

Seasonal growth of the submerged macrophyte *Ceratophyllum demersum* L. in mesotrophic Lake Vechten in relation to insolation, temperature and reserve carbohydrates

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Abstract

Seasonal growth of a *Ceratophyllum demersum* stand in Lake Vechten, The Netherlands, varied considerably during 1978, '79 and '81. The biomass was highest in 1981 (max. 115 g ash-free dry weight m⁻²). The 1978 growth trend was similar to that of 1981 with slightly lower net annual production (max. 92 g AFDW m⁻²). The vegetation almost disappeared in 1979 (max. 24 g AFDW m⁻²). These large differences in biomass could not be explained by differences in insolation but were mainly attributed to the severe winter of 1978–'79 which slowed plant development and full maturity was attained only after the diurnal insolation had decreased.

Reserve carbohydrates were primarily starch and water-soluble sugars. Starch concentrations varied between 71.5 and 24.7 mg g⁻¹ AFDW in the winter and summer, and total sugar concentrations between 24.9 and 20.2 mg g⁻¹ AFDW, respectively. The non-reducing sugars tended to predominate in summer and the reducing sugars in winter. The value of these reserves for maintenance, growth and survival was assessed by calculating plant carbon budgets for several seasons.

It was concluded that *C. demersum* relies heavily on its developmental timing and energy-conserving physiological mechanisms to survive extended periods of stress and in these respects is analogous to a typical terrestrial shade plant.

Introduction

Ceratophyllum demersum L. is a cosmopolitan, submerged angiosperm, which grows in standing and slowly flowing fresh waters. It is usually attached to silted, muddy bottoms by leaves modified as rhizoids, but it may also occur free-floating (Sculthorpe, 1967a). This plant species has evolved

morphological and physiological characteristics suitable to its usual environment.

Under conditions where nutrients are readily available, such as in the meso- to eutrophic waters which comprise most Dutch surface waters, growth of submerged plants is likely to be limited by light, temperature or both (Barko & Smart, 1981; Best, 1981a). The light climate received by submerged

plants is similar to a terrestrial shade habitat when expressed in terms of radiant energy. However, light quality is heavily influenced by particles (dead or alive) within the water column and greatly affects plant growth (Kirk, 1983).

Plant growth is only possible when the energy fixed by photosynthesis exceeds the energy required to maintain the plant. The quantity of carbon fixed depends on environmental conditions such as the concentration of inorganic carbon and solar irradiation, and on plant specific factors such as photosynthetic capacity and age (Best & Meulemans, 1979). Part of the energy fixed by photosynthesis may be stored in different biochemical reservoirs, usually distributed over various plant organs, to sustain plants during periods of adverse environmental conditions. It may be expected that submerged angiosperms growing under conditions of low temperature and solar irradiation, which have virtually no underground organs for storage purposes, may benefit from energy-conserving mechanisms. For *C. demersum* these may be represented by the chemical nature of the carbohydrate storage substances (Best, 1977; Best & Visser, 1983; Janauer, 1981; Janauer, 1982) and the formation of hibernacula (Sculthorpe, 1967b).

In the present study the specific growth behaviour of a *Ceratophyllum demersum* L. stand over a three year period is described under the prevailing environmental conditions in a mesotrophic lake. The temporal changes in the carbohydrate storage substances (composition, concentration and distribution) were measured. The timing of changes in morphology, the biomass production and the use of storage substances are discussed in terms of survival value.

Materials and methods

Site description

All observations were made on stands of *Ceratophyllum demersum* L., attached to the sediment at 2–2.5 m depth in the meso- eutrophic Lake Vechten, The Netherlands. This lake originated from sand excavation in the early 1940's. The sur-

face area was 4.7 ha and the average and maximum depth 6.0 and 11.9 m, respectively. A general description of the lake and its macrophyte populations has been given by Best (1982).

Sampling of plant material

Standing crop. One plot (0.25 by 0.25 m) was harvested each time by SCUBA divers in the middle of the *C. demersum* vegetation, between 10.00 and 10.30 a.m. The size of the harvest was kept as small as possible to prevent damaging of the plant stands. Harvesting triplicate plots in August-September showed an S.D. of 17% in ash-free dry weight (AFDW) determinations. Plant material was sampled bimonthly from March to November in 1978. In 1979 the growth season was delayed because of the severe winter. Therefore the bimonthly samples were taken from the end of April until mid December. In 1981 a growth simulation model cf. Best (1981b) was employed as a conceptual aid. As a result the sampling frequency was increased from January to December. The standing crop was calculated from these harvests, expressed in g AFDW m⁻².

Individual plants. Three individual plants were harvested, between 10.00 and 10.30 a.m. at each sampling. In 1978 these plants had been marked with metal tags *in situ* in March, and the biomass above the tag was determined every three weeks during the remainder of the year. This method was used to avoid confusion about age differences (Best, 1981c). The individual plant biomass was not recorded in 1980. In 1981 biomass of non-tagged plants was measured at times indicated by a growth simulation model.

The plant density (number of plants m⁻²) was determined in 1978 by dividing the values on standing crop by those of the individual plant weights. In 1979 it was determined by dividing the values on standing crop by the average of the individual plant weights in 1978 and 1981. In 1981 the number m⁻² was actually counted when the individual plants were sampled (three plots of 0.25 by 0.25 m).

After harvesting, the fresh plant material was transported to the laboratory in plastic bags placed

in vessels containing lake water. The plant material and periphyton were separated after cutting the macrophyte into sections. A vibromixer (Chemap, Zürich) was used, if necessary. In 1978 carbonate encrustations were dissociated by lowering the pH of the water with 0.1 N HCl to 5 (Gons, 1982). The macrophyte was rinsed with water of neutral pH after this treatment. However, the lowering of the pH caused carbohydrate leakage and therefore macrophyte and periphyton were separated at ambient pH in the samples of 1979 and '81. The macrophyte material was clipped into small pieces with scissors, rapidly frozen in liquid nitrogen and freeze-dried.

Measurements of solar irradiation and water temperature

Data on irradiation were used from the De Bilt weather station, located at a distance of 4 km of Lake Vechten. Only the photosynthetically active radiation (PAR; 400–700 nm) was taken into account. The vertical extinction coefficient of the lake water was measured biweekly at 11.00 a.m. using a Licor model Li-185 A radiometer with a submersible cell. The irradiation at 1 m depth, the

depth where the plant apices occurred in summer, was calculated using the formula: $I_{(z)} = I_{(0)} \times e^{-1z}$, where $I_{(z)}$ is the irradiation at depth z , $I_{(0)}$ is the irradiation at the water surface, 1 is the extinction coefficient per m depth and z the depth in m (Wetzel, 1975).

The temperature of the lake water was recorded biweekly at 11.00 a.m.

Development state

The development state of *C. demersum* was described in terms of extension rate, specific leaf area (concerning branching and leaf expansion) and photosynthetic capacity (Best & Meulemans, 1979). Eighteen developmental stages were distinguished based on field observations made in 1978, which are described in detail elsewhere (Best & Dassen, 1987b). According to this description the plants were nearing full development and close to having their maximum photosynthetic capacity at day 180 (Fig. 1).

For comparison of the developmental rates in the various years the development process was made independent of calendar time by relating it to temper-

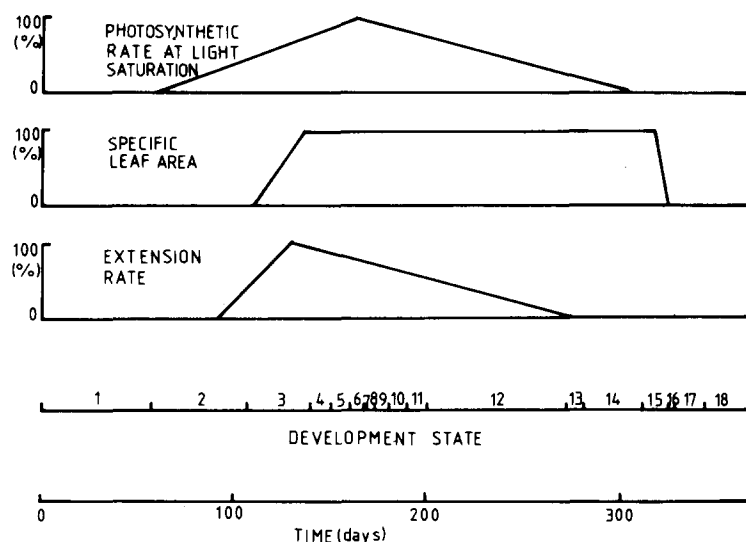


Fig. 1. Stylized representation of the timing of the various phases of development state and the morphogenetical and physiological characteristics of *C. demersum*. The morphogenetical (extension, expansion of photosynthetic area) and physiological (photosynthetic capacity) data were collected from a *C. demersum* stand in Lake Vechten, in 1978.

ature. The temperature was expressed for this purpose in degree days, calculated as the sum of the daily temperature (average of the 0–2.5 m depth water layer in Lake Vechten) decreased with a base temperature of 3°C. Base temperatures of 4 and 5°C were tried also, but 3°C resulted in the most regular curve. This description of development process is commonly used for summer crops by crop physiologists (Hesketh *et al.*, 1980).

Chemical analyses

The dry plant material in liquid nitrogen was ground into a fine powder with a JKA mill (Janke & Kunkel, Stauffen, West Germany). The ash free dry weight content of a portion of the powder was determined after combustion at 550°C.

Carbohydrates were determined in plants harvested in 1981. The plants from stands higher than 0.5 m were divided into 0.5 m apical and subsequent 0.1 m sections after transporting them to the laboratory. This was done because in growing *C. demersum* stands the individual plants started to shade each other from a height of 0.5 m onwards and therefore it was expected that the carbohydrates were more or less homogeneously distributed over the well-lit plant parts, but that shading would affect the carbohydrate distribution. Starch was measured in duplicate in perchloric acid extracts of the plant material (Hewitt, 1958).

The soluble sugars were determined in plants harvested from Lake Vechten using enzymatic techniques (Bergmeyer, 1970). A hot water (40°C) extract was prepared from 100 mg dry plant material (3 successive extractions with 4 ml water, 15 min in an ultrasonic vibration bath). The fats and remaining particles were removed by filtration over a paper filter. Subsequently, the proteins were removed by diluting the aqueous extract with an equal volume of 1 M perchloric acid, centrifuging at 500 G and discarding the pellet. The supernatant was cooled in ice and neutralized with 2 N KOH. The KClO₄ precipitate which formed was sedimented by centrifugation at 500 G and removed. Glucose and fructose were determined successively in the same enzymatic assay in aliquots of

this extract. Sucrose was assayed separately using Bergmeyers' method as described by Boehringer. The enzymatic assays were performed in duplicate. Variation between replicate extracts was always less than 10%. The analytical precision, replicate enzymatic assays of the same extract, was 3%.

The total soluble sugars were determined in *C. demersum* plants harvested from an outdoor pond in the Limnological Institute's garden in winter (February) and in summer (July) at 10.00 a.m. The sugars of these samples were extracted as described above and determined using GLC according to Best & Dassen (1987a).

Results

Life history and phenology

C. demersum, an evergreen perennial, occurred in distinct stands in Lake Vechten. The presence of this plant species in this lake has been documented from 1972 onwards. In the period of observation it did not flower but perennated by dormant buds and propagated vegetatively.

C. demersum is a herbaceous plant. In winter its shoots varied from 6 cm long, dormant, apices with tightly clustered leaves, to meters long vestiges of the previous seasons' growth which usually largely decayed during winter. In summer the species achieved lengths of up to 2.5 m (at 3.5 m rooting depth), consisted of 0 to 8 cm long internodes and whorls of twofold bifurcated, leathery leaves. The plants were multi-branched and tended to concentrate most biomass in the upper 0.4 to 0.5 m of their length.

Biomass and plant density

The standing crop of the stand varied greatly between the years studied (Fig. 2A). It was highest in 1981 and showed a similar seasonal trend although somewhat lower mass in 1978. The standing crop varied from 40 to 115 g AFDW m⁻² in 1981 and from 25 to 92 g AFDW m⁻² in 1978. In 1979 the vegetation had almost disappeared and biomass

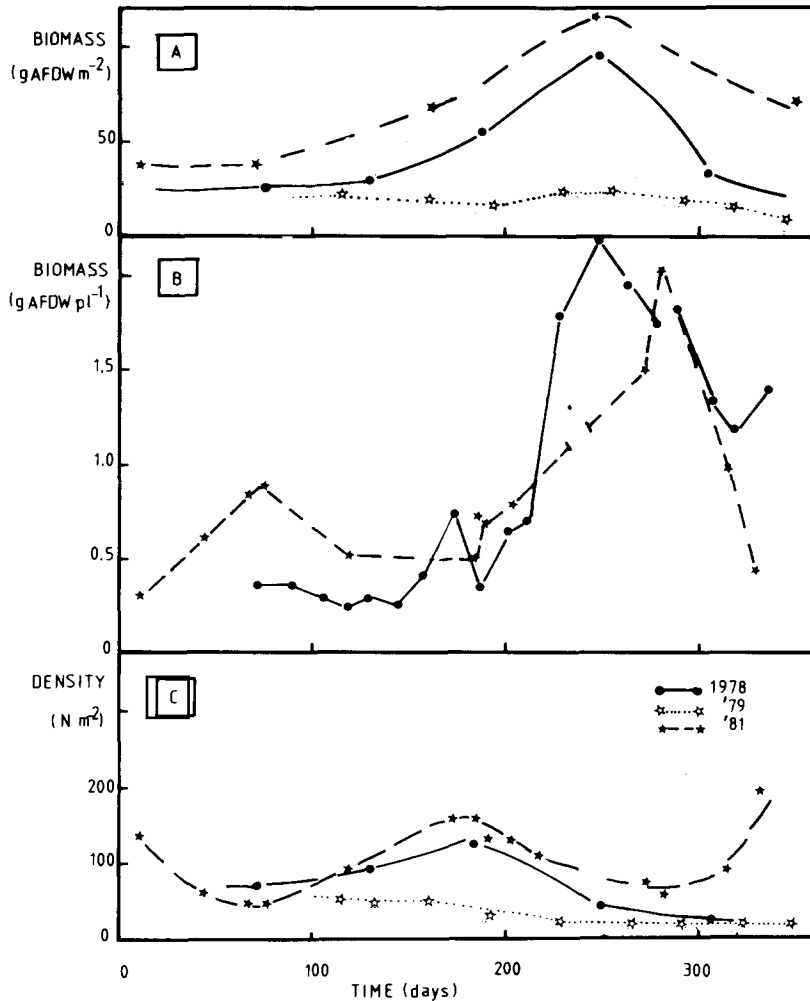


Fig. 2. Temporal changes in biomass of *C. demersum* in Lake Vechten, during 1978, '79 and '81. A: standing crop; B: weight of individual plants (averages of 3 determinations; no record of '79); C: plant density.

varied from 10 to 24 g AFDW m⁻².

The individual plants showed similar growth curves in 1978 and 1981, with most rapid growth occurring in the period between day 230 and 290 and slowest from day 0 to 170 (Fig. 2B). Individual plants were heavier during the first half of 1981 than in the same period of 1978 (Fig. 2B). The weights ranged from 0.24 to 2.18 g AFDW plant⁻¹ in 1978 and from 0.29 to 2.01 g AFDW plant⁻¹ in 1981. The weights of the individual plants were not recorded in 1979.

The plant density varied during the growth season of 1978 (day 150 to 300; Fig. 2C) between 12

and 126 m⁻², the highest value occurring at day 180. In 1979 a far lower plant density was found, varying from 9 to 39 m⁻². A distinct seasonal maximum did not occur, although the number of plants m⁻² was higher during the first half of the season than later on. In 1981 the measuring period was extended, starting earlier and finishing later in the year. The plant density was usually higher compared in 1978 and '79 and varied from 44 to 183 m⁻². In 1978 a similar tendency was recorded but a second maximum occurred at mid-winter.

Solar radiation and water temperature

Total annual solar insolation for 1978, '79 and '81 was similar, 331 124, 324 088 and 333 879 J cm⁻² y⁻¹, respectively. However, the seasonal timing in 1981 differed from that in 1978 and '79. In 1981 the irradiation was higher in March and from July to October than in both other years. However, it was relatively low in April and June, 1981, compared to the irradiation in the same period in 1978 and '79. The pattern of light attenuation within the water column followed that of irradiation with a lag period of 1 to 1.5 months. This is probably due to the growth response of the algal populations in the lake. The attenuation coefficient was relatively high (compared to both other years) in April and Oc-

tober to mid-November, but it was relatively low from August to mid-September (Fig. 3A, B).

The temperature sums increased most rapidly from day 150 to 275 (Fig. 4B). The temperature sum of 1979 lagged initially behind that of 1978, but was higher from day 136 onwards. The temperature sum of 1981 increased more rapidly and attained a higher final level than those of 1978 and '79.

Development state

The development rate was recorded in 1978 and related to temperature sum (Fig. 4A). Development state was predicted for 1979 and 1981 from their

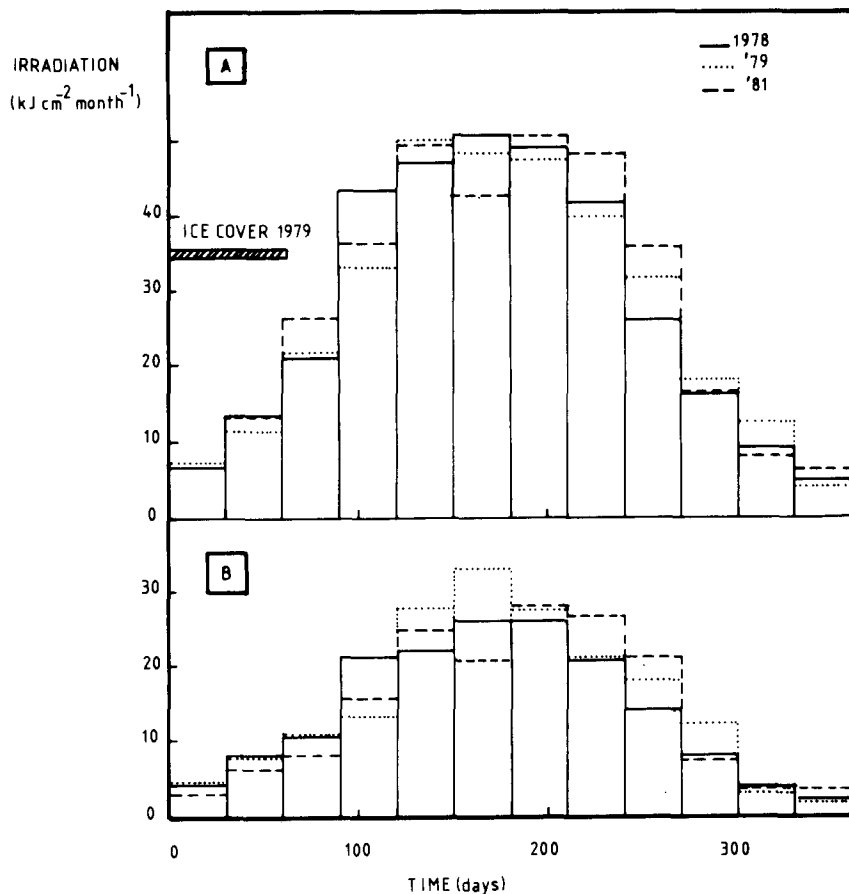


Fig. 3. Temporal changes in monthly solar irradiation at Lake Vechten, during 1978, '79 and '81. A: at the water surface; B: at 1 m depth. At maximum height the 2 m depth stand of *C. demersum* reached 1 m below the water surface.

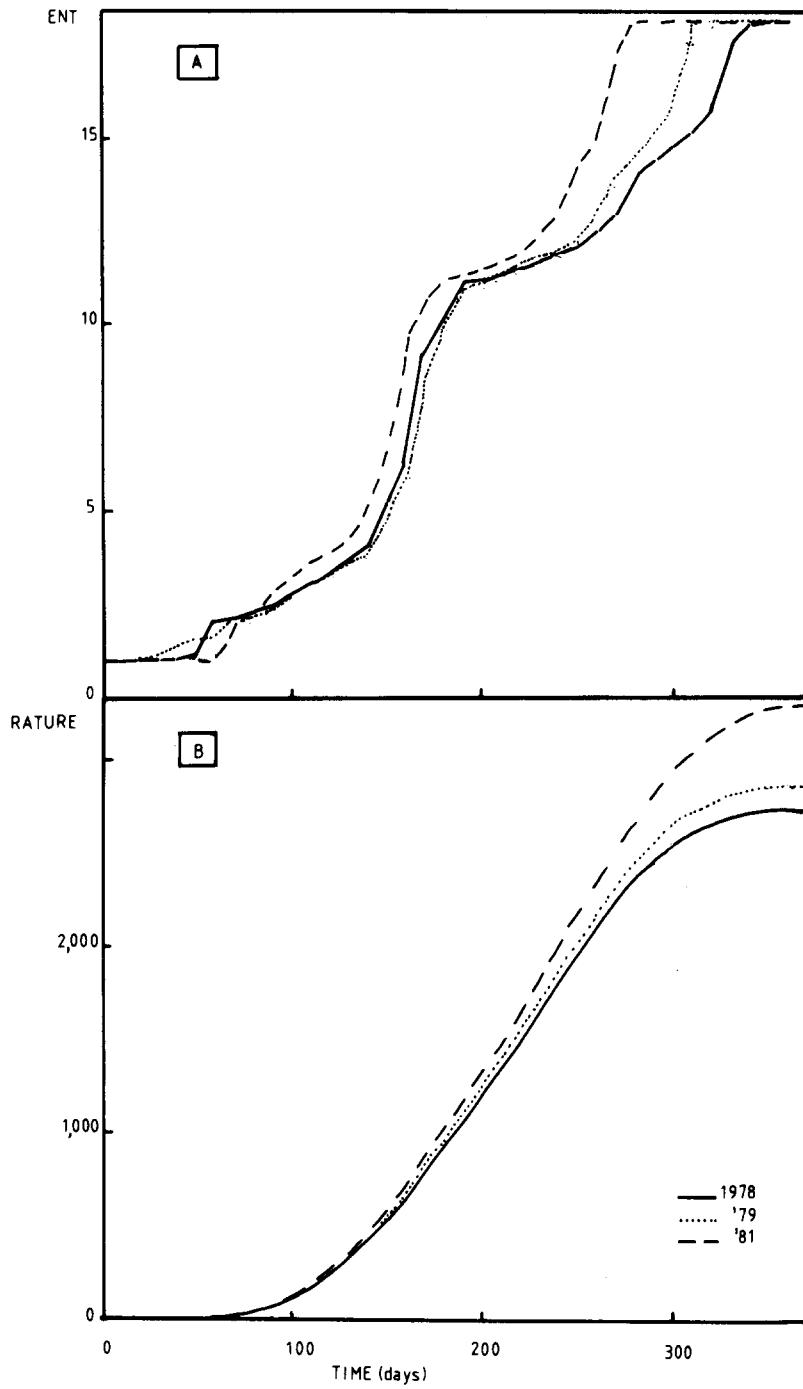


Fig. 4. A: the development state of a 2 m depth class of *C. demersum* in Lake Vechten, in 1978, '79 and '81, governed by temperature; B: the 3°C temperature sum, calculated for the surface water of Lake Vechten, in 1978, '79 and '81.

respective temperature sums. The predicted development state proved accurate for 1981. However, the temperature sum predicted development rate in 1979 was not accurate. The morphology at day 200 should have been characterized by extended shoots and fully expanded specific leaf area (Fig. 1). This morphology was only partially achieved by day 150. Therefore in 1979 the plants lagged in development state during the period of the highest solar radiation.

Carbohydrate storage substances: composition, concentration and distribution

Most sugars were present in the aqueous extracts of *C. demersum* in summer as well as in winter (Table 1), but showed seasonal changes in concentration (Table 2, 3, 4). Stachyose and melibiose predominated in winter, while non-reducing sugars, sucrose and raffinose, represented only 3.2% of the total extractable sugars (Table 1). In summer, raffinose, fructose, glucose and an unknown component 3 were predominant and the non-reducing sugars comprised 33.1% of the total extractable sugars. Stachyose and the unknown component 6, which eluted between raffinose and stachyose, were

Table 1. The composition of the water-soluble sugars of *C. demersum* in 1981, determined using GLC. The plants were harvested at 10.00 a.m.

Date	12 February	14 July
Sugars (% of total)		
xylose/arabinose	-	-
1	-	2.5
ribose	-	-
fructose	0.9	14.3
glucose	2.3	11.3
myo-inositol	1.9	3.5
2	2.0	3.7
sucrose	1.9	6.6
melibiose	39.6	6.7
3	-	10.0
4	2.4	9.0
raffinose	2.7	26.5
5	1.9	3.0
6	2.5	-
stachyose	41.5	-

Table 2. Seasonal changes in the composition and concentration of water-soluble and reserve carbohydrates (water-soluble sugars and starch) of *C. demersum* in Lake Vechten during 1981. The plants were harvested at 10.00 a.m.

Date	Reserve substances (% whole plant reserves)				Reserve conc. (mg g ⁻¹ AFDW)
	suc	glu + fruc	raff + stach	starch	
4 Jan.	1.0	2.7	27.2	69.1	88.17
11	0.6	8.3	11.3	79.8	61.94
21	0.6	2.8	21.3	75.2	77.12
12 Feb.	0.4	3.6	15.3	80.7	104.83
4 March	0.8	6.4	26.0	66.8	63.21
11	0.4	9.5	5.2	84.9	90.92
18	0.9	4.1	18.9	76.1	75.28
29 April	1.6	9.8	21.5	67.1	41.30
23 June	5.7	11.9	17.7	64.7	36.57
2 July	2.2	13.2	21.4	63.2	41.73
8	6.5	17.6	22.1	53.8	41.75
22	7.5	10.4	11.9	70.2	43.83
30 Sept.	7.2	15.1	27.4	50.3	33.70
7 Oct.	1.8	6.6	13.3	78.3	63.35
25 Nov.	0.6	3.0	20.7	75.7	94.14

characteristic for the plant material harvested in February.

The unknown components 1 and 3, eluted between xylose/arabinose and ribose, and melibiose and raffinose, respectively, occurred only in plants harvested in summer. About half of the water-soluble sugars consisted of fructose, glucose, sucrose and raffinose/stachyose.

The concentrations of carbohydrate reserves (water-soluble sugars and starch) were higher in winter than in summer (Table 2), averaging 79.88 mg g⁻¹ AFDW from October to February and 39.81 mg g⁻¹ AFDW from April to September. The average sugar concentration was 24.9 mg g⁻¹ AFDW in winter and 20.2 mg g⁻¹ AFDW in summer. The average winter starch concentration was 71.5 mg g⁻¹ AFDW and in summer it was 24.7 mg g⁻¹ AFDW. The contributions of sucrose and reducing sugars to the total extractable sugar pool were lower in winter than in summer, averaging 0.8 and 5.2% versus 5.1 and 13.0%, respectively. The stachyose/raffinose concentration was usually higher than that of the other sugars but relatively

Table 3. Seasonal changes in the composition and concentrations of water-soluble and reserve carbohydrates (water-soluble sugars and starch) of *C. demersum* in Lake Vechten during 1981. The plants were harvested at 10.00 a.m. Tip, 0.5 m apical plant section; S1 to S6, successive 0.1 m sections; *, abscised distal plant parts.

Date		Reserve substances (% section reserves)				Reserve conc. (mg g ⁻¹ AFDW)
		suc	glu + fruc	raff/stach	starch	
12 Feb.	Tip	0.4	3.6	15.3	80.7	104.83
	S1*	1.1	7.1	27.1	64.7	44.07
23 June	Tip	5.8	11.2	17.5	65.5	39.67
	S1	4.1	19.2	20.0	56.7	19.56
2 July	Tip	2.4	13.6	21.1	62.9	43.86
	S1	2.2	11.0	19.8	67.0	45.07
	S2	3.4	18.4	16.8	61.4	33.08
	S3	2.3	13.0	24.1	60.6	38.28
	S4	1.4	12.2	25.1	61.3	40.77
22 July	Tip	7.2	11.2	11.7	69.9	51.47
	S1	1.2	2.2	4.5	92.2	42.32
	S2	12.3	8.5	13.0	66.2	33.38
	S3	23.6	24.5	35.2	16.7	15.52
	S4	13.4	14.7	20.8	51.1	26.81
30 Sept.	Tip	6.1	17.0	23.7	53.2	42.19
	S1	8.3	11.0	35.3	45.4	30.17
	S2	8.1	12.2	46.4	33.3	24.29
	S3	15.5	19.3	56.5	8.7	13.87
	S4	17.0	21.1	50.4	11.5	13.05
	S5	16.7	22.1	50.5	10.7	12.19
	S6	7.3	9.0	16.9	66.8	30.39
7 Oct.	Tip	1.6	7.1	12.0	79.3	72.39
	S1	1.8	3.6	15.7	78.9	57.66
	S2	4.0	7.6	20.8	67.6	31.65

constant, averaging 17.7 of the total extractable sugar pool in winter and 20.3% in summer. Starch was the major reserve substance, contributing 76.3% of the total extractable carbohydrates in winter and 61.6% in summer.

The distribution of extractable carbohydrates over the height of the vegetation is represented in Table 3. The concentration usually decreased from the apex to the distal plant parts in the period October to June. From July to September it decreased with distance from the apex but increased again in the extreme distal section. Starch concentrations showed the same trend as soluble sugars regardless

of season. The highest sucrose concentrations were found at the end of July in the lower, largely shaded, plant portions to which considerable transport of assimilates from the actively photosynthesizing apical portions occurred. From October to February the sucrose concentrations were relatively higher in the lower sections than in the upper ones, possibly due to local reserve mobilization and subsequent transport to support maintenance of the upper plant parts. Raffinose served probably as major transport sugar (Table 1). Regrettably it could not be distinguished from stachyose in the samples for which the enzymatic method was used.

Table 4. Seasonal changes in the concentrations of water-soluble and reserve carbohydrates (water-soluble sugars and starch) of *C. demersum* in Lake Vechten during 1981. The plants were harvested at 10.00 a.m. Tip, 0.5 m apical plant section; S1 to S6, successive 0.1 m sections. *, abscised distal plant parts.

Date		Reserve conc. (mg g ⁻¹ AFDW)			Biomass (g AFDW plant ⁻¹)
		sugar	starch	total	
12 Feb.	Tip	20.23	84.60	104.83	0.305
	S1*	15.56	28.51	44.07	0.296
23 June	Tip	13.68	25.98	39.66	0.410
	S1	8.47	11.09	19.56	0.075
2 July	Tip	16.27	27.59	43.86	0.194
	S1	14.87	30.20	45.07	0.093
	S2	12.77	20.31	33.08	0.048
	S3	15.08	23.20	38.28	0.066
	S4	15.77	25.00	40.77	0.068
22 July	Tip	15.49	35.98	51.47	0.478
	S1	3.30	39.02	42.32	0.102
	S2	11.29	22.10	33.39	0.080
	S3	12.92	2.59	15.51	0.045
	S4	13.11	13.70	26.81	0.081
30 Sept.	Tip	19.74	22.45	42.19	0.736
	S1	16.47	13.70	30.17	0.255
	S2	16.20	8.09	24.29	0.106
	S3	12.66	1.21	13.87	0.071
	S4	11.55	1.50	13.05	0.046
	S5	10.89	1.30	12.19	0.065
	S6	10.09	20.30	30.39	0.182
7 Oct.	Tip	14.98	57.41	72.39	1.365
	S1	12.17	45.49	57.66	0.314
	S2	10.26	10.25	20.51	0.333

Discussion

Relation of growth behaviour to light and temperature

Yearly biomass production of *C. demersum* in the littoral zone of a small meso-eutrophic lake was studied for three years in relation to insolation and water temperature. Large differences in yearly biomass production between 1981 and 1978 could be explained by differences in cumulative yearly water temperature and seasonal timing of insolation.

However, the large differences in yearly biomass production between 1978 and 1979 could not be explained by only insolation and water temperatures.

1981 Proved the most productive year. In 1981 solar irradiation was relatively high in early spring (March) and the second half of the growth season (July to October) but relatively low during the first half of the growth season (April to July), with its consequences for attenuation by the overlying water column. Elongation and development of photosynthetic area in the plants occurred in time to intercept the peak in insolation, and plant development was successfully predicted from the temperature sum. Consequently, the highest biomass was found. 1979 was the least productive year. The differences in biomass production could only partly be attributed to the temporarily lower insolation and water temperatures, or to both. However, unexpected large differences were also found between the years 1978 and '79, despite the similarities in the monthly totals and timing of solar irradiation and water temperature. In 1979 the plant development was retarded and occurred far later than predicted from the relationship between water temperature and development rate established in 1978. This delay in development of the plants in 1979 might have been due to the late initiation of the development process, which is usually triggered by light. During the winter of 1978-'79 the lake surface was frozen and heavily covered with snow from the beginning of the year until the end of February (day 0 to 60), permitting virtually no light penetration. Therefore, the developmental clock in 1979 probably started to run later, i.e. at day 61, and the development state of the plants lagged behind the standard development until day 260, providing little opportunity to utilize the high summer irradiation. Consequently, only the plants with sufficient reserves (plants with the highest biomass and reserve concentration) survived while the others died, causing a gradually decreasing standing crop.

The effects of temperature are manifold and therefore only an indirect relationship between temperature and biomass was expected. Temperature affects both the development rate once it is initiated (Van Dobben, 1962) and biomass production, the latter by increasing or decreasing respiration. Late

initiation and slowly increasing water temperatures during the first half of the year affected the development of *C. demersum* negatively by preventing the plants from attaining in due time their full height and leaf area. Subsequent growth (i.e. increase in biomass), however, depended probably on solar radiation levels, light penetration in the water column and vegetation, and water temperature. In temperate regions insolation decreases during the second half of the summer while water temperatures are still high, both favouring a negative net carbon balance. In 1981, the rapidly developing plants may have benefitted from their higher position in the water column and their early attainment of full photosynthetic capacity in absorbing relatively more light, despite the relatively unfavourable environmental conditions in June (low irradiation) and October–November (high water temperatures). On the other hand, high temperatures in the latter period may be less important in determining a positive net carbon balance because of the plants' relatively low growth respiration rate. In 1979 both, mainly the lag in development and the environmental conditions, which were less favourable than in 1978 for a positive net carbon balance, must have been responsible for the poor growth observed because during July–August irradiation at 1 m depth was slightly higher and water temperatures generally lower than in 1978.

The changes in plant density might be explained as follows. Usually, as in 1981, the plant density decreases from January onwards because of the death of the relatively small dormant buds due to depletion of their reserves. Around day 100 the largest also gradually lose their dormant buds and therefore the plant density increases because each plant usually carries more than one bud. These buds start developing photosynthetic area largely at the expense of their reserves, which process occurs earliest in apical buds. The other, usually smaller, buds become increasingly shaded, compete unsuccessfully for light with their original parent plants and finally disappear. In 1979 the normal pattern was disturbed possibly by the long winter of 1978–79.

Carbohydrate reserves, respiration and seasonal growth

Reserves have an important function in plants, serving as internal sources of energy for survival during unfavourable periods. Carbohydrates are generally the main substrates for respiration, although it is known that not all carbohydrates are used simultaneously or with equal ease.

Starch was usually the major carbohydrate reserve, but sugars also contributed considerably. About 50% of the extractable sugars consisted of glucose, fructose, sucrose and raffinose/stachyose. The remainder consisted mainly of melibiose and several unknown components. Raffinose and, to lesser extent, sucrose were probably the transportable sugars. Non-reducing sugars tended to predominate in summer, an indication of assimilate transport (Ziegler, 1975), and reducing sugars were generally more abundant in winter. The sugar and starch concentrations were in the range reported by Janauer (1981, '82) for several other submerged aquatics, but higher than those found in *Elodea sp.* from the same lake (Best & Dassen, 1987a). The sugar composition in summer was similar to those found by Janauer and Best & Dassen, but for the winter material the presence of stachyose was distinctive. Myo-inositol occurred only in small amounts in *C. demersum* and may therefore not play an important role. The high melibiose contribution in winter may point to degradation of raffinose during transport (Ziegler, 1975), as was suggested also for *Elodea sp.* (Best & Dassen, 1987a).

The value of the reserves for the plants' survival was assessed. In winter, the respiration rate of quiescent *C. demersum* plants at 5 °C in the dark (the plants are covered by detritus and sediment) is 0.07 mg C g⁻¹ AFDW h⁻¹, 0.14 mmol CO₂ g⁻¹ AFDW d⁻¹ or 4.20 mg sugar g⁻¹ AFDW d⁻¹ (Best & Van der Werf, 1986). On 12 February the plant tips contained enough sugars to maintain their whole biomass for 4.8 days (Table 4), and for 25.0 days when they also mobilized their starch reserves. The situation was far less favourable for the abscised distal plant parts where the reserve substrates sufficed only for maintenance during

10.5 days. The plant usually starts its initial stages of growth about mid-March, depending on the water temperature sum (Fig. 4), and the respiration rate increases from 0.07 to 0.17 mg C g⁻¹ AFDW h⁻¹ or a sugar requirement of 10.2 mg g⁻¹ AFDW d⁻¹ (Best & Van der Werf, 1986). Because the photosynthetic capacity is then very low the substrate for respiration can only be provided by translocation of reserves from distal plant parts to the apex resulting in loss of mass from the distal parts. The relatively higher sucrose concentrations in the lower plant parts (Table 3) and the decrease in biomass of the plants (Fig. 1) in winter and early spring indicate that this phenomenon occurs.

The summer physiological situation of *C. demersum* is exemplified by the data of 22 July. At that time the upper 0.5 m of the vegetation is well-lit, while the lower portions received far less light or no light at all due to selfshading of the vegetation and the detritus cover (Best & Dassen, 1987b). The plant has passed its maximum photosynthetic capacity (Fig. 1) of 4.48 mg C g⁻¹ AFDW h⁻¹. It is not fully light-saturated and a photosynthetic rate of about 2.24 mg C g⁻¹ AFDW h⁻¹ is common (Best & Dassen, 1987b; a situation similar to that of *Myriophyllum spicatum*, cf. Adams & McCracken, 1974). Under these conditions the daily (12 h) yield would be 67.2 mg sugar g⁻¹ AFDW (12 h × 2.24 mg C g⁻¹ AFDW h⁻¹ × 30/12) or for the whole plant 32.12 mg sugar. The respiration rate of *C. demersum* plants growing in steady state at 20 °C is 0.26 mg C g⁻¹ AFDW h⁻¹, 15.60 mg sugar g⁻¹ AFDW d⁻¹ (Best & Van der Werf, 1986) or for the whole plant 12.26 mg sugar d⁻¹. Thus, in this period a surplus of assimilates is produced in the plant tips, which is readily transported to distal plant parts (Table 4) and biomass increases.

At the end of September, however, the photosynthetic capacity has declined further to about one third of the maximum value, the daylength has shortened and the irradiation is about 5% of the midsummer value. Under these conditions a daily photosynthetic rate for the upper 0.5 m of the vegetation of 1.49 mg sugar g⁻¹ AFDW (8 h × 1.49 mg C g⁻¹ AFDW h⁻¹ × 30/12 × 0.05%) is common, or 1.10 mg sugar per plant. The daily respiration rate, however, would be 15.60 mg sugar g⁻¹ AFDW or 22.79 mg sugar per plant, leaving a daily short-

age of 21.30 mg sugar per plant. To maintain the tips, and thus most meristems, mobilization of the reserves takes place and apparently this concerns at first largely the starch of the lower plant portions and to lesser extent the distal, anchorage section (Table 3, 4). The latter, however, is resorbed later.

The carbon budgets calculated for summer and autumn indicate the likelihood of a more rapid carbon deficit than would actually occur in the lake. Taking the measured sugar concentrations into account, being generally lower than 60 mg g⁻¹ AFDW, the respiration rates would have been probably 30 to 50% of the ones used (Best & Van der Werf, 1986). Even temporarily lower respiration rates would be expected in situations where several carbohydrates are temporarily depleted, for instance at the end of the night (Best & Visser, 1983; Challa, 1976).

The survival value of growth pattern and carbon allocation in C. demersum

The present study demonstrates the importance of coordinating the plant development processes and the insolation maxima. This was illustrated by the situation of 1979 when full development of *C. demersum* was attained only after the insolation maxima and plant biomass remained extremely low as was the number of propagules. In 1981 and 1978 plant development occurred on time and insolation was reflected in the formation of considerable biomass and in the dynamics of the propagules.

The storage systems for carbohydrates in the stem base and, particularly, in the apical leaves represented valuable survival potential for *C. demersum* during adverse conditions. The low sugar concentrations point to an energy conserving strategy directed to maintain a positive net carbon balance in environmental conditions where energy is usually scarce.

Respective to production and utilization of storage substances and the from literature known versatility in carbon metabolism (Bowes, 1986; Keeley & Morton, 1982), suitable morphology for light interception and longevity *C. demersum* resembles terrestrial shade plants (Grime, 1979, 1981).

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