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THE GROWTH OF *CHARA GLOBULARIS* AND ITS RELATIONSHIP TO CALCIUM CARBONATE DEPOSITION IN MALHAM TARN

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Abstract

The growth, photosynthesis and carbonate deposition rates of *C. globularis* were measured directly and by the $^{14}CO_2$ method. A positive correlation was found between the rate of $^{14}CO_2$ fixed in photosynthesis and the rate of uptake into carbonate ($r = +.77$, $p < 0.001$). During the growth period from May to August, the calcium concentration in Malham Tarn fell by 45 mg l^{-1} and measurements of the summer standing crop showed that this fall could be attributed to the growth of *Chara*. The growth period was found to coincide with that predicted from measurements of photosynthesis and light attenuation in Malham Tarn.

Introduction

Charophytes often dominate the submerged macrophyte communities of shallow lakes yet little is known of their growth rates, contribution to primary production, or their influence on lake water chemistry. Many species develop a series of band-shaped carbonate incrustations on their internodal cells due to the formation of alternating acid and alkaline regions surrounding the cell walls (Hope and Walker, 1975). These alkaline bands are caused by a local efflux of OH^- ions (Lucas and Smith, 1973) which appears to be linked to HCO_3^- ion uptake induced by photosynthesis (Lucas, 1975). The OH^- ion efflux causes the precipitation of calcium carbonate in hard waters which can eventually result in the entire plant becoming densely encrusted. For this reason, these algae are often referred to as stoneworts, although the extent and significance of this encrustation have not been investigated in detail.

This study attempts to determine the extent of carbonate deposition in Malham Tarn, an upland calcareous lake whose benthos is dominated by *Chara globularis* Thuill. The lake is subject to large seasonal fluctuations in dissolved calcium (Lund, 1961) which may be directly related to the growth of *Chara*.

Methods

Chara globularis was obtained from grab samples taken in 2–3 m of water in Malham Tarn, North Yorkshire. For the $^{14}CO_2$ experiments, plants were placed in clear and blackened 50 ml glass bottles with 40 mls lake water and 10 μC $NaH^{14}CO_3$. They were incubated in the laboratory under light intensities ranging from 10–470 W m^{-2} supplied by daylight fluorescent tubes at 20°C. After 3 hours the plants were removed, washed in lake water, dried and ground, and the radioactivity determined with a Tracerlab G. M. counter for a minimum of 10^4 counts and an end window efficiency of 40–44%. $^{14}CO_2$ uptake into calcium carbonate was found by difference following mild acidification (Paasche, 1963). Corrections for self absorption were found to be unnecessary but photosynthetic carbon fixation was corrected for dark uptake. No correction was applied to uptake into calcium carbonate and four replicates were run for each sample.

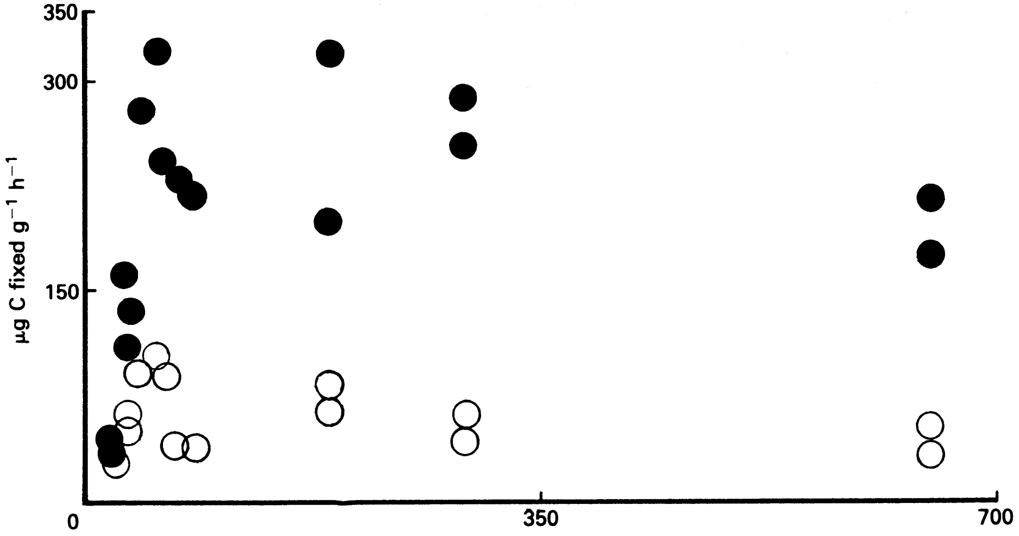

FIG. 1.

$^{14}CO_2$ uptake by *C. globularis* vs. light intensity during July. Closed circles, photosynthetic carbon fixation; open circles, uptake into calcium carbonate deposited onto plants.

To study *Chara* growth *in situ*, samples were collected at about fortnightly intervals from a single site. A minimum of 25 plants were separated and the current season's growth measured. This was possible because the previous season's growth had begun to decay and contrasted with the recent fresh green growth. Additional samples were collected in July, then air dried and analysed for a) calcium carbonate content using a method adapted from Umbreit *et al.* (1959) and b) chlorophyll-a content (Vollenweider, 1969; equation of Talling and Driver, 1963). The carbon content of decalcified, oven-dried *Chara* was obtained using a Hewlitt-Packard Analyser and the minimum extinction coefficient (e_{min}) of the lake water was calculated from readings taken from a combined Mackereth probe (Mackereth, 1964). Calcium concentration in the water was determined by titration with EDTA (Golterman and Clymo, 1969).

RESULTS

a) $^{14}CO_2$ *uptake*

The uptake of $^{14}CO_2$ over a range of light intensities is shown in Fig. 1. Photosynthetic carbon fixation exceeded uptake into $CaCO_3$ by a factor of about 3 with a maximum light-saturated uptake rate of 330 µg C g^{-1} h^{-1}. The onset of light saturation, defined as I_k, occurred at 85 W m^{-2} with an indication of light inhibition at high intensities. The uptake of isotope into $CaCO_3$ showed no clear relationship with light intensity but a significant correlation was found between uptake into $CaCO_3$ and photosynthetic carbon fixation (Table 1).

b) Growth measurements

Growth began in mid-May (Fig. 2a) and a steady increase in the length of *Chara* was observed until early August. A significant value of the regression coefficient b was found for the length of *Chara* on the dry weight (Table 1) so changes in length may be equated to

Table 1. *Statistical data*

a) Correlation and regression analyses.

Variables	Sample statistic	Significance level	Sample number
Photosynthetic carbon fixation vs. carbonate deposition.	$r = +0.77$	**	16
Chara (c) dry weight vs. $CaCO_3$ content	$r = -0.19$	Not significant	25
Chara (c) dry weight mg. (Y) vs. length cm. (X)	$a = -39$ $b = 2.12$	*	50
Chara (c) dry weight vs. chlorophyll-a.	$r = -0.70$	**	25
Chara length vs. water temperature	$r = +0.82$	**	13
Chara length vs. Calcium concentration	$r = -0.89$	**	13

b) Means and ranges.

	mean	range
Chara (d) summer standing crop	0.51 kg m^{-2}	0.36–0.64
$CaCO_3$ in standing crop	0.89 kg m^{-2}	0.62–1.1
Chara (c) chlorophyll-a content %	0.13	0.03–0.21
Chara $CaCO_3$ content %	63.5	57–86
Chara (d) organic carbon content %	34.1	33.5–34.6
Tarn calcium mg.l^{-1}		84–140
Tarn temperature °C		0–16
Tarn e_{min} value	0.71	0.5–1.05
Chara I_k value W m^{-2}	90	

Levels of significance: $^*p < 0.05$ $^{**}p < 0.01$.
r Pearson's correlation coefficient.
a, b Linear regression coefficients.
Chara (c) dry weight includes $CaCO_3$, *Chara*(d) excludes $CaCO_3$.

changes in biomass. Between May and August, the mean length increased from 2.1 cm to 30.4 cm, equivalent to a dry weight increase of 21 mg per plant. As the plants grew, the chlorophyll-a content fell, resulting in a significant negative correlation between these variables.

C. globularis is monoecious. The sex organs began developing in early June and attained maturity by mid-July (Fig. 2a). Fertilization soon followed and this coincided with the cessation of growth in mid-August. During the growing period, secondary axes often developed from the nodal cells although their growth rate tended to be considerably lower than that of the main axis. During September and throughout the winter, all but the uppermost extremities of the main axes and secondary axes underwent a slow decay. The shoot tips appeared to act as overwintering organs.

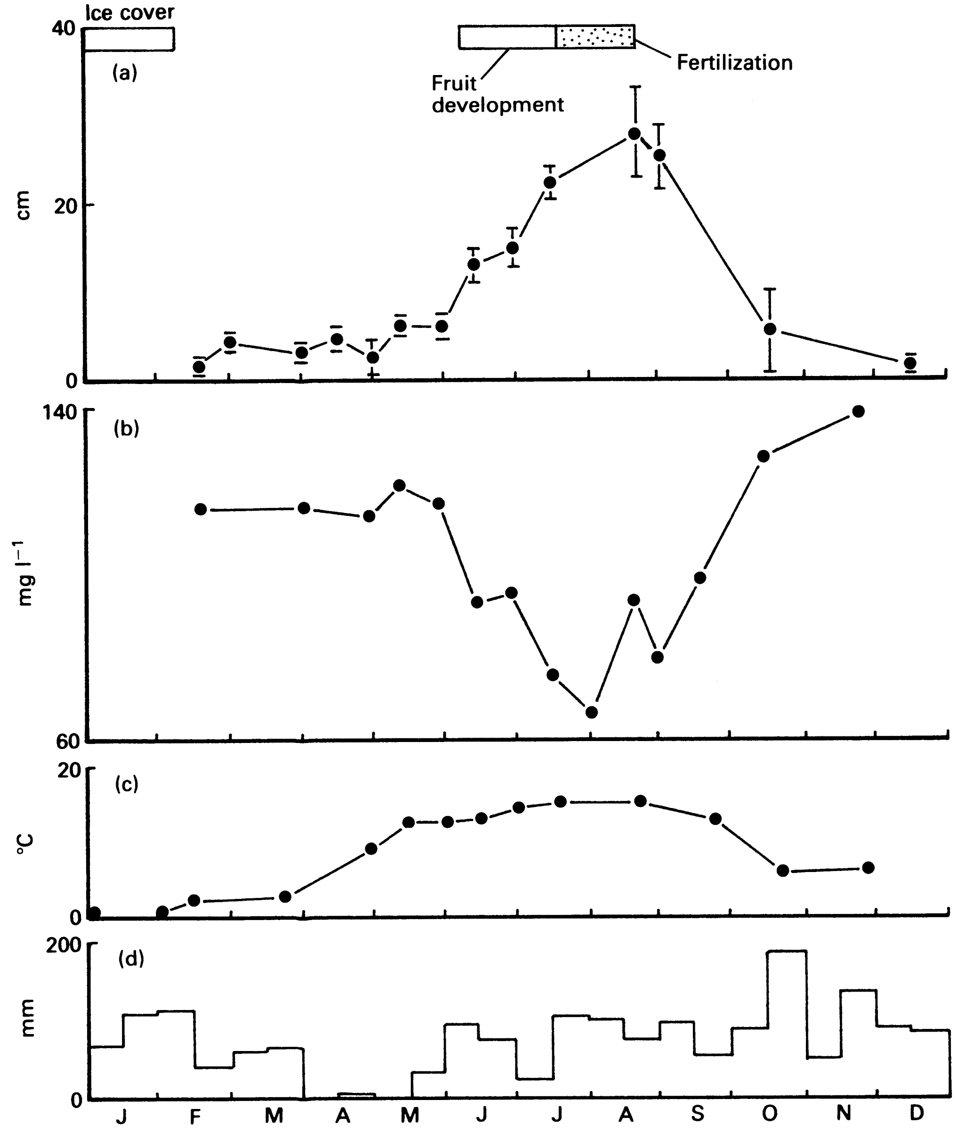

FIG. 2.
a) Growth of *C. globularis* measured as plant length during 1980. Bars enclose 95% confidence limits of the mean. b) Calcium carbonate concentration (mg l^{-1}) in Malham Tarn. c) Water temperature. d) Rainfall (mm).

From February to May the calcium carbonate concentration in the Tarn remained approximately constant at 120 mg l^{-1} (Fig. 2b) but it fell steadily after May to a value of 84 mg l^{-1} in early August after which it began to rise to its former level and there was a significant negative correlation between calcium concentration and *Chara* biomass (Table 1). Water temperature remained close to 2°C from January to March (Fig. 2c) and then rose steadily to a maximum of 16°C in July resulting in a significant positive correlation with *Chara* biomass. Dilution of the lake water calcium by direct rainfall was negligible and about 300 mm of rain fell in the district during the period of *Chara* growth (Fig. 2d).

c) Standing crop and carbonate budget

During the growth period, the calcium carbonate concentration in the Tarn fell by 45 mg l^{-1}. Since *Chara* is known to cover between 80–90% of the Tarn floor and the Tarn is of approximately uniform depth (2.5 m), it is possible to estimate the deposition rate of calcium carbonate as 0.28 kg $m^{-2}a^{-1}$. This is considerably lower than the quantity found encrusting the summer standing crop, which was equivalent to a mean of 0.89 kg $m^{-2}a^{-1}$ (Table 1). There was no significant difference between the degree of encrustation of *Chara* and biomass. About 60% of the dry weight of this species consisted of $CaCO_3$ (Table 1). Because of this degree of carbonate deposition, quantities have been calculated with and without encrustation in Table 1.

DISCUSSION

The deposition of calcium carbonate on the surfaces of charophyte cells is dependent upon both the rate of photosynthesis and the saturation state of the waters with respect to calcite which is the mineral form produced. Carbonate deposition does not occur in calcium-poor waters because the solubility product is not normally exceeded—a necessary condition for precipitation to occur (Dragunova, 1970; Pentecost, 1981). The precipitation of calcite is also dependent upon the presence of suitable nucleation sites (Walton, 1967) and in the absence of these, supersaturation may occur instead of deposition. The precipitation of sparingly soluble salts is often a slow process and this may account for the low uptake rates of $^{14}CO_2$ into calcium carbonate compared with photosynthetic carbon fixation (Table 1). However, this loss might also be accounted for if some of the precipitated carbonate formed upon the vessel walls rather than the plants themselves. Previous published estimates of the $CaCO_3$ content of *Chara* species range from 30–86% of the dry weight (Schuette and Alder, 1929; Boyd and Lawrence, 1966; Straskraba, 1968) but most of these estimates are based upon small numbers of samples and are of doubtful accuracy since they were obtained from ash analyses.

The onset of light saturation for photosynthesis and the minimum extinction coefficient for light attenuation can be used to obtain an approximate threshold for the surface light intensity necessary for light saturated growth. This value, which corresponds to 300 W m^{-2}, when referred to the average illumination curves for the appropriate latitude (Walsh, 1961), indicates that lightsaturated photosynthesis could occur only during the period April–September, which coincides with the actual growth season. The maximum rate of photosynthetic carbon fixation agrees well with the recorded growth rate of *Chara* during the early summer, and the growth rate, which was found to be negatively correlated with calcium concentration, supports the suggestion by Lund (1961) that the regular summer fall in calcium levels which were recorded between 1949 and 1953 were a consequence of *Chara* growth. It could be argued that these changes occur in the inflow streams and not the Tarn itself, but recent unpublished studies and the data of Lund (1961) do not support this.

The positive correlation between *Chara* biomass and water temperature is of interest because there is no indication that the rate of growth actually increased at temperatures above 12°C. Unfortunately, little progress has been made in elucidating the putative role of auxin and nutrient depletion in the growth of *Chara,* both of which probably play an important part during the period of growth and its termination in August.

Malham Tarn has one major inflow and a single outflow situated at opposite ends of the lake. The residence time of the water is known to be 6–9 months, so that during the growing season of about 4 months, between 40% and 70% of the Tarn water will have been replenished and the measured fall in calcium concentration would be underestimated by this amount. This may account for much of the difference between the estimated and observed loss of $CaCO_3$ to *Chara*.

The mean summer standing crop of 0.5 kg m^{-2} is low compared to the values quoted by Westlake (1963) for aquatic macrophytes and this must reflect the climate of this upland, well mixed lake, whose summer temperature rarely exceeds 15°C.

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