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Growth rates and morphological adaptations of aquatic and terrestrial forms of amphibious *Littorella uniflora* (L.) Aschers.

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Abstract

Morphological – anatomical features of the terrestrial and the aquatic life form of the rosette species *Littorella uniflora*, inhabiting nutrient poor soils of oligotrophic lakes, were investigated together with growth rates of both life forms and of transplants. Growth rates were the same for the two life forms. However, growth of transplanted plants was somewhat reduced by transition from one environment to another. This was especially true for aquatic plants, which may be stressed by desiccation when moved to the terrestrial environment. The morphological – anatomical differences between the life forms were small compared with many other amphibious species which produce highly specialized leaves and life forms in air and under water. It is suggested that the conservative leaf morphology of *Littorella* is a consequence of the high dependence on rhizospheric CO_2 of both the aquatic and the terrestrial form of *Littorella*, making production of leaves specialized for carbon uptake in one specific environment unnecessary.

Introduction

Amphibious plants constitute a taxonomically diverse group of plants (Sand-Jensen et al. 1992), that attracts particular interest due to the ability to photosynthesize and grow in terrestrial as well as aquatic environments. It is commonly claimed that water is a less suitable habitat for plant growth than the terrestrial environment (e.g. Maberly & Spence 1989). The availability of light is reduced under water due to surface reflection and absorbance and scattering in the water column. The accessibility of CO_2 is usually also reduced under water due to 10^4 times lower diffusion coefficients and thicker boundary layers around the leaves, but this may be compensated for by the availability of HCO_3^- ions, present in high concentrations (1-5 mm) in alkaline waters, and CO_2 oversaturation in habitats receiving CO_2-rich groundwater and respiratory CO_2 (e.g. from sediment surfaces). Many amphibious plants do actually form continuous and dominant populations under water (Moeslund et al. 1990; Sand-Jensen & Søndergaard 1979; Sand-Jensen et al. 1992), while the emergent forms of the same species rarely dominate the shore vegetation.

In this study, we worked with the amphibious rosette plant *Littorella uniflora* (L.) Aschers., found in temperate, oligotrophic, soft-water lakes. The submerged life form of *Littorella* often dominates the vegetation in shallow water of these lakes (Hutchinson 1975), and the emergent form is usually less abundant, though it can form dense stands of flowering plants particularly during summer on recently exposed soils (Moeslund et al. 1990). *Littorella* has several adaptations enabling it to grow in this carbon and nutrient poor environment. The rosette life form, the high root:shoot ratio, and well-developed continuous gas lacunae facilitate the uptake of CO_2 from the sediment, and $>80\%$ of the carbon uptake takes place through the roots in submerged as well as in emergent forms (Boston & Adams 1987; Nielsen et al. 1991; Søndergaard & Sand-Jensen 1979). Furthermore, the possession of Crassulacean Acid Metabolism (CAM) enables dark uptake and recycling of CO_2 (Boston & Adams 1983; Madsen 1985, 1987). Dark uptake of

CO_2 has been shown to constitute 20–35% of the light uptake in both submerged and emergent forms (Madsen 1985; Nielsen et al. 1991), while recycling of CO_2 from the lacunae constitutes as much as 75–85% of the CO_2 uptake during the first 6 hours of the light period (Madsen 1987). The relatively slow inherent growth rates, the evergreen leaves and the large root systems also facilitate nutrient uptake and nutrient conservation in *Littorella* (Boston & Adams 1987). The emergent life form of *Littorella* resembles the submerged form. Quantitative measurements of morphological and anatomical differences are few, but Hostrup & Wiegleb (1991) have shown that *Littorella* leaves upon emergence develops stomata, thicker cuticula and smaller lacunar gas spaces. Hostrup & Wiegleb (1991) note that both life forms grow quickly, but provide no measurements of growth rates that enable us to evaluate the suitability of the submerged and aerial environments.

The aim of the present work was to determine the growth rates and some morphological, anatomical and chemical adaptations of aerial and submerged life forms of *Littorella* and the changes in growth rates taking place in the transition from one life form to the other. This allows us to evaluate, for a single, abundant amphibious species, the common claim that the terrestrial habitat is more suitable to plant growth.

Methods

Experimental *Littorella* grew on a coarse sand and gravel sediment on the shores of the oligotrophic soft-water Lake Hampen (56°N, 9°E) in mid-Jutland, Denmark (Christiansen et al. 1985). The population is subject to alternating submergence and emergence during the year or between very wet or dry years because of fluctuations in water level (up to about 1 m). Because the slope of the shore is very shallow, extensive populations over a 100 m wide zone alternate between air exposure and submergence. Growth experiments were performed in the field during July. For growth experiments mature, field collected *Littorella* plants with 20 cm of sediment were transferred to plastic pots (diameter 6 cm). A sediment depth of 20 cm was considered to be sufficient as the rooting depth of *Littorella* is 5–15 cm, with most roots less than 7 cm long. Plant characteristics are given in Table 1. Growth experiments with the two life forms of *Littorella* were performed in their original environment (ca. 40 cm above and 30 cm below the water surface), and with emergent *Littorella* transferred to water and submerged *Littorella* transferred to land. The pots were placed among the native vegetation of *Littorella* plants in a submerged and an emergent position respectively. Each treatment consisted of 60 plants. Water levels may have fluctuated slightly during the experiment, but plants referred to as submerged remained submerged during the duration of the experiment, and, likewise, plants referred to as emergent remained emergent during the entire experiment. The plants were subjected to natural fluctuations in light intensity (up to 2000 μE m^{-2} s^{-1}) and temperature (between 15 – 30 °C). Effects on light and temperature regimes as a consequence of water level fluctuations during the experiment can be regarded as negligible, as the lake had a mean Secchi depth of 3.5 m during the study period (County of Vejle, pers. comm.). The concentration of dissolved inorganic carbon (DIC) in the sediment pore water was measured as described by Nielsen et al. (1991), and was 1.58 mM at pH 6.03, yielding 1.12 mM free CO_2. The lake water contained 0.41 mM DIC at pH 7.43, yielding 0.036 mM free CO_2. The sediment content of N and P was not measured, but dissolved N and P in sediment pore water in this lake is known to be low or below detection limits (Christiansen et al. 1985) and P in particular is probably made available through mycorrhiza associations (Søndergaard & Lægaard 1977). We therefore preferred to measure the N and P content in the plants, which provides a better description of whether or not the growth was nutrient limited (Gerloff & Krombholz 1966).

Leaf growth rate was measured by marking the youngest leaf on the plants and repeatedly counting the number of new leaves over 21 days and by repeatedly measuring the length of the individual leaves. Relative growth rates in weight units were then calculated from known weight/length relationships of leaves with different locations on the shoot (Nielsen & Sand-Jensen 1989). The conversion to weight was based on leaf age/weight and length/weight relationships measured repeatedly throughout experiment. Separate relationships were used for the individual treatments. The R^2-values of the regressions were high (0.75-0.98).

Morphological and anatomical differences between the aerial and water forms of *Littorella* were measured at the start of the experiments and between the transplants at the end of the experiment. Leaf area and volume were calculated from measurements of leaf length and diameter. The specific leaf area (SLA) was expressed as cm^2 cm^{-3} and as cm^2 mg^{-1} dry weight (DW). Leaves and roots were dried over 24 h at 105 °C to obtain dry weight (DW), and ash free

Table 1. Various morphological, anatomical and chemical features of the two leaf forms of *Littorella uniflora*. Numbers are means ± 1SD, n = 20 plants. All numbers referring to individual leaves are averages of the mean values for 20 plants. *l/d* ratio = length/diameter ratio, DW = dry weight, AFDW = ash free dry weight, SLA = specific leaf area, LWR: leaf weight ratio

Feature	Emerged	Submerged
Leaf length (cm)	1.7 ± 0.6	1.4 ± 0.5
Leaf diam. (cm)	0.18 ± 0.03	0.15 ± 0.02
l/d ratio	10.24 ± 5.0	8.20 ± 3.94
Total plant weight (mg DW)	8.53 ± 1.50	11.53 ± 3.88
Leaf weight plant^{-1} (mg DW)	1.90 ± 0.16	5.85 ± 0.33
Root weight plant^{-1} (mg DW)	6.63 ± 0.56	5.68 ± 0.32
SLA volume (cm^2 cm^{-3})	30.97 ± 3.26	41.63 ± 4.95
SLA weight (cm^2 mg^{-1}DW)	0.59 ± 0.15	0.26 ± 0.04
LWR (%)	22.3 ± 4.5	50.7 ± 4.7
% lacunar space	41.60 ± 4.06	60.10 ± 17.92
% Leaf AFDW of DW	86.72 ± 1.15	81.83 ± 0.26
% Root AFDW of DW	83.09 ± 1.50	91.96 ± 3.90
Chlorophyll (*a*+*b*) (mg g^{-1})	6.35 ± 1.05	4.26 ± 0.05
Carbon (mg g^{-1})	411.0 ± 3.0	385.1 ± 3.1
Nitrogen (mg g^{-1})	27.3 ± 0.3	29.4 ± 0.3
Phosphorus (mg g^{-1})	1.97 ± 0.11	2.06 ± 0.10

dry weight (AFDW) was measured as loss on ignition at 550 °C. Chlorophyll *a*+*b* was measured by extraction with ethanol according to Wintermans & DeMots (1967) and content of carbon and nitrogen was measured by a Carlo-Erba EA-1108 CHN-analyzer. Phosphorus content was measured spectrophotometrically after destruction in concentrated H_2SO_4 according to Koroleff (1983). Light microscopy was used to quantify leaf area and lacunar area of cross sections of leaves, enabling an estimate of lacunar space as a percentage of leaf volume. Leaf permeability to water vapor and thus the susceptibility of leaves to desiccation in the different life forms of *Littorella* was obtained by placing leaves vertically in a desiccator with their basal parts in water free lanoline, thus closing the air lacunae (Pedersen & Sand-Jensen 1992), and weighing them repeatedly over a period of 7 hours.

Results

Relative growth rates ranged from 0.0180 g g^{-1} d^{-1} to 0.0340 g g^{-1} d^{-1}. A one-way analysis of variance (ANOVA) showed significant differences in relative growth rates among the four treatments (ANOVA, $p<0.0005$). A Tukey test identified two homogenous groups: The relative growth rate of aquatic plants transferred to the terrestrial environment (0.0180 g g^{-1} d^{-1}) was significantly lower than the relative growth rate of either parental form (0.0340 g g^{-1} d^{-1} for aquatic plants and 0.0317 g g^{-1} d^{-1} for terrestrial plants). These, in turn, were not significantly different from each other (Figure 1). The relative growth rate of terrestrial plants transferred to the aquatic environment (0.0278 g g^{-1} d^{-1}) was intermediate and did not differ significantly from the relative growth rates of either of the three other treatments (Figure 1). Growth rates were well above growth rates measured after acclimation and over long intervals in the laboratory (0.013 g g^{-1} d^{-1}, recalculated after Nielsen & Sand-Jensen 1991), indicating that transplantation did not in itself affect growth rates adversely.

Leaves of submerged plants were – as expected – more susceptible to desiccation in air than leaves of emergent plants, estimated from fitting an exponential loss function to the data. Leaves of emergent plants attained a weight specific loss rate of 0.0042 g H_2O g^{-1} FW min^{-1}, while submerged plants had a loss rate of 0.0091 g H_2O g^{-1} FW min^{-1} (Figure 2). *Littorella* plants along the shore of Lake Hampen were small (Table 1) compared to those normally found in

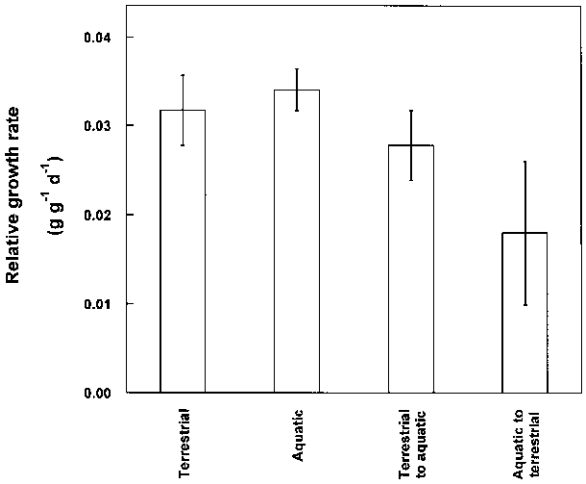

Figure 1. Relative leaf growth rates (g g^{-1} d^{-1}) for the two life forms of *Littorella* and of the transplants. Mean rates over 21 days are shown, error bars are 95% C.I., n = 60 plants for each treatment.

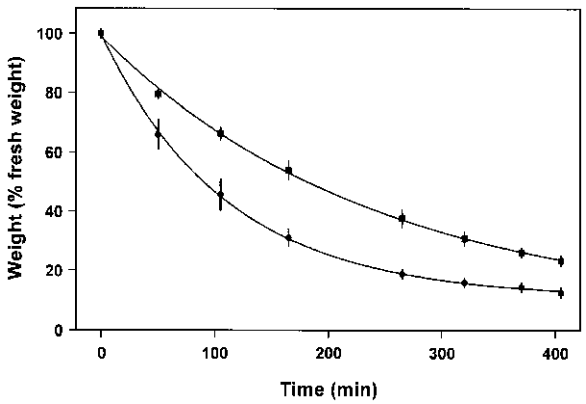

Figure 2. Water loss to dry air of *Littorella* leaves from land (–■–) and water forms (–●–). The lines represent fitted exponential loss functions ($A * e^{-kX} + R$). $R^2 > 0.99$ for both forms. Error bars are 1 SD, n = 20 leaves for each treatment.

Danish softwater lakes (Søndergaard & Sand-Jensen 1979). They represent the typical sand plants of the most infertile sediments, described from nearby Lake Kalgaard (Søndergaard & Sand-Jensen 1979). Length and length/diameter ratio of emergent plants was not significantly different from that of submerged plants (Table 1). Likewise, leaf diameter was not significantly different between the two leaf forms (Table 1). Leaves constituted a significantly higher proportion of total plant weight in submerged (mean LWR 50.7%) than in emergent plants (mean LWR 22.3%; Table 1).

There were no differences in specific leaf area (SLA) between the two forms of *Littorella*, but as anticipated, submerged leaves had higher proportions of lacunar gas spaces than emergent leaves (Table 1). The organic percentage of the dry weight was not significantly different between the life forms (Table 1), but there was a tendency for both forms of transplanted plants to have a lower organic percentage in the roots than their parent forms (Table 2), and for submerged plants transferred to the terrestrial environment this was also true for the leaves (Table 2). Plants transplanted from the aquatic to the terrestrial environment also had lower total plant weights than either parent form (Table 2).

Table 2. Total plant weight (mg DW) and% leaf and root ash free dry weight (AFDW) of dry weight (DW) of transplants of *Littorella uniflora*. Numbers are mean ± 1SD, n = 20 plants

Feature	Emergent to submerged	Submerged to emergent
Total plant weight (mg DW)	13.25 ± 2.23	6.07 ± 1.22
% Leaf AFDW of DW	89.5 ± 5.9	64.8 ± 9.8
% Root AFDW of DW	76.9 ± 8.4	76.0 ± 8.8

Chlorophyll content was always lower in submerged plants, relative to emergent plants (Table 1), while the content of nitrogen and phosphorus in general was high and differences among plant types were small, though submerged plants appeared to contain relatively more nitrogen and phosphorus and less carbon than emergent plants (Table 1).

Discussion

As previously mentioned, it is often claimed that the aquatic habitat is less beneficial for growth of higher plants than the terrestrial environment (Maberly & Spence 1989). Especially the availability of inorganic carbon is assumed to be a limiting factor for the photosynthesis and growth of submerged angiosperms (Madsen & Sand-Jensen 1991), and these plants have evolved a number of strategies to cope with this situation, including bicarbonate utilization, uptake of CO_2 from the rhizosphere and recycling in lacunar spaces, and the development of floating or otherwise aerial leaves (Madsen & Sand-Jensen 1991, and references therein). The effect of emergence on photosynthetic carbon utilization in amphibious plants has been

studied in some detail (e.g. Nielsen 1993; Nielsen & Sand-Jensen 1993; Salvucci & Bowes 1982) and, although studies of the growth of amphibious plants upon emergence are scarce, it has been shown that air contact has a significant effect on the growth of the non-bicarbonate user *Callitriche cophocarpa* (Madsen & Breinholt 1995).

In contrast, we did not find any significant differences in the growth rates of submerged and emergent forms of *Littorella uniflora* in this study. While a plant with the growth form characteristic for *Callitriche* can not be assumed to received any significant amount of inorganic carbon from the rhizosphere due to the long diffusive path from roots to leaves (Madsen & Sand-Jensen 1991), the short rosette plant *Littorella* receives almost all its inorganic carbon for photosynthesis from the sediment in both its submerged and its emergent form (Boston & Adams 1987; Boston et al. 1987; Nielsen et al. 1991; Søndergaard & Sand-Jensen 1979). In addition to this, *Littorella* has extensive lacunar spaces, which together with its possession of CAM facilitates recycling of respired CO_2 (Madsen 1987). It can thus be argued, that while some amphibious plants benefits vastly from air contact, where diffusion of CO_2 is four orders of magnitude faster than in water, *Littorella* which, through lacunar diffusion, receives 80–95% of its CO_2 from the sediment, does not experience any significant change in inorganic carbon availability as a consequence of the transition between water and air.

The decline in growth rate resulting from the transference of aquatic *Littorella* plants to an aerial environment can be hypothesized to be caused by the detrimental effect of desiccation of the leaves, rather than by the aquatic leaves having inferior carbon uptake capabilities in the aerial environment, as no similar effect was observed when terrestrial plants were transferred to the aquatic environment. The aquatic leaves lost water at a rate about twice that of terrestrial plants, and similar differences between aquatic and terrestrial leaves has been observed for other species of amphibious plants (Nielsen & Sand-Jensen 1993; Pedersen & Sand-Jensen 1992). Upon emergence *Littorella* produces terrestrial leaves, differing from aquatic leaves by having a thicker cuticula (Hostrup & Wiegleb 1991), although this study shows that the plants do not necessary discard all the aquatic leaves simultaneously, as stated by Hostrup and Wiegleb (1991).

The nutrient concentration of *Littorella* plants was generally high and probably not limiting for growth (Gerloff & Krombholz 1966), despite the nutrient poor environment (Christiansen et al. 1985). *Littorella* probably maintains a high leaf nutrient concentration as a result of a high leaf longevity (Chabot & Hicks 1982).

The *Littorella* plants of Lake Hampen exhibit only small differences between the aquatic and the terrestrial form. However, the relative leaf weight ratio (LWR) is significantly larger in the aquatic form, something that has also been observed in other amphibious plants (Grace 1989; Rea & Ganf 1994), and which has been attributed to adaptations to improve harvest of the more limiting resource – light in aquatic environment (Rea & Ganf 1994). Apart from this, the plants show only limited heterophylly compared to what is found in other species of amphibious plants (Hutchinson 1975; Nielsen & Sand-Jensen 1993; Sculthorpe 1967). Heterophylly has been found to be controlled mainly by the availability of inorganic carbon, temperature and light quality (Bristow 1969; Bristow & Looi 1968; Johnson 1967; Kane & Albert 1987). It can thus be hypothesized that the slight heterophylly of *Littorella* is due to the fact that this plant – because of its dependence on rhizospheric and recycled CO_2 – does not experience any significant change in inorganic carbon availability on emergence, and that changes in temperature regime and light quality also are small when the plant is transferred from shallow water to air. It has been demonstrated that the degree of heterophylly in amphibious plants is coupled to the heterogeneity of their environment (Cook & Johnson 1968), and while the environment of *Littorella* apparently changes drastically upon emergence, its environment with regards to inorganic carbon does not change significantly. In that perspective, the adaptations of *Littorella* to effective uptake of CO_2 from the sediment and to internal recycling, can be viewed as adaptations not only to a carbon poor environment, but also to a nutrient poor environment by reducing the need for new leaves upon transference from one environment to an other.

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