J. Phycol. **18,** 226–232 (1982)

AUTECOLOGY OF AN ULTRAPLANKTONIC SHADE ALGA IN LAKE TAHOE[1]

Warwick F. Vincent[2]

Institute of Ecology, University of California, Davis, California 95616

ABSTRACT

The ultraplanktonic green alga Monoraphidium contortum *Korm. in Lake Tahoe (California-Nevada) demonstrated several ecological and physiological attributes of a genetically adapted shade species.* Monoraphidium contortum *achieved maximum biomass during deep mixing in winter when light availability was at a minimum. During stratification it was found in maximum abundance in the deep euphotic region, 100–150 m. This species was also distributed through the deep aphotic zone where, despite prolonged darkness, it remained capable of immediate photosynthesis when re-exposed to light levels in the euphotic zone. The spirally twisted cells were grazed by two calanoid copepods in Lake Tahoe as readily as much larger-celled phytoplankton species of less complex morphology. Slow growth rates in combination with high susceptibility to copepod grazing may effectively exclude* M. contortum *from the upper 75 m, where it was rarely recorded. In culture it showed a marked incapacity to adjust to 'sun' conditions but was well adapted to low light regimes. Under a wide range of irradiances, photochemical capacity, photosynthetic capacity and growth rates were low, but cellular pigment content remained high. The ratio of* P_{max} *to respiration was at the lower end of the range for shade plants. Genetically distinct sun and shade populations of phytoplankton may play a determining role in major shifts of community structure over depth and time in Lake Tahoe.*

Key index words: algae; aphotic; chlorophyll; grazing; lake plankton; Monoraphidium contortum; *oligotrophic; photosynthesis; phytoplankton; respiration; shade adaptation; zooplankton*

Shade adaptation in natural phytoplankton communities has been commonly ascribed to phenotypic shifts in cellular physiology. Many algal species appear to be capable of wide adjustments to photosynthetic performance, for example, in their light-capturing ability (Myers and Graham 1971), capacity for light-induced electron transport (Fleischhacker and Senger 1978) or the pathways used for photosynthetic carboxylation (Graham and Whittingham 1968). By contrast, little has been reported of species lacking in such flexibility but genetically adapted towards light climate extremes. Higher plants representative of this type are well known; for example, clones of *Solidago virgaurea* native to shaded habitats are incapable of adjusting to sunny conditions (Bjorkman and Holmgren 1963). A macroscopic shade alga, *Hydrodictyon africanum* Yamonouchi, has also been described (Raven and Glidewell 1975). If sun and shade species of phytoplankton also exist, they would conceivably play a determining role in major shifts of community structure over time and space.

The present paper describes a small-celled green alga, *Monoraphidium contortum* Korm., found in ultra-oligotrophic Lake Tahoe where it demonstrates several ecophysiological attributes of a genetically adapted shade species. The seasonal and depth distribution patterns of this alga are first outlined in relation to grazing pressure, aphotic viability and the distribution of other numerical dominants in the phytoplankton community of the lake. The photosynthetic characteristics of this species are then examined in culture with respect to irradiance conditions during growth.

METHODS

Phytoplankton collection and counts. All natural samples were collected at a mid-lake station (maximum depth of 460–500 m) with an opaque 30 L Niskin bottle. Samples for algal enumeration were preserved with Lugol's iodine solution (acidified) and later filtered onto 30 mm diameter 0.45 μm Millipore membranes. These were mounted on glass slides, cleared with 25% glutaraldehyde (cf. 50% used by Dozier and Richerson 1975) and counted at 1200× magnification under phase contrast illumination. Algal cells in samples from culture flask experiments were counted by hemacytometer. Cell volumes were estimated from measurements of 25 individual cells; mean volumes were converted to biomass carbon by the equation of Mullin et al. (1966).

Phytoplankton culture. To isolate algal species from Lake Tahoe into unialgal culture, 10 mL quantities of lakewater were poured over inorganic media (Chu No. 10, Chu 1942; ASM, Gorham et al. 1964, both diluted to one-tenth strength) agar plates and incubated at 5° C under 20 $\mu E \cdot m^{-2} \cdot s^{-1}$ cool white fluorescent light for 4 to 6 weeks. Individual colonies were then aseptically removed and transferred to liquid culture (one-tenth strength ASM or Chu No. 10). Several alternations of liquid culture and streak plating were required before unialgal conditions were reliably obtained. The cultures were not axenic for the photosynthetic experiments, but bacterial contamination determined by epifluorescence microscopy was always very low.

Photosynthetic measurements. Photosynthetic rates were measured on both natural and cultured material with $H^{14}CO_3^-$, generally added to a final radioactivity of 0.05 μCi per mL. At the end of each incubation in replicate light and dark containers, the labelled cells were filtered onto 0.45 μm Millipore membranes and air-dried. These were then counted in either a Nuclear Chicago gas flow Geiger-Müller counter (samples for microautoradiography) or in a Beckman LS100C liquid scintillation spectrometer. Dissolved inorganic carbon was measured by infrared gas analysis.

For microautoradiography, the filters were next attached to glass slides and cleared by brief exposure to boiling acetone fumes. The samples were subsequently prepared for fission-track autoradiography using Kodak NTB-3 nuclear-track emulsion and the method of Knoechel and Kalff (1976).

[1] *Accepted: 24 November 1981.*

[2] Present address: Freshwater Section, Ecology Division, DSIR, Box 415, Taupo, New Zealand.

Respiration measurements. Respiration rates were determined on cultures of *M. contortum* by direct oxygen uptake measurements. Exponentially growing cultures were incubated at 5° C or 10° C under 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ irradiance for 2 days before measurement. Subsamples were then transferred to darkened 250 mL Quickfit conical flasks which were filled completely and then fitted and sealed with an Orbisphere 638 dissolved oxygen probe and stirrer. Changes in dissolved oxygen were continuously monitored over 2–4 h of dark incubation with an Orbisphere 2603 oxygen meter. Other subsamples were removed from the cultures for concurrent photosynthetic measurement with $H^{14}CO_3^-$ (as above) at 100 $\mu E \cdot m^{-2} \cdot s^{-1}$. At the end of each incubation period the cells were harvested for chlorophyll determinations.

Chlorophyll measurements. The lakewater or culture samples were filtered onto GF/C glass-fiber filters which were stored frozen and later homogenized in 90% acetone/water with a Teflon tissue grinder. The homogenates were cleared by centrifugation and assayed (Strickland and Parsons 1968) by a Turner 111 fluorometer or a Cary 219 spectrophotometer.

In vivo measurements of chlorophyll *a* fluorescence were made with a Turner 111 fluorometer fitted with a blue (CS5-60 excitation filter and red (CS2-64) emission filter. Plankton cells were dark-adapted for 2 h and their fluorescence was then measured both without (F_a) and with (F_b) 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU). These values were used to calculate an index of photochemical capacity per unit chlorophyll *a*, the cellular fluorescence capacity (CFC, Vincent 1980), equivalent to the CPC of Vincent (1981) and defined as $(F_b - F_a)/F_b$.

Grazing experiments. Two of the dominant zooplankton species in Lake Tahoe throughout the period of study were the calanoid copepods *Epischura nevadensis* Lilljeborg and *Diaptomus tyrrelli* Poppe. Both of these species occurred at maximum abundance at around 50 m during the day and moved towards the surface at night (P. Richerson, J. Rybock, unpublished data). A series of grazing experiments was run to determine the potential influence of zooplankton on the depth distribution of *M. contortum* relative to other constituents of the algal community.

Adult calanoid copepods were collected by Clarke-Bumpus net and immediately transferred to 100 mL quantities of 0.45 μm membrane-filtered lakewater in 150 mL sampling jars. Four individuals were placed in each container and maintained in the dark for 12 h at 5° C. Unialgal isolates of Tahoe phytoplankton which had previously been labelled with $H^{14}CO_3^-$ were added to duplicate containers of *Diaptomus* or *Epischura* at the following final cell concentrations per mL: 3.6×10^3 (*M. contortum*), 1.5×10^3 (*Synedra* sp. Ehr.), 8.0×10^4 (*Friedmannia* sp. Chant. et Bold), 9.5×10^4 (*Choricystis coccoides* Fott). Subsamples of algae were removed immediately upon inoculation and filtered onto membranes for counting by liquid scintillation spectrometry. After 12 h (6 h light, 6 h dark) the zooplankton were removed, washed and placed into scintillation vials in a desiccator. After 2 days drying, the organisms were macerated in small quantities of scintillation cocktail and then counted.

Description of species. Monoraphidium contortum Korm. is a small-celled (18.2 μm^3, 4.7 pg carbon per cell) green alga (Chlorophyceae, Chlorococcales, Oocystaceae; generic details given by Kormáková-Legnerová 1969). The cells are solitary, narrowly fusiform and sometimes narrowly cylindrical at the center. They are 1.5–2.5 μm wide, 10–15 μm long, and variably twisted into a spiral. The chloroplast lacks a pyrenoid and extends into the ends of the cell. Reproduction is by 2–4 autospores, released by rupture of the parent cell wall which persists in culture as a single unit.

Study site. Ultra-oligotrophic Lake Tahoe lies on the California-Nevada border at 1898 m above sea level. The lake is 499 km^2 in area and occupies a deep graben basin (maximum water depth 501 m, average depth 313 m). The water column is remarkably transparent; the 1% illuminance level of blue light (the most penetrating waveband) lies at ca. 87 m, the 0.1% level at ca. 130 m (from extinction coefficient data of Tilzer and Goldman 1978).

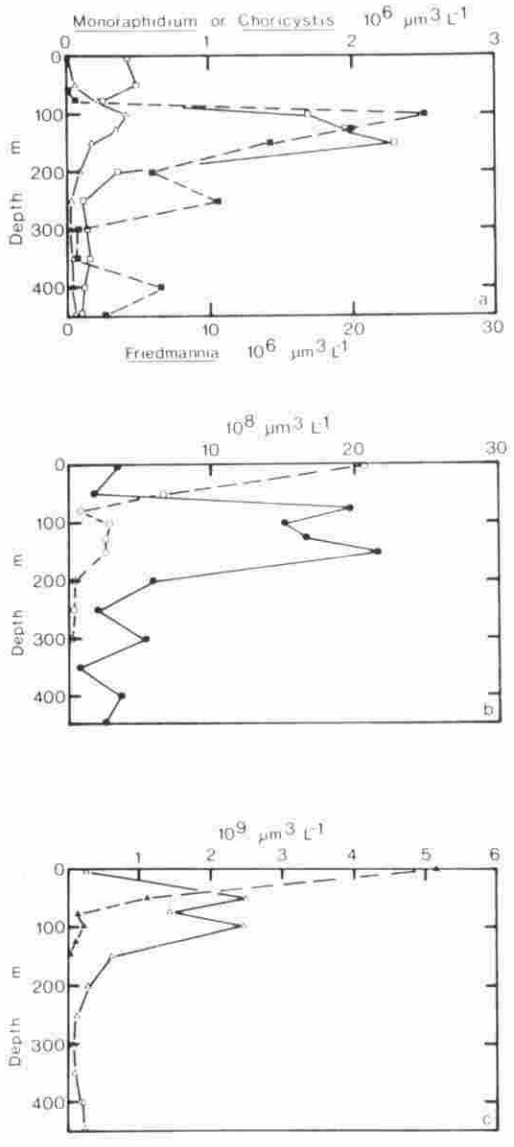

FIG. 1. Distribution of algal species with depth in Lake Tahoe, 14 September 1976, at a deep mid-lake station: (a) *Monoraphidium contortum* = ■, *Friedmannia* sp. = □, *Choricystis coccoides* = △; (b) *Cyclotella stelligera* = ○, *Synedra* sp. = ●; (c) flagellates = ▲, *Cyclotella ocellata* = △.

RESULTS

Vertical distribution. Over the period of sampling (February 1976–January 1977) *M. contortum* was only detected in the surface waters (0–50 m) of Lake Tahoe during late winter mixing in March. The rest of the year it was never found above 75 m (Fig. 1a). Below this depth, cell concentrations usually increased to a maximum in the region 100–150 m. The depth of 150 m corresponds with the lowermost limit of photosynthetic CO_2 uptake as measured by in situ light and dark bottle $H^{14}CO_3^-$ incubations (Vincent and Goldman 1980). Cell concentrations of *M. contortum* declined below 150 m, but the species was detected at most aphotic depths throughout the year.

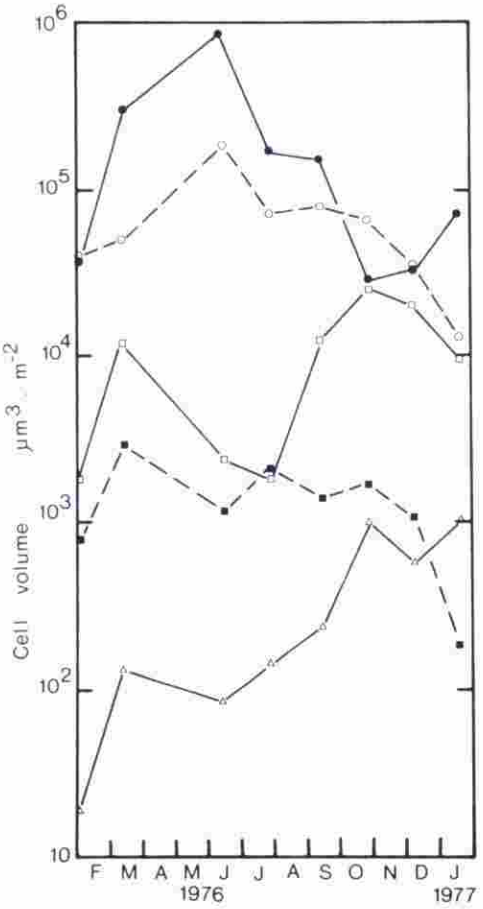

FIG. 2. Seasonal succession of five phytoplankton species in the euphotic zone of Lake Tahoe. *M. contortum* = ■, *Friedmannia* sp. = □, *Choricystis coccoides* = △, *Cyclotella stelligera* = ○, *Synedra* sp. = ●.

The vertical distribution of *M. contortum* was closely paralleled by two other species of small-celled green algae (Fig. 1a): the reniform coccomyxan *Choricystis coccoides* (0.5 μm^3) and a coccoid chlorosphaeralean, *Friedmannia* sp. (4.4 μm^3). Also attaining maximum abundance in the deep aphotic region throughout stratification were two species of relatively large-celled diatoms (Fig. 1b, c): *Synedra* sp. (341 μm^3; incorrectly reported as *Fragilaria crotonensis* Kitton by Vincent 1978) and *Cyclotella ocellata* Pont. (494 μm^3). A number of small-celled diatoms (e.g. *Cyclotella stelligera* Cl. et Brun, 37.8 μm^3, Fig. 1b) were common in the surface euphotic zone of Lake Tahoe, but rare in the region of green algal abundance. Several species of flagellates [*Kephyrion* Pasch., *Kephyriopsis* Pasch., *Mallomonas* Perty and *Peridinium* Ehr. (Stein)] were similarly distributed at the surface but not in the lower euphotic zone throughout the year (Fig. 1c).

The deep euphotic zone of Lake Tahoe was characterized throughout the period of stratification by elevated levels of nitrate (1.5–3 times the levels in the surface euphotic zone), low temperatures (ca. 5° C) and light levels of ca. 1% (75 m) to ca. 0.05% (150 m) of surface illuminance. Chlorophyll levels per unit biomass were highest in this region of the water column, as in previous years (Paerl et al. 1976).

TABLE 1. *Feeding rates of two Lake Tahoe zooplankton spp. on algal isolates in dense suspension at 5° C. Each value is the mean of duplicate tests, expressed as algal cells ingested (and retained) per zooplankton per hour, and algal biomass (ng C) ingested per hour per animal.*

	Ingestion rate (animal^{-1}·h^{-1})			
	Diaptomus tyrrelli		*Epischura nevadensis*	
Algal isolate	cells	ng C	cells	ng C
Monoraphidium contortum	4365	20.36	965	4.50
Friedmannia sp.	158	0.24	3	0.01
Choricystis coccoides	3	0.01	1	0.01
Synedra sp.	646	27.86	179	7.72

Seasonal distribution. The maximum increase in biomass of *M. contortum* was recorded during late winter mixing (Fig. 2). Populations then declined in spring to a relatively constant cell biomass that persisted over summer. A rapid decrease in cell counts was recorded in autumn and early winter.

The two other ultraplanktonic green algae, *Friedmannia* sp. and *Choricystis coccoides*, also reached a maximum abundance in late winter, but in addition demonstrated a second, larger maximum in late summer. This pattern differed markedly from the seasonal distribution of diatoms, in which all continued to rise in abundance through spring and then decline in summer (Fig. 2).

Grazing experiments. All species of algae tested were grazed more heavily by *Diaptomus* than by the larger animal *Epischura* (Table 1). Both animals were capable of filtering out *M. contortum* and *Synedra* sp. with almost equal effectiveness in terms of biomass ingested and retained, despite the order of magnitude difference in cellular biomass between these two phytoplankton species. The zooplankton filtered out two other green algae from the deep euphotic zone either at very slow rates (*Friedmannia* by *Diaptomus*) or not at all (*Choricystis* by both animals, *Friedmannia* by *Epischura*). *Monoraphidium contortum* is therefore susceptible to zooplankton grazing, and much more so than other ultraplanktonic constituents of the deep euphotic community.

Aphotic viability. Monoraphidium contortum was found at most aphotic depths over the period of study. Cells which can photosynthesize immediately upon re-exposure to light are known to occur throughout Lake Tahoe's deep aphotic zone at all times of the year (Tilzer et al. 1977, Vincent 1978). The viability of deep-living populations of *M. contortum* was tested in January 1977. By this date the lake had not completely mixed to the bottom for almost 2 years, and some algal cells had probably been in the bottom waters of the lake, several hundred meters below the euphotic zone, for a period in excess of 18 months (Vincent 1978).

Water samples collected on 20 January 1977 at

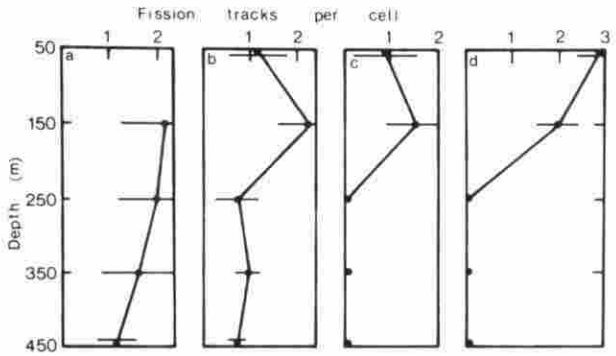

FIG. 3. Species specific photosynthetic potential of aphotic and euphotic phytoplankton on 20 January 1977. Each point is the mean number of fission tracks per algal cell for 20 individual cells at each depth ±95% confidence limits: a = *M. contortum*, b = *Friedmannia* sp., c = *Synedra* sp., d = *C. ocellata*.

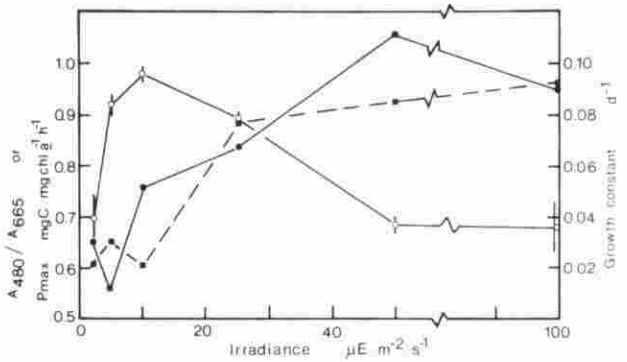

FIG. 4. Characteristics of *M. contortum* cultured at different irradiances. Growth = ○, maximum photosynthesis per unit chlorophyll = ■, carotenoid to chlorophyll *a* ratio (A_{480}/A_{665}) = ●. Bars are ± range for duplicate cultures.

100 m intervals between 50 m and 450 m were dispensed into duplicate 125 mL light and dark bottles, and photosynthetic rates were measured in a laboratory incubator at 5° C with ca. 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ irradiance. The filters were counted by Geiger-Müller counter and then prepared for fission-track autoradiography. The number of fission tracks per cell, directly proportional to the number of ^{14}C atoms per cell (Knoechel and Kalff 1976), were counted for 20 indiviuals of *M. contortum* and for three other species found throughout the aphotic water column.

Despite the prolonged period of stratification before this experiment, significant differences ($P < 0.05$) were detected between light and dark bottle carbon uptake for all depths tested. Average rates of photosynthetic uptake for the assemblages as a whole, in $\mu g\ C \cdot m^{-3} \cdot h^{-1}$, were: 463.3 (50 m), 136.7 (150 m), 22.8 (250 m), 10.5 (350 m) and 6.9 (450 m).

Viable individuals of *M. contortum* were found at all aphotic depths (Fig. 3a). There was a decline in average photosynthetic rates per cell with increasing depth; mean photosynthetic carbon incorporation for the 450 m populations was approximately half that for the 150 m population, but the variance was wide for all populations sampled. *Monoraphidium contortum* could not be found at 50 m and no data are therefore available for individuals from this depth.

Viable populations of *Friedmannia* sp. were also found at all aphotic depths (Fig. 3b). However, no individuals of *C. ocellata* or *Synedra* sp. capable of immediate photosynthesis were found below 150 m despite the occurrence of these species throughout the aphotic zone (Figs. 3c, d). Aphotic populations of *M. contortum* therefore retain a fully operational photosynthetic apparatus throughout prolonged stratification, but this is not a feature common to all species found below the compensation depth in Lake Tahoe.

Photosynthesis and growth characteristics. Monoraphidium contortum grew slowly on all inorganic media tested (ASM, Gorham et al. 1964; Woods Hole MBL, Nichols 1973; Chu No. 10, Chu 1942) and at all light intensities. Under 40 $\mu E \cdot m^{-2} \cdot s^{-1}$ at 5° C, the growth rate constant for this species on one-tenth strength Chu No. 10 medium was 0.116 d^{-1}; under the same conditions growth rates of two other isolates from Lake Tahoe's deep euphotic zone were also low, but higher than for *M. contortum* (*Friedmannia* = 0.293 d^{-1}, *Choricystis* = 0.220 d^{-1}).

The relationship between growth of *M. contortum* and irradiance demonstrated light saturation at very low levels (Fig. 4); the I_k value for growth of this species in ASM at 5° C was ca. 4 $\mu E \cdot m^{-2} \cdot s^{-1}$. Above 10 $\mu E \cdot m^{-2} \cdot s^{-1}$, growth rates decreased with increasing irradiance.

Subsamples were removed from cultures of *M. contortum* grown for 20 days at various irradiances for analysis of pigment content and photosynthetic capacity. At all light intensities, cells of *M. contortum* contained approximately the same weight of chlorophyll *a* (Table 2). Spectrophotometric scans of acetone extracts of *M. contortum* cells revealed a well-defined chlorophyll *b* peak at 460 nm; in cells from all irradiances this pigment accounted for about 36% of total chlorophyll (Table 2). The ratio of absorbance at 480 nm relative to 663 nm provides some measure of carotenoid content; in the cultured *M. contortum* this ratio markedly increased with increasing irradiance above 5 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. 4).

The photochemical capacity of exponentially growing cells, as measured by CFC, was extremely low at all irradiances, increasing from 0.235 at 2.5 $\mu E \cdot m^{-2} \cdot s^{-1}$ to 0.306 at 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Table 2). Over this range, a 58% increase in maximum photosynthetic rates per unit chlorophyll was measured (Fig. 4), but even at 100 $\mu E \cdot m^{-2} \cdot s^{-1}$, P_{max} values were low (0.958 cf. 0.605 $\mu g\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}$ at 2.5 $\mu E \cdot m^{-2} \cdot s^{-1}$).

The photosynthesis/irradiance curves demonstrated some variation between cultures, but the differences were not marked (Fig. 5). I_k values for photosynthesis varied from 7 $\mu E \cdot m^{-2} \cdot s^{-1}$ (2.5

TABLE 2. *Chlorophyll content and DCMU-induced fluorescence (measured by CFC ratio) of* M. contortum *cells grown for 20 days under different light regimes.*

Irradiance $\mu E \cdot m^{-2} \cdot s^{-1}$	Chlorophyll (pg cell^{-1}) chl *a*	chl *b*	total	CFC
2.5	1.17	0.75	1.92	0.235
5	1.01	0.47	1.48	0.278
10	1.14	0.66	1.80	0.267
25	0.89	0.41	1.30	0.298
50	1.25	0.82	2.07	0.280
100	1.23	0.66	1.89	0.306
$\bar{x} \pm 2$ SE	1.11 ± 0.12	0.63 ± 0.13	1.74 ± 0.24	0.277 ± 0.021

$\mu E \cdot m^{-2} \cdot s^{-1}$ cells) to 12 $\mu E \cdot m^{-2} \cdot s^{-1}$ (100 $\mu E \cdot m^{-2} \cdot s^{-1}$ cells).

Photosynthetic rates were 23% higher at 10° C relative to 5° C but respiration rates more than doubled over the same temperature range (Table 3). The molar ratio of P_{max} to respiration rate was low at 5° C, and even lower at 10° C (Table 3).

DISCUSSION

In a recent review, Boardman (1977) noted that species are "classified into sun and shade plants depending on their adaptability to a selected light intensity" and that this adaptability is genetically determined. *Monoraphidium contortum* demonstrates a marked incapacity to adapt to 'sun' conditions; conversely, the species does possess many attributes of a genetically adapted shade plant:

(i) High chlorophyll *a* levels per cell. Improved light-capturing ability by cellular increases in chlorophyll *a* content are well known for many algae grown under low irradiances (e.g. Myers and Graham 1971). Ratios of chlorophyll to *a* to biomass carbon in natural plankton communities commonly fall around 0.06:1 (Paerl et al. 1976). In cultures of *M. contortum* the cellular chlorophyll *a* content averaged 1.11 pg (Table 2), equivalent to a chlorophyll *a* to carbon ratio of ca. 0.24:1. This approximates the maximum ratio found at the bottom of Lake Tahoe's euphotic zone 0.17:1 (Paerl et al. 1976).

(ii) High cellular concentrations of chlorophyll *b*. A decrease in the ratio of chlorophyll *a* to chlorophyll *b* is a general feature of shade adaptation. In *Atriplex patula*, for example, the ratio decreases from 3.38 under high-irradiance conditions to 2.97 under low light (Bjorkman et al. 1972). *Scenedesmus obliquus* colonies grown under weak irradiance (23 $\mu E \cdot m^{-2} \cdot s^{-1}$) have a chlorophyll *a* to *b* ratio of 2.5. In cultures of *M. contortum* this ratio averaged a low 1.8 over the wide range of light regimes tested.

(iii) Low photochemical capacity as measured by DCMU-induced chlorophyll fluorescence. This is a relative guide to non-cyclic electron transport capacity. In natural phytoplankton populations this value is typically 0.4–0.6 CFC units (Vincent 1980); for *M. contortum* it varies from 0.2 to 0.3. Many plant species are known to adapt to low light regimes by

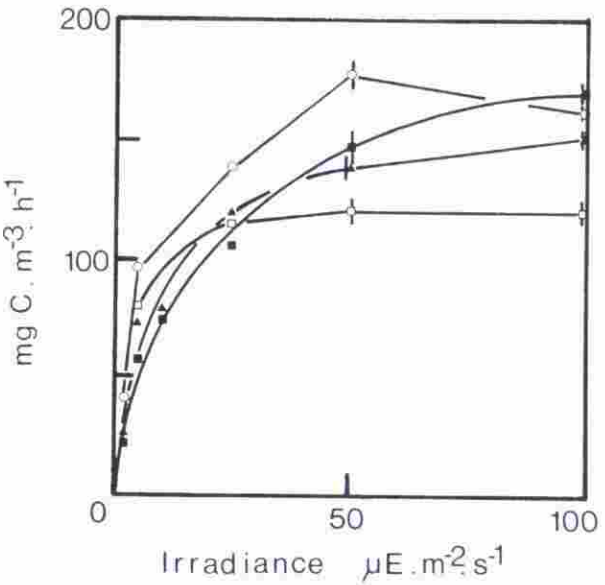

FIG. 5. Photosynthesis/irradiance curves for *M. contortum*. Cultures grown at 5° C under irradiances of 2.5 = □, 5 = ▲, 10 = ○, and 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ = ■, of cool-white fluorescent light. Bars are ± range for duplicate cultures.

reducing their cellular concentration of redox components in the non-cyclic electron transport chain (reviewed by Vincent 1980), which results in a reduced CFC value.

(iv) Low P_{max} per chlorophyll *a*. Light-saturated photosynthetic rates for lake plankton typically fall in the range 1–10 $\mu g\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}$. Shade-adapted cultures of *Scenedesmus obliquus* demonstrate a maximum rate of 3.2 $\mu g\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}$ (Senger and Fleischhacker 1978). For *M. contortum*, light-saturated photosynthesis ranged from 0.61 to 0.96 $\mu g\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}$.

(v) Low I_k values for growth and photosynthesis, with optimal growth rates at only 10 $\mu E \cdot m^{-2} \cdot s^{-1}$.

(vi) Slow growth rates at all irradiances, and low rates of respiration at both 5° C and 10° C. Reduced rates of metabolism are a general feature of shade populations. Respiration by *Scenedesmus obliquus* grown under weak light, for example, is one-sixth of that for cultures grown under strong light (Fleischhacker and Senger 1978). Shade plants appear to have decreased respiration requirements for growth and/or maintenance, and some species may supplement their respiratory ATP supply by photosynthetic partial reactions (Raven and Glidewell 1975).

The slow growth rate of *M. contortum* is not simply a consequence of low temperatures. Eppley's (1972) empirical relationship between growth and temperature for a wide range of algal species in culture predicts a maximum growth rate of 1.17 d^{-1} at 5° C. Growth rates for *M. contortum* in culture were less than one-tenth of this estimated k value at all irradiances.

(vii) Low ratio of P_{max} to respiration. Raven and Glidewell (1975) report that for macroscopic species

of algae this ratio is typically 4–15 in shade species but up to 25 for sun species. In *M. contortum* this ratio was 2–5, at the lower end of the range for shade species.

(viii) Onset of carotenoid pigmentation at a low threshold light intensity. Carotenoids are known to play an important protective role for plants exposed to elevated irradiances (Krinsky 1978). The absorbance ratios suggest that these sun-screening pigments are increasingly produced by *M. contortum* above the growth optimum of 10 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. 4).

Two ecological features further emphasize the shade adaptiveness of *M. contortum*. This species achieved maximum biomass in 1976 during late winter mixing when average light availability for the entire phytoplankton community was at a minimum. Mixing regimes in Lake Tahoe are known to exert a controlling influence on primary production rates. During deep lake mixing net productivity falls to a minimum in response to low average irradiances, and the community as a whole appears to be shade adapted (Tilzer and Goldman 1978). During 1976, water column mixing probably extended to a maximum depth of 300 m (Vincent 1978). Average light intensities experienced by the plankton were:

$$\frac{1}{Z_m} \cdot \int_{z=0}^{z=z_m} I_0 e^{-kz}\, dz$$

which approximates to: $I_0/(Z_m \cdot k)$, where I_0 = surface light intensity; z_m = depth of mixing (300 m); k = extinction coefficient (0.066 for white light).

Average light intensity may therefore be calculated as 5% of surface light levels. Even under dim surface irradiance conditions typical of this time of year, the average irradiance experienced during mixing would be above the saturation value for photosynthesis by *M. contortum* and perhaps other ultraplanktonic species that similarly occur in Lake Tahoe's deep euphotic zone during stratification. For example, a subsurface irradiance of 250 $\mu E \cdot m^{-2} \cdot s^{-1}$ would result in an average irradiance of ca. 12.5 $\mu E \cdot m^{-2} \cdot s^{-1}$. Tilzer and Goldman (1978, table 1, p. 812) also recorded a marked increase in abundance of small-celled (unidentified) algae, with high chlorophyll *a* levels per unit biomass, during late winter mixing on 21 March 1974. The photosynthetic shifts towards a shade-adapted community, as recorded by Tilzer and Goldman, may therefore be due to an increased abundance of shade species of algae rather than cellular adjustments by all members of the community towards a low light regime.

The second ecological feature which distinguishes the shade-adaptiveness of *M. contortum* is the distinctive vertical distribution of this species. During stratification *M. contortum* was rarely found above 75 m, but achieved maximum abundance in the deep euphotic zone. This species is clearly well-suited to growth at low irradiances. The high susceptibility of *Monoraphidium* to copepod grazing combined with its inability to grow faster at elevated irradiances may effectively eliminate it from the surface waters of Tahoe. By contrast, the smaller-celled species *Friedmannia* and *Choricystis* are much less subject to loss by grazing, and this may account for their detectable presence in the surface euphotic zone. Thus, selective grazing pressure and the shade adaptability of Lake Tahoe plankton may be important determinants of vertical community structure.

TABLE 3. *Photosynthetic and respiration rates for* M. contortum *at two temperatures. Each figure is the mean for duplicate incubations.*

	5° C	10° C
Photosynthesis (P_{max}) (μmol $O_2 \cdot$ mg chl $a^{-1} \cdot h^{-1}$)	26.9	33.1
Respiration (dark) (μmol $O_2 \cdot$ mg chl $a^{-1} \cdot h^{-1}$)	6	13
P_{max}/Respiration	4.5	2.6

Monoraphidium contortum is one of several species in Lake Tahoe capable of sustaining a fully operational photosynthetic apparatus during prolonged residence in the aphotic zone. This alga is also capable of organic nutrient transport and utilization, and a heterotrophic mode of metabolism may contribute towards its success in the deep euphotic zone and the aphotic viability of this species (Vincent and Goldman 1980). Shade plants in general and *M. contortum* specifically are characterized by low rates of metabolism. Slow catabolic losses may further promote the long term viability of *Monoraphidium* cells trapped in the subcompensatory light conditions below Lake Tahoe's euphotic zone.

I thank Professor Charles R. Goldman for his support; Drs. A. Horne, N. Lang, P. Richerson and M. Tilzer for their input at critical phases of this work; R. C. Richards for skilled assistance in the field; Ms. S. Dryden for valuable aid with the culture studies; Drs. E. White, C. Howard-Williams and two anonymous referees for critically reviewing the manuscript; Dr. J. A. Gibb and A. D. Pritchard for editorial comments; and Ms. Jan Simmiss for typing each draft. This research was supported in part by a New Zealand National Research Advisory Council Fellowship to the author and NSF grant DEB 76-11095 to C. R. Goldman.

Bjorkman, O. & Holmgren, P. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiol. Plant.* 16:889–914.

Bjorkman, O., Boardman, N. K., Anderson, J. M., Thorne, S. W., Goodchild, D. J. & Pyliotis, N. A. 1972. Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carnegie Inst. Wash. Year Book* 71:115–135.

Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28:355–377.

Chu, S. P. 1942. The influence of the mineral composition of the medium on the growth of planktonic algae. I. Methods and culture media. *J. Ecol.* 30:284–325.

Dozier, B. J. & Richerson, P. J. 1975. An improved membrane filter method for the enumeration of phytoplankton. *Verh. Int. Verein. Theor. Angew Limnol.* 19:1524–9.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* 70:1063–85.

Fleischhacker, P. & Senger, H. 1978. Adaptation of the photosynthetic apparatus of *Scenedesmus obliquus* to strong and weak light conditions. II. Differences in photochemical reactions, the photosynthetic electron transport and photosynthetic units. *Physiol. Plant.* 43:43–51.

Gorham, P. R., MacLachlan, J. L., Hammer, V. T. & Kim, W. K. 1964. Isolation and culture of toxic strains of *Anabaena flos-aquae* (Lyngb.) Bréb. *Verh. Int. Verein. Theor. Angew Limnol.* 15:796–804.

Graham, D. & Whittingham, C. P. 1968. The path of carbon during photosynthesis in *Chlorella pyrenoidosa* at high and low CO_2 concentrations. *Z. Pflanzenphysiol.* 58:418–427.

Knoechel, R. & Kalff, J. 1976. Track autoradiography: a method for the determination of phytoplankton species productivity. *Limnol. Oceanogr.* 21:590–5.

Kormáková-Legnerová, J. 1969. The systematics and ontogenesis of the genera *Ankistrodesmus Corda* and *Monoraphidium* gen. nov. *In* Fott, B. [Ed.] *Studies in Phycology*, E. Schweiz. Verlags., Stuttgart, pp. 75–144.

Krinsky, N. I. 1978. Non-photosynthetic functions of carotenoids. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 284:581–90.

Mullin, M. M., Sloan, P. R. & Eppley, R. W. 1966. Relationship between carbon content, cell volume and area in phytoplankton. *Limnol. Oceanogr.* 11:307–11.

Myers, J. & Graham, J. 1971. The photosynthetic unit in *Chlorella* measured by repetitive short flashes. *Plant Physiol.* 48:282–6.

Nichols, H. W. 1973. Growth media—freshwater. *In* Stein, J. R. [Ed.] *Handbook of Phycological Methods, Culture Methods and Growth Measurements*, Cambridge University Press, pp. 7–24.

Paerl, H. W., Tilzer, M. M. & Goldman, C. R. 1976. Chlorophyll *a* versus adenosine triphosphate as algal biomass indicators in lakes. *J. Phycol.* 12:242–6.

Raven, J. A. & Glidewell, S. M. 1975. Photosynthesis, respiration and growth in the shade alga *Hydrodictyon africanum*. *Photosynthetica* 9:361–7.

Senger, H. & Fleischhacker, P. 1978. Adaptation of photosynthetic apparatus of *Scenedesmus obliquus* to strong and weak light conditions. I. Differences in pigments, photosynthetic capacity, quantum yield and dark reactions. *Physiol. Plant.* 43:35–42.

Strickland, J. D. H. & Parsons, T. R. 1968. A practical handbook of seawater analysis. *Bull. Fish. Res. Board Can.* No. 167. 311 pp.

Tilzer, M. M. & Goldman, C. R. 1978. Importance of mixing, thermal stratification and light adaptation for phytoplankton productivity in Lake Tahoe (California-Nevada). *Ecology* 59:810–21.

Tilzer, M. M., Paerl, H. W. & Goldman, C. R. 1977. Sustained viability of aphotic phytoplankton in Lake Tahoe, California-Nevada. *Limnol. Oceanogr.* 22:84–91.

Vincent, W. F. 1978. Survival of aphotic phytoplankton in Lake Tahoe throughout prolonged stratification. *Verh. Int. Verein. Theor. Angew. Limnol.* 20:401–6.

——— 1980. Mechanisms of rapid photosynthetic adaptation in natural phytoplankton communities. II. Changes in photochemical capacity as measured by DCMU-induced chlorophyll fluorescence. *J. Phycol.* 16:568–77.

——— 1981. Photosynthetic capacity measured by DCMU-induced chlorophyll fluorescence in an oligotrophic lake. *Freshw. Biol.* 11:61–78.

Vincent, W. F. & Goldman, C. R. 1980. Evidence for algal heterotrophy in Lake Tahoe, California-Nevada. *Limnol. Oceanogr.* 25:89–99.

J. Phycol. **18,** 232–240 (1982)

STRUCTURE AND DEVELOPMENT OF THE SECRETORY CELLS AND DUCT SYSTEM IN *MACROCYSTIS PYRIFERA* (L.) C. A. AGARDH[1]

D. J. Grenville, R. L. Peterson, H. L. Barrales and J. F. Gerrath

Department of Botany and Genetics, University of Guelph, Guelph, Ontario N1G 2W1, Canada

ABSTRACT

Sporophytes of Macrocystis pyrifera *(L.) C. A. Agardh of various stages of growth were studied by light microscopy to determine the initiation and ontogeny of secretory cells and the accompanying duct system. Secretory cells are initiated by asymmetric, periclinal divisions of meristoderm cells; subsequent mitoses increase the number of secretory cells associated with each duct. Duct formation occurs by schizogeny of anticlinal cell walls adjacent to the site of secretory cell initiation. Differences in distribution and structure of the duct system occur in various parts of the sporophyte. The duct system does not have openings directly to the sporophyte surface. Histochemical techniques showed that the duct contents are mostly sulfated polysaccharides with perhaps some lipid.*

Key index words: secretory cells; ducts; ontogeny; histochemistry; sulphated polysaccharides; Macrocystis; *Laminariales*

Sporophytes of genera in the Laminariales consist of complex tissue systems involved in photosynthesis, translocation of photosynthates to various sinks, the synthesis and storage of mucilage, and the production of spores. The tissue system involved in the conduction of photosynthates has received the most attention from a structure-function point of view. Tissues involved in the synthesis and storage of mucilage have been studied from various perspectives, including ontogeny (Guignard 1892, MacMillan 1899, Skottsberg 1907, Fritsch 1945, Walker and Bisalputra 1977), histochemistry (Walker and Bisalputra 1977), biosynthetic capabilities (Evans et al.

[1] *Accepted: 28 November 1981.*