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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

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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 CO₂ and O₂ diffusion resistance in water compared to air. Terrestrial species and most amphibious macrophytes are unable to use HCO₃⁻ 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 CO₂ and O₂ (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 CO₂, 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. lacustris* show the strongest morphological responses to submergence and *S. maritimus* the weakest, and that *S.l. tabernaemontani* behaves intermediately, 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. lacustris* L. ssp. *lacustris*, synonymous with *Schoenoplectus lacustris* (L.) Palla; *S. lacustris* 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 *Bolboschoenus 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 (60 × 40 × 40 cm; l × w × 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 H₂SO₄ 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

from submerged to terrestrial conditions or vice versa. 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 terrestrially, using a light/dark regime of 16 h ($300 \mu\text{mol m}^{-2} \text{s}^{-1}$) 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 \times taxon \times 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:

$$W \vee 1 = W \vee 0 \cdot e^{\wedge RGR(t \vee 1 - t \vee 0)}$$

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. 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 $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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.

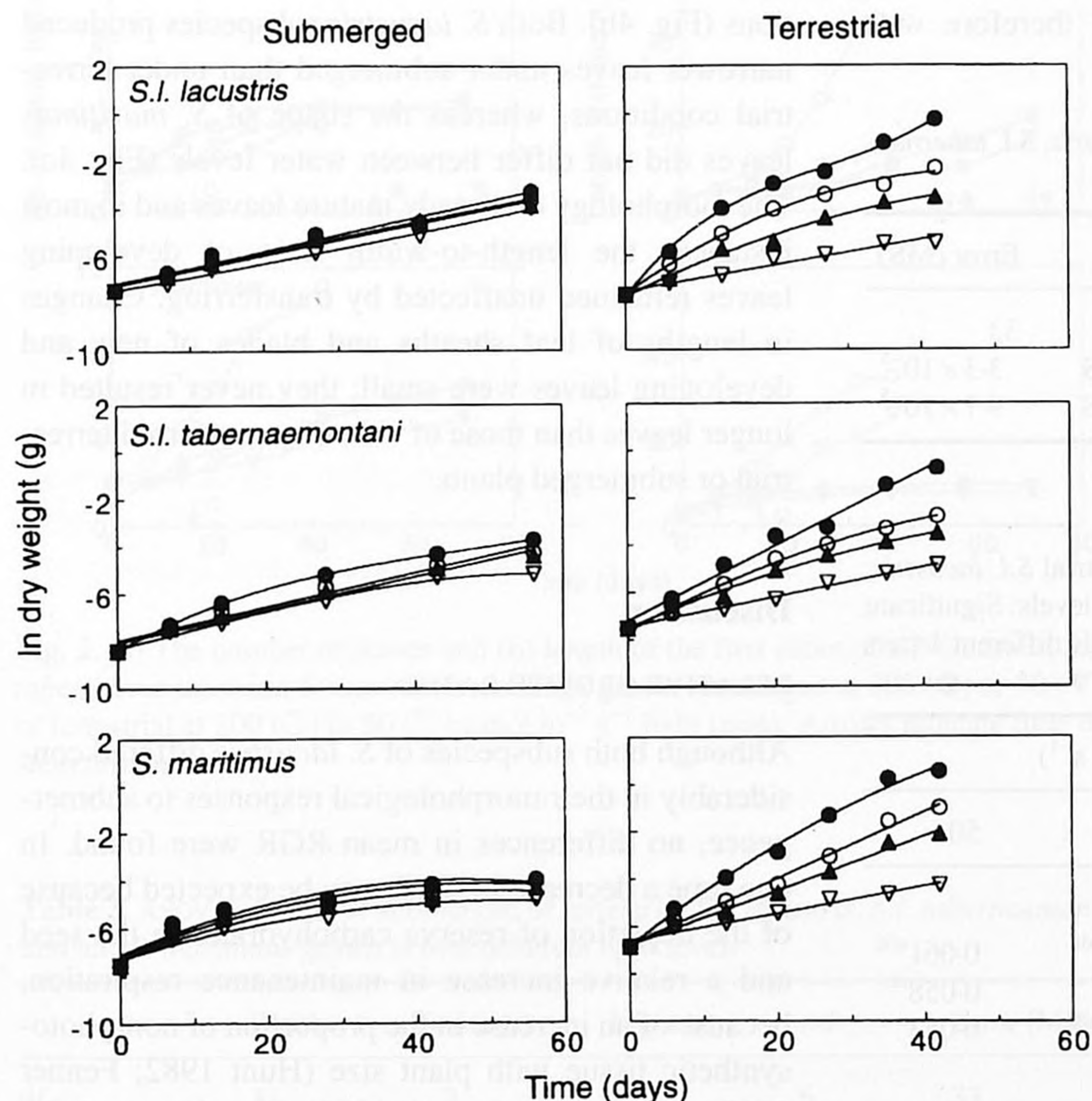


Fig. 1. Growth curves of submerged and terrestrial *S.l. lacustris*, *S.l. tabernaemontani* and *S. maritimus* seedlings grown at 300 (●), 150 (○), 100 (▲) or 50 (▽) $\mu\text{mol m}^{-2} \text{s}^{-1}$ light ($n=4$). A first, second or third order polynomial was fitted to ln-transformed data of total dry weight depending on the results of a trend analysis over time.

Some of the submerged seedlings that were grown at $300\mu\text{mol m}^{-2} \text{s}^{-1}$ 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 l. tabernaemontani* behaved intermediately (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 ($300\mu\text{mol m}^{-2} \text{s}^{-1}$) 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 submerged *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 terrestrial 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.

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

	Block	Taxon (t)	Light (l)	t×l	Error (MS)
df	3	2	3	6	33
Submerged	1.3 NS	9.0 ***	15.6 ***	1.0 NS	3.3×10^{-5}
Terrestrial	0.2 NS	8.6 ***	273.9 ***	1.7 NS	9.7×10^{-5}

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: $P < 0.05$)

	Light levels ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			
	300	150	100	50
Submerged				
<i>S.l. lacustris</i>	0.073 ^{ef}	0.066 ^{cde}	0.065 ^{bcde}	0.061 ^{abc}
<i>S.l. tabernaemontani</i>	0.081 ^f	0.072 ^e	0.070 ^e	0.058 ^{ab}
<i>S. maritimus</i>	0.066 ^{bcde}	0.065 ^{bcde}	0.061 ^{abcd}	0.053 ^a
Terrestrial				
<i>S.l. lacustris</i>	0.169 ^{fg}	0.125 ^d	0.103 ^{bc}	0.055 ^a
<i>S.l. tabernaemontani</i>	0.162 ^f	0.124 ^d	0.098 ^b	0.064 ^a
<i>S. maritimus</i>	0.183 ^g	0.142 ^e	0.116 ^{cd}	0.058 ^a

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-photosynthetic 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.*

lacustris 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 (Shiple & Peters 1990). The strong decrease in RGR in terrestrial seedlings upon shading showed that they were relatively shade intolerant (Grime 1966).

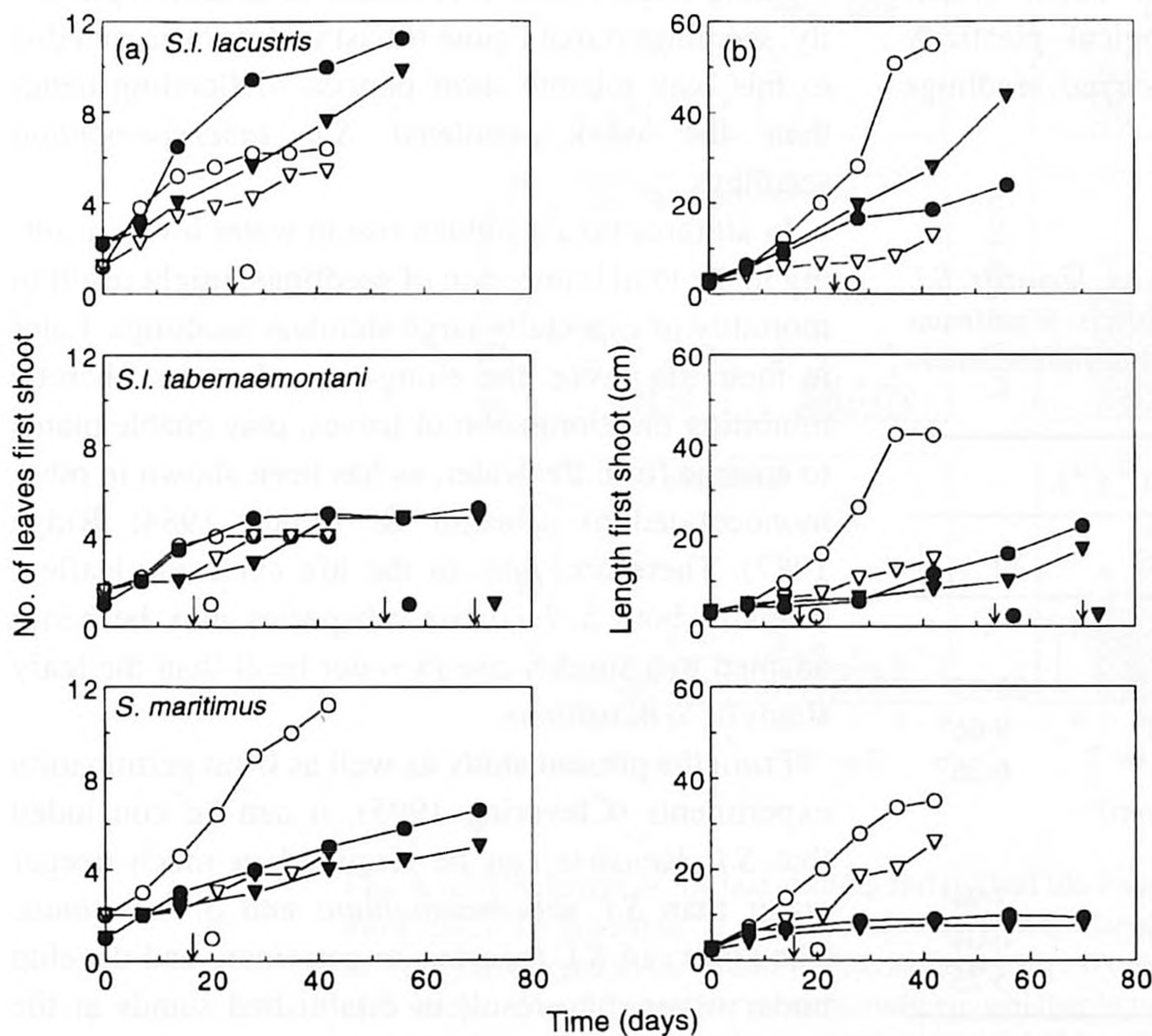


Fig. 2. (a) The number of leaves and (b) length of the first shoot of *S.l. lacustris*, *S.l. tabernaemontani* and *S. maritimus* seedlings grown submerged at 300 (●) or 50 (▼) or terrestrial at 300 (○) or 50 (▽) μmol m⁻² s⁻¹ light ($n=4$). Arrows indicate time of stem formation.

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

	Block	Taxon (t)	Light (l)	$t \times l$	Error (MS)
df	3	2	3	6	33
Submerged	0.4 NS	148.7 ***	5.7 **	1.8 NS	1.5×10^{-3}
Terrestrial	1.3 NS	3.1 NS	61.5 ***	1.6 NS	4.0×10^{-4}

NS, not significant. ** $P < 0.01$, *** $P < 0.001$.

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). Voeselek *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.l. lacustris* seedlings transferred to terrestrial growing conditions were very vulnerable to desiccation. In contrast, submerged *S.l. 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.l. lacustris* seedlings produced a relatively high number of narrow and thin leaves that had the ability to float, whereas *S.l. tabernaemontani* produced narrow, erect and less thin leaves. *Scirpus maritimus* showed almost no plasticity in leaf morphology. In the seedling stage *S.l. 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 (Sculthorpe 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; Voeselek *et al.* 1993).

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

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 ($\text{dm}^2 \text{g}^{-1}$) 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 arcs sqrt-transformed prior to analysis

	Light levels ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			
	300	150	100	50
Submerged				
<i>S.l. lacustris</i>	14.03 ^e	15.30 ^{ef}	21.01 ^{fg}	22.35 ^g
<i>S.l. tabernaemontani</i>	8.93 ^{cd}	10.26 ^d	9.88 ^d	9.66 ^d
<i>S. maritimus</i>	3.56 ^a	3.31 ^a	4.21 ^{ab}	6.26 ^{bc}
Terrestrial				
<i>S.l. lacustris</i>	2.19 ^{ab}	3.02 ^{cde}	3.87 ^{de}	7.94 ^g
<i>S.l. tabernaemontani</i>	2.04 ^a	2.88 ^{abc}	3.99 ^e	6.04 ^f
<i>S. maritimus</i>	2.03 ^a	2.88 ^{abc}	3.59 ^{de}	5.23 ^f

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

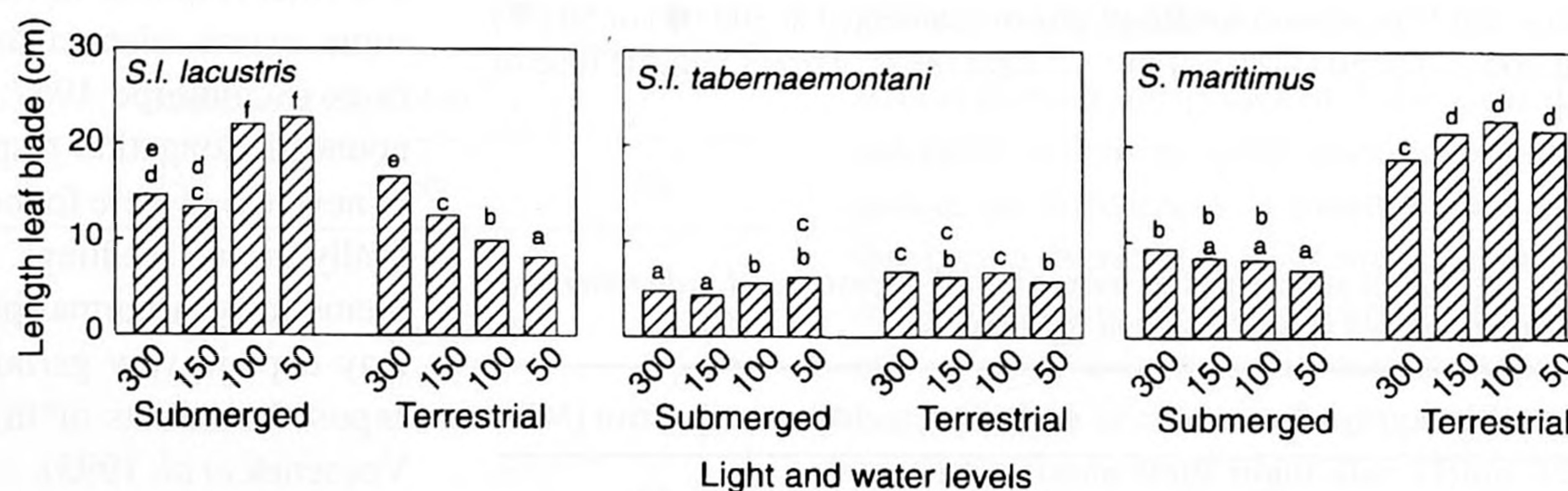


Fig. 3. Length of the fully-grown fourth leaf blade of *S.l. lacustris* and *S. maritimus* and second leaf blade of *S.l. tabernaemontani* grown under submerged or terrestrial conditions at light levels of 300, 150, 100 or 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Data of two successive harvests were pooled ($n = 8$). The data were sqrt-transformed prior to the analysis. Per taxon significant differences are indicated with different letters (LSD; $P < 0.05$).

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

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

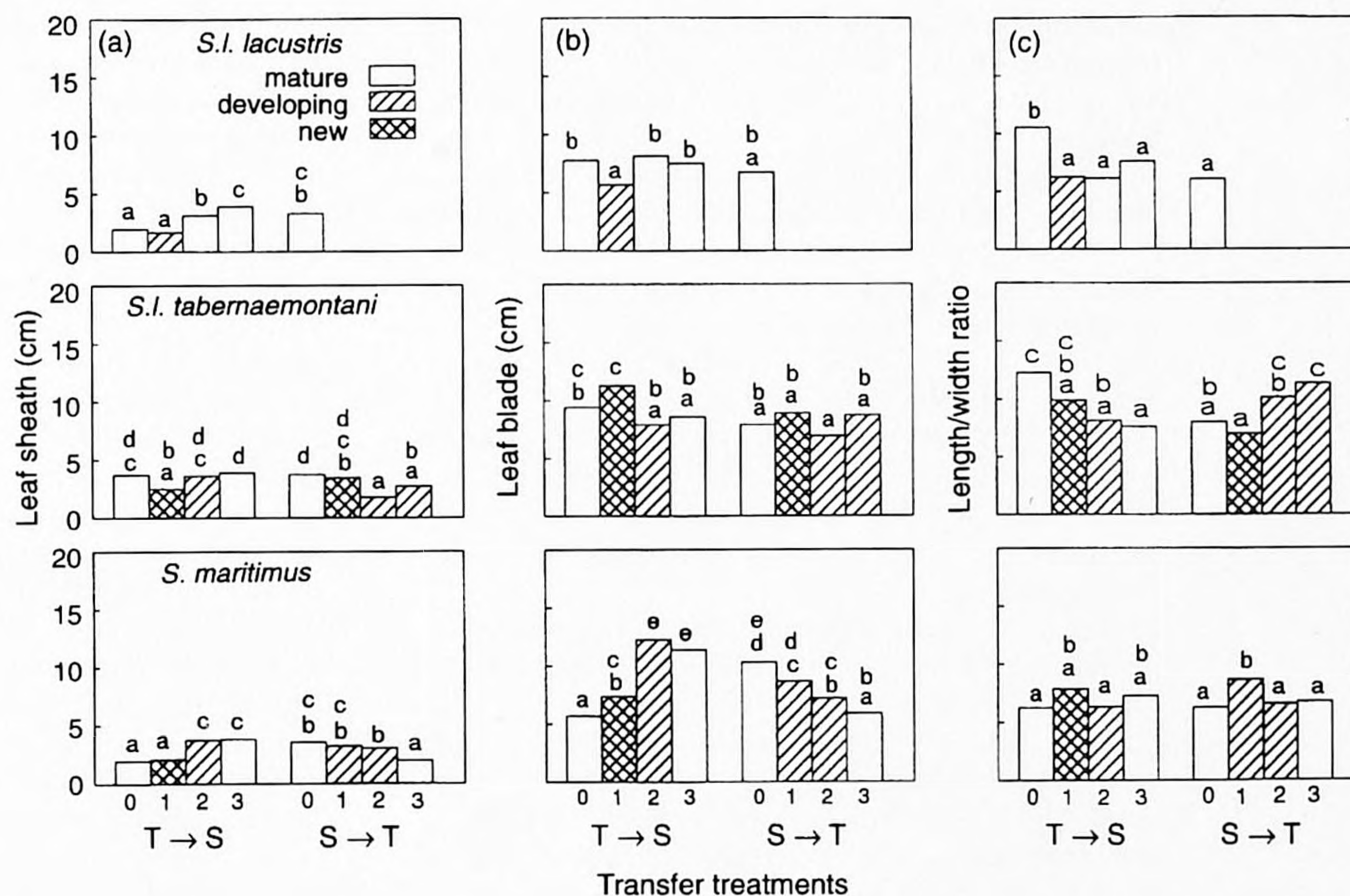


Fig. 4. (a) The length of the leaf sheaths and (b) leaf blades, and (c) the length-to-width ratio of the leaf blade of the fully grown third leaf of *S.l. lacustris*, *S.l. tabernaemontani* and *S. maritimus* seedlings transferred from either terrestrial to submerged (TS) or from submerged to terrestrial (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 arcs sqrt-transformed prior to the analysis. Differences between means were calculated per taxon and per leaf characteristic and are indicated by different letters (LSD; $P < 0.05$).

lakeward side of an existing *Phragmites australis* (Cav.) Trin. ex Steudel belt in shallow, sheltered lakes (Haslam 1978; Weisner *et al.* 1993). Under terrestrial conditions, *S. maritimus* may be the better competitor, because it shows a higher relative and absolute growth rate than both *S. lacustris* subspecies.

It can be concluded that in the transitional zone between water and land, water levels are a strong selective force during seedling establishment. Differences in morphological plasticity of seedlings may result in differences in the distribution of adult *Scirpus* taxa

along a gradient in water depth. It has been shown that fluctuation in water level is an important selective force as well. At sites with frequent changing water levels *S. maritimus* may be the best adapted taxon.

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References

- Armstrong, W. (1979) Aeration in higher plants. *Advances in Botanical Research* **7**, 225–332.
- Bakker, D. (1954) Miscellaneous notes on *Scirpus lacustris* L. sensu lat. in the Netherlands. *Acta Botanica Neerlandica* **3**, 425–445.
- Beer, S., Sand-Jensen, K., Madsen, T.V. & Nielsen, S.L. (1991) The carboxylase activity of rubisco and the photosynthetic performance in aquatic plants. *Oecologia* **87**, 429–434.
- Boston, H.L., Adams, M.S. & Madsen, J.D. (1989) Photosynthetic strategies and productivity in aquatic systems. *Aquatic Botany* **34**, 27–57.
- Bowes, G. & Salvucci, M.E. (1989) Plasticity in the photosynthetic carbon metabolism of submerged aquatic macrophytes. *Aquatic Botany* **34**, 233–266.
- Clevering, O.A. (1995) Germination and seedling emergence of *Scirpus lacustris* and *S. maritimus* with special reference to the restoration of wetlands. *Aquatic Botany* **50**, 63–78.
- Clevering, O.A. & Van Gulik, W.J.M. (1991) The establishment of *Scirpus lacustris* ssp. *lacustris* and *S. maritimus* in the northern Delta area, the Netherlands. *Verhandlungen der Internationalen Vereinigung für Limnologie* **24**, 2711–2713.
- Dykjová, D. & Květ, J. (1978) *Pond littoral ecosystems*. Springer-Verlag, Berlin.
- Fenner, M. (1987) Seedlings. *New Phytologist* **106**, 35–47.
- Grime, J.P. (1966) Shade avoidance and tolerance in flowering plants. *Light as an Ecological Factor* (eds R. Bainbridge, G.C. Evans & O. Rachham), pp. 281–301. Blackwell Scientific Publications, Oxford.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester.
- Harper, J.P. (1977) *Population Biology of Plants*. Academic Press, London.
- Haslam, S.M. (1978) *Riverplants: the Macrophytic Vegetation of Water courses*. Cambridge University Press, Cambridge.
- Hunt, R. (1982) *Plant Growth Curves. The Functional Approach to Plant Growth Analysis*. Edward Arnold, London.
- Hutchinson, G.E. (1975) *A Treatise on Limnology, Vol. III. Limnological Botany*. John Wiley, New York.
- Jackson, M.B. (1985) Ethylene and responses of plants to soil waterlogging and submergence. *Annual Review of Plant Physiology* **36**, 145–174.
- Kadlec, J.A. (1962) Effects of a drawdown on a waterfowl impoundment. *Ecology* **43**, 267–281.
- Maberly, S.C. & Spence, D.H.N. (1989) Photosynthesis and photorespiration in freshwater organisms: amphibious plants. *Aquatic Botany* **34**, 267–286.
- Madsen, T.V. & Sand-Jensen, K. (1991) Photosynthetic carbon assimilation in aquatic macrophytes. *Aquatic Botany* **41**, 5–40.
- Nielsen, S.L. (1993) A comparison of aerial and submerged photosynthesis in some Danish amphibious plants. *Aquatic Botany* **45**, 27–40.
- Penning de Vries, F.W.T. (1983) Modelling of growth and production. *Encyclopedia of Plant Physiology*. (eds O. L. Lange, P. S. Nobel, C. B. Osmond & H. Ziegler) Vol. 12D, pp 117–150. Berlin Springer Verlag.
- Poorter, H. & Lewis, C. (1986) Testing differences in relative growth rate: a method avoiding curve fitting and pairing. *Physiologia Plantarum* **67**, 223–226.
- Poorter, H. & Remkes, C. (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* **83**, 553–559.
- Potvin, C. & Roff, D.A. (1993) Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology* **74**, 1617–1628.
- Raskin, I. & Kende, H. (1984) Regulation of growth in stem sections of deep-water rice. *Planta* **160**, 66–72.
- Ridge, I. (1987) Ethylene and growth control in amphibious plants. *Plant Life in Aquatic and Amphibious Habitats* (ed. R.M.M. Crawford), pp. 53–76. Blackwell Scientific Publications, Oxford.
- Salvucci, M.E. & Bowes, G. (1982) Photosynthetic and photorespiratory responses of the aerial and submerged leaves of *Myriophyllum brasiliense*. *Aquatic Botany* **13**, 147–164.
- Sand-Jensen, K., Pedersen, M.F. & Nielsen, S.L. (1992) Photosynthetic use of inorganic carbon among primary and secondary water plants in streams. *Freshwater Biology* **27**, 283–293.
- Sculthorpe, C.D. (1967) *The Biology of Aquatic Vascular Plants*. Edward Arnold, London.
- Sharma, K.P. & Gopal, B. (1979) The effect of water regimes on the growth and establishment of *Typha angustata* seedlings. *International Journal of Ecology and Environmental Sciences* **5**, 69–74.
- Shipley, B. & Peters, R.H. (1990) A test of the Tilman model of plant strategies: relative growth rate and biomass partitioning. *The American Naturalist* **136**, 139–153.
- Spence, D.H.N. & Chrystal, J. (1970) Photosynthesis and zonation of freshwater macrophytes. II. Adaptability of species of deep and shallow water. *New Phytologist* **69**, 217–227.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (1980) *Flora Europaea Vol. 5*. Cambridge University Press, London.
- van der Valk, A.G. & Davis, C.B. (1978) The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**, 322–335.
- Voesenek, L.A.C.J. & Blom, C.W.P.M. (1989) Growth responses of *Rumex* species in relation to submergence and ethylene. *Plant, Cell and Environment* **12**, 433–439.
- Voesenek, L.A.C.J., van Oorschot, F.J.M.M., Smits, A.J.M. & Blom, C.W.P.M. (1993) The role of flooding resistance in the establishment of *Rumex* seedlings in river flood plains. *Functional Ecology* **7**, 105–114.
- Weisner, S.E.B., Granéli, W. & Ekstam, B. (1993) Influence of submergence on growth of seedlings of *Scirpus lacustris* and *Phragmites australis*. *Freshwater Biology* **29**, 371–375.
- Welling, C.H., Pederson, R.L. & van der Valk, A. G. (1988) Recruitment from the seed bank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. *Journal of Ecology* **76**, 483–496.
- van der Werf, A., Kooijman, A., Welschen, R. & Lambers, H. (1988) Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. *Physiologia Plantarum* **72**, 483–491.
- Zonneveld, I.S. (1960) *De Brabantse Biesbosch. A study of soil and vegetation of a fresh water tidal area (in Dutch with English summary)*. PhD thesis, Agricultural University, Wageningen, the Netherlands.

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