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Growth, photosynthesis and carbohydrate utilization in submerged *Scirpus maritimus* L. during spring growth

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SUMMARY

The importance of underwater photosynthesis and the use of reserve-carbohydrates were assessed in submerged *Scirpus maritimus* L. during spring growth. Submerged plants were grown in outdoor ponds (90 cm deep) using different initial tuber sizes (mean 8.9 and 16.2 g f. wt) and different light treatments (0, 40, 70 and 100% of full daylight). After shoot emergence the recovery from shading and darkness was studied.

The period of submerged growth lasted 9 wk. During this period the mean relative growth rate (RGR) was independently affected by shading and tuber size. At the end of this period dry weight of plants grown in darkness was only 50% of that of plants grown in full daylight or shade (70 or 40% of full daylight), whereas that of plants from small tubers was only 67% of that from large ones. As a result plants grown from small tubers in darkness had only 33% of the dry weight of those grown from large tubers in full daylight or shade.

Despite these large differences in total dry weight at the end of the submerged period, shoot length remained unaffected by shading and tuber size. Shoots grown in darkness were strongly etiolated, with a slower rate of leaf appearance, but with longer leaves, than those grown in full daylight or shade. Only after emergence was shoot length as well as dry matter production greater in plants grown previously in full daylight or shade than in darkness, and greater in plants grown from large than from small tubers.

During the submerged period, the relative depletion rate of reserve-carbohydrates increased with time, but remained unaffected by shading and tuber size. The reserve-carbohydrates were replenished after plants emerged.

It was concluded that both underwater photosynthesis and tuber size had a large impact on total dry matter production in *S. maritimus*. They did not, however, affect the ability of *S. maritimus* to emerge from 90 cm deep water.

Key words: Emergent macrophytes, maximum water depth, submerged growth, reserve carbohydrates, photosynthesis.

INTRODUCTION

The ability of emergent macrophytes to cope with low oxygen concentrations in the environment is a major factor determining the occurrence of these species (Crawford, 1992). Research has been focused on the survival of perennating organs in anaerobic mud during winter on the one hand, and on growth and survival in deep water during summer on the other.

The ability of perennating organs to survive anaerobiosis might differ widely among species; for

example, *Juncus effusus* L. rhizomes survive only 4 d of anaerobiosis, whereas *Scirpus maritimus* L. tubers can survive nearly 3 months (Brändle & Crawford, 1987). The ability to survive without oxygen has great adaptive value; during winter *S. maritimus* tubers can be completely covered with anaerobic mud, but in early spring the tubers succeed in producing shoots that emerge from the soil, where access to oxygen is restored (Crawford, 1989). The ability to tolerate anaerobiosis during winter has been found to depend on the amount of reserve carbohydrates and their metabolic conservation (see

e.g. Barclay & Crawford, 1982, 1983; Brändle & Crawford, 1987; Crawford, 1989, 1992; Brändle, 1990). After plants again have access to air, oxygen is transported to the below-ground parts, where it is used for root respiration and oxidation of the rhizosphere (Armstrong & Armstrong, 1988; Laan & Blom, 1990). In deep water the oxygen transport from shoots to below-ground parts might be restricted by the length of the emergent part of the shoot and a long O₂ transport distance (Yamasaki, 1984, 1987; Weisner, 1988, 1991)

In contrast to the knowledge available on survival and growth during winter and summer, little is known about the submerged shoot-growth of emergent macrophytes during spring. Generally, it is assumed that the maximum water depth submerged shoots can overcome depends on the amount of reserve carbohydrates (Grace & Wetzel, 1982; Spence, 1982; Grace, 1989). Although the importance of the amount of reserve-carbohydrates seems obvious, there have been no experimental studies to date which investigated the relationship between the amount of reserve-carbohydrates and the maximum depth of water from which macrophytes can emerge. Grace & Wetzel (1982) observed that *Typha latifolia* L. and *T. angustifolia* L. had larger rhizomes if they grew in deeper water. In *S. maritimus*, however, the tuber size is unaffected by water depth, but is strongly correlated with the size of the whole clone (O. A. Clevering, unpublished). Besides the availability of reserve-carbohydrates, that of oxygen has also been found to be of major importance for submerged shoot growth of emergent macrophytes (Jordan & Whigham, 1988; Granéli, 1989). Plants which are not provided with oxygen from dead overwintering shoots have to take up oxygen from the water or they might produce oxygen by underwater photosynthesis which will also supply plants with carbohydrates for shoot growth. Although Grace & Wetzel (1982) assumed that underwater photosynthesis contributes very little to the growth of submerged ramets of *T. latifolia*, it has been shown that underwater photosynthesis supplies a number of wetland species with both oxygen and/or carbohydrates (Palada & Vergara, 1972; Gaynard & Armstrong, 1987; Laan & Blom, 1990; Voesenek *et al.*, 1993). When underwater photosynthesis is an important phenomenon in spring, shoot growth of emergent macrophytes could be considerably reduced in shallow water bodies, where turbidity of the water is of frequent occurrence.

The present study was conducted using the emergent macrophyte *Scirpus maritimus* (syn. *Bolboschoenus maritimus* (L.) Palla). It occurs along the outer zone of emergent macrophyte vegetation, in fresh and brackish tidal areas as well as in inland waters (Hejný, 1960; Zonneveld, 1960; Kötter, 1961; Dykyjová, 1986). Within the group of emergent macrophytes *S. maritimus* is one of the most

tolerant to anoxia of the substrate (Barclay & Crawford, 1982). The species is able to emerge from deep water, obviously without the provision of oxygen from standing dead shoots. This paper assesses the relative importance of photosynthesis and reserve carbohydrates for the submerged shoot growth of *S. maritimus*. Using tubers from two different size classes, growth, photosynthesis and tuber depletion rates were calculated for plants grown under different light treatments. To assess whether ample oxygen was available for respiration, the efficiency of the conversion of reserve carbohydrates into newly produced dry matter and respiration of plants grown in darkness were calculated.

MATERIALS AND METHODS

Experimental design

In February 1991, tubers of *S. maritimus* L. were collected from 3-yr-old clones, which were grown at Ventjagersplaten (Haringvliet, The Netherlands). The clones were established from seed originating from a natural stand near Willemstad (Hollandsch Diep.). Directly after the tubers were collected dead stems were cut back close to the stem base and roots were removed. To avoid bud damage, stems were not completely removed. The tubers were split up into two size classes, small (8.9 ± 2.6 g) and large (16.2 ± 2.8 g) tubers based on their fresh weights. Tubers were planted in 1 l pots in a mixture of sand and potting soil (2/1 v/v). On 9 March, tubers were placed in two adjacent outdoor ponds at the University of Nijmegen with two blocks per pond and four plots of 1×1 m² within each block. The four plots received a different light treatment; 100, 70, 40 and 0% of full daylight. Tubers of both size classes were assigned randomly to the plots. Tubers which were shaded or grown in total darkness were placed under constructions ($1 \times w \times h$: $1 \times 1 \times 1.1$ m³) covered with neutral density netting of different mesh width. Full darkness was obtained by opaque PVC sheeting. The ponds were filled with tap water up to a depth of 90 cm. At each harvest date a total number of 32 tubers was harvested, namely 1 sprouted tuber per size class per plot.

Period of submergence. After buds started to sprout, plants were harvested weekly, over a period of 9 wk (20 March–15 May 1991).

Period of emergence. After these 9 wk of growth, about 80% of the remaining plants had reached the water surface. These plants were re-assigned randomly to different harvest dates for each tuber size class and plot. Plants were grown for another period of 6 wk (15 May–30 June 1991) under full daylight conditions. In this period plants were harvested each fortnight.

Light and temperature measurements

Light measurements were made at the end of the experiment in each plot, at 10, 30, 50 and 70 cm above ground level (LICOR photometer; LI-185B, Lambda Instr. Corp., USA). Control measurements were made in air (above water level) after each underwater measurement. Hourly total radiation measurements (J m^{-2}) were obtained from Meteoconsult Wageningen (station Terlet) for the period of submerged growth. These radiation measurements were converted to $\mu\text{mol m}^{-2} \text{s}^{-1}$ according to McCree (1972) and were multiplied by the water/air light ratio for all shade levels. To obtain corresponding temperatures for the underwater photosynthesis measurements, the water temperature was measured during the submerged period.

Growth characteristics

At each harvest, plants were carefully cleaned and fresh weight of tubers, as well as dry weights (dried at 70 °C) of planted tubers, shoots, roots, rhizomes, newly formed tubers and ramets were determined separately. Ash-free dry weights of shoots were determined after drying at 70 °C (until constant weight) and ashing at 550 °C for 4 h. At each harvest, the length of all shoots, the leaf appearance rate and the length of the individual leaves of the longest shoot were determined.

Total soluble carbohydrates were determined after grinding the tubers, by the method of Allen (1974). They were extracted in 10 ml 3% HCl. In both instances anthrone was used as a reagent.

Photosynthesis

Flooding shoots. Measuring photosynthesis of aerenchymous plants might be complicated because of the internal storage and/or cycling of O_2 . This phenomenon can lead to an underestimation of the photosynthesis and respiration rate as has been found in *Egeria densa* Planchon (Sorrell & Dromgoole, 1986). Therefore the internal storage of oxygen by *S. maritimus* was studied by flooding the lacunae. Plants were grown submerged in a greenhouse in Heteren at 20 °C. At the end of the day before photosynthesis was measured, whole plants were harvested and transported from Heteren to the laboratory (IHE Delft) in PVC tubes of 1 m length and 10 cm diameter filled with tap water. During the night in between collecting and measuring, plants remained in the PVC tubes. Before measuring photosynthesis the below-ground plant parts were removed and shoots were cut in parts of 30 cm. The flooding of the lacunae was achieved by placing the shoots in a container filled with water. The air pressure was reduced until hardly any air was released from the cut shoot parts, using a manual vacuum pump.

Photosynthesis was measured according to Hootsmans & Vermaat (1994). A 100 l aquarium tank was filled with tap water and 20 g NaHCO_3 was added to produce saturating concentrations of inorganic carbon. The temperature was kept at 20 °C. Photosynthesis was measured in three replicate closed systems, each consisting of a circulation pump, a perspex electrode chamber and a perspex tube of 30 cm length and 5 cm diameter, interconnected with PVC tubes. The perspex tubes were submerged horizontally in the aquarium and the tube surface was kept 1 cm beneath the water surface. The flow rate of the system was 1.5 l min^{-1} , using a Watson and Marlowe peristaltic pump. The shoot parts were attached on a grid of 20 cm length which was placed in the perspex tubes.

Measurements of oxygen concentration and temperature were made using a Clark type oxygen electrode (WTW EO196) connected with a read-out unit (WTW OXI 196). Data were registered every 10 s by a datalogger. Light was provided by a Philips 400 W HPIT metal halide lamp. Different light levels were created by changing the distance between lamp and aquarium and using a neutral density filter. After dark respiration, net photosynthesis was measured at nine light levels between 25 and $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, from low to high. Each incubation session took 20–30 min, and the systems were opened between incubations to replenish the medium.

Pond experiment. Photosynthesis of flooded shoots of plants grown in the pond was measured in weeks 5, 7 and 9, as it was assumed that the plants became photosynthetically active after the shoots started to develop green leaves in week 4. Handling and transporting plants from Nijmegen to Delft were done as before. During measurements of photosynthesis, the temperature was kept between 14 and 16 °C, corresponding with the mean daily water temperature during the period of submerged growth in the ponds.

Data analyses

Growth characteristics. For both the submerged and emerged period, differences between treatments were calculated for all parameters according to a completely randomized block design (a three-way ANOVA) with factors time, light level and tuber size. All weights were \log_e transformed, lengths were square-root (sqrt)-transformed and ratios arcsin-sqrt transformed. To obtain more replicate measurements leaf lengths of full-grown leaves of three successive harvest weeks were pooled prior to a two-way ANOVA, with light level and tuber size as factors. Differences between means were calculated with the Least Significant Difference (LSD) procedure (Sokal & Rohlf, 1981). In the period of submerged growth the mean relative growth rates (RGR) of the whole

plant and of the above- and below-ground parts were calculated for each combination of tuber size and plot (light level).

The RGR was calculated using the formula:

$$W_2 = W_1 \cdot e^{RGR(t_2 - t_1)}$$

Because plants started to develop roots and became photosynthetically active in week 4, growth rates were calculated for the whole period and for the first 4 wk (non-photosynthetic period) and the second 5 wk (photosynthetic period) separately. Differences in growth rates were tested using a two-way ANOVA, followed by the LSD-procedure for testing differences between means.

Extrapolating data. Reserve-carbohydrate depletion was estimated by fitting a first- and a second-order polynomial to both untransformed and \log_e transformed data. The depletion of carbohydrates was slightly better described using a second-degree polynomial on untransformed rather than on \log_e transformed data. Therefore, a second-degree polynomial on untransformed data was used to calculate the point of zero carbohydrates and the length of submerged plants at that time, for each combination of tuber size and plot (light level). Significant differences were calculated using a two-way ANOVA, followed by the LSD-procedure for testing differences between means.

Conversion efficiency. The conversion efficiency (CE), the ratio of newly produced dry matter/used reserve carbohydrates, was calculated using data from second-degree polynomials fitted to data of newly produced dry matter and of reserve carbohydrates of plants grown in darkness.

Photosynthesis. O_2 exchange rates were calculated according to Hootsmans & Vermaat (1994). The data were fitted using the rectangular hyperbola (Michaelis–Menten) model:

$$P = \frac{P_{\max} \times I}{K_m + I} - R,$$

in which (I) is the independent variable light, (P) the dependent variable net productivity, (P_{\max}) is the maximum rate of gross productivity, (K_m) the Michaelis–Menten constant (light level where gross productivity is half the maximum gross productivity (P_{\max})) and (R) is dark respiration (P and R in $\mu\text{g } O_2 \text{ g}^{-1} \text{ min}^{-1}$ and I and K_m in $\mu\text{mol m}^{-2} \text{ s}^{-1}$). Differences between light response curves of control and flooded shoots were calculated using light intensity as a within-shoots repeated factor, using the repeated measurement analysis of variance procedure (SPSS-procedure MANOVA; Norusis, 1986).

In the pond experiment the model parameters P_{\max} , K_m , and R and the light compensation point

(LCP) were used for comparisons between treatments. Two-way ANOVAs were performed with light level and census date as factors. Prior to the ANOVA, the data were \log_e transformed in order to obtain homogeneity of variances. Differences between means were calculated by the LSD-procedure.

Net photosynthesis of shoots in the ponds was calculated using the hourly radiation data and the P_{\max} , R , and K_m values obtained from the photosynthesis measurements in the laboratory.

RESULTS

Growth rates and morphology

Growth rates. During the period of submergence the relative growth rates (RGRs) of total, above- and below-ground plant parts were significantly affected by a light level \times tuber size interaction (Table 1). Between weeks 1–4, plants were not yet photosynthetically active and had no roots. In this period no significant differences in dry weight production were present (Fig. 1a) and plants had a mean RGR of 0.077 d^{-1} (data not shown). For weeks 4–9, plants grown in full daylight and shade (40 and 70% of full daylight) became photosynthetically active. From week 5 onwards differences in dry matter production became apparent, leading to significant differences in mean RGRs (Table 2). In contrast to changes with time in RGR (Table 1), mean RGRs were independently affected by shading and tuber size (Table 2). The mean RGRs of the whole plant and of the above-ground parts were lower in plants grown in darkness than in full daylight or shade, whereas the mean RGR of below-ground parts decreased with increasing level of shading. Mean RGRs were also lower for plants from small than from large tubers (Table 2).

In the period of emergence, no significant interactions with time were present, and the RGRs did not differ between treatments (Table 1). Dry weight of plants grown in darkness in the previous period remained smaller than that of plants grown in full daylight (Fig. 1a) or shade (data not shown). In this period dry weights were more strongly affected by tuber size than by shading (Table 1; Fig. 1a). In this period new tillers were produced, but no significant differences in tiller formation were present (data not shown).

Morphology. In the submerged period the lengths of the first shoots did not differ between light levels and tuber sizes (Table 1). A slower leaf appearance rate of plants grown in darkness than in full daylight or shade (Table 1; data not shown) was compensated for by the production of longer leaves (Fig. 2). After plants emerged, the length of the first shoot was independently affected by light level in the period of submergence and by tuber size (Table 1). In this period, shoots which had grown previously at 40%

Table 1. Submerged and emerged period: *F*-values and significances of an ANOVA of newly produced dry matter, shoot morphology and reserve carbohydrates (absolute and as a percentage of dry weight) in the tubers of *S. maritimus* grown under different light treatments and from small or large tubers. In the first 3 wk no below-ground parts were developed. (*df*-values in parentheses)

	df	Newly produced dry matter			Shoot morphology		Reserve carbohydrates	
		Total	Above-ground	Below-ground	Length first shoot	Leaf appearance rate	Carbo-hydrates (g)	Carbo-hydrates (%)
Submerged								
Block	3 (3)	0.9 ns	0.9 ns	1.5 ns	0.4 ns	1.0 ns	1.3 ns	1.1 ns
Time (t)	8 (5)	287.2***	251.5***	56.3***	506.4***	7.2**	22.2***	35.7***
Light (l)	3 (3)	18.2***	13.7***	44.5***	2.4 ns	4.8**	0.5 ns	1.1 ns
Size (s)	1 (1)	9.6**	12.7**	10.2**	0.1 ns	0.1 ns	114.1***	23.5***
t × l	24 (15)	1.5 ns	1.3 ns	6.2***	0.9 ns	0.9 ns	1.2 ns	1.5 ns
t × s	8 (5)	1.8 ns	1.7 ns	2.5**	0.7 ns	1.1 ns	0.2 ns	0.6 ns
l × s	3 (3)	1.4 ns	1.3 ns	0.1 ns	0.5 ns	0.6 ns	0.4 ns	0.2 ns
t × l × s	24 (15)	2.1**	2.0**	1.6*	1.2 ns	1.0 ns	0.4 ns	0.7 ns
Error (MS)		191 (0.44)	191 (0.44)	128 (0.61)	191 (0.40)	191 (0.03)	181 (0.28)	181 (0.01)
Emerged								
Block	3	0.0 ns	0.0 ns	0.5 ns	2.3 ns	2.3 ns	1.0 ns	1.5 ns
Time (t)	2	43.2***	32.3***	41.4***	32.0***	14.3***	15.4***	30.8***
Light (l)	3	16.1***	8.3***	12.5***	8.1***	0.5 ns	0.5 ns	0.5 ns
Size (s)	1	66.9**	53.3***	35.9***	5.9*	10.8**	88.9***	39.5***
t × l	6	0.8 ns	0.5 ns	1.1 ns	1.5 ns	1.1 ns	0.4 ns	1.0 ns
t × s	2	1.7 ns	1.7 ns	0.9 ns	2.1 ns	0.3 ns	0.6 ns	0.7 ns
l × s	3	1.4 ns	0.2 ns	2.4 ns	1.4 ns	0.6 ns	1.8 ns	1.2 ns
t × l × s	6	1.3 ns	0.8 ns	1.3 ns	0.9 ns	1.0 ns	1.1 ns	1.4 ns
Error (MS)		55 (0.10)	55 (0.12)	55 (0.24)	55 (0.24)	63 (0.03)	59 (0.25)	59 (0.004)

Data of weights were \log_e -transformed, lengths were sqrt-transformed, and ratios arcs sqrt-transformed prior to analysis. ns = not significant; * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ in this and subsequent tables.

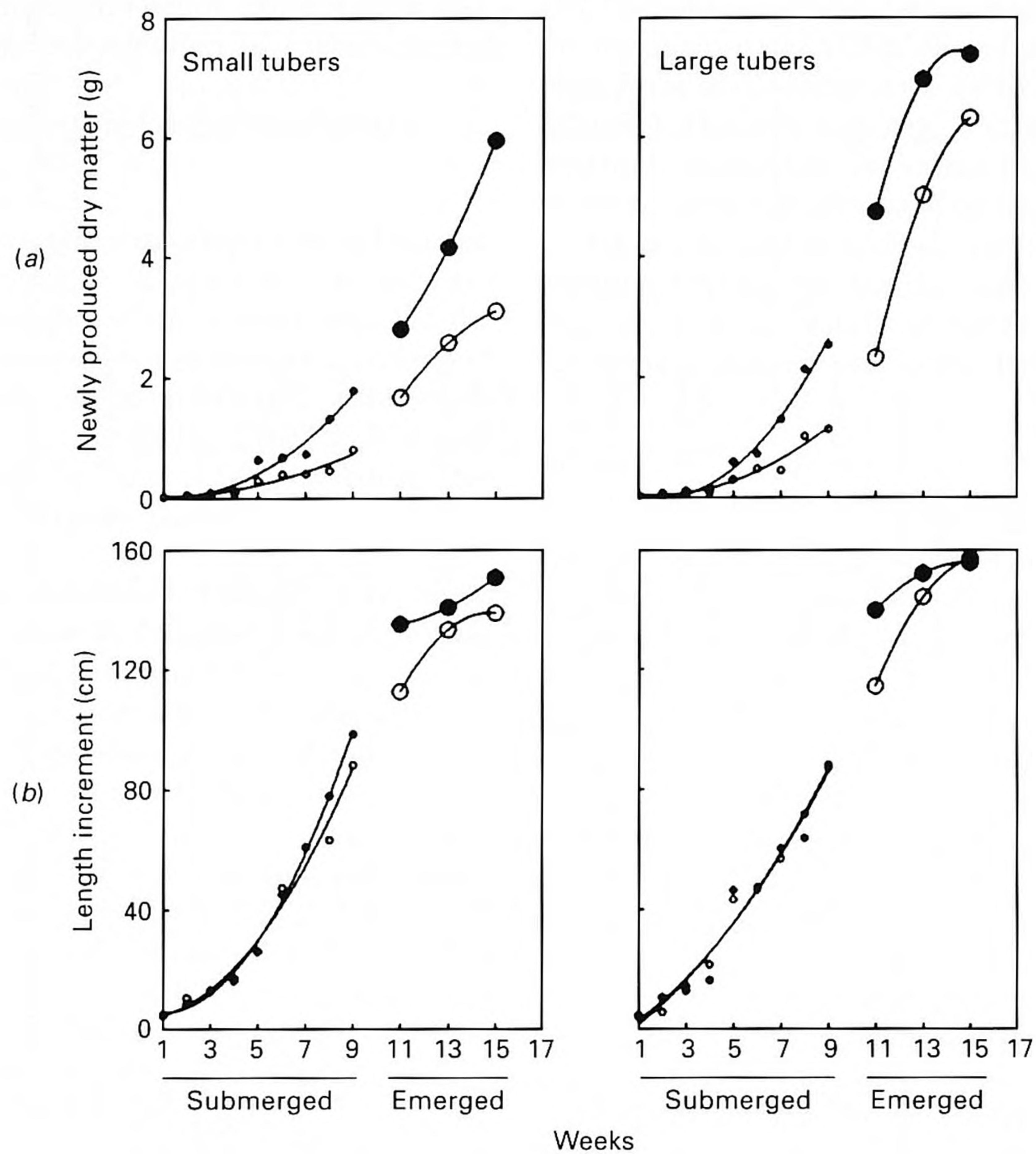


Figure 1. Submerged and emerged period: (a) Newly produced dry matter and (b) length increment of *S. maritimus* grown from small and large tubers in full daylight (●) or darkness (○). Data of the submerged period (small dots) were fitted using second-degree polynomials. Emerged period: Large dots ($n = 4$).

Table 2. Submerged, photosynthetic period: *F*-values of ANOVA and means of RGRs (d^{-1}) of the whole plant, and of the above- and below-ground parts, respectively

	df	Total	Above-ground	Below-ground
Block	3	0.0 ns	0.1 ns	3.9*
Light (l)	3	4.1*	3.4*	25.2***
Size (s)	1	9.5**	9.5**	10.0**
l × s	4	0.4 ns	0.4 ns	0.3 ns
Error (MS)	24	2×10^{-4}	3×10^{-4}	2×10^{-6}
% of full daylight				
100		0.077 b	0.070 b	0.0078 c
70		0.070 b	0.065 b	0.0067 bc
40		0.075 b	0.073 b	0.0056 b
0		0.051 a	0.049 a	0.0023 a
Tuber size				
Small		0.056 a	0.055 a	0.0049 a
Large		0.077 b	0.072 b	0.0064 b

Significant differences are indicated with different letters ($P < 0.05$).

of full daylight were longer than those which had grown in darkness. The lengths of the shoots grown at 100 and 70% of full daylight were intermediate (Fig. 1b, for full daylight and darkness only). The leaf appearance rate remained unaffected by shading

(Table 1), whereas the length of leaves, which became full-grown after emergence, was shorter for plants grown in darkness than in full daylight or shade in the period of submergence (Fig. 2). The first shoot was shorter (Fig. 1b) with a slower rate of

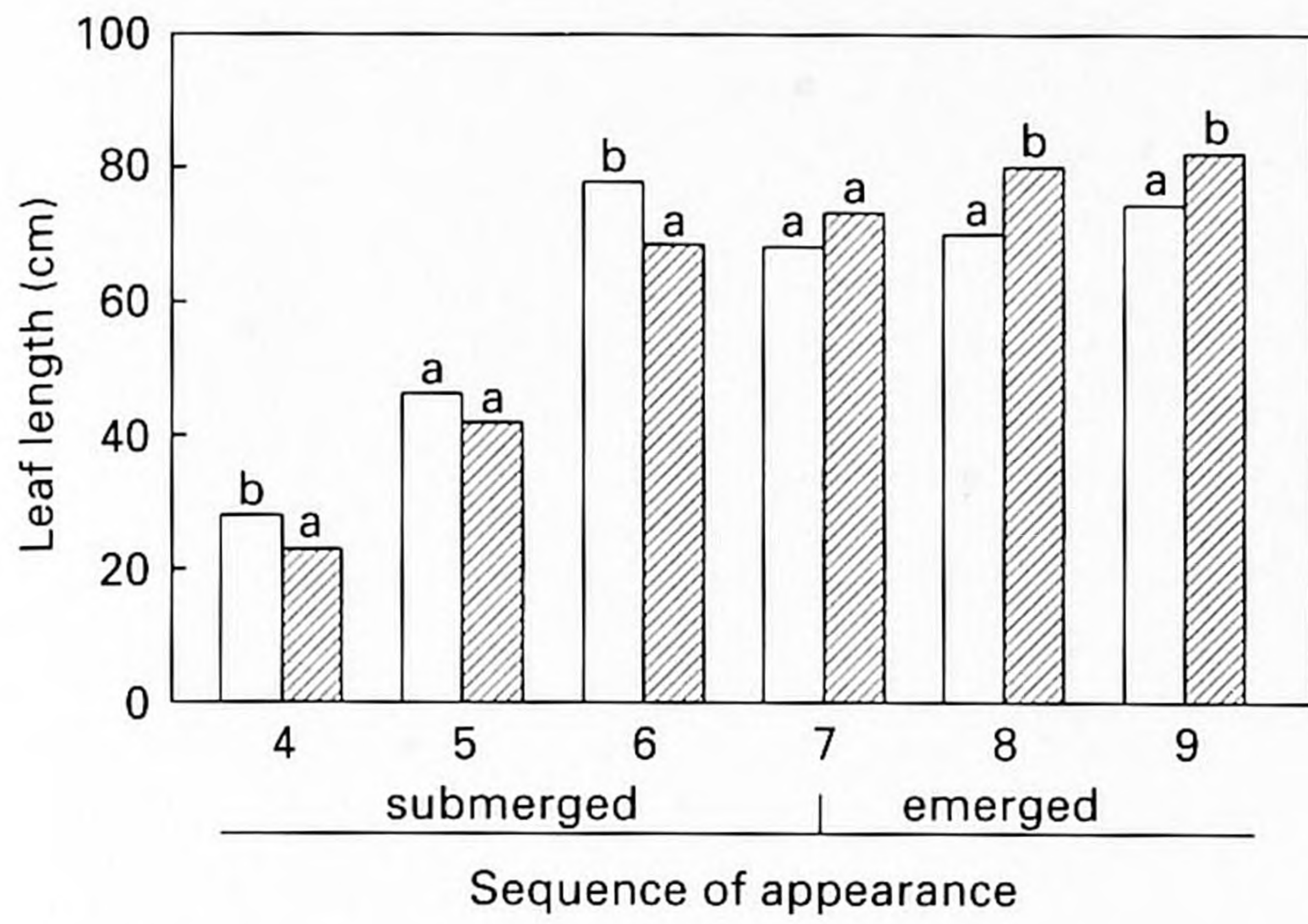


Figure 2. Submerged and emerged period: leaf length of full-grown leaves in full daylight (▨) and darkness (□). Data of these successive census dates and tuber size classes were pooled. Leaves 4, 5 and 6 were full-grown in the submerged period, leaf 7 during emerging and leaves 8, 9 and 10 in the emerged period. Significant differences between light treatments were calculated per leaf and are indicated with different letters ($P < 0.05$; $n = 24$).

leaf appearance (data not shown) when grown from small tubers than from large ones. In both periods tuber size had no effect on the length of full-grown leaves (data not shown).

Depletion of carbohydrates, conversion efficiency and maximum water depth

The relative depletion rate was unaffected by shading and tuber weight (Table 1). Partitioning the sum of squares for the factor time showed that the relative depletion rate was best described using a second-degree polynomial ($P < 0.01$); this indicated that the relative depletion rate increased with time. In both the submerged and emerged period the absolute as well as the relative (% of d. wt) carbohydrate content

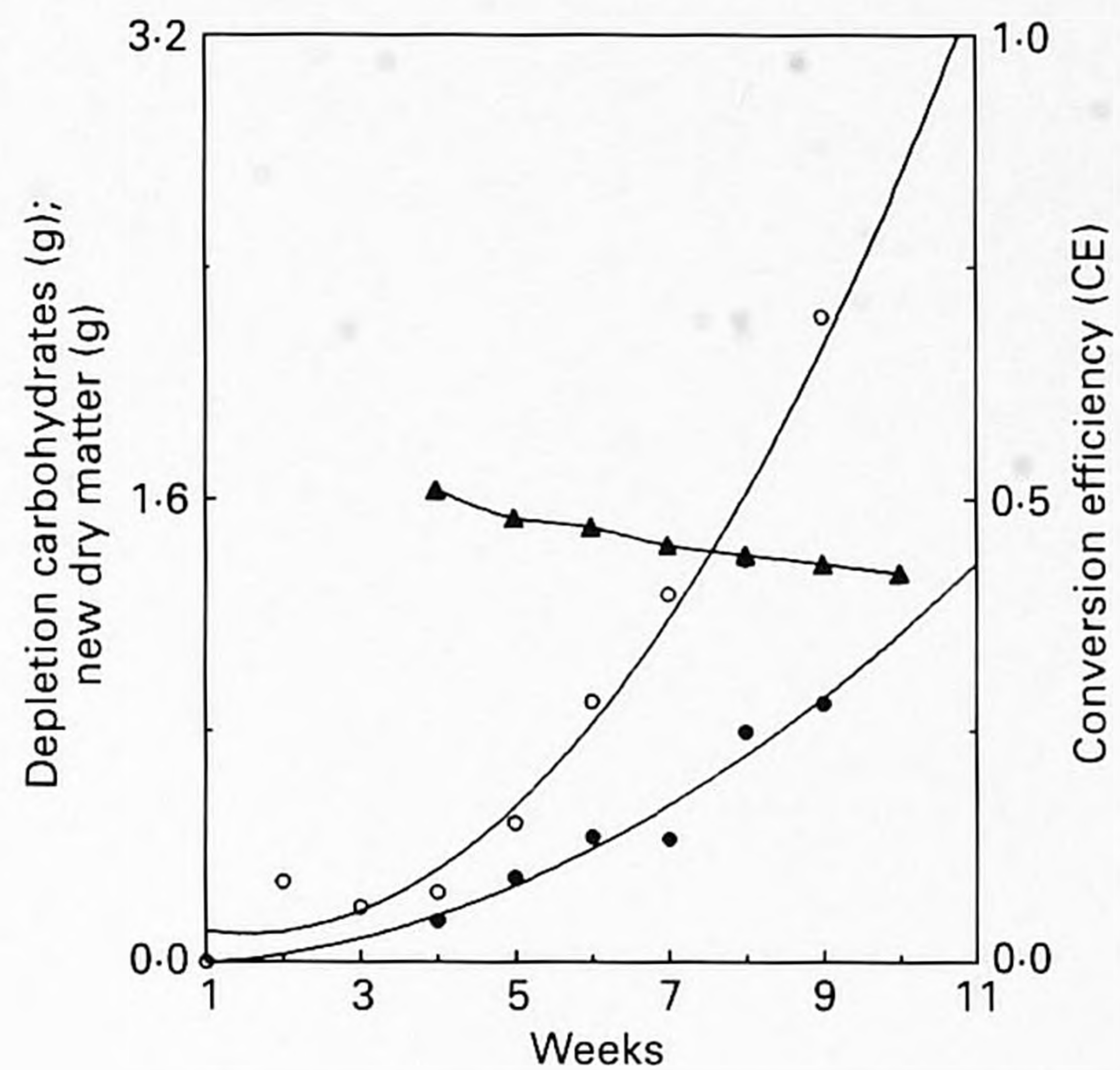


Figure 4. Submerged, photosynthetic period: relationship between carbohydrate use (○) and newly produced dry matter (●) of plants grown in darkness ($n = 8$). Data of dry weights were fitted using a second-degree polynomial. The conversion efficiency (CE, ▲) is given as the ratio newly formed dry matter/used carbohydrates. (The values at the time of zero carbohydrates were extrapolated.)

of the tubers remained unaffected by shading, whereas both were higher in larger than in small tubers (Table 1; Fig. 3). After emerging, carbohydrates were replenished, owing to the translocation of newly produced photosynthates.

Extrapolating the curves of reserve carbohydrates to the time of zero reserves resulted in a time of 71 and 78 d for small and large tubers, respectively. These values were, however, not significantly different (t -test; $df 1,30$; $F = 0.35$), and therefore data on tuber depletion of small and large tubers were pooled in order to calculate the efficiency of the conversion of carbohydrates and the maximum depth of water at which shoots can emerge.

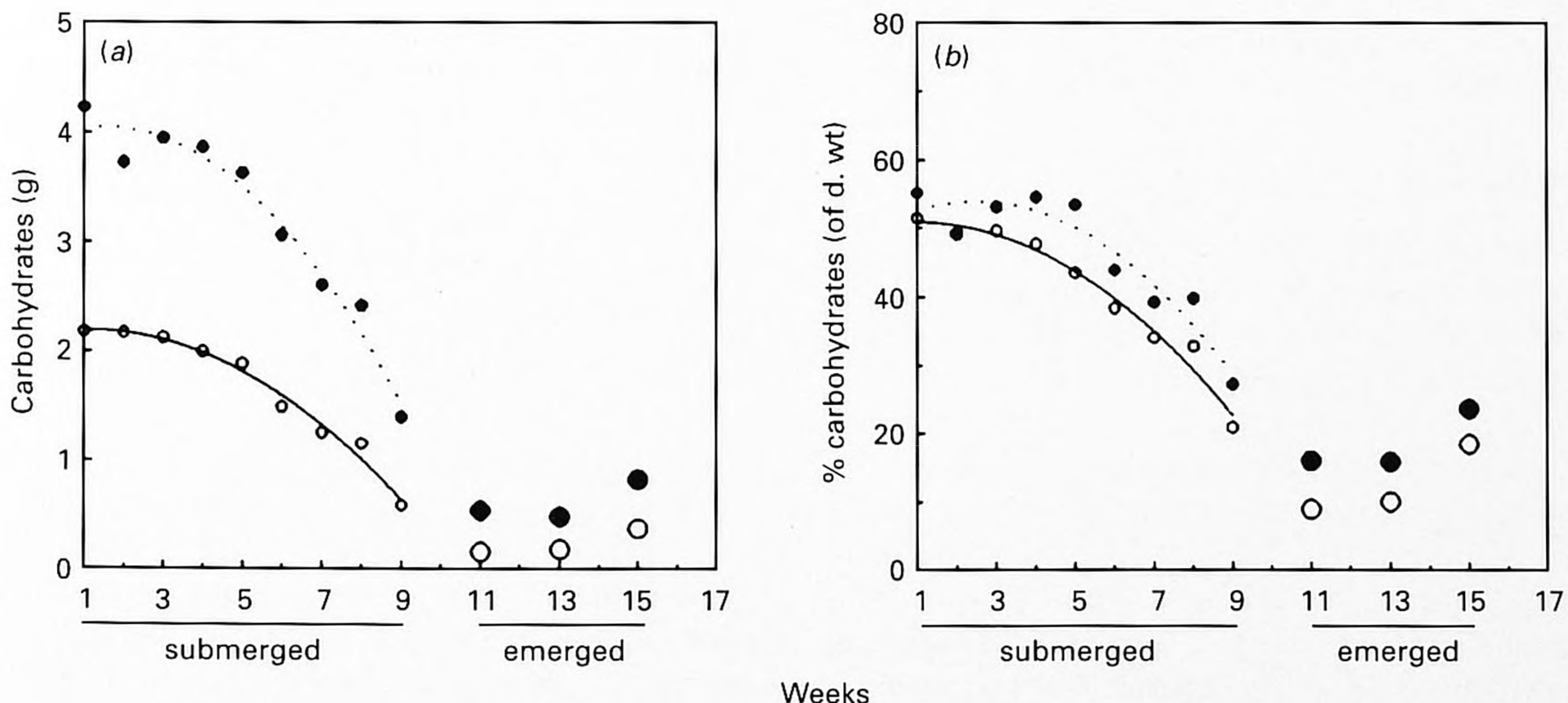


Figure 3. Submerged and emerged period: (a) Absolute amount of reserve carbohydrates and (b) relative amount of carbohydrates (% of d. wt) of small (○) and large (●) tubers pooled for the four light treatments ($n = 16$). Data of the submerged period (small dots) were fitted using second-degree polynomials.

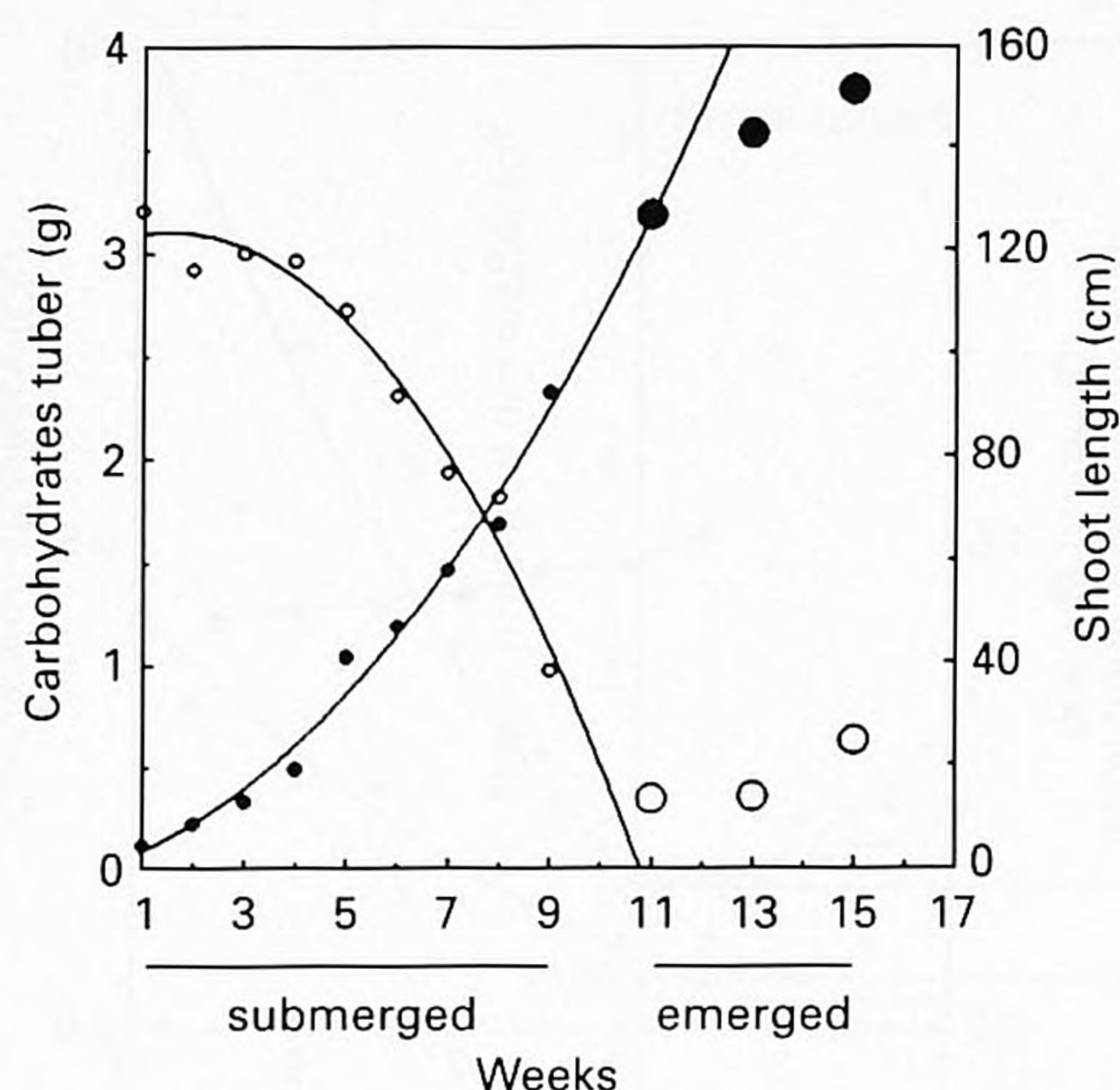


Figure 5. Submerged and emerged period: amount of reserve carbohydrates (g; ○) and length increment of the first shoot ($n = 32$; ●). A polynomial of the second degree was fitted to the data obtained from the submerged period. Submerged period, small dots; emerged period, large dots.

Table 3. *F*-values of an ANOVA on photosynthesis in control and flooded shoots of *S. maritimus*

	df	<i>F</i> -values
Flooding (f)	1,4	12.7*
Light (l)	6,24	149.8***
f × l	6,24	4.3**

Light treatments were used as a within-shoot repeated factor. Light treatments with missing values were omitted from the analysis.

The conversion efficiency (CE) of carbohydrates into newly produced dry matter of plants grown in darkness was only calculated for the last 5 wk of the submerged period, because of the high variance in the amount of carbohydrates present in the first weeks (Fig. 4). The CE-value declined slowly in time, with a mean value of 0.47.

The shoot length at the time of zero carbohydrates was calculated to be about 120 cm (Fig. 5).

Photosynthesis

Flooding shoots. The light-response curves of control and flooded shoots differed significantly (Table 3) and are shown in Figure 6. The values of gross photosynthesis (P_{\max}) were higher in flooded than in control shoots (t -test; df 1,4; $F = 16.2$; $P < 0.05$), indicating that O_2 was stored and/or recycled in the control plants. The Michaelis-Menten constant (K_m), dark-respiration (R) and the light compensation point (LCP) did not differ significantly between control and flooded shoots, although the mean R and K_m -values tended to be higher in flooded than in control shoots (Fig. 6). At the end of the experiment the storage of O_2 in the lacunae of the flooded plants was checked by placing the shoots

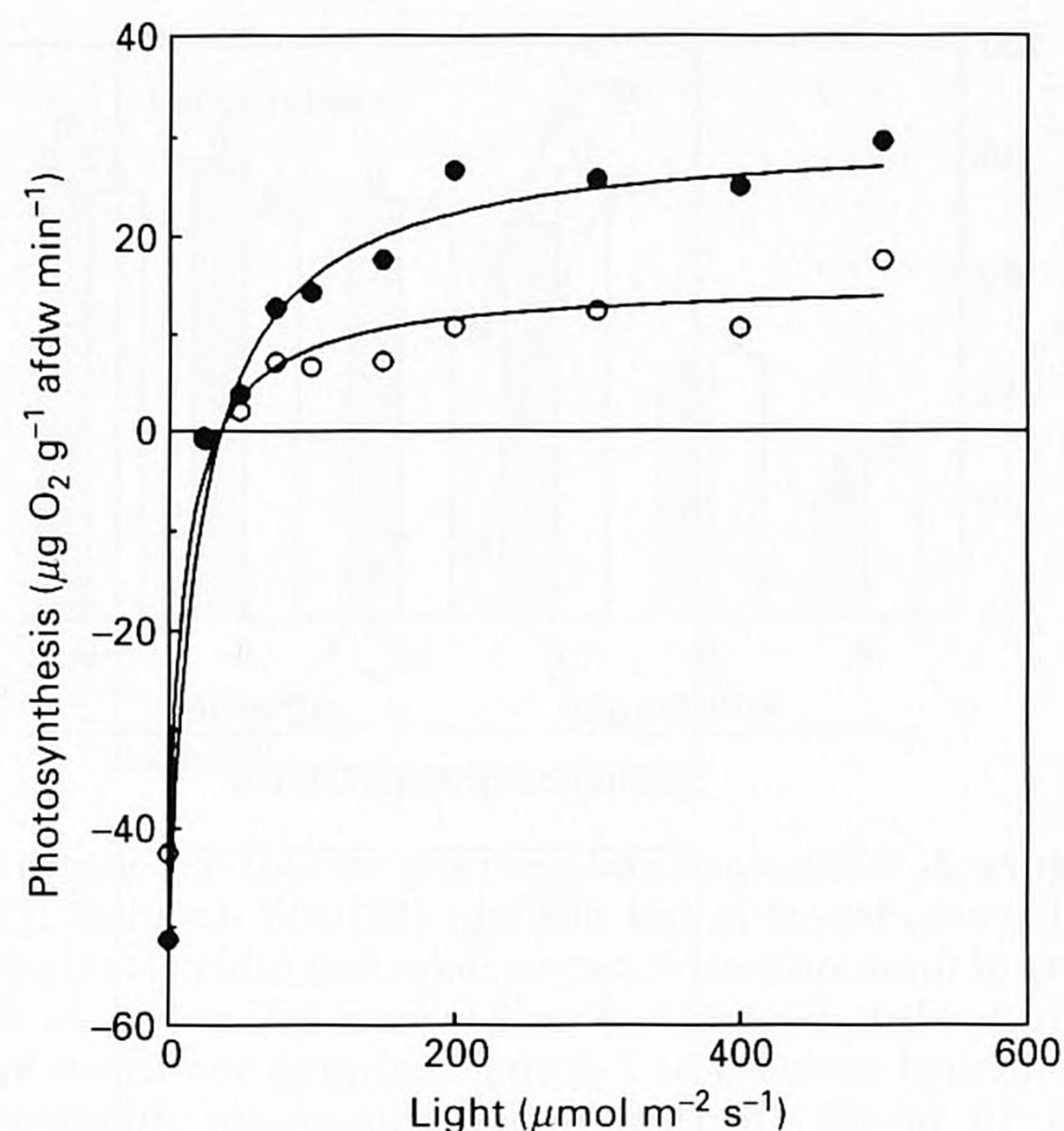


Figure 6. Light response curves of control (○) and flooded (●) shoots of *S. maritimus*.

again under low pressure. Only tiny bubbles were released from the shoots, indicating that the lacunae were only slightly refilled with O_2 .

Pond experiment. Photosynthesis was measured in flooded shoots. Values of P_{\max} as well as R decreased with increasing age of the shoots (Table 4). The P_{\max} was not affected by light level, but R was higher in shoots grown in darkness than in full daylight or shade. The net photosynthesis of plants grown in darkness remained negative. In week 5, K_m of plants grown in darkness was lower than in the other treatments, resulting in a significant interaction between time and light level. The LCP, only calculated for plants grown in full daylight or shade, did not differ between treatments (Table 4).

During the photosynthetic period, plants in full daylight had a positive net photosynthesis rate of 6.2 during 13 h, plants in 70% of full daylight of 8.6 during 12 h and plants in 40% of full daylight of 5.4 $\mu g O_2 g^{-1} min^{-1}$ during 11 h (Fig. 7).

DISCUSSION

Growth characteristics

Light availability did not affect the ability of *S. maritimus* to emerge from 90 cm deep water, although after a period of 9 wk of submerged growth, shoots grown in full daylight and shade (70 and 40% of full daylight) were twice as heavy, with a greater rate of leaf appearance, and shorter leaves than those grown in darkness. In response to light exposure the etiolated shoots grown previously in darkness increased their dry weight/length ratio, resulting in a retarded length increment compared to those grown in full daylight or shade.

Table 4. Submerged, photosynthetic period: *F*-values of ANOVA and means of p_{\max} (maximum rate of gross photosynthesis), *R* (respiration), K_m (the Michaelis-Menten constant) and LCP (light compensation point)

	df	P_{\max}	<i>R</i>	K_m	df	LCP
Time (t)	2	18.9***	19.2***	5.7**	2	1.2 ns
Light (l)	3	1.3 ns	8.0***	3.1*	2	1.2 ns
t × l	6	0.5 ns	0.2 ns	3.0*	4	0.2 ns
Error (MS)	22	0.05	0.057	0.501	17	0.24
		$\mu\text{g O}_2 \text{ g}^{-1} \text{ afdw min}^{-1}$		$\mu\text{mol m}^{-2} \text{ s}^{-1}$		
Time						
week 5		54.2 b	49.2 c	20.2 a		127.9 a
week 7		48.2 b	40.5 b	31.1 b		90.3 a
week 9		32.5 a	29.9 a	26.2 b		144.6 a
% of full daylight						
100		40.8 a	32.8 a	22.9 ab		125.4 a
70		49.0 a	37.7 a	30.2 b		90.8 a
40		46.0 a	36.5 a	30.8 b		146.7 a
0		44.0 a	52.4 b	19.6 a		

Data were \log_e transformed prior to analysis. Differences among means are indicated with different letters ($P < 0.05$). (The untransformed data are shown.) LCP could not be calculated for plants grown in darkness. (The significant interaction of K_m originated from a different K_m value of plants grown in darkness measured in week 5 compared to all other treatments.)

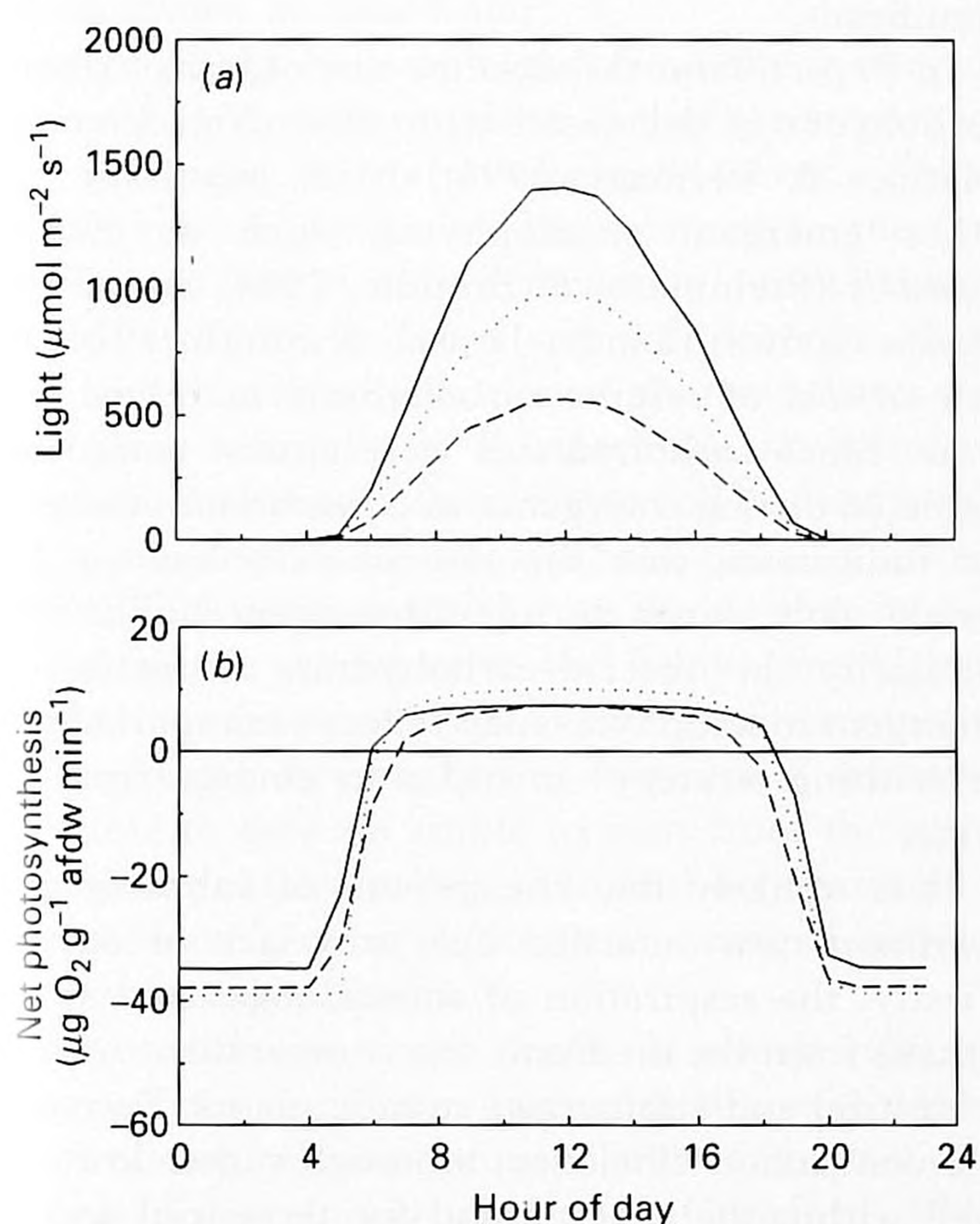


Figure 7. Submerged, photosynthetic period: (a) Mean hourly irradiance and (b) calculated net photosynthesis of plants at 100 (—), 70 (····) and 40 (---) % of full daylight in the photosynthetic period.

Also tuber size did not affect the ability of plants to emerge from 90 cm deep water, although during the period of submerged growth plants from large tubers produced 1.6 times more dry matter than those from small ones, which was allocated in similar proportions to the different plant parts. These differences in dry matter production were more or

less of the same magnitude as the initial differences in tuber dry weight. Only in the emergent period, when small tubers were almost completely depleted of carbohydrate, were length increments of shoots lower in plants from small than from large tubers. In this period plants from small tubers allocated relatively more biomass to the first shoot than to secondary shoots as compared to plants grown from large tubers. Abortion of secondary shoots in deep water as reported by Lieffers & Shay (1981) did not occur in the present study.

The calculated maximum water depth of 120 cm from which *S. maritimus* can emerge using only reserve carbohydrates is higher than the maximum water depth of 80–90 cm mentioned in Dykyjová (1986), but corresponds with the water depth the species was just able to reach in outdoor basins (Coops & Smit, 1991). It is likely that under field conditions, depending on the burial depth and occurrence of anaerobiosis in the soil, the maximum water depth will be less, as carbohydrates might be partly used for emergence from the soil as well. In these studies as well as in ours the submerged leaves of *S. maritimus* turned yellow as soon as the shoots emerged above the water. The loss of submerged leaves might be functional, as it might be expected that the photosynthesis of emerged leaves is much higher. Submerged leaves would increase the total respiration, while contributing relatively little to photosynthesis.

Photosynthesis

The control shoots of *S. maritimus* probably accumulated O_2 in the lacunae, resulting in an

underestimation of gross photosynthesis (P_{\max}). Similar results were found in *Egeria densa* (Sorrell & Dromgoole, 1986). Although plants were measured at a relatively low temperature of 20 °C, high concentrations of oxygen might have accumulated in the control plants, leading to an increase in photorespiration with time (Hartman & Brown, 1967; Søndergaard, 1979; Pokorný & Ondok, 1991). In this study no evidence for photorespiration has been found, as no decline in net photosynthesis of control and flooded shoots was found during the photosynthesis measurements.

Photosynthesis of *S. maritimus* was measured at pH 8.2, which might have been suboptimal, as the concentration of free- CO_2 decreases with increasing pH (Sand-Jensen, 1983; Bowes, 1987; Boston, Adams & Madsen, 1989). This pH, however, corresponds well with that of the field situation (De Lyon & Roelofs, 1986; J. E. Vermaat, unpublished). According to Beer *et al.* (1991), *Scirpus lacustris* L., closely related to *S. maritimus*, is unable to use HCO_3^- , and Sand-Jensen, Pedersen & Nielsen (1992) concluded that a number of emergent and amphibious plants were unable to use HCO_3^- as an alternative C-source. Therefore, it seems unlikely that *S. maritimus* can use HCO_3^- . Søndergaard (1979) and Salvucci & Bowes (1982) suggested that aerenchymatous species might increase the availability of CO_2 , by storing and re-fixing CO_2 , produced during photo- and dark-respiration, in the lacunae.

The mean net photosynthesis of $9.6 \mu\text{g O}_2 \text{ g}^{-1} \text{ d.wt min}^{-1}$ ($0.51 \text{ mg O}_2 \text{ g}^{-1} \text{ d.wt h}^{-1}$) of plants grown in light at 15 °C and pH 8.2 is about 15 to 60 times lower than that of the relatively thin leaves of submerged aquatic plants, but lies well within the range found for submerged terrestrial and amphibious species (Nielsen & Sand-Jensen, 1989; Sand-Jensen *et al.*, 1992). In air the net photosynthesis of emergent macrophytes is 10 to 30 times higher (McNaughton, 1973) than our values for submerged *S. maritimus*.

The mean respiration rate of *S. maritimus* grown in full daylight or shade (40 or 70 % of full daylight) was within the range of respiration rates found for different submerged species (Nielsen & Sand-Jensen, 1989). Generally, photosynthesis characteristics of leaves of submerged plants resemble those of shade leaves of terrestrial plants, i.e. a low P_{\max} , a low LCP ($< 60 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and a low K_m (Björkman & Holmgren, 1963; Sand-Jensen, 1983; Bowes & Salvucci, 1989). In the present study the K_m values are low and the LCP high as compared to those of submerged macrophytes (Hootsmans & Vermaat, 1994). The high respiration rate of plants grown in darkness is difficult to explain, especially because the tuber depletion rate did not differ between light treatments.

Owing to the low light saturation point of submerged *S. maritimus* shoots, no differences in the

mean daily net photosynthesis of plants grown in 100 and 70 % of full daylight were apparent. Differences were larger when compared with plants grown in 40 % of full daylight; however, they were not reflected in differences in dry matter gain.

Utilization of carbohydrates

In the submerged macrophyte *Potamogeton pectinatus* L. it has been found that tuber depletion was also independent of shading. In this species, however, the relative depletion rate was higher in small tubers than in large ones (Vermaat & Hootsmans, 1994). In both *P. pectinatus* and *S. maritimus* the relative reserve-carbohydrate content (% of d. wt) was higher in large than in small tubers, probably because of differences in the volume to surface ratio. Since in *S. maritimus* the relative depletion rates were unaffected by tuber size, it might be expected that large tubers are depleted later in time than small ones. Probably, owing to relatively small differences in tuber sizes and a high variation in time of zero-carbohydrates between replicate measurements this was, however, not significant.

In *P. pectinatus* the absolute rate of loss of reserve carbohydrates decreased with time (Van Vierssen, Mathies & Vermaat, 1994). In *S. maritimus* and other emergent macrophytes, such as *Scirpus lacustris* (Steinmann & Brändle, 1984) and *Typha glauca* Godron (Linde, Janisch & Smith, 1976) the rate of loss of reserve carbohydrate increased with time. Since carbohydrates were almost completely depleted during emergence in *S. maritimus*, there are no indications that the rate of carbohydrate loss would slow down during submergence. The high similarity in reserve-carbohydrate depletion of emergent macrophytes may reflect a comparable 'all or nothing strategy' in order to emerge from the water.

It is unlikely that the growth of submerged *S. maritimus* was retarded due to a lack of oxygen. Firstly, the respiration of shoots, measured as O_2 -uptake from the medium, was comparable to that of terrestrial and submerged aquatic plants. Secondly, the conversion efficiency, although rather low, was well within the range found for terrestrial and for emergent species growing in shallow waters (Van Keulen, 1976; Fiala, 1978; Grace & Wetzel, 1982; Granéli, Sytsma & Weisner, 1983; Lambers & Rychter, 1990).

The utilization of photosynthates had a considerable impact on growth. The observed difference in RGR between plants in full daylight or shade and darkness was 0.018 d^{-1} . Once tubers are depleted *S. maritimus* plants might be just able to survive under water, without showing any significant length increment, if a maintenance respiration of 0.011 d^{-1} of the newly produced dry matter at 15 °C (Penning de

Vries, 1983) is assumed to occur and if the proportion of non-photosynthetic tissue is not too high. Eventually however, mortality will occur, because the rate of underwater photosynthesis will decrease with increasing plant age (Hootsmans & Vermaat, 1994).

Ecological implications

In early spring, *S. maritimus*, like other emergent species grows to get access to air as soon as possible. In darkness shoots are etiolated and biomass production rather than the shoot length is reduced in response to low carbohydrate availability. Etiolation might have adverse side effects, like reduced mechanical strength and increased vulnerability to infection (Grime, 1966). In a greenhouse experiment (at 22 °C) *S. maritimus* grown in darkness became infected by *Pseudomonas* species at the shoot-base. As a consequence shoots died off (O. A. Clevering, unpublished). This was not the case with plants grown in light. In the field shoots infected by *Pseudomonas* species were also found and in the spring plants growing in turbid water might be more susceptible to wave action and diseases than are plants grown in clear water.

After plants have emerged from the water, the submerged leaves turn yellow so that photosynthates are produced only by emerged leaves. *Scirpus maritimus* is, however, unable to increase the total number of leaves before flowering (unpublished). The photosynthetic active area will decrease, therefore, and thus the production of photosynthates with increasing water depth. Furthermore, an increasing proportion of the photosynthates will be used for the maintenance of non-photosynthetic tissue. Yamasaki (1984) and Weisner (1988) concluded that in deep water oxygen transport to the below-ground parts might limit the occurrence of emergent macrophytes in deep water. In early spring, however, *S. maritimus* was able to take up ample oxygen from the water. The ability to take up oxygen from the water might be lost, however, once plants have emerged and lost their submerged leaves.

The maximum water depth, at which emergent macrophytes occur at a particular site, will depend on physiological adaptations, like the conservation of carbohydrates during winter (cf. Crawford, 1992), spring sprouting (this study) and the efficiency of oxygen transport to, and utilization of oxygen by, roots, and the storage of carbohydrates during summer (Weisner, 1988; Granéli, Weisner & Sytsma, 1992). However, morphological adaptations might be important as well. Although *S. maritimus* is well adapted to overwintering in anaerobic mud and shows submerged shoot growth without the provision of oxygen by overwintering dead shoots, the species occurs in shallower water than *Phragmites australis* (Cav.) Trin. ex Steudel (Haslam, 1972), *Scirpus lacustris* (Seidel, 1955) and *Typha*

angustifolia (Grace & Wetzel, 1982), which show less or similar physiological adaptations (Crawford, 1992). These latter species might form longer shoots and may be better able to elongate shoots in response to submergence. Therefore, *Scirpus maritimus* seems to be adapted to periods of oxygen deprivation rather than to growth in deeper water.

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