989).

In a Monte-Carlo analysis there is a probability that a parameter has a positive sensitivity coefficient because it is related to the model outcomes by chance. To determine the significance level of the sensitivity coefficients, we added 100 dummy parameters that had no effect on the model (Van Nes et al. 2003). These dummy parameters were arbitrarily set to 1. As the real model parameters, the dummy parameters were drawn from uniform distributions, and their ‘sensitivity coefficients’ were calculated. The 0.02 significance level of the sensitivity coefficients was estimated by the 98% percentile of the sensitivity coefficients of the dummy parameters. In the cluster analyses we only included parameters with a significant sensitivity coefficient.

Results

Architecture and growth parameters

The simulation produces complex architectural patterns of shoot and rhizome connections (Fig. 7.4) which compare well with field data from Lake Constance (Wolfer & Straile 2004b). For example, the observed increase in length of younger rhizomes during one season (Wolfer & Straile 2004a, 2004b) is reproduced by the model.
A 20 years simulation starting with 5 propagules m$^{-2}$ yielded the following results: Annual curves of most growth parameters (Fig. 7.5a) start in May, increase more or less exponentially, peak in August, and fall back to zero after September. With regard to area, there is a net patch growth each year (difference between end-of-season and before-season turion occurrence). In 20 years (Fig. 7.5b), biomass, ramet number and total patch size initially increase and then stabilize after 10 - 15 years; ramet number per plant and rhizome length decrease slightly, spacer length, shoot length, belowground biomass and limitation stay about the same.

The values of simulated growth parameters such as shoot length, rhizome spacer length, rhizome length etc. are in the range of the field data (Wolfer & Straile 2004b; Tab. 7.3). In general, growth parameters of macrophytes are extremely variable and also the cited reference only covers a small part of the repertoire. The simulated biomass and ramet densities occur frequently in-situ (Wolfer, unpublished observation); for the cited field work, lower densities were deliberately chosen. The simulated number of ramets per plant is rather low, but this is partly due to the high equilibrium density of ramets, implying strong light limitation. At lower ramet densities the number of ramets per plant is quite realistic (Fig. 7.6).

**Tab. 7.3** Model results of growth parameters in comparison to in-situ and mesocosm assessments (average site values)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Model result</th>
<th>In-situ (Wolfer and Straile, 2004b)</th>
<th>Mesocosm (Wolfer and Straile, 2004a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>biomass</td>
<td>280 g dw m$^{-2}$</td>
<td>17 - 200 g dw m$^{-2}$</td>
<td>na</td>
</tr>
<tr>
<td>ramets</td>
<td>350 m$^{-2}$</td>
<td>90 - 210</td>
<td>na</td>
</tr>
<tr>
<td>ramets per plant</td>
<td>5.5</td>
<td>5 - 8</td>
<td>7 - 13</td>
</tr>
<tr>
<td>shoot length</td>
<td>100 cm</td>
<td>12 - 66 cm</td>
<td>na</td>
</tr>
<tr>
<td>rhizome spacer length</td>
<td>8.5 cm</td>
<td>7.6 - 8 cm</td>
<td>7 - 10 cm</td>
</tr>
<tr>
<td>rhizome length</td>
<td>0.4 m</td>
<td>0.4 - 0.63 m</td>
<td>0.6 - 1.25 m</td>
</tr>
</tbody>
</table>
Fig. 7.5 20 years run, (a) year 2009 (b) 1990 - 2010.
Stabilization of biomass and ramet number after an initial colonization phase is common in aquatic macrophytes (Duarte & Sand-Jensen 1990). Ramet number per plant and total rhizome length decrease because of higher density and the resulting light limitation (Wolfer & Straile 2004a).

Average spacer length, shoot length and belowground fractions do not change much during the 20 simulated years. The behaviour of spacer length does not comply with observations which show that average spacer length decreases with increasing light limitation (Wolfer & Straile 2004a). This decrease must be an active light foraging strategy of the plants (shoot growth for light capturing at the expense of rhizome growth) which could not be reproduced by the simplified plant strategy in the model.

As in Wolfer & Straile 2004a, we found lower patch expansion at low plant density and at higher density, and highest patch expansion at medium density. Long-term stabilization of patch sizes under model conditions (no disturbance, homogeneous environment) is probably related to field observations, where patches appear at the same site and in a very similar size from year to year (Walser 1996; Gafny & Gasith 1991). In-situ, patches may even keep their distinct shape over long time periods, although, according to expectations, they should expand until they fill up homogeneous lake compartments. The growth curves suggest that this could be a result of the stabilization of biomass and ramet number which in turn are due to light limitation in a dense patch.

**Branchings**

A variation of the branching probability per plant from 0 to 1 reveals strong consequences for equilibrium summer biomasses and total number of ramets (Fig. 7.7). Plants with zero branching die. Due to the clonal growth architecture of *P. perfoliatus*, each plant with zero branching produces exactly one turion at the end of the rhizome axis (Wolfer & Straile 2004b). Under the assumption of zero mortality, the number of plants will remain the same forever. However, turions are usually subjected to waterbird foraging, fungus infection, or mortality of stochastic reasons. Additionally, it is assumed that turions also fail to propagate if their weight is too low (for example due to bad shoot...
biomass growth in the previous season). The model shows that, if there is no branching, even the lowest turion mortality will eventually lead to the extinction of the plant.

![Graph](image)

**Fig. 7.7** Modelling results on the influence of branching probability on (a) summer biomass and (b) number of ramets in *P. perfoliatus* after a simulation period of 20 years

Maximum summer biomass and maximum density are achieved at the (relatively low) branching intensity of 0.1 - 0.2. At higher branching rates, biomass and number of ramets decrease again. The optimum branching probabilities found by the model are equal to those found in the field in patches with favourable plant growth (Wolfer & Straile 2004b), and lower than those found under experimental conditions (Wolfer & Straile 2004a), probably because of lower water level and more light in the experimental water basin. The decreasing biomass at higher branching is due to our assumption that energy reserves at the end of the growing season are equally divided up into the number of turions. Branching increases the number of turions, therefore individual turions will have not enough reserves to sprout successfully in the next season.

**Spatial expansion with and without reversing turions**

The main rhizomes axes of *P. perfoliatus* usually grow relatively straight and terminate with a turion at the end of the season. During winter, the rhizomes decompose and only the turion remains intact. In the following year, the growth of the new rhizome can theoretically (a) be random, (b) continue in the
direction of the previous year, or (c) reverse its direction. In practice however, the growth direction of the new rhizome is probably not random but rather determined by the position of the meristem along the clonal growth axis (Watson & Cook 1982). There is some indication of growth reversal, since turions grow basipetally in the sediment in a hook-like fashion (Wolfer & Straile 2004b).

The model allowed us to compare the influence of random, continuing, and reverse rhizome growth. There are dramatic effects on patch density and expansion after a 20 year simulation (Fig. 7.8). Reversal leads to a very compact patch with high density (Fig. 7.8b). Continuation of growth into last years direction creates a larger, sparser patch (Fig. 7.8d) and a random direction lies in between the two (Fig. 7.8c).

![Fig. 7.8 Patch density and expansion in dependence to rhizome growth direction relative to the previous year. (a) common starting condition (b) growth reversal (c) random growth (d) continuing growth (simulation period 20 years)](image)

These model results show that not only extrinsic growth conditions but also intrinsic architectural growth rules are of major importance for the patch characteristics. There are intra-specific feed-backs of patch density and structure such as modification of light, nutrients, and sediment detritus (Cebrián & Duarte 2001), regulation of flowering (Thompson et al. 1990), or susceptibility against wave attack (Coops et al. 1991). The observed differences in patch size, pattern and density will have impacts on processes in the littoral ecosystem, such as element cycles (Barko & James 1997), as well as on
littoral food webs (Lauridsen et al. 1996) and the distribution and age-characteristics of littoral fish (Weaver et al. 1997) and macro-invertebrates (Webster et al. 1998).

Scanning of asymptotic regimes

Although the new model ‘CLOMO’ is much more complex than the original model Charisma, the results were quite similar (Van Nes & Scheffer 2005). Starting from the turbid state, *P. perfoliatus* growth tolerates less turbidity, than starting from the clear state. We can therefore show that *Potamogeton* influences its own environment through feedback mechanisms and that the system can have two alternative stable states at higher turbidity: one with vegetation and one with little or no vegetation. The main difference is that the zone with alternative equilibria is much smaller in the clonal model (Fig. 7.9) which is due to the fact that *P. perfoliatus* is assumed to have a much smaller effect on water clarity than *P. pectinatus*.

![Biomass vs Vertical light attenuation](image)

**Fig. 7.9** Simulation of the response of *P. perfoliatus* biomass to increasing and subsequently decreasing turbidity without resetting the model

Monte Carlo sensitivity analysis of clonal architecture

Cluster analysis of the sensitivity coefficients shows that there are only two clear clusters of parameters that determine the clonal architecture. The strongest effect is due to a group of parameters with a strong effect on photosynthesis. This group includes hPhotoTemp, pMax, sPhotoTemp and hAge (Fig. 7.10). These parameters have a strong effect on the expansion area and the number of ramets per clone (Fig. 7.11). In an earlier analysis, they also had the strongest effect on biomass and numbers in the model Charisma (Van Nes et al. 2003).
Fig. 7.10 Cluster analysis of the sensitivity parameters of the model. Parameters with the same or opposite effect on the model results of 4 subsequent years at 3 points in time (day 189, 219 and 249). Sensitivity was based on the following model output: mean spacer length, mean shoot length, fraction belowground biomass, mean number of ramets per clone, approximate expansion area, mean expansion per clone. All parameters shown have a significant effect on model results (p > 0.01).

A second smaller cluster (Fig. 7.10) includes the parameter Alpha which determines the fraction of transported biomass that is used for the growth of subsequent ramets (Fig. 7.2). The parameters determining the length/weight relationship of the rhizomes (RhizomeWeightPerM) and the length of the shoots at which a new ramet is created (NewRametLength) are also included in this cluster (Fig. 7.10). These parameters also have a strong effect on the clonal expansion because they determine total rhizome length, but also on rhizome spacer length (Fig 7.11). Furthermore there are some parameters that belong to no cluster, but also have a significant effect. It seems plausible that the day of turion germination (TurionGerminationDay) influences the growth of the clones because any additional day of growth increases the biomass. The importance of earlier germination is also confirmed by experiments and in-situ observations (Spencer & Rejmanek 1989, Spencer et al. 2000). In the model, it strongly affects all variables in the first year but has much less effect the next years.
Fig. 7.11 Time course of the relative sensitivity coefficients of various representative parameters (expressed as sensitivity coefficients) on model outcomes
Discussion

Comparison with other models

The models available for clonal plant growth can be classified into empirical models and mechanistic models (Carr et al. 1997).

(1) The majority of aquatic plant models are mechanistic biomass models that calculate plant growth from physiological processes such as photosynthesis but disregard clonal architecture. These models can be (a) non-spatial (Collins & Wlosinski 1989, Scheffer et al. 1993, van Dijk & Janse 1993, Davis & McDonnell 1997, Hootsmans 1999, Asaeda & Karunaratne 2000, Calado & Duarte 2000, Best et al. 2001) or (b) spatial (Wortmann et al. 1997, Van Nes et al. 2003). Compared to such models our model needs many extra parameters that have to be assessed or calibrated. Complex rules have to be set up which make the model complex and prone to uncertainties. The advantage of our model is that it gives more insight into plant growth strategies than non-architectural mechanistic models. The model allows us to study the effects and implications of specific growth rules for growth characteristics. For example: is branching necessary for successful propagation? It also allows for insights into patch formation and growth.

(2) In contrast to mechanistic models, there are some empirical ‘design models’ of clonal architecture (Bell 1976, Bell et al. 1979), including submersed species (Molenaar et al. 2000). Empirical models use the ranges and standard deviations of rhizome lengths, branching frequency, branching angles etc. and generate simulations of growth patterns. They provide insights into possible variability of patterns but can not explain the underlying mechanisms nor simulate the patterns under different environmental conditions. In contrast, our rhizome architecture is growth related and consequently ruled by environmental factors.

(3) Deterministic and stochastic spatio-temporal models (cellular automata) are also used for clonal plants in competition models (Colasanti & Grime 1993, Chiarello & Barrat-Segretain 1997, Balzter et al. 1998) but they describe clonal expansion on a grid basis using simple empirical rules, or random processes. They can be used to predict patterns on a larger scale, but being empirical, they do not provide mechanistic insight.


(5) Models of clonal integration exist for theoretical plants and are usually non-spatial (Stuefer et al. 1998, Chesson & Peterson 2002, Suzuki 2002). Only a few spatial models include clonal integration (Oborny et al. 2000, Herben & Suzuki 2002, Oborny & Kun 2002), but in contrast to our model these models are not truly mechanistic, ignore clonal architecture or have a rigid architecture, i.e. do not assume any plastic adjustment of clonal architecture to resource availability.

To our knowledge there is no other model that includes all following components: submersed species, mechanistic biomass growth (dependent on environment), individually based, spatially concise, non-rigid clonal architecture, and clonal integration.
Chapter 7

Controlling complexity of the model

Being complex and detailed, our model has also several drawbacks (Van Nes & Scheffer 2005). The model includes many unknown parameters and processes, resulting in a high uncertainty of the results. Although our results were qualitatively correct, we cannot be sure that we get good results for the correct reason. Therefore, it is not sure whether this model can also be applied to other lakes and sites.

In particular, the results of the simulation of branching variability are sensitive to some parameters for which we do not have good field data, such as fraction of biomass allocated to turions or minimum turion weight for sprouting. The description of poorly known processes was kept as simple as possible in the model, ignoring more flexible plant strategies like omitting small side branches or forming a few big turions to overcome the problem of too small turions. Moreover, the model does not include biomass allocation strategies and foraging by means of rhizome length control, as we lack enough knowledge of these processes.

We tried to manage the complexity of the model by implementing detailed visualisation of the results which we regard as essential for keeping track of the complexity (Grimm 2002). Our modelling environment could visualise the clones and the various features of the ramets, including shoot length, roots and rhizomes, transport between shoot and rhizomes and between rhizomes and patch expansion in 2D and 3D graphs. Furthermore, it was essential that the generated patterns could be compared with real data of P. perfoliatus in Lake Constance at the same level of detail (Wolfer & Straile 2004a,b). Keeping track of several properties of the clones (spacer length, biomass, number of ramets) simultaneously, we could reduce the probability of getting realistic results for wrong reasons. Finally, we compared our results with a simpler version of the model (Van Nes & Scheffer 2005), namely the original Charisma model. This way we could show that some behaviour of the model, like the existence of alternative stable states, is not sensitive to the complexity of clonal growth.

The benefits of our model approach are detailed ecological insights through qualitatively correct results. The model has also provided first insights into the understanding of growth architecture and patch expansion of submersed macrophytes. The strong graphical user interface makes it possible to analyse the existing patterns and find the underlying mechanisms. In future, the model will be used for more detailed analyses and to generate hypotheses about macrophyte growth rules which can be tested experimentally. It can easily be extended by additional parameters and processes, for example wave mortality, or heterogeneous grid cells in order to provide an improved picture of the growth of submersed macrophytes.
CHAPTER 8. SYNTHESIS AND DISCUSSION

Our study on *Potamogeton perfoliatus* provides the first insights into clonal architecture of this species and its plasticity in response to the environmental factors light and nutrients. The results show that architectural growth rules govern spatial patterns, but that local environmental factors may also affect architecture. Based on our experimental results and the literature, we are able to construct models that simulate patch growth quite well. Nevertheless we are still far from understanding all details of patch growth found in-situ. A number of factors that potentially influence patch patterns have not been investigated in this study and provide possibilities for future research (Fig. 8.1). Below, a summary of our findings with respect to architectural features and the effects of nutrients, light and clonal integration will be presented. Subsequently, some other factors that seem likely to be influential in the field will be highlighted.

![Diagram of factors influencing patch characteristics](image.png)

**Fig. 8.1** Factors that influence patch characteristics; bold font: investigated in this study; standard font: studies available; italic font: further research required

*Architecture*

The investigation of small-scale quadrats (1 m²) of *P. perfoliatus* by divers in Lower Lake Constance (Chapter 3) has provided the first detailed data on architectural features such as number of ramets per clonal fragment, rhizome spacer length, branching angles of rhizomes, frequency of branching and turion formation. We found recurring architectural rules, among them a particularly interesting feature that has not been described before for this species: spacer length tended to increase considerably with the order of rhizome spacers i.e. the younger the spacer, the longer. We attributed this to the larger amount of photosynthetic activity of both individual shoots and the whole plant and to the transfer of resources to younger sections of the clonal system. Spacing between ramets of the same
rhizome system was larger than spacing between nearest (non-clonal) neighbours which has interesting implications for competition.

The architectural information collected was used as input in the new simulation model 'CLOMO' (Chapter 7). Using parameterization of data from our experiments, the model generated distinct patches similar to those in the field, rather than all-covering ‘plant carpets’. The simulations also revealed that the direction of rhizome growth relative to that in the previous year determines the patch density and patch expansion rate. Moreover, the model showed that a lack of branching will lead to the extinction of the clonal fragment if the turion (i.e. the propagation unit) is non-productive. The reason for this is the fact that only one single turion is formed at the tip of each unbranched rhizome axis, whereas each branch may produce one additional turion.

Besides architectural mechanisms, the explanations for different patch sizes and shapes of *P. perfoliatus* lie also in various environmental factors that cause plastic growth of plants. As summarized in the following sections, our results demonstrate that clonal growth and patch architecture are affected by nutrients, light conditions and clonal integration (Tab 8.1).

**Nutrients**

Our experiments have shown that nutrients control parameters of clonal growth morphology such as branching, rhizome spacer length and biomass allocation of *P. perfoliatus* as well as total productivity, density and size of patches. The lack of *P. perfoliatus* patches in parts of Upper Lake Constance as well as the poor growth patches we found next to good growth patches in Lower Lake Constance can be explained by insufficient nutrients in the sediment porewater (Chapters 3, 5). Only *P. perfoliatus* shoots planted with additional nutrient supply (slow-release N-P-K fertilizer) survived in the Upper Lake, whereas unfertilized controls vanished eventually. Moreover, poor growth of plant patches in Lower Lake Constance showed increased growth after fertilization. An associated tissue analysis confirmed the positive relationship between nutrient availability, growth and tissue nutrient concentration. By contrast, in the mesocosm, fertilization did not enhance productivity on naturally nutrient-rich sediment of Lower Lake Constance. Since productive sites are dominant in the Lower Lake, we assumed that the unproductive sites were a product of either sediment disturbance or nutrient depletion. As an example of the influence of nutrients on the clonal architecture of *P. perfoliatus*, we showed increased branching at higher nutrient availability (e.g. Chapter 3). Furthermore, reduced allocation to rhizomes and (relatively) shorter rhizomes were found at higher nutrient concentrations (Chapters 3, 5). Under nutrient poor conditions, in contrast, *P. perfoliatus* allocated more biomass to roots and rhizomes - primarily by means of a reduction of shoot length - and developed (relatively) longer rhizomes.

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Branching</th>
<th>Spacer Length</th>
<th>Rhizome Allocation</th>
<th>Root Allocation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrients</td>
<td>+</td>
<td>- / =</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Light</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>=</td>
</tr>
<tr>
<td>Clonal Integration</td>
<td>n.t.</td>
<td>- / +</td>
<td>= / +</td>
<td>- / +</td>
</tr>
</tbody>
</table>

**Tab. 8.1** Simplified responses of clonal architecture on the growth factors nutrients, light and clonal integration as found in this study. + : positive relationship, - : negative relationship, = : indifferent, n.t. : not tested; integration may also change the local effects of light and nutrients on architecture (not shown in the table)
Synthesis and discussion

Light / shade

Planting density had a clear effect on total productivity and parameters of clonal growth morphology such as branching, rhizome spacer length and biomass allocation of *P. perfoliatus* in a mesocosm. Nutrient or light competition seem obvious potential explanations for these effects. However, since fertilization did hardly affect growth on the same sediment (Chapter 5), we suppose that light effects are dominant. Remarkably, production of *P. perfoliatus* was highest at medium initial plant density. It remains uncertain if the lower production at low initial density is a result of physiological damage by excessive irradiation or other allee effects. Lower production at higher initial density might be due to light competition. The findings imply that the number of primary shoots i.e. propagules available in the beginning of the season can strongly influence patterns of growth and clonal reproduction. Higher light levels significantly increased the number of branchings, while medium and lower light levels resulted in reduced branching, implying that branching also works indirectly as self-regulation of ramet numbers (Chapter 4). Shading stimulated vertical growth of shoots at the expense of rhizome allocation and rhizome spacer length.

Clonal integration

An experiment in which parts of the growing clones were disconnected showed that translocation of resources between different ramets of the same plant may modify the effects of shading (Chapter 6). We showed that *P. perfoliatus* ramets were capable of sharing resources acropetally (i.e. from the primary shoot in direction of the younger shoots) with recipient ramets. As a consequence, integrated ramets improve nutrient supply of younger ramets and influence the productivity of the patch in a positive way. However, overall dynamics of redistribution of resources may be quite variable. For instance, if ramets occupy patchy environments, support by other ramets may be unavailable to ramets at unfavourable micro-sites but may be shifted to ramets at better micro-sites. Besides, rhizome spacer length of integrated ramets decreased in the shade (Chapters 6, 4), whereas in single ramets, spacer length increased in the shade (Chapter 6). Moreover, root allocation was affected by integration and shading as well as the interaction between the two. This shows that integration is a complex process that likely works towards optimum performance of the total plant. Implementation of integration in our simulation model may therefore be important to improve realism.

Patch size and density

The reactions of biomass and rhizome spacer lengths of individual plants to environmental factors influence the characteristics of the patch as a whole. Patch sizes increase with decreasing branching, increasing rhizome spacer length, increasing rhizome allocation, or straight rhizome growth direction and decrease with increasing branching, decreasing rhizome spacer length or reversing rhizome growth direction (Tab. 8.2). The trends found in the course of our nutrient and light experiments had the following implications (Fig 8.2): Nutrient supply decreased rhizome spacer lengths and resulted in dense and compact patches with smaller patch expansion and discrete patch shapes whereas a lack of nutrients stimulated horizontal expansion and larger (but low density and low height) patches. Besides, increased nutrient supply also increased branching. Since higher branching rates decrease patch size, the reactions of spacer lengths and branching to increased nutrients both worked in the same direction, i.e. a reduction of patch size. Responses to the factor light were more complicated. On one hand, increasing rhizome spacer lengths with increasing light led to larger patches and reduced rhizome spacer lengths in the shade led to reduced horizontal growth and resulted in dense and
compact patches with smaller patch expansion and discrete patch shapes. On the other hand, increased branching with light resulted in reduced patch sizes. Therefore, reactions of rhizome spacer lengths and branching to different light levels may partially cancel each other out.

**Tab. 8.2** Simplified relationships between clonal architecture / growth factors and patch size as found in this study. + : positive relationship, - : negative relationship

<table>
<thead>
<tr>
<th>factor</th>
<th>patch size</th>
</tr>
</thead>
<tbody>
<tr>
<td>branching</td>
<td>-</td>
</tr>
<tr>
<td>spacer length</td>
<td>+</td>
</tr>
<tr>
<td>rhizome allocation</td>
<td>+</td>
</tr>
<tr>
<td>reversing growth direction</td>
<td>-</td>
</tr>
</tbody>
</table>

**Fig. 8.2** Simplified responses of patch growth to light and nutrients as found in this study

Several aspects were not addressed in our study, but might nevertheless have an important effect on clonal growth. In the following, the potential role of exposure, periphyton, interspecific competition and feedback between plants and their environment will be briefly highlighted.

**Exposure**

Among the environmental factors that influence patch growth, exposure has received considerable attention. Wave action and currents affect submersed macrophyte stands directly or indirectly. The most obvious direct effect in shallow water zones is mechanical disturbance through uprooting (Keddy 1982, Lehmann 1997). Although *P. perfoliatus* is often present at exposed sites (Luther 1951, Schmieder 1995), waves can prevent patch establishment (Coops et al. 1991), impact patch growth, or destroy parts of patches (Walser 1996). It has been shown that exposure leads to more compact outlines of macrophyte patches (Fonseca & Bell 1998). Indirect effects of exposure on macrophytes may include light attenuation by particle resuspension or partial removal of periphyton (Coops et al. 1991, Fonseca 1996). This may affect species composition (Keddy 1983), biomass (Kautsky 1987, Duarte & Kalf 1990a) and percent cover of submerged macrophyte species (Fonseca & Bell 1998) as well as clonal architecture, patch characteristics and aspects such as shoot lengths (Kautsky 1987),
root number and length (Koch 1999), shoot branching and shoot internode length (Kautsky 1987), shoot density (Lundholm & Simser 1999) and stolon length (Puijalon & Bornette 2006). Importantly, plants also influence current velocity (Fonseca et al. 1983, Losee & Wetzel 1993, Koch 1996), implying a two-way interaction between plants and their environment.

**Epiphyton and periphyton**

Since epiphytes take up the same nutrients as macrophytes and additionally reduce light and CO\(_2\) availability (Jones et al. 2000), they may consequently decrease macrophyte chlorophyll contents, reduce macrophyte growth (Ozimek et al. 1991), or even kill the host plant (Jones et al. 2000). Blindow (1987) could show that epiphyte colonization differed between plant parts, sites and macrophyte species. As epiphyte species also affect the amount of marl encrustation (i.e. carbonate deposits), they may considerably influence patch characteristics. Since epiphyte layers increase during the growing season, fast growth is favourable. Moreover, it may well be that shading by epiphytes has similar effects to self-shading or experimental shading: reduced rhizome spacer lengths, less roots, more shoots, and reduced branching.

**Interspecific competition**

In the context of this study, we have tried to work on mono-specific stands where ever possible. However, *P. perfoliatus* occurs also in intermixed stands. In Lake Constance, for example, important associated species are *Chara sp.*, *Potamogeton pectinatus* and *Najas marina*. In such intermixed stands, there is likely to be some competition for space occupancy, light and nutrients which might influence patch characteristics. Competitive reactions of *P. perfoliatus* include elongation and concentration of photoreceptive biomass at the water surface (light foraging, see below). Since simulations show that spatial aggregation has a dramatic effect in reducing the rate at which stronger competitors are able to exclude weaker ones (Silvertown 1992), we would expect shorter rhizome spacer lengths, and increased branching at higher levels of competition. Furthermore, in case of nutrient competition, foraging by root systems should increase (Campbell et al. 1991). Further competitive actions involve the change of sediment characteristics or the release of allelopathic substances and might affect the positioning of macrophyte patches.

**Effects on own environment**

Once a plant has established itself on a formerly uncolonized area, it will influence its own environment. After the sprouting of ramets and building up of biomass, patches act like sediment traps. During the vegetation period, suspended allochthonous and autochthonous organic matter (Sand-Jensen 1998, Lee et al. 2001) or sand (Sánchez et al. 2001) accumulates within the patch thereby changing both density of the sediment (Barko & Smart 1986b) and nutrient status (Szczepanska & Szczepanski 1973). In Lake Constance, detritus at macrophyte sites can amount to 10 cm thickness, but after the growing season, the site might be completely eroded by autumn storms (Walser 1996). Plants on old growth sites may profit from increased nutrients or might be negatively influenced by high concentrations of nutrients and/or toxic decomposition products. Indeed, the lowest density is sometimes found at the centre and patches may take on a ring-shaped appearance (Sánchez et al. 2001). These could, however, also be explained by nutrient depletion in the centre due to proliferate growth and nutrient uptake.
Theories of architectural responses to habitat quality

Clonal responses and plastic morphological changes in architecture of modular plants as found in this study have received much attention and are often interpreted as strategies to optimize space occupation and utilization. Here we discuss whether our results are in line with the predictions from two main theories in this field: foraging theory and allometric growth rules.

The 'foraging theory' considers changes in branching frequency, biomass allocation and spacer length as mechanism for the increase of ramet density in favourable microsites, and as means of improving exploitation of resources such as light or nutrients (Hutchings 1988, Sutherland & Stillman 1988, De Kroon & Knops 1990, Vermaat & Verhagen 1996, Marbà et al. 1996).

Some definitions of foraging

- Grime (1979): ‘the ability of plants to project leaves and roots into patches of high resource supply within the environment’ (the word foraging as such was not used; pertaining non-clonal species).
- Bell (1984): clonal plants consist of ‘feeding sites’ and spacers that connect the feeding sites
- Slade and Hutchings (1987b): ‘plasticity [in stolons] enables clones to consolidate occupation of favourable sites, through intensive foraging, and to grow through less favourable sites’
- De Kroon & Hutchings (1995): ‘the processes whereby an organism searches, or ramifies within its habitat, which enhance its acquisition of essential resources’.
- Oborny & Cain (1997): ‘Plant foraging occurs when a plant exhibits any morphological plasticity that is selectively advantageous for resource acquisition at a particular spatiotemporal distribution of the resource.’

As predicted by the foraging theory, we found reduced branching at low nutrient availability (Chapter 5) or low light levels (Chapter 4). Such reduced branching allows for larger spatial extension and for searching for better sites whereas increased branching at higher nutrient and high light availability allows for denser stands and placement of more shoots at the favourable site (Oborny 1994, Sutherland & Stillman 1988). As in other plant species, branching patterns are thought to be regulated by hormones such as auxins, cytokinins and gibberellins which strengthen apical dominance of rhizomes in case of low nutrient availability (see Jackson et al. 1985).

In recent years, the foraging theory has been rejected by many authors including the original authors, especially with regard to spacer length of rhizomatous species (De Kroon & Hutchings 1995). The main reason is that many studies did not find shorter spacer lengths in favourable environments (e.g. Hartnett & Bazzaz 1985). Furthermore, experiments showed that plasticity in spacer length did not succeed in concentrating ramets in favourable habitat (De Kroon & Hutchings 1995). On the other hand, some rhizomatous species definitely showed foraging (Slade & Hutchings 1987a, De Kroon & Knops 1990, Dong et al. 1997, Klimes et al. 1997) and simulation models suggested that foraging can succeed in concentrating ramets in favourable patches (Sutherland & Stillman 1988, Oborny 1994, Cain et al. 1996). According to a literature review (Miller 1999), 15 % of examined rhizomatous species (all terrestrial) showed foraging. Unfortunately, the presented growth parameters generally suffer from a lack of completeness and comparability. In our study, as predicted by the foraging theory, we found longer rhizome spacers at non-fertilized sites (Chapter 5) which resulted in sparsely vegetated patches with a relatively large horizontal expansion rate. By contrast, the foraging theory
seems not to be appropriate to explain some of our other results such as decreasing rhizome spacer lengths with shade (Chapter 4) or equal spacer lengths of good and bad growth sites in-situ (Chapter 3).

The main problem of the foraging theory is that relevant studies mostly compare absolute rhizome spacer lengths at ‘good’ and ‘bad’ sites, disregarding that plants may differ considerably in biomass, shoot length, number of ramets and weight-density relationships. However, when resources increase, plant growth increases including both shoots and rhizomes. This is the main prediction of the ‘growth hypothesis’ according to which spacer length should increase at favourable sites as they allow a higher productivity (Hutchings & De Kroon 1994, De Kroon & Hutchings 1995, Stoll et al. 1998). However, if rhizomes increase at a slower rate than shoots, this foraging sensu latu might be easily overseen. In this case only a closer look at biomass allocation will reveal foraging, following the newer definitions of De Kroon & Hutchings (1995) or Oborny & Cain (1997). Principally, longer rhizomes can be achieved by means of increased biomass allocation into rhizome tissue, a reduced rhizome diameter or reduced tissue-mass density. The latter aspects have hardly received any attention by researchers and are not covered by this study. In our study, reactions of spacer length to changing resources were usually related to changes in biomass allocation. In-situ, rhizome spacers had the same length whereas rhizome allocation was five-fold higher on unfavourable sites compared to favourable sites (Chapter 3). Increased allocation to rhizomes under bad conditions, however, is only possible at the expense of shoot growth because the total biomass can at most be equal to that at a favourable site. In fact, we would expect total biomass to be lower as reduced resources decrease photosynthesis. Indeed, our study showed that the ramets on unfavourable sites had less biomass, were much smaller and had higher rhizome allocation than those on favourable sites. This is also in line with the ‘allometry theory’ which argues that allocation differences are a consequence of allometric growth rules rather than of morphological plasticity, as smaller plants frequently show a higher biomass allocation to rhizomes and roots (Duarte 1991, Gedroc et al. 1996, Müller et al. 2000). Allometric rules should not be confounded with morphological plasticity (Coleman & McConnaughay 1995, Huber & Stuefer 1997, Huber et al. 1999, Preston & Ackerly 2004) and have been complemented with the concept of ‘developmental reaction norms’ (DRN) to include the ontogenetic stage of plants (Schlichting & Pigliucci 1998).

We cannot determine whether spacer length in *P. perfoliatus* follows the foraging or the allometry theory. This is because both theories lead to the same predictions: favourable sites in the context of the foraging theory should produce large plants in the context of the allometry theory, and both result in shorter rhizomes respectively less allocation into belowground parts. Foraging and allometry theory differ only in terms of causation which is an active ‘search’ in the former and an ontogenetic growth rule which may also have been evolved through natural selection in the latter (Preston & Ackerly 2004). If we associate foraging with morphological plasticity, we have to compare responses of spacer length / belowground allocation to a resource at the same ontogenetic level which is rather difficult. Allometric relationships differ considerably between species (Duarte 1991, Müller et al. 2000) and adequate data for *P. perfoliatus* are missing. However, it seems very unlikely that, at the course of their ontogenetic growth, ramets might grow by more than 50 cm without any changes in rhizomes (Chapter 3). Therefore it seems likely that there is indeed some kind of foraging in *P. perfoliatus* and that its effects add to allometric rules of ontogenetic growth. The systematic increase of younger rhizome spacer lengths within the season suggests, however, that *P. perfoliatus* does not ‘search’ actively by sensing a favourable site and placing an individual ramet, as the earlier definitions of foraging would suggest (Slade & Hutchings 1987a,b,c) because in that case we would expect to find a
more diverse picture. As the growing rhizome is initially rootless until a new ramet is established, the sensor for microsite quality remains unclear. We suggest that ramet placement is rather influenced by the conditions of the older ramets than the new ramet. This would be beneficial in environments with a scale of heterogeneity in the range of plant size where a systematically smaller or larger increase of all rhizome spacers of a plant may succeed in increasing overall fitness of the genet fragment. In addition, localized morphological responses of biomass allocation are highly important (De Kroon & Hutchings 1995).

With respect to foraging, the mechanism for different biomass allocation may also be interpreted in the light of stochiometric theory. Under nutrient limitation, for example, nutrients and CO$_2$ invested in photosynthetic tissue can not further increase biomass production because of missing nutrients. Consequently, it would be better for the plant to invest nutrients either in rhizomes in order to grow faster out of the bad site, or in roots to capture more nutrients. Only when CO$_2$ becomes the limiting factor, it is beneficial for the plant to produce aboveground photosynthetic active biomass. Likewise, allometry is based on ‘economic’ allocation for optimal resource acquisition (Bloom et al. 1985). Overall, plants must function as a balanced system in terms of resource uptake and use, and resources may not be allocated independently from each other (Hirose 1986, Ågren & Ingestad 1987). Higher allocation to roots in smaller plants might also be due to the need for anchorage, the lower possibility to take up additional nutrients over their surface and the faster uptake due to a higher growth rate.

The decreasing rhizome allocation with shade (Chapter 4) seems to contradict the allometry theory since mean shoot length and mean shoot weight remained the same. In case of shading, however, investment into aboveground biomass at the expense of rhizomes enabled shoots to escape the shading of neighbours by growing up to the light. The decrease of spacer length with shade can definitely be interpreted as light foraging if the more general definitions of Grime (1979) and Oborny & Cain (1997) are applied instead of the original definition of shorter rhizomes at good sites. When the foraging rule was originally formulated, research was done on terrestrial plants with rosette growth forms or on grasses which have the strategy to grow sideward out of the shade (Slade & Hutchings 1987a). As light diminishes sharply with depth, the better strategy is to develop tall shoots and to grow upwards out of the shade, partly by etiolation.

Besides appropriate placement of ramets, a clonal plant must optimally exploit the resources, e.g. take-up nutrients by roots. As predicted by the foraging theory, plants at the nutrient-deficient site allocated considerably more biomass to roots than plants at the rich site, and plants in the controls of the in-situ fertilization experiment allocated more biomass to roots than the fertilized plants (Chapter 3) whereas in the mesocosm, root allocation was not affected by fertilization due to the fact that biomass was not affected either (Chapter 5). This allocation rule has been confirmed by a variety of experiments with clonal terrestrial plants (review of Hutchings 1997) and submersed macrophytes (Barko & Smart 1981b, Kautsky 1991, Reusch et al. 1994, Wertz & Weisner 1997). Such shifts in allocation patterns under changing environments have been proven to maximize plant growth (Hirose 1987) and can be interpreted in the light of both foraging and allometry theories analogous to rhizome allocation (see above).

In summary, the dynamics of clonal architecture we found in _P. perfoliatus_ are in line with predictions by allometric rules as well as foraging theory. While this is a poorly explored area of research in aquatic ecology, the responses we demonstrated may be the key to explaining the ecological success of clonally growing submerged plants.
References


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Summary

Clonal growth governs the aboveground growth pattern of submerged clonal macrophytes. This study provides detailed data on the architectural growth rules of *Potamogeton perfoliatus* L. (perfoliate pondweed) such as rhizome spacer lengths, biomass allocation, branching frequencies, branching angles, as well as maps of rhizome networks and their seasonal development at Lake Constance.

Besides architectural reasons, the causes for different sizes and shapes of *P. perfoliatus* patches are dependent on nutrients, light conditions, and clonal integration. Branching was positively related to both irradiation and nutrient supply. Rhizome spacer lengths were negatively related to nutrient supply and positively related to irradiation. Where absolute rhizome lengths did not respond to the habitat conditions, relative rhizome lengths did. Rhizome allocation tended to increase with irradiation and shoot allocation tended to decrease with irradiation. Root allocation was higher at low nutrient supply. Clonal growth is further complicated because the species shows complex sharing of resources between older and younger ramets, aiming at optimal resource partitioning.

We present an individual-based clonal model which shows that architectural growth affects patch characteristics: both rhizome spacer lengths and growth of rhizome axes relative to those in the previous year considerably determine patch density and patch expansion rates. Furthermore, the model is able to simulate seasonal growth of *Potamogeton* patches.

All results on clonal architecture are discussed in the light of foraging theory and allometric rules.
Samenvatting

De bovengrondse groeipatronen van ondergedoken kлонаal groeiende waterplanten worden in grote mate bepaald door de processen die kлонale groei bepalen. Deze studie geeft gedetailleerde informatie over de factoren die de klonale groei van Potamogeton perfoliatus L. (Doorgroeid fonteinkuid) bepalen. Onder andere wordt de lengte tussen de scheuten van de wortelstokken (rhizomen), de biomassa verdeling, vertakkingsfrequenties en -hoeken precies beschreven. Bovendien zijn gedurende een seizoen gedetailleerde kaarten van de ondergrondse en bovengrondse delen van P. perfoliatus in de Bodensee bepaald.

De groeiformen en -partonen van P. perfoliatus zijn ook afhankelijk van omgevingsfactoren zoals nutriënten (meststoffen), licht en voeding vanuit andere delen van de plant via de wortelstokken. De vertakkingsfrequentie was positief gerelateerd aan zowel de lichtbeschikbaarheid en de nutriënten. De lengte van de rhizomen tussen de scheuten was negatief gerelateerd aan de beschikbaarheid van nutriënten en positief met de hoeveelheid licht. Terwijl de totale lengte van de rhizomen niet afhankelijk was van het habitat, was de relatieve lengte tussen de scheuten dat wel. De allocatie van biomassa aan rhizomen nam meestal toe met de hoeveelheid lichtbeschikbaarheid, en de allocatie van biomassa aan de scheuten nam meestal af met licht. Klonale groei is complex omdat voedsel op een complexe manier uitgewisseld wordt tussen oude en jonge scheuten. Experimenteel is het belang van de rhizomen ook vastgesteld.

We presenteren een individu-gebaseerd ruimtelijk model dat de klonale groei van P. perfoliatus over meerdere seizoenen beschrijft. Het model toont aan hoe fotosynthese en groeiregels van scheuten ruimtelijke patronen in een macrofytenveld kan genereren. Zowel de lengte tussen de scheuten en de groeirichting van een rhizoom ten opzichte van het vorige jaar bepaalt in grote mate hoe dicht de scheutdichtheid zal zijn en hoe snel een macrofytenveld zich kan uitbreiden.

De resultaten van deze studie worden in het licht van verschillende theorieën besproken. Met name de ‘foraging’ theorie en allometrische regels.
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List of publications


Curriculum vitae

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University education: Geography and biology, Universität des Saarlandes, Saarbrücken, Germany and Simon Fraser University, Burnaby, Canada (1986 - 1991)
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04/1992 - 04/1993 Project leader, CSIR (Council for Industrial and Scientific Research), Division of Water Quality Information Systems, Pretoria, South Africa:
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