Growth and morphology of *Scirpus lacustris* and *S. maritimus* seedlings as affected by water level and light availability

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**Summary**

1. Adults of the emergent macrophytes *Scirpus lacustris* ssp. *lacustris* (*S.l. lacustris*), *S. lacustris* ssp. *tabernaemontani* (*S.l. tabernaemontani*) and *S. maritimus* occur along a gradient in water depth from deep to shallow water. This study examined whether seedlings of these taxa respond differently to changing hydrological conditions.

2. Seedlings of both *S. lacustris* subspecies showed the highest relative growth rate (RGR) under terrestrial growth conditions, whereas *S. maritimus* did so under submerged growth conditions. In all three taxa, shading reduced the mean RGR of terrestrial seedlings more strongly than that of submerged ones.

3. *Scirpus maritimus* and *S.l. tabernaemontani* maintained an erect growth form under water, whereas *S.l. lacustris* produced numerous long, floating leaves.

4. Under terrestrial growth conditions the specific leaf area (SLA) did not differ between taxa. Under submerged growth conditions the SLA differed as follows: *S.l. lacustris* > *S.l. tabernaemontani* > *S. maritimus*. Irrespective of taxon and water level, the SLA was increased by shading.

5. Growth of all three taxa was reduced considerably after seedlings were transferred from terrestrial to submerged growth conditions. This effect was stronger with increasing age of seedlings. When transferred the other way round, seedlings of *S.l. tabernaemontani* and *S. maritimus* adapted quickly to the terrestrial growth conditions, whereas the thin leaves of *S.l. lacustris* partly dried out.

6. It was concluded that although seedling establishment of all three *Scirpus* taxa will be most successful under terrestrial conditions, subsequent fluctuating water levels may act as a strong selective force. This may determine the distribution of *Scirpus* taxa along a gradient in water depth during seedling establishment.

**Key-words:** Emergent macrophytes, heterophylly, plant size, relative growth rate, shading, submergence

**Introduction**

*Scirpus lacustris* L. ssp. *lacustris* (*S.l. lacustris*), *S. lacustris* L. ssp. *tabernaemontani* (C.C. Gmelin) Syme (*S.l. tabernaemontani*) and *S. maritimus* L. can be found at outer fringes of emergent macrophyte belts in both tidal and inland waters. They occur along a gradient from deep to shallow water as follows: *S.l. lacustris* > *S.l. tabernaemontani* > *S. maritimus* (Bakker 1954; Zonneveld 1960; Dykyjová & Květ 1978).

The occurrence of emergent macrophytes at different water depths may be related directly to differences in sexual recruitment (i.e. germination and seedling establishment). Germination is supposed to occur at sites most suitable for seedling establishment (Harper, 1977; Grime, 1979). In *Scirpus*, as in other emergent macrophytes, germination is predominately restricted to the transitional zone between land and water, or to bare mudflats which become exposed in periods of drought, the so-called drawdowns (Kadlec 1962; van der Valk & Davis 1978; Welling, Pederson & van der Valk 1988). In wetlands, however, water levels may change unpredictably, and even small changes may result in alternating periods of submergence and desiccation of seedlings. Owing to the shallowness of the water and wave action, changes in water level may be accompanied by a high turbidity of the water.
Under water, aeration of roots and shoots, as well as photosynthesis, may become strongly reduced (Boston Adams & Madsen 1989; Bowes & Salvucci 1989) because of the high CO$_2$ and O$_2$ diffusion resistance in water compared to air. Terrestrial species and most amphibious macrophytes are unable to use HCO$_3^-$ as an alternative C source for photosynthesis, but may form aerenchyma and respond morphologically to submergence (Sculthorpe 1967; Hutchinson 1975; Armstrong 1979; Maberly & Spence 1989; Beer et al. 1991). Although morphological responses may enable these species to photosynthesize under water to some extent, they are predominately directed towards the uptake of aerial CO$_2$ and O$_2$ (Madsen & Sand-Jensen 1991; Voesenek et al. 1993). Access to air can be reached in two different ways, by (1) forming long, thin floating leaves, such as occurs in many amphibious species (Sculthorpe 1967; Hutchinson 1975; Nielsen 1993), or by (2) the elongation of leaves, petioles or stems in order to emerge from the water, the so-called depth-accommodation response (Jackson 1985; Ridge 1987; Voesenek & Blom 1989). When plants fail to reach the water surface they may die, because of anaerobiosis in roots and shoots and to a lack of carbohydrates (Sand-Jensen, Pedersen & Nielsen 1992; Voesenek et al. 1993). Apart from CO$_2$, turbidity of the water may affect plant growth as well. To avoid shade, plants may also elongate their shoots (Grime 1966; Ridge 1987), which in combination with submergence may result in strongly etiolated plants.

A disadvantage of strong morphological responses to submergence is that elongated shoots may easily fall over and leaves may desiccate once the water level drops (Ridge 1987). On the other hand when water levels rise, especially large seedlings with a low morphological plasticity may suffer from inadequate underwater photosynthesis, because of a high maintenance respiration of large plants (Penning de Vries 1983; Ridge 1987).

This paper reports on the study of the relative growth rates (RGR) and morphological responses of Scirpus seedlings related to water level, changes in water level and shading during establishment. The hypothesis that seedlings of S.l. lacastris show the strongest morphological responses to submergence and S. maritimus the weakest, and that S.l. tabernaemontani behaves intermediate, was tested. Also, the possibility that submergence reinforces the elongation response to shade was examined.

**Materials and methods**

**NOMENCLATURE**

The nomenclature follows the Flora Europaea (Tutin et al. 1980), i.e. *S. lacastris* L. ssp. *lacastris*, synonymous with *Schoenoplectus lacastris* (L.) Palla; *S. lacastris* L. ssp. *tabernaemontani* (C.C. Gmelin) Syme, synonymous with *S. glaucus* Sm., non Lam., *S. tabernaemontani*

C.C. Gmelin and *Schoenoplectus tabernaemontani* (C.C. Gmelin) Palla; and *S. maritimus* L., synonymous with *Bolboschoenous maritimus* (L.) Palla.

**RESPONSES TO WATER LEVEL AND LIGHT AVAILABILITY**

In this experiment RGR and morphology of *Scirpus* seedlings were studied under submerged and terrestrial conditions at four different light levels. Stratified seeds, obtained from the same sources as described in Clevering (1995) were germinated in an incubator with a light/dark regime of 12 h at 30 °C and 12 h at 10 °C in 2-cm deep water (submerged treatment) or in waterlogged (terrestrial treatment) sandy substrate. One week after germination, the submerged seedlings were planted in pots of 150 ml and the terrestrial ones in pots of 500 ml. All pots were filled with sandy loam (1% organic matter) collected from Ventjagersplaten, the Netherlands (Clevering & van Gulik, 1991). The pots were placed in eight 100-litre (60x40x40 cm; 1xw x h) aquaria, which were placed in two controlled growth chambers with a light/dark regime of 16 h at 20 °C and 8 h at 15 °C and a relative air humidity of c. 80%. The water levels of the aquaria were kept at 25 cm above (submerged treatment) or 1 cm below the substrate level (terrestrial treatment). The pH of the water was checked regularly and maintained at pH 8.2 using H$_2$SO$_4$ for seedlings grown under water. This pH is comparable to the field situation (J. Vermaat, personal communication). Water was circulated using pumps (Eheim, Deizisau, Germany) with a capacity of 60 litres h$^{-1}$. Both the submerged and terrestrial seedlings were supplied with ground water. Light levels of 300 and 100 μmol m$^{-2}$ s$^{-1}$ (photosynthetically active radiation; PAR) were obtained by adjusting one of the growth chambers to 300 and the other one to 100 μmol m$^{-2}$ s$^{-1}$. 150 and 50 μmol m$^{-2}$ s$^{-1}$ (PAR) were obtained using neutral density netting with 50% light reduction. The three *Scirpus* taxa were grown in succession using only one water level at a time with two aquaria per light level and two replicates per aquarium.

Because an inherently slower growth of submerged seedlings was expected, they were harvested at larger time intervals (after 0, 1, 2, 4, 6, 8 and 10 weeks) than the terrestrial ones (after 0, 1, 2, 3, 4, 5 and 6 weeks of growth in the growth chambers). At each harvest the length of the first shoot, the number of leaves and the lengths of fully grown leaf blades were determined. Plants were dried at 70 °C for a period of at least 48 h. At the penultimate harvest the leaf area was determined using a digital image processor (Imaging Technology Inc., Woburn, MA).

**RESPONSES TO A CHANGE IN WATER LEVEL**

In this experiment sudden changes in water level were simulated by transferring seedlings of different age
Responses to changing water levels in Scirpus seedlings

Seedlings were obtained as in the previous experiment. One week after germination, seedlings were planted in pots of 150 ml filled with the same substrate as in the previous experiment. Half of the seedlings were grown submerged, the other half terrestrial, using a light/dark regime of 16 h (300 μmol m$^{-2}$ s$^{-1}$) at 20 °C and 8 h at 15 °C and a relative air humidity of c. 80%. The experimental conditions were the same as in the previous experiment. After 1, 2 and 3 weeks of growth, seedlings were reciprocally transferred. Untransferred seedlings were used as a control. Plants were harvested weekly during a period of 6 weeks. As the experiment was repeated once, with one replicate in each of the two growth chambers, four replicates were obtained.

At each harvest date, shoot length, the number of leaves and the length of the leaf blades and leaf sheaths were determined. Furthermore, the leaf width of fully grown leaves was determined. Dry weights were determined as described before.

**Statistical analyses**

Results of the first experiment were analysed per water level, except for growth characteristics of fully grown leaves because submerged and terrestrial seedlings were grown for different periods of time. In both instances results were analysed according to a completely randomized block design, with each of the two aquaria containing two blocks. A trend analysis in growth over time was conducted by performing an ANOVA on ln-transformed data of dry weights using the factors time x taxon x light level (Hunt 1982; Poorter & Lewis 1986). As submerged *S.l. lacustris* seedlings suffered from epiphytic algae at the end of the experiment, results of the final harvest were omitted for all three taxa.

Results of the second experiment were analysed according to a completely randomized block design, with growth chambers used at a particular time regarded as blocks. For each individual combination of taxon and date of transfer, the mean RGR was calculated after the plants were transferred, regarding the date of transfer as $t = 0$ using the formula:

$$W_v (t) = W_v (0) e^{RGR(t - 0)}.$$

Because of heterogeneity in *S.l. lacustris*, it was decided to assign rank numbers to the data of all three taxa and to perform one-way ANOVAs on these rank numbers per taxon (Potvin & Roff 1993). In contrast to the variances of RGR, those of rank numbers proved to be homogeneous (data not shown). Differences between means were calculated by the least-significant difference (LSD) procedure.

**Results**

**Responses to water level and light availability**

In a growth analysis it was shown that changes in RGR of submerged and terrestrial seedlings of the different taxa were affected differently by light levels (data not shown). The RGR of submerged *S.l. lacustris* remained constant in time, whereas those of *S. maritimus* decreased strongly (Fig. 1). Changes in RGR with time for *S.l. tabernaemontani* were intermediate, but resembled those of *S.l. lacustris* more than those of *S. maritimus*. The terrestrial seedlings showed reversed responses (Fig. 1). The RGR of both *S.l. lacustris* subspecies decreased with time under intermediate light levels, whereas those of *S. maritimus* remained rather constant. Mean RGR differed between taxa and light levels (Tables 1 and 2). Pooled for all light levels, they were lower in submerged *S. maritimus* than in both *S.l. lacustris* subspecies, whereas the opposite occurred in terrestrial seedlings ($P < 0.05$). Shading decreased the RGR of terrestrial seedlings more strongly than those of submerged ones (Fig. 1 and Table 2).

Submerged *S.l. lacustris* seedlings produced numerous floating leaves, whereas no stem was produced during the course of the experiment. In contrast, terrestrial seedlings grown at 300 μmol m$^{-2}$ s$^{-1}$ formed maximally six erect leaves and then a leafless stem (Fig. 2). Both submerged and terrestrial seedlings of *S.l. tabernaemontani* produced leafless stems, after producing four or five and four leaves, respectively.
Some of the submerged seedlings that were grown at 300 µmol m⁻² s⁻¹ succeeded in emerging from the water by the end of the experiment. Scirpus maritimus seedlings produced maximally six leaves before a leafy stem was produced. In contrast to terrestrial S. maritimus seedlings, the submerged ones did not show a significant increase in shoot length (Fig. 2).

The specific leaf area (SLA) of submerged seedlings varied widely between taxa, whereas those of terrestrial ones were similar (Table 3). Differences in SLA between submerged and terrestrially grown seedlings were higher in S.L. lacustris than in S. maritimus. Scirpus I. tabernaemontani behaved intermediate (Table 4). Irrespective of the taxon, a reduction in light resulted in an increase in SLA. This reaction was much smaller, however, than the response to submergence.

At the highest light level (300 µmol m⁻² s⁻¹) the length of mature leaf blades did not differ between submerged and terrestrially grown S.L. lacustris, but submerged S.L. tabernaemontani and S. maritimus leaf blades were shorter than terrestrial ones (Fig. 3). In response to shade the length of leaf blades of both submersed S. lacustris subspecies increased, whereas that of S. maritimus decreased. The opposite occurred in terrestrial leaves, although this was less pronounced in S.L. tabernaemontani (Fig. 3).

RESPONSES TO CHANGES IN WATER LEVEL

The mean RGR, especially of untransferred terrestrial seedlings, decreased with time and therefore with increasing plant size (Table 5). Transferring seedlings from terrestrial to submerged growth conditions resulted in a strong decrease in RGR, leading to an almost complete standstill of submerged growth in S.L. lacustris and S. maritimus when transferred after 3 weeks of terrestrial growth. Some of the then already large 3-week-old S.L. tabernaemontani seedlings were able to emerge from the water, resulting in a mean RGR comparable with those transferred after 1 and 2 weeks. After a transfer to terrestrial conditions, the mean RGR of S.L. lacustris was much lower than that of untransferred terrestrial ones, due to the desiccation of leaves. Larger seedlings were better able to overcome desiccation than smaller ones. In contrast, S.L. tabernaemontani and S. maritimus seedlings had RGR similar to the untransferred terrestrial ones, irrespective of the time of transfer (Table 5).

Because leaves of submerged S.L. lacustris partly desiccated after transfer to terrestrial growth conditions, no leaf characteristics of this taxon could be determined. Generally, the number of leaves of all three taxa was intermediate between the untransferred and submerged seedlings (data not shown). Characteristics of the third leaf are given in connection with the stage of development at the time of transfer (Fig. 4). Untransferred seedlings of S.L. lacustris and S. maritimus had longer terrestrial than submerged leaf sheaths, whereas those of S.L. tabernaemontani were similar (Fig. 4a). Only S. maritimus showed differences in leaf blade lengths, which were longer under terrestrial than under submerged conditions (Fig. 4b). Both S. lacustris subspecies produced narrower leaves under submerged than under terrestrial conditions, whereas the shape of S. maritimus leaves did not differ between water levels (Fig. 4c). The morphology of already mature leaves and in most instances the length-to-width ratio of developing leaves remained unaffected by transferring. Changes in lengths of leaf sheaths and blades of new and developing leaves were small; they never resulted in longer leaves than those of either untransferred terrestrial or submerged plants.

**Discussion**

**RELATIVE GROWTH RATES**

Although both subspecies of S. lacustris differed considerably in their morphological responses to submergence, no differences in mean RGR were found. In due time a decrease in RGR may be expected because of the depletion of reserve carbohydrates in the seed and a relative increase in maintenance respiration, because of an increase in the proportion of non-photsynthetic tissue with plant size (Hunt 1982; Fenner 1987; van der Werf et al. 1988). In submerged S.L. lacustris no decline in RGR with time was apparent, whereas in some instances that of submerged S.L. tabernaemontani did decrease. Therefore, S.L.

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**Table 1. ANOVA of mean RGR of submerged or terrestrial S.L. lacustris, S.L. tabernaemontani and S. maritimus grown at four different light levels**

<table>
<thead>
<tr>
<th>Block</th>
<th>Taxon (t)</th>
<th>Light (l)</th>
<th>rsl</th>
<th>Error (MS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>df</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>m</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>33</td>
</tr>
<tr>
<td>Submerged</td>
<td>1.3 NS</td>
<td>9.0 ***</td>
<td>15.6 ***</td>
<td>1.0 NS</td>
</tr>
<tr>
<td>Terrestrial</td>
<td>0.2 NS</td>
<td>8.6 ***</td>
<td>273.9 ***</td>
<td>1.7 NS</td>
</tr>
</tbody>
</table>

NS, not significant. ***P < 0.001.

**Table 2. Means of the mean RGR (day⁻¹) of submerged or terrestrial S.L. lacustris, S.L. tabernaemontani and S. maritimus grown at four different light levels. Significant differences were calculated per water level and are indicated with different letters (LSD: P < 0.05)**

<table>
<thead>
<tr>
<th>Light levels (µmol m⁻² s⁻¹)</th>
<th>Submerged</th>
<th>Terrestrial</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S.L. lacustris</td>
<td>S.L. tabernaemontani</td>
</tr>
<tr>
<td>300</td>
<td>0.073ef</td>
<td>0.066dce</td>
</tr>
<tr>
<td>150</td>
<td>0.066bde</td>
<td>0.065bde</td>
</tr>
<tr>
<td>100</td>
<td>0.072de</td>
<td>0.065bde</td>
</tr>
<tr>
<td>50</td>
<td>0.066bde</td>
<td>0.065bde</td>
</tr>
</tbody>
</table>
Responses to changing water levels in Scirpus seedlings

*S.lacusaris* may be the better submerged grower. The decline in RGR with time was especially pronounced in *S. maritimus*, the taxon with lowest morphological plasticity. Differences in mean RGR probably remained small because seedlings may have been supplied with reserve carbohydrates during the greater part of the experiment, whereas in all three taxa the rate of underwater photosynthesis remained low (O. A. Clevering, unpublished results) as a consequence of a low availability of CO₂ at a high pH. Also, the small differences in RGR between light levels in submerged *Scirpus* indicated that CO₂ availability was limiting rather than light (Salvucci & Bowes 1982; Boston et al. 1989; Nielsen 1993). The mean RGR of 0.17 day⁻¹ of terrestrial *Scirpus* seedlings falls within the range found for other emergent macrophytes under optimal growth conditions (Shipley & Peters 1990). The strong decrease in RGR in terrestrial seedlings upon shading showed that they were relatively shade intolerant (Grime 1966).

The transfer to submerged conditions after 1 or 2 weeks of terrestrial growth did not result in different RGR between taxa. It seems that seedlings, irrespective of the taxon, once adapted to terrestrial conditions may not be able to adapt quickly to submerged conditions later in their life cycle. Also, the strong decrease in RGR with increasing size of transferred *Scirpus* seedlings may be due to the absence of morphological changes in leaves, especially of those already produced under terrestrial conditions. As a consequence, large plants will have a high proportion of non-photosynthetic tissue, whereas they have a high absolute maintenance respiration (Penning de Vries 1983; van der Werf et al. 1988). Voesenek et al. (1993) argued that mortality in large transferred *Rumex* plants was probably due to a shift in the balance between the use (respiration) and availability of carbohydrates (seed reserves and photosynthates).

The submerged *S.lacustris* seedlings transferred to terrestrial growing conditions were very vulnerable to desiccation. In contrast, submerged *S. tabernaemontani* and *S. maritimus* seedlings were able to adapt quickly to terrestrial growth conditions. Apparently transferring these latter taxa did not seem to require costly adjustments of the plants, in terms of carbon use. It has been found in other taxa that the efficiency of photosynthesis of submerged leaves exposed to air may not differ from that of terrestrial ones (Salvucci & Bowes 1982; Nielsen 1993).

**MORPHOLOGICAL CHARACTERISTICS**

The three *Scirpus* taxa differed widely in their morphological responses to submergence. Submerged *S.lacusaris* seedlings produced a relatively high number of narrow and thin leaves that had the ability to float, whereas *S. tabernaemontani* produced narrow, erect and less thin leaves. *Scirpus maritimus* showed almost no plasticity in leaf morphology. In the seedling stage *S.lacustris* may be called a heterophyllous amphibious taxon. The existence of heterophyllous seedlings has also been found in other clonal emergent macrophytes, but seems to be an exception rather than the rule (Hutchinson 1975; Sharma & Gopal 1979). The formation of narrow, thin leaves upon submergence is a normal response in terrestrial species, which are to some extent adapted to submerged growing conditions (Scultihorpe 1967; Hutchinson 1975). No pronounced elongation responses of mature, developing or new leaves were found after submergence of terrestrially grown seedlings. The absence of this response seems to be a normal phenomenon in seedlings, and may explain why germination is only successful on exposed mudflats or in shallow water (Ridge 1987; Voesenek et al. 1993).

Plasticity in the SLA was higher in *S.lacusaris* than in *S. maritimus*, whereas *S. I. tabernaemontani* was intermediate. The SLA of submerged leaves of *S. lacusaris* subspecies was comparable to that of sub-

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**Table 3. ANOVA of SLA of submerged or terrestrial S.l. lacustris, S.l. tabernaemontani and S. maritimus grown at four different light levels**

<table>
<thead>
<tr>
<th>df</th>
<th>Block</th>
<th>Taxon (t)</th>
<th>Light (l)</th>
<th>p&lt;sub&gt;d&lt;/sub&gt;</th>
<th>Error (MS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Submerged</td>
<td>0-4 NS</td>
<td>148-7 ***</td>
<td>3-7 **</td>
<td>1-8 NS</td>
<td>1-5 x 10⁻³</td>
</tr>
<tr>
<td>Terrestrial</td>
<td>1-3 NS</td>
<td>3-1 NS</td>
<td>61-5 ***</td>
<td>1-6 NS</td>
<td>4-0 x 10⁻⁴</td>
</tr>
</tbody>
</table>

NS, not significant. **P < 0-01, ***P < 0-001.
merged or amphibious species, whereas that of terrestrial leaves resembled that of terrestrial species (Spence & Chrystal 1970; Poorter & Remkes 1990; Nielsen 1993). Shading reinforced the response in SLA upon submergence, but no differences between taxa were present. This may indicate that these reactions are mediated by different hormones. Only in submerged S.l. lacustris was a clear elongation response upon shading present. In S. maritimus, leaves were shorter with increasing shade, which may indicate a shortage in photosynthates. In terrestrially grown S. lacustris seedlings, as in S. maritimus, an elongation response to shade was expected. However, in the case of S. lacustris the maintenance of a relative high leaf appearance rate and, finally, the production of a stem, may be a better strategy to avoid shade.

**ECOLOGICAL IMPLICATIONS**

It can be concluded that morphological responses to submergence in *Scirpus* may primarily serve as a mechanism to have access to air, rather than to provide for a substantial carbon gain under water. Therefore, differences in morphological plasticity may reflect best the distribution of *Scirpus* seedlings along a gradient in water depth.

### Table 4. Means of the SLA (dm$^2$ g$^{-1}$) of submerged or terrestrial S.l. lacustris, S.l. tabernaemontani, and S. maritimus grown at four different light levels. Significant differences were calculated per water level and are indicated with different letters (LSD; $P < 0.05$). Data were arcsqrt-transformed prior to analysis

<table>
<thead>
<tr>
<th></th>
<th>Light levels (μmol m$^{-2}$ s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>300</td>
</tr>
<tr>
<td><strong>Submerged</strong></td>
<td></td>
</tr>
<tr>
<td>S.l. lacustris</td>
<td>14.03$^d$</td>
</tr>
<tr>
<td>S.l. tabernaemontani</td>
<td>8.93$^d$</td>
</tr>
<tr>
<td>S. maritimus</td>
<td>3.56$^a$</td>
</tr>
<tr>
<td><strong>Terrestrial</strong></td>
<td></td>
</tr>
<tr>
<td>S.l. lacustris</td>
<td>2.19$^{ab}$</td>
</tr>
<tr>
<td>S.l. tabernaemontani</td>
<td>2.04$^a$</td>
</tr>
<tr>
<td>S. maritimus</td>
<td>2.03$^a$</td>
</tr>
</tbody>
</table>

The strong morphological responses of *S.l. lacustris* to submergence may indicate that germination occurs under water and that seedlings emerge from the water later in their life cycle (Ridge 1987). This may be the case in streams and shallow, stagnant waters (Sand-Jensen et al. 1992; Weisner, Granéli & Ekstam 1993). However, seedlings from seed of the same population are also able to germinate (Clevering 1995) and grow terrestrially, as has been shown in the present study, without showing differences in RGR with S.l. tabernaemontani. Therefore, the occurrence of *S.l. lacustris* in back swamps (Zonneveld 1960) may be the result of entirely terrestrial establishment.

Despite their similar RGR, the production of very long leaves may enable *S.l. lacustris* to have access to air in much deeper water than *S.l. tabernaemontani*. *Scirpus l. tabernaemontani* seedlings are able to overcome a water depth of 20–30 cm, whereas those of *S. maritimus* are probably unable to show any growth after the seed reserves are depleted. This latter taxon is only able to grow under terrestrial conditions during its seedling stage. However, because of its lack in plasticity, seedlings remain quite robust under water, and due to this may tolerate short periods of flooding better than the weak, etiolated *S.l. tabernaemontani* seedlings.

In all three taxa a sudden rise in water level, resulting in the total immersion of seedlings, might result in mortality of especially large stemless seedlings. Later in their life cycle, the elongation of stems, thereby inhibiting the elongation of leaves, may enable plants to emerge from the water, as has been shown in other monocotyledons (Raskin & Kende 1984; Ridge 1987). Therefore, later in the life cycle the leafless stems of both *S. lacustris* subspecies may be better adapted to a sudden rise in water level than the leafy stems of *S. maritimus*.

From the present study as well as from germination experiments (Clevering 1995), it can be concluded that *S.l. lacustris* can be recruited in much deeper water than *S.l. tabernaemontani* and *S. maritimus*. The ability of *S.l. lacustris* to germinate and develop under water may result in established stands at the
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Table 5. The mean RGR (day\(^{-1}\)) of *S.l. lacustris*, *S.l. tabernaemontani* and *S. maritimus* (a) under submerged growth conditions after transfer from terrestrial to submerged or (b) under terrestrial conditions after transfer from submerged to terrestrial growth conditions. Per taxon differences between means were calculated using rank orders and are indicated by different letters (LSD; \(P < 0.05\)). The mean RGR of untransferred submerged (a) and terrestrial (b) plants during the same period are given in parentheses.

<table>
<thead>
<tr>
<th></th>
<th><em>S.l. lacustris</em></th>
<th><em>S.l. tabernaemontani</em></th>
<th><em>S. maritimus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Terrestrial → submerged</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weeks of terrestrial growth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.057(^c) (0.057)</td>
<td>0.072(^c) (0.072)</td>
<td>0.060(^c) (0.060)</td>
</tr>
<tr>
<td>1 week</td>
<td>0.043(^b) (0.046)</td>
<td>0.039(^b) (0.061)</td>
<td>0.041(^b) (0.043)</td>
</tr>
<tr>
<td>2 weeks</td>
<td>0.013(^\ast) (0.045)</td>
<td>0.010(^\ast) (0.049)</td>
<td>0.010(^\ast) (0.032)</td>
</tr>
<tr>
<td>3 weeks</td>
<td>0.006(^\ast) (0.052)</td>
<td>0.020(^\ast) (0.055)</td>
<td>0.004(^\ast) (0.034)</td>
</tr>
<tr>
<td>(b) Submerged → terrestrial</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weeks of submerged growth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.170(^d) (0.170)</td>
<td>0.165(^d) (0.165)</td>
<td>0.174(^d) (0.174)</td>
</tr>
<tr>
<td>1 week</td>
<td>0.046(^b) (0.167)</td>
<td>0.167(^d) (0.162)</td>
<td>0.162(^d) (0.172)</td>
</tr>
<tr>
<td>2 weeks</td>
<td>0.051(^b) (0.155)</td>
<td>0.153(^d) (0.152)</td>
<td>0.159(^d) (0.166)</td>
</tr>
<tr>
<td>3 weeks</td>
<td>0.088(^c) (0.149)</td>
<td>0.150(^d) (0.152)</td>
<td>0.163(^d) (0.135)</td>
</tr>
</tbody>
</table>

Fig. 4. (a) The length of the leaf sheaths and (b) leaf blades, and (c) the length-to-width ratio of the leaf blade of the fully grown third leaf of *S.l. lacustris*, *S.l. tabernaemontani* and *S. maritimus* seedlings transferred from either terrestrial to submerged (TS) or from submerged to terrestrial (ST) conditions after 0 (untransferred submerged and terrestrial seedlings, respectively), 1, 2 or 3 weeks. The different bar patterns indicate whether leaves were mature, developing or not yet formed (new) at the time of transfer. Data of two successive harvests were pooled (\(n = 8\)). Data of lengths were sqrt-transformed, and of the length to width ratio arcsqrt-transformed prior to the analysis. Differences between means were calculated per taxon and per leaf characteristic and are indicated by different letters (LSD; \(P < 0.05\)).

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