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Coexistence and the Comparative Light Relations of the Submersed Macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx.

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Summary. The Eurasian watermilfoil (*Myriophyllum spicatum* L.) has partially replaced wild celery (*Vallisneria americana* Michx.) as a community dominant in the littoral zones of lakes of Madison, Wisconsin. The two species have very different growth forms, with that of *M. spicatum* corresponding more closely to the optimal growth form simulated by the macrophyte production model WEED. The objective of this research was to investigate the mechanisms by which *Vallisneria* could compensate for its nonoptimal growth form and coexist with *Myriophyllum.*

A quantification of midsummer growth form for the two species at a rooting depth of 80–90 cm showed that *M. spicatum* had 68% of its shoot biomass within 30 cm of the surface, whereas *V. americana* had 62% of its leaf biomass within 30 cm of the bottom. *Vallisneria* had a light extinction coefficient ranging from 0.013 to 0.019 $m^2 \cdot g^{-1}$, much higher than the value (ca. 0.006 $m^2 \cdot g^{-1}$) for *M. spicatum.* This indicates less effective penetration of light to lower leaves of *V. americana.* Half-saturation constants describing the light-dependence of carbon uptake in "shade" and "sun" tissues ranged from 60–197 microeinsteins$\cdot m^{-2} \cdot s^{-1}$ for *V. americana*, and 164–365 µeinsteins$\cdot m^{-2} \cdot s^{-1}$ for *M. spicatum.* The optimum temperature for photosynthesis was 33.6° C for *M. spicatum* and 32.6° C for *V. americana*, but *Myriophyllum* was nearly twice as effective at carbon uptake at 10° C. Integration of all of the above features with WEED showed that, for midsummer conditions, *V. americana* more than compensated for apparently disadvantageous morphological features by its greater physiological adaptability to low light regimes. Coupled with the temperature-dependence of photosynthesis, it appears that *V. americana* is favored by midsummer conditions, whereas *M. spicatum* is at an advantage at other times.

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Introduction

The general importance of submersed macrophytes in carbon and nutrient cycling (Wetzel, 1975) justifies expanded research on dominant species. Because of the varied roles of different species in providing habitat for *Aufwuchs*, invertebrates, and fishes (Fassett, 1957), great benefit could be derived from the capability to predict compositional changes in macrophyte communities resulting from environmental changes. The low diversity characteristic of such communities (Curtis, 1959) imparts a particular significance to the nature of constituent species and their influences on community structure.

Simulations with the macrophyte production model WEED (Titus et al., 1975) generated the intuitively comfortable hypothesis that, on the basis of maximizing carbon gain in relation to light availability, the optimum growth form for submersed macrophytes is represented by a concentration of photosynthetic tissues near the water surface. The model suggested that biomass concentration near the surface should be especially favorable in waters characterized by low available light. Field data on plant distribution (Fassett, 1930) were consistent with this hypothesis. Thus, we were intrigued to observe the coexistence of two species with very different growth forms in the littoral zones of University Bay, Lake Mendota, and Lake Wingra (Madison, Wisconsin). The Eurasian watermilfoil (*Myriophyllum spicatum* L.) is quite capable of concentrating photosynthetic tissues near the surface, as shown by Titus et al. (1975). As *Myriophyllum* plants grow upward, lower leaves are shaded and sloughed from the stems, resulting in a canopy-like cover near the water surface. In contrast, wild celery (*Vallisneria americana* Michx.) has a basal rosette of leaves which may extend to the surface but do not form a canopy. We view the growth form of *V. americana* as a constraint on its fitness in eutrophic waters with low transparency and dense macrophyte growths. Indeed, *M. spicatum* has replaced *V. americana* as a community dominant, partially in University Bay (Lind and Cottam, 1969) and more completely in Lake Wingra (Nichols and Mori, 1971).[1] The objective of this research was to investigate the mechanisms by which *V. americana* could compensate for its nonoptimal growth form and coexist with *M. spicatum*.

Research on adaptations essential for coexistence should also provide insight into their relevance for competitive replacement in the face of changing environmental regimes. Several studies have documented compositional changes in submersed macrophyte communities (e.g., Volker and Smith, 1965; Lind and Cottam, 1969; Harman and Doane, 1970; Stuckey, 1971; Chesnut and Barman, 1974), but did not consider the particular plant features which allowed such changes. We have taken the approach of Mooney (1972) that patterns of resource gain and allocation must be understood before one can predict the outcome of interactions between species. Certainly, several aspects of the environmental relations of macrophytes shape these patterns. We will report elsewhere on photosynthetic response to inorganic carbon availability (Titus, Stone, and Adams, unpublished manuscript) and on storage and utilization of nonstructural carbohydrates (Titus and Adams, unpublished manuscript). In this paper we focus on light availability and carbon gain.

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[1] *Vallisneria*, however, retains dominance in certain areas of University Bay and appears to be reestablishing itself in Lake Wingra (Titus, 1977; Johnsen, personal communication)

Light Relations

Light availability has been cited as an important factor controlling the distribution and abundance of submersed macrophytes (Denny, 1972; Sculthorpe, 1967; Spence and Chrystal 1970a). It is an obvious factor to consider in aquatic systems where light may be attenuated very rapidly by water and its suspended load, and by macrophytes themselves. We have observed the attenuation of more than 99% of incident light by dense macrophyte growths within 50 cm of the water surface. Spence and Chrystal (1970a, b) found that plasticity in morphological and physiologial features relevant to light relations provided important determinants of depth ranges for selected *Potamogeton* species. We were more interested in investigating light relations over a relatively narrow depth range which included the interface between *M. spicatum* and *V. americana* in University Bay. We presumed that mechanisms of coexistence would be most important at this interface.

We considered three aspects of light relations of *M. spicatum* and *V. americana*: vertical biomass profiles, macrophyte light extinction coefficients, and the light-dependence of photosynthesis. The first two items relate to light availability as calculated from Eq. (1) (Titus et al., 1975):

$$I_z = I_0 e^{-k_w z - k_m M} \tag{1}$$

where I_z is the photosynthetically active radiation (Phar) at depth z
I_0 is the Phar immediately below the surface
k_w is the light extinction coefficient of water and its suspended load
k_m is the light extinction coefficient of macrophyte shoot tissue M
and M is the dry weight of macrophyte tissue found in a m^2 water column above depth z.

The negative exponential relation for light attenuation by lake water and its suspended load is an approximation that assumes no changes in light quality with depth. Exponential light attenuation by plant tissues has been tested for crop species (see Duncan et al., 1967) and used for submersed macrophytes by Westlake (1964) and Owens et al. (1967). For a given shoot biomass M, more light will be available to lower leaves of a macrophyte with a lower light extinction coefficient. This k_m should depend on leaf shape, thickness, pigment content, and orientation. We reasoned that a macrophyte which allows considerable light penetration to lower leaves should be at an advantage over a second macrophyte species with comparable maximum photosynthetic rates, but which allowed less effective light penetration. In midsummer, maximal carbon uptake rates were similar for *M. spicatum* and *V. americana* at 1400 µeinsteins$\cdot m^{-2} \cdot s^{-1}$ and 25° C (Titus, 1977), indicating that they are nearly equally efficient carbon fixers at high light. Thus, we hypothesized that *Vallisneria* would have a lower k_m than *Myriophyllum* as a partial compensation for nonoptimal growth form.

In addition to facilitating greater light penetration, macrophytes may adapt physiologically to low light availability. Adaptation of the photosynthetic apparatus of submersed aquatic macrophytes was the subject of many early investigations. The studies of Ruttner (1926), Schomer (1934), Manning et al., (1938), Meyer and Heritage (1941) and Meyer et al., (1943) stressed photosynthesis profiles of plants incubated at different depths in various lakes. Some investigators found indications of high light inhibition of photosynthesis, while others did not. Gessner (1938), Ikusima (1966) and Spence and Chrystal (1970 b) directly measured photosynthetic response of selected species of submersed macrophytes to various light intensities. These authors found substantial differences among and within species adapted to different light regimes. Recently Van et al. (1976) measured the light dependence of photosynthesis of three submersed macrophytes, including *Myriophyllum spicatum.* They emphasized differences among rather than within species. We hypothesized that *Vallisneria* would exhibit relatively more efficient use of low light than *Myriophyllum,* again to compensate for apparently disadvantageous growth form.

To interpret the significance to carbon gain of interspecific differences in plant features discussed above, we used the macrophyte production model WEED. This model requires information on the temperature-dependence of photosynthesis, which we also describe in this paper for midsummer conditions. Thus, in this research effort we confirm qualitative observations of differences in biomass profiles in *M. spicatum* and *V. americana,* test two specific hypotheses relevant to compensation by *V. americana* for its nonoptimal biomass profiles, and integrate light relations with the temperature-dependence of photosynthesis via WEED.

Methods

We collected *Myriophyllum spicatum* from Lake Wingra and *Vallisneria americana* from University Bay. Two study sites were necessary because of inadequate *Vallisneria* in Lake Wingra, the site of intensive studies on *M. spicatum* during the International Biological Program. The sites are similar in size (140 and 106 ha, respectively), and are both relatively shallow, alkaline, and eutrophic. University Bay generally has somewhat greater water transparency than Wingra (Titus, 1977).

For the biomass profile of *Vallisneria,* 100 shoots collected at 90 cm near the time of maximum standing crop (July 1976) were separated into 30 cm depth classes, dried and weighed. For comparative purposes, we used similar profiles for *M. spicatum* collected at 80 cm in July 1972 (Titus, 1973).

Macrophyte Light Extinction Coefficients

To measure light extinction coefficients of macrophyte tissues, terminal sections of *Myriophyllum* or basal sections of *Vallisneria,* about 65–70 cm long, were secured to a 1.4 × 1.4 m framed screen. Four vertical poles embedded in lake sediment supported the screen at a water depth of 60 cm for most determinations, allowing the attached plants to just reach the surface and attain a more or less natural orientation. For some readings the frame was raised to within 30 cm of the surface to simulate a surface canopy and assess the effects of changed orientation of plant shoots. With a regular arrangement of plants, this apparatus minimized variability among light readings and thus facilitated the determination of macrophyte light extinction coefficients. A submersible quantum sensor (Lambda Instruments Model LI-185) could readily be held beneath the attached plants without disturbing them. Generally ca. 40–50 light readings were taken at 6 central locations beneath the screen and compared to subsurface light intensities. Readings corrected for light extinction due to water and suspended materials, and due to the frame itself were more stable on cloudless days. Several sets of readings for each species at various times of the day permitted assessment of changes in light extinction coefficients due to differing orientation of plant tissues relative to the sun. At the conclusion of readings plants were harvested, dried, and weighed, and macrophyte light extinction coefficients (k_m) were calculated on the basis of dry weight according to Eq. [2]:

$$k_m = \frac{\ln(I_0/I_z) - k_w z}{M} \tag{2}$$

Equation (2) results directly from manipulations of Eq. (1) to solve for k_m.

The Light-Dependence of Photosynthesis

We collected entire plants and surface leaf tips of *Vallisneria* to provide plant tissues preconditioned to a range of light regimes. Similarly, we collected "sun" and "shade" tissues of *Myriophyllum* and washed all plants to remove loosely attached algae. Plant tissues collected from low light regimes were maintained in shaded containers until we monitored photosynthetic response to different light intensities with differential infrared gas analysis the day after collection. With this method, we secured plants to a central partition within a "Plexiglas" chamber containing filtered (Whatman GFC) lake water. A continuous bubbling air stream generated a rapid flow of water to minimize boundary layer resistance to diffusion of dissolved carbon to leaf surfaces. Titus et al. (unpublished manuscript) demonstrated that it was possible to achieve steady state for this air/water/plant system, at which point changes in airstream CO_2 reflected net photosynthesis of chamber plants. This chamber was situated within a water bath thermostatically maintained at $25 \pm 1°$ C. Plants were exposed first to darkness, then to different light intensities provided from the side by positioning a General Electric "Lucalox" lamp at various distances from the "Plexiglas" water bath, and in some cases by interposing cheesecloth screens between the lamp and the water bath. Light intensities encompassing a range from darkness to full sun (2,000 μeinsteins $\cdot$ $m^{-2} \cdot s^{-1}$) were the same for both species, but the order of exposure was random and thus probably unique for each light curve. Using a Beckman 215-B infrared gas analyzer in an open system arrangement, approximately 1–2 h were required to attain an apparent steady state for the air/water/plant system.

Using nonlinear regression and the subroutine NREG (Madison Academic Computing Center), the resulting photoassimilation (net photosynthesis + the absolute value of "dark" respiration; Marker and Westlake, in press) rates were fit to the following formula:

$$P = P_{\max} \cdot \frac{I}{I + A} \tag{3}$$

where P is photoassimilation rate at light intensity I

$P_{\max}$ is photoassimilation rate at very high light

and A is the light intensity at which half the maximum photoassimilation rate is observed. The use of photoassimilation is operationally simpler than gross photosynthesis, which must include photorespiration. We use this rectangular hyperbola, analogous to Michaelis-Menten enzyme kinetics, simply as a convenient formulation to describe the data. This formulation has been widely used in productivity models (e.g., Duncan et al., 1967; Shugart et al., 1974; Titus et al., 1975) but is not designed to incorporate high light inhibition of photosynthesis, which we observed in a few instances. Thus we excluded photoassimilation rates observed at supraoptimal light intensities from regressions.

The Temperature-Dependence of Net Photosynthesis

To monitor the temperature-dependence of photosynthesis we collected small but entire shoots of *Vallisneria* when water temperatures ranged from 21–25° C. We collected growing tips of *Myriophyllum* from a broader temperature range. Procedures were the same as described above for the light-dependence of photosynthesis, except that we exposed these plants to constant saturating light (1,400 μeinsteins $\cdot$ $m^{-2} \cdot s^{-1}$) at temperatures increasing from 13–39° C. We did not correct for the effects of temperature on CO_2 solubility, as did Stanley and Naylor (1972). Experiments with filtered lake water alone showed no significant difference in dissolved inorganic carbon at steady-state between 15 and 35° C. Thus this lake water did not obey Henry's Law in the limited experimental duration of 1–2 h, and we deemed a correction based on Henry's Law inappropriate. Temperature responses of photosynthesis were always monitored the day after collection of plant material and water.

We normalized the resulting net photosynthetic rates and applied nonlinear regression using subroutine NREG (Madison Academic Computing Center) to fit the data to the following formula:

$$\text{Relative } P = V^X e^{X(1-V)} \tag{4}$$

where

$$V = \frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}}$$

$$X = \frac{W^2\left[1 + \sqrt{1 + \frac{40}{W}}\right]^2}{400}$$

and

$$W = (S-1)\cdot(T_{\max} - T_{\text{opt}})$$

In the formulas defining V, X, and W, T is ambient temperature, T_{opt} is the temperature at which net photosynthetic response is a maximum, $T_{\max}$ is the upper temperature compensation point, and S is the Q10 value for photosynthesis between T_{opt} and (T_{opt} – 10°C). This is an empirical formulation described by Shugart et al. (1974) and used by Titus et al. (1975) in WEED. The function involves a response which rises slowly then more rapidly as the temperature increases to T_{opt}, then declines to zero at $T_{\max}$.

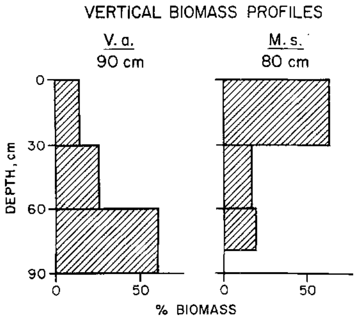
Simulations with WEED

We used the photosynthesis submodel of the macrophyte production model WEED (Titus et al., 1975) to integrate several plant features. This submodel incorporates the effects of light and low light adaptation on macrophyte photosynthesis, as well as temperature effects. For low light adaptation, we assumed a linear decline in A (Eq. 3) with depth in the water column. This assumption has been used in other productivity models (see Duncan et al., 1967). This photosynthesis submodel also incorporates light extinction due to water and that due to macrophyte tissue integrated over 10 cm depth classes in the water column. For both species we used midsummer biomass profiles and a total shoot biomass of 350 g dw·m^{-2}, a figure consistent with *Myriophyllum* (Titus et al., 1975) and *Vallisneria* (Titus, 1977) biomass samples. We used the same maximum photoassimilation rate for *Myriophyllum* and *Vallisneria*, based on laboratory studies under standard conditions (Titus, 1977). For all cases, we simulated total photoassimilation for a sunny summer day in g C for a m^2 water column at a rooting depth of 1.2 m with different water transparencies for *Vallisneria* and *Myriophyllum*.

Results and Discussion

Biomass Profiles

Vallisneria and *Myriophyllum* exhibited inverse patterns of allocation of shoot biomass at 80–90 cm rooting depths (Fig. 1). *Myriophyllum* had 68% of its shoot biomass within 30 cm of the surface, and *Vallisneria* had 62% of its shoot biomass within 30 cm of the sediment/water interface. This clearly quanti-



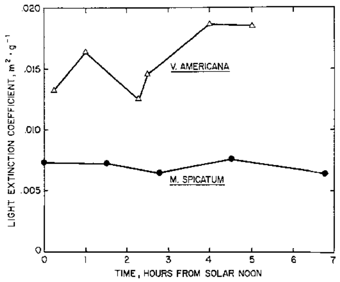


Fig. 1. Midsummer vertical biomass profiles for *Myriophyllum spicatum* and *Vallisneria americana*

Fig. 2. Light extinction coefficients of macrophyte tissue (k_m) for *Myriophyllum spicatum* and *Vallisneria americana* at different times of the day. Each point is the result of ca. 40–50 light readings

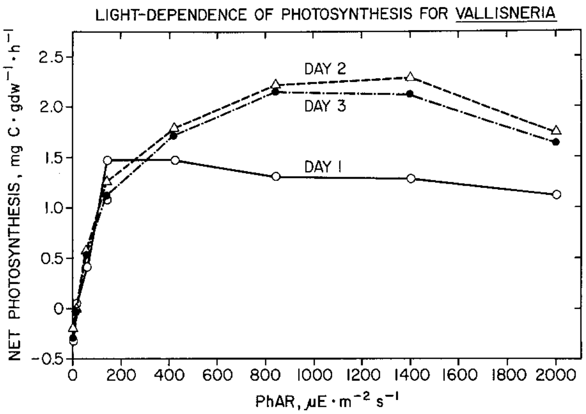
Table 1. Ranges of light extinction coefficients (k_m) of plants with vertical orientation vs. those with "canopy" orientation. k_m in $m^2 \cdot g^{-1}$

	Vertical k_m	"Canopy" k_m
Myriophyllum spicatum	0.0055–0.0066	0.0066–0.0077
Vallisneria americana	0.0126–0.0188	0.0235

fied the apparently non-optimal growth form of *Vallisneria* relative to *Myriophyllum*.

Macrophyte Light Extinction Coefficients

Light extinction coefficients for both macrophytes are plotted (Fig. 2) vs. time in hours from solar noon. The k_m for *Myriophyllum* was constant through the day, as contrasted to the extinction coefficient for *Vallisneria*, which increased with decreasing sun angle. In other words, the orientation of *Vallisneria* plants was less conducive to light penetration at low than at high sun angles. More importantly, *Vallisneria* did not compensate for its presumed disadvantageous growth form by facilitating light penetration. Extinction coefficients for *Vallisneria* were generally twice as high as those of *Myriophyllum*. Approximately 30% of subsurface light will penetrate 200 g dw of plants·m^{-2} with a k_m of 0.006, while only about 5% will penetrate the same biomass with a k_m of 0.015. Ranges of light extinction coefficients for vertically oriented vs. "canopy" tissues for both species are shown in Table 1. They indicate that in general, "canopy" tissues have higher light extinction coefficients than vertically oriented shoots. The difference between the two orientations was particularly noticeable for



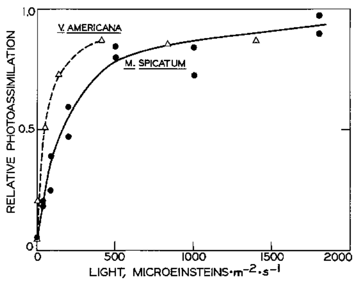


Fig. 3. Light-dependence of net photosynthesis of a *V. americana* plant on the first, second, and third days after collection

Fig. 4. Light-dependence of photoassimilation for *M. spicatum* and *V. americana* with regression curves described by Eq. 3. The A values for these "shade" tissues are 60 μE · m^{-2} · s^{-1} for *V. americana* and 175 μE · m^{-2} · s^{-1} for *M. spicatum*

Vallisneria, suggesting that it could be especially disadvantageous for *Vallisneria* to form a canopy. Thus, on the basis of overall growth form and light extinction coefficients, *Vallisneria* is at a disadvantage compared to *Myriophyllum*.

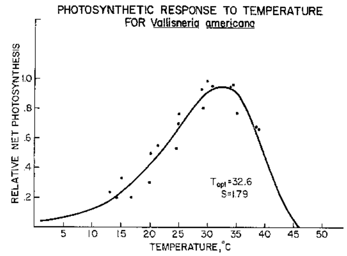
The Light-Dependence of Photosynthesis

To evaluate potential physiological compensation for disadvantageous morphological features, we first collected entire *Vallisneria* plants, with the intention to document light response in "sun" tissues. We were surprised to find the response shown as "Day 1" in Fig. 3. This response with light saturation at 140 μeinsteins·m^{-2}·s^{-1} and apparent high light inhibition of photosynthesis is more like that of a typical "shade" plant. Manning et al. (1938) found no high light inhibition in *V. americana*. Either *Vallisneria* cannot effectively use high light or the shorter leaves and basal parts of the longer leaves, preconditioned to low light, dominated the response of the whole plant. We resumed work on the same plant for the following two days to find the responses for Days 2 and 3 (Fig. 3). A marked change in the light response of this plant occurred within 24 h, apparently induced solely by the exposure to high light during measurement of the light-dependence of photosynthesis. An increase in the light intensity required to saturate *Vallisneria* photosynthesis was observed, concomitant with higher photosynthetic rates at 2,000 μeinsteins·m^{-2}·s^{-1}, though some high light inhibition remained. Thus, *Vallisneria* appears to acclimate very rapidly to increasing light.

Data points and regression curves for shade-adapted tissues of *Vallisneria* and *Myriophyllum* are shown in Fig. 4. Relative photoassimilation is comparable for the two species at high light (full sun is ca. 2,000 μE·m^{-2}·s^{-1}), but quite

Table 2. Range of A values (Eq. 3) describing the light-dependence of photoassimilation. A in μeinsteins·m^{-2}·s^{-1}

	A range	Number of curves fit
Myriophyllum spicatum	164–365	11
Vallisneria americana	60–197	7



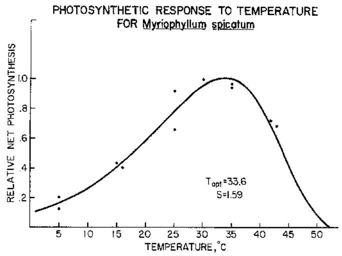


Fig. 5. Temperature-dependence of net photosynthesis for *Vallisneria americana*. Regression curve (solid line) results from fitting data to Eq. 4.

Fig. 6. Temperature-dependence of net photosynthesis for *Myriophyllum spicatum*. Regression curve determined as in Fig. 5

different at low light. As indicated by the differences in half-saturation constants, or *A* values, *Vallisneria* is a much more efficient fixer of carbon at low light intensities. This is supported not simply by these two extreme cases, but also from the ranges of *A* values (Table 2) for all replicated responses of both species. The ranges barely overlap, with that of *Vallisneria* consistently indicating more efficient use of low light. This is in line with the results of Meyer et al. (1943), who found *V. americana* to be the most shade-adapted of 5 submersed macrophytes.

The foregoing results indiate that *Vallisneria* can at least partially compensate for non-optimal morphology by physiological adaptation to low light availability, but did not reveal the significance of this compensation. To evaluate this question for *Vallisneria* with WEED, we needed to know parameters of the temperature-dependence of photosynthesis.

Temperature-Dependence of Photosynthesis

Results of nonlinear regressions on temperature response data for *Vallisneria* and *Myriophyllum* are shown in Figs. 5 and 6, respectively. Table 3 summarizes parameter values for these regression lines. Temperature optima do not differ substantially between the species. The upper temperature compensation points do differ considerably, and suggest that *Myriophyllum* would respond better to very high temperatures than would *Vallisneria*, at least on a short-term

Table 3. Parameters of Eq. (4) from nonlinear regressions on the temperature-dependence of net photosynthesis

	T_{opt}	S	T_{max}
Myriophyllum spicatum	33.6	1.59	54.7
Vallisneria americana	32.6	1.79	47.1

basis. There are few data points in this range, however, and these temperatures are so high as to have little significance in Lake Wingra and University Bay. The most important differences between the species are reflected by their values of S (Eq. 4), an indicator of the rate of increase of net photosynthetic response to increasing temperatures. *Vallisneria* has the higher S value, indicating that, on a relative basis, *Vallisneria* is more "specialized" for midsummer temperatures, and *Myriophyllum* is better able to photosynthesize at low temperature. This is apparent from Figs. 5 and 6. If both species had net photosynthetic rates of 1.0 at T_{opt}, *Myriophyllum* net photosynthesis would be 1.9 times as high as *Vallisneria* photosynthesis at 10° C. These differences are based on the temperature-dependence of net photosynthesis in plants adapted to summer temperature regimes, and the apparent ability of *Myriophyllum* to acclimate to different temperature regimes (Adams and Stone, unpublished) would probably enhance the distinction between *Myriophyllum* and *Vallisneria* in spring and fall. This distinction is consistent with observed phenologies. *Vallisneria americana* has photosynthetic tissues in the water column for just over four months in University Bay, whereas *M. spicatum* has green tissues throughout the year. The ability of *Myriophyllum* to extend its growing season relative to that of *Vallisneria* by fixing carbon effectively at low temperature has probably been an important factor in its virtual replacement of *Vallisneria* in Lake Wingra and its partial replacement of *Vallisneria* in University Bay.

Simulations

The results of simulations are shown in Fig. 7 as total daily photoassimilation for *M. spicatum* and *V. americana* for several values of k_w, the light extinction coefficient of water and suspended matter. Within the range of light extinction coefficients we have measured for Lake Wingra and University Bay (0.7–$1.7\ m^{-1}$), the simulations indicate that *Vallisneria* is at a distinct advantage over *Myriophyllum* with respect to carbon gain. Thus, the superior physiological adaptation of *Vallisneria* to low light more than compensates for its disadvantageous morphological features relative to *Myriophyllum*, a result we found surprising. This result also serves as a reminder of the probable sensitivity of most models to subtle variations in the light-dependence of photosynthesis, and thus the importance of such variations. Furthermore, these simulations lead to a conclusion consistent with the temperature-dependence of photosynthesis for

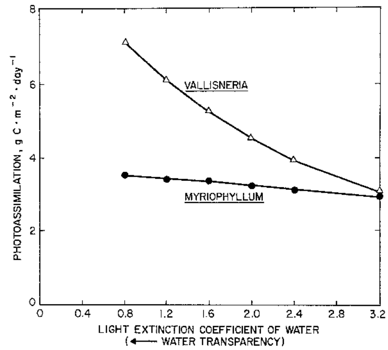


Fig. 7. Results of simulations with WEED for total daily photoassimilation of *Myriophyllum spicatum* and *Vallisneria americana* with different water transparencies. WEED incorporates biomass profiles, light extinction due to water and macrophytes, maximum photosynthetic rates, and the light- and temperature-dependence of photoassimilation

Vallisneria: *Vallisneria* is a summer "specialist", and appears capable of relatively high rates of carbon gain even in dense stands in midsummer.

Another point of interest in Fig. 7 is that photoassimilation rates of *Myriophyllum* are little affected by marked decreases in water transparency. This appears reasonable, as photosynthetic tissues of *Myriophyllum* are concentrated near the surface in midsummer and barely subject to changes in water transparency. On the other hand, photoassimilation rates for *Vallisneria* decline rapidly with decreasing water transparency. This is in accord with the distribution of *Vallisneria* leaves toward the bottom, and clearly reveals the greater reliance of *Vallisneria* on water clarity. With an extremely high light extinction coefficient of water, there is essentially no difference between photoassimilation by *Vallisneria* and *Myriophyllum* as predicted by WEED. This trend in the simulations leads to the prediction that a decrease in water transparency in University Bay (Lake Mendota) would be advantageous for *Myriophyllum* over *Vallisneria*, whereas increasing water transparency in Lake Wingra would favor *Vallisneria*. This prediction is most appropriate for areas transitional between those dominated by each of the two species, and is consistent with observed vegetational changes. With decreasing water transparency, *Vallisneria americana* has disappeared or declined in importance in lakes in New York (Oglesby et al., 1976) and Florida (Chesnut and Barman, 1974), although not in Lake Erie (Stuckey, 1971). Declining water transparency was probably also involved in the near elimination of *Vallisneria* from Lake Wingra.

University Bay apparently presents a different situation from the more turbid Lake Wingra. According to Stewart and Hasler (1972), the water transparency in Lake Mendota has not changed since Birge took readings in 1916. The replacement of *Vallisneria* by *Myriophyllum* appears to have occurred primarily in deeper water, as the present distribution of *Vallisneria* in depths less than 2 m represents a considerable restriction from its former distribution to depths in excess of 5 m (Denniston, 1921). We now have enough data to speculate on the important adaptations involved in this replacement pattern, a seemingly counterintuitive pattern in which the species better able to fix carbon at low light intensities is restricted to shallower water. Increasing depth can be viewed as an agent reducing the availability of light to short-statured plants, such as *Vallisneria*. *Myriophyllum*, although well-suited to deeper water in midsummer by virtue of its long stems and concentration of leaves near the surface, must face the problem of growth toward the surface with limited available light. We speculate that the low light extinction coefficient of *Myriophyllum* tissue coupled with its demonstrated ability to store considerable quantities of non-structural carbohydrates (Titus, 1977; Titus and Adams, unpublished manuscript) are adequate to compensate for its relatively inefficient carbon fixation at low light intensities. Growth toward the surface in spring when water temperatures are low could reduce the costs of maintenance respiration at a critical growth phase. Further research will be required to test these speculations regarding the depth zonation of these two plants.

Conclusion

Myriophyllum spicatum is able to adapt to low light availability via leaf sloughing and the attendant plasticity in growth form. In contrast, *Vallisneria americana* adjusts to low light by virtue of its greater physiological adaptability as evidenced by more efficient carbon fixation at low light. Although *Vallisneria* can not have the morphological plasticity of *Myriophyllum*, the basis for the limitations to the physiological adaptability of *Myriophyllum* to low light is not obvious. Efforts to determine the nature of such constraints could yield valuable insight into the limits to adaptation (Antonovics, 1976).

This study provides an example of coexistence which has elements of both spatial and temporal partitioning of resources. These macrophytes are like the herbaceous plants of Bratton (1976) and Thomas and Dale (1976) in that they occupy different microhabitats within the community. The former distribution of *V. americana* to much greater depths in University Bay and the presence of *M. spicatum* in shallow water in Lake Wingra attest to the ability of each species to survive at depths well beyond the observed interface, however.

A degree of temporal partitioning occurs in that *V. americana* is a summer "specialist". This is not as strong as the temporal partitioning observed by Bratton (1976) or Taylor and Pearcy (1976), however, since the growing season of *V. americana* is completely included within the growing season of *M. spicatum*. Because there is considerable temporal overlap and potential spatial overlap, it seems reasonable to view the interface between the two species as a result of balances involving both the benefits of establishment and different constellations of adaptations. This balance could be disrupted either by disturbance or more gradual environmental changes.

An interaction of light, temperature, and food relations contributes to an explanation of the coexistence of two plants with very different growth forms, and at the same time provides insight into temporal and spatial variation in the distribution of these plants.

We believe it has been informative to consider both physiological and morphological features of plants, as Bradshaw (1965) advocated, in conjunction with a modeling approach. Although revising assumptions of the model may modify our estimate of the water transparency at which photoassimilation by *Myriophyllum* and *Vallisneria* is equivalent, our approach has clarified circumstances under which each of our study species is at an advantage over the other. Understanding such advantages is a necessary, though only partial, basis for the prediction of the outcome of competition under a wide range of environmental conditions.

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