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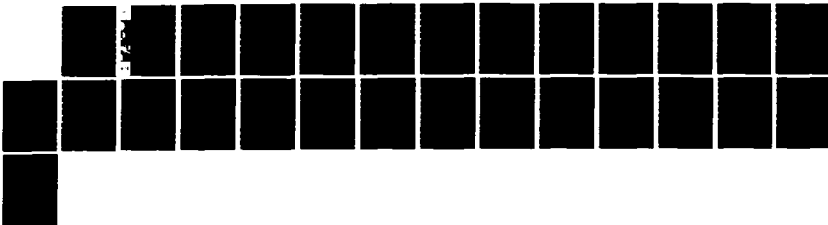
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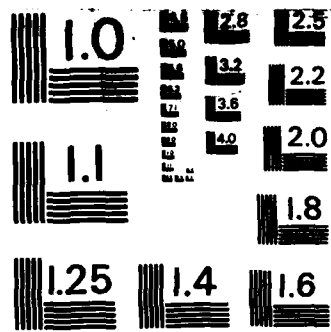
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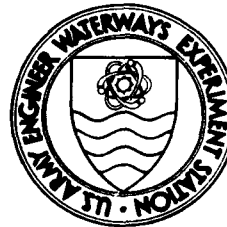
**INTERACTIVE INFLUENCES OF LIGHT
AND TEMPERATURE ON THE GROWTH
AND MORPHOLOGY OF SUBMERSED
FRESHWATER MACROPHYTES**

by

John W. Barko, Dwilette G. Hardin, M. Susan Matthews

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February 1984

Final Report

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20. ABSTRACT (Continued).

Total biomass production in all species generally increased with both increasing light and increasing temperature (to at least 28°C). However, variations in biomass and other parameters as well were highly influenced by the interactive relationship between light and temperature. Shoot density correlated directly with biomass production in these species under all experimental conditions. In contrast, light and temperature elicited opposing responses in shoot length, which decreased with increasing light but increased with increasing temperature. The extent of variations in leaf morphology differed among species, apparently reflecting intrinsic differences in heterophyllous capabilities.

Light and temperature appear to interact in influencing lower limits of macrophyte depth distribution and related variations in the duration of seasonal growth. Temperature is likely to assert a strong influence on the latitudinal distribution of submersed freshwater macrophytes, dependent upon species-specific differences in response to temperature and basic differences in macrophyte life cycle.

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Preface

This investigation was supported by the Aquatic Plant Control Research Program (APCRP), sponsored by the Office, Chief of Engineers (OCE), and managed by the U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. The OCE Technical Monitor was Mr. Dwight L. Quarles.

Manager of the APCRP was Mr. J. Lewis Decell. General supervision was provided by Drs. Rex L. Eley and Robert M. Engler, Division and Group Chiefs, respectively, in the Ecosystem Research and Simulation Division of the Environmental Laboratory (EL). Investigators were Dr. John W. Barko, Ms. Dwilette G. Hardin, and Ms. M. Susan Matthews. Dr. Barko wrote this report.

The authors wish to acknowledge the constructive review comments provided by Mr. Derrick J. Bates and Mr. R. Michael Smart of the EL. Mr. Bates also provided statistical assistance during the conduct of the investigation. The sediment used in the investigation was collected by Dr. Jack C. Serwold.

Chief of the EL during the conduct of this investigation was Dr. John Harrison. Commanders and Directors of the WES during the investigation and preparation of the report were COL Nelson P. Conover, CE, and COL Tilford C. Creel, CE. Technical Director was Mr. F. R. Brown.

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INTERACTIVE INFLUENCES OF LIGHT AND TEMPERATURE
ON THE GROWTH AND MORPHOLOGY OF SUBMERSED
FRESHWATER MACROPHYTES

Introduction

1. In most aquatic systems, variations in incident solar radiation with season and/or depth promote corresponding variations in water temperature. Particularly in systems supporting dense aquatic macrophyte populations, vertical profiles of light and water temperature in the littoral zone roughly parallel one another (Dale and Gillespie 1977; Bowes, Holaday, and Haller 1979). The influences of light and water temperature on the growth of submersed macrophytes are difficult to separate from one another in nature; yet, both of these factors may be of equal importance with regard to macrophyte growth (refer to Barko and Smart 1981a and literature cited therein).

2. Morphology is linked with growth in submersed macrophytes; however, the extent to which differences in growth promote morphological variations or vice versa is not always clear. Species capable of morphological adjustments over a broad range of environmental conditions, particularly if these adjustments confer advantaged growth, may be more competitive than less adaptable species. A high degree of morphological flexibility may also promote increased distributional potential. For example, Spence and Chrystal (1970a, b) provide experimental evidence suggesting that differences in the maximum rooting depth of two coexisting *Potamogeton* species may reflect intrinsically different ranges in their specific leaf area since this characteristic apparently affects the light compensation point in photosynthesis. In a related connection, the rapid spread of the introduced species, *Hydrilla verticillata*, in Florida reflects its tremendous competitive ability imparted by extensive foliar canopy formation at the water surface (Haller and Sutton 1975).

3. The presently reported investigation is an extension of the work described in Barko and Smart (1981a), wherein variations in the growth

and metabolism of several submersed macrophytes introduced into North America were examined over broad experimental ranges of light and temperature. This report will provide similar information, but with greater emphases on morphological variations in considering the responses of three native North American species, *Elodea canadensis* Michx., *Potamogeton nodosus* Poiret (*P. americanus*), and *Vallisneria americana* Michx., to light and temperature.

Materials and Methods

4. The investigation was conducted during the months of June and July 1980 in white fiberglass tanks housed in the greenhouse facility of the U. S. Army Engineer Waterways Experiment Station (WES) Environmental Laboratory, Vicksburg, Miss. Eighteen tanks were used in the study. Each tank provided a volume of ca. 1200 l and a water depth of ca. 83 cm. Tanks were positioned into six groups of three tanks each. Water temperature was assigned to each group at one of six levels ranging between 12° and 32°C in 4°C increments. Within all groups a single light level (low, mid, or high) was randomly assigned to each of the three composite tanks, providing a broad range of irradiance at all temperature levels. Midday irradiance (PAR*) measured at a midpoint in the tanks on a cloudless day was ca. 100, 600, and 1500 $\mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at low, mid, and high light levels, respectively. Water temperatures were continuously maintained at specified levels ($\pm 1^\circ\text{C}$) using water circulating units possessing both heating and cooling capacities. Light levels were provided by neutrally absorptive shade fabrics allowing natural diel fluctuations in irradiance. A more detailed description of the greenhouse facility and ancillary apparatus providing semicontrolled conditions for macrophyte research is presented in Barko and Smart (1981a) and Smart and Barko (1978).

5. Macrophytes were grown on well-mixed surficial sediment obtained by dredging from Lake Washington in the State of Washington. Physical and chemical characteristics of this sediment (not presented)

* PAR = photosynthetically active radiation.

were very similar to those reported in Barko and Smart (1981a) for sediment obtained from approximately the same location 1 year previously.

6. The chemical composition of the solution used in the investigation is provided in Table 1. This solution differed only slightly (owing to the addition of KCl) from the solution used in the related investigation of Barko and Smart (1981a). As in the previous study, most essential nutrients were excluded from the solution in order to minimize algal growth in the tanks. It was assumed that the sediment would provide these nutrients via root uptake (refer to Barko and Smart 1981b; Barko and Smart 1980; Patterson and Brown 1979).

Table 1
Solution Chemical Composition

<u>Solution Chemistry</u>	<u>Concentration, mg·ℓ⁻¹</u>
Constituent*	
NaHCO ₃	84.0
CaCl ₂	66.0
KCl	2.9
HCl	5.1
Determination**	
Alkalinity	1.0 meq·ℓ ⁻¹
Conductivity	290 μmhos·cm ⁻¹ (20°C)
pH	7.5

* Added to distilled water.

** Determinations made 24 hr after solution preparation.

7. The macrophyte species included in this investigation were obtained from commercial sources in the United States. The rhizomatous species, *Potamogeton* and *Vallisneria*, were planted in sediment containers providing a surface area of ca. 560 cm². *Elodea* was planted in smaller containers providing a surface area of ca. 100 cm². Sediment depths in the large and small containers were similar at ca. 10 and 13 cm, respectively. Propagule type, number, and biomass of each species initially allocated to individual sediment containers are summarized in Table 2. Three replicate containers of each species were introduced into each of

Table 2
Propagule Type, Number, and Biomass of Each Species Allocated
to Sediment Containers

	Plant Species		
	<u><i>Elodea</i></u>	<u><i>Potamogeton</i></u>	<u><i>Vallisneria</i></u>
Propagule type*	Apical tip	Rhizome	Juvenile plant
Number of propagules per container	6	9	6
Biomass per container**	0.15 \pm 0.02	1.18 \pm 0.05	0.81 \pm 0.04

* Apical tips of *Elodea* and juvenile plants of *Vallisneria* were ca. 10 cm in length. Rhizomes of *Potamogeton* in which growth had been initiated were selected for uniformity in both size and number of nodal points.

** Biomass means and standard errors were based on triplicate determinations and are presented as grams dry mass.

the 18 tanks. *Elodea* and *Potamogeton*, anticipated to form dense foliar canopies, were positioned at opposite ends of each tank to avoid cross-species entanglement of shoots. *Vallisneria*, with a lower vertical growth profile, was positioned in the middle of each tank. Durations of growth were chosen to allow adequate time for the development of treatment-related differences in growth and morphology, yet to minimize tissue deterioration associated with senescence under maximal growth conditions. *Potamogeton*, the most rapidly growing species, was harvested after 6 weeks compared to 8 weeks of growth allowed for *Elodea* and *Vallisneria*.

8. Harvesting procedures and subsequent determinations of a variety of growth and morphological characteristics were accomplished over several days for each species. The exposure of plants to nonexperimental conditions during harvesting was usually limited to less than 0.5 hr. Containers were individually removed from the greenhouse tanks with the immediate processing of plant materials performed in a controlled environment at 24°C under subdued light. Shoot length in *Elodea* and *Potamogeton* was determined as the distance from shoot bases cut at the sediment surface to the average position of shoot apices. Because of

the prostrate condition of *Elodea* under some experimental conditions, the actual height of its shoots was measured in the greenhouse tanks prior to harvesting. Shoot density (the number of shoots per container in *Elodea* and *Potamogeton* and the number of whole plants per container in *Vallisneria*) was determined by direct counting. Branch density (number of branches per shoot) in *Elodea* was determined as an average for five representative shoots from each container. Similarly, leaf length and breadth in *Potamogeton* and *Vallisneria* were determined as averages for each container calculated from measurements made on 10 leaves. Leaf length was measured from the point of leaf intersection with the shoot to the leaf apex. In *Vallisneria*, this parameter was equated with shoot height. Leaf breadth was measured at the widest point along the length of the leaf in both species. Leaf area was calculated from length (L) and breadth (B) data ($\text{area} = \pi L B/4$) assuming approximate conformity in leaf shape to an ellipse. Shoot and root biomass were determined for plants according to the procedures described in Barko and Smart (1981a). Root biomass in *Potamogeton* and *Vallisneria* included rhizomatous materials in addition to true roots.

9. All experimental data considered in this report were statistically analyzed using the analysis of variance (ANOVA) and post-ANOVA capabilities of the Statistical Analysis System (Raleigh, N. C.). Growth and morphological response variables included in Figures 1-4 are presented as means (N = 3) and are contrasted across experimental ranges of both light and temperature using Duncan's multiple range test. All statements of significance made in the text refer to the 5-percent level or less of statistical significance.

Results

Biomass and shoot morphology

10. *Elodea*. Shoot biomass, root biomass, and shoot density in *Elodea* increased with increasing light, particularly between low and mid levels, across the entire range of temperature conditions (Figure 1). At the two higher light levels (mid and high), shoot biomass increased

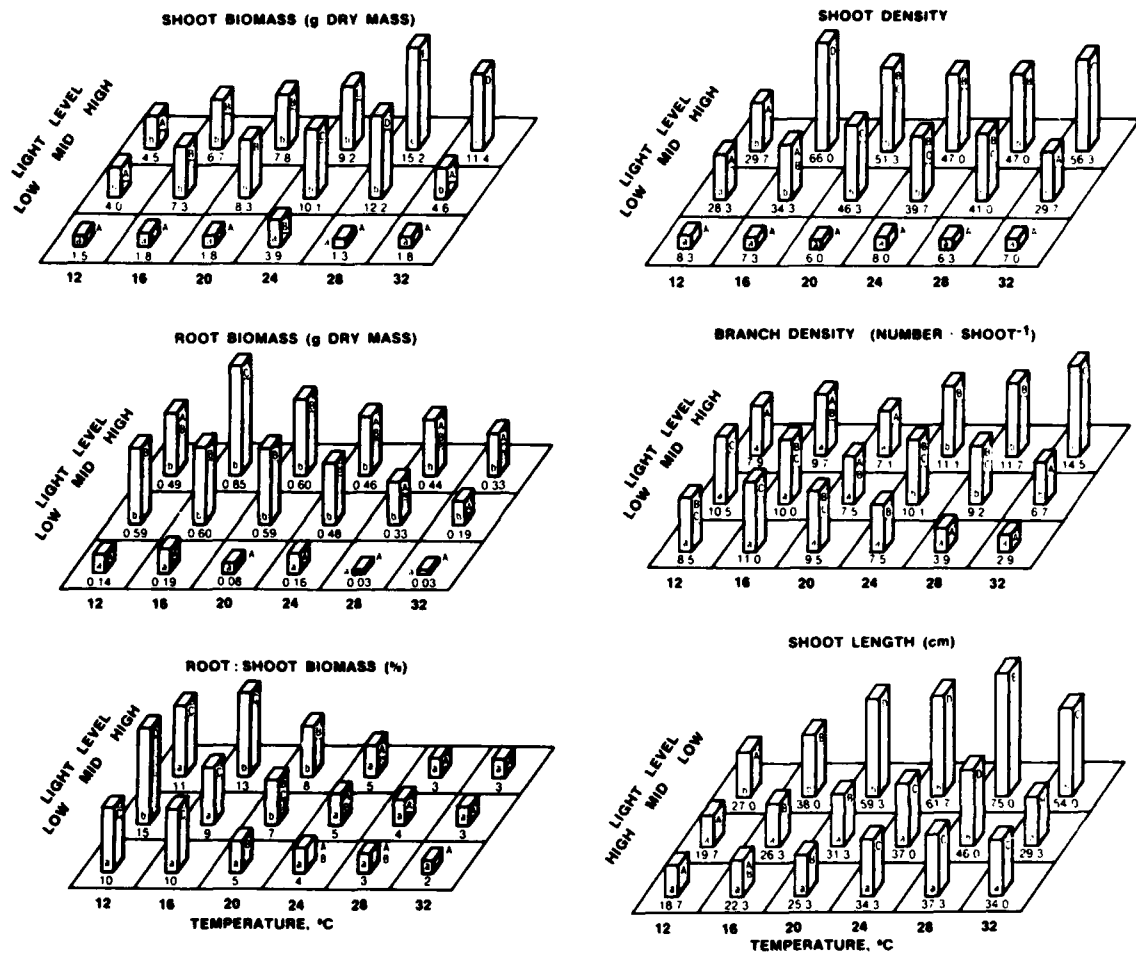


Figure 1. Growth and shoot morphology in *Elodea*. Within each subfigure, numerical values printed at the base of bars sharing the same letter (upper case among temperature levels and lower case among light levels) do not differ significantly from each other. The order of presenting light levels in the shoot length subfigure is reversed in comparison with the order used in the other subfigures

with increasing temperature up to 28°C. In direct contrast, root biomass increased with decreasing temperature down to 16°C. At the low light level, overall biomass production (shoots and roots) and shoot density in *Elodea* were essentially unresponsive to temperature. Ratios of root to shoot biomass varied to only a minor extent with light, but increased dramatically with decreasing temperature across the entire range of light conditions. Roots contributed very little to overall biomass production in *Elodea*.

11. Unlike the consistently positive response of shoot density to increasing light, branch density was unaffected by light except at the higher temperature levels ($>24^{\circ}\text{C}$), where the response of these two variables mimicked one another. Although temperature promoted significant variations in shoot and branch densities, these variations demonstrated no clearly consistent patterns.

12. Shoot length in *Elodea* increased with increasing temperature up to 28°C at all (particularly at the lower) light levels, and increased with decreasing light across the entire range of temperature conditions. At mid and high light levels, respectively, only 24 (+13) and 14 (+8) percent of the length of *Elodea* shoots contributed to actual shoot height (i.e. vertical growth) measured in the greenhouse tanks. At these higher light levels, *Elodea* grew in a dense and distinctly prostrate fashion that contrasted with the near completely vertical profile of shoots at the low light level. Temperature had no effect on vertical shoot elongation in *Elodea*.

13. *Potamogeton*. Shoot biomass, root biomass, and shoot density in *Potamogeton* increased with increasing light across the entire range of temperature conditions (Figure 2). At the two higher light levels, shoot biomass and shoot density increased continuously with increasing temperature, but maximum root biomass occurred at intermediate (20° - 24°C) temperature levels. An increased production of shoot biomass and increased shoot density with increasing temperature occurred in a pronounced fashion at the high light level and to a more moderate extent at the mid light level. Overall biomass and shoot density were largely unresponsive to differences in temperature at the low light level. Root to shoot biomass ratios responded rather erratically to temperature at the low light level, but at the higher light levels demonstrated a general increase with both increasing light (at temperatures $<28^{\circ}\text{C}$) and with decreasing temperature. The production of roots and rhizomes (root biomass) represented a substantial fraction of overall biomass production in *Potamogeton*.

14. Shoot length in *Potamogeton* was uniquely responsive to differences in temperature at the low light level, where a distinct maximum in

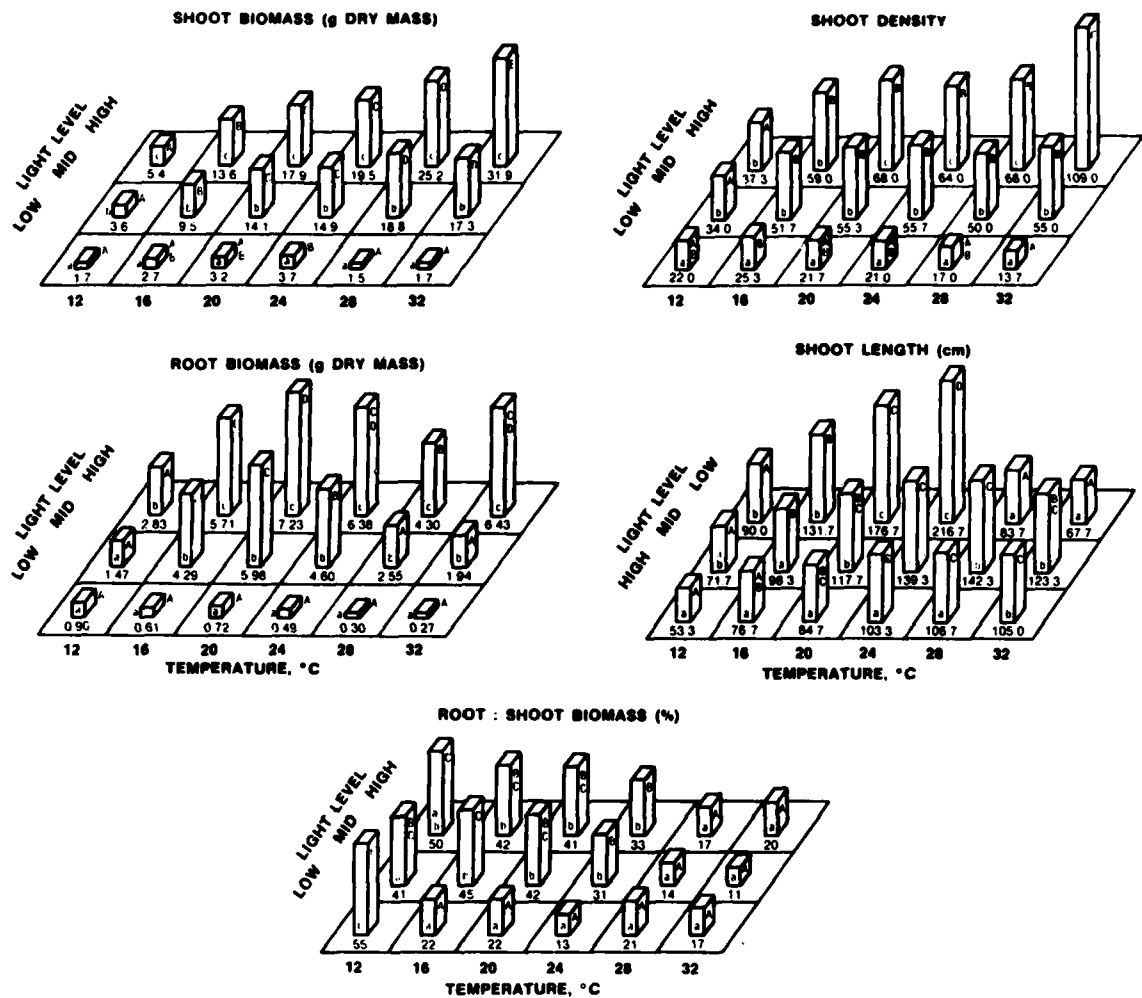


Figure 2. Growth and shoot morphology in *Potamogeton*. Within each subfigure, numerical values printed at the base of bars sharing the same letter (upper case among temperature levels and lower case among light levels) do not differ significantly from each other. The order of presenting light levels in the shoot length subfigure is reversed in comparison with the order used in the other subfigures

this variable occurred at 24°C. At higher light levels, shoot length increased moderately with increasing temperature up to 24°-28°C. At temperatures between 12° and 24°C, shoot length increased with decreasing light, but at 28° and 32°C maximum elongation of shoots occurred at the mid light level.

15. *Vallisneria*. At temperatures of 20°C and above, overall biomass production and shoot density in *Vallisneria* generally increased

with increasing light, particularly between the low and mid levels (Figure 3). Shoot length at temperatures between 20° and 32°C increased with decreasing irradiance. Shoot biomass, root biomass, shoot density, and shoot length increased with increasing temperature up to 28°C at mid and high light levels. It is apparent in the response of each of these variables that the growth of *Vallisneria* was severely restricted at temperatures below 20°C. Root to shoot biomass ratios increased with

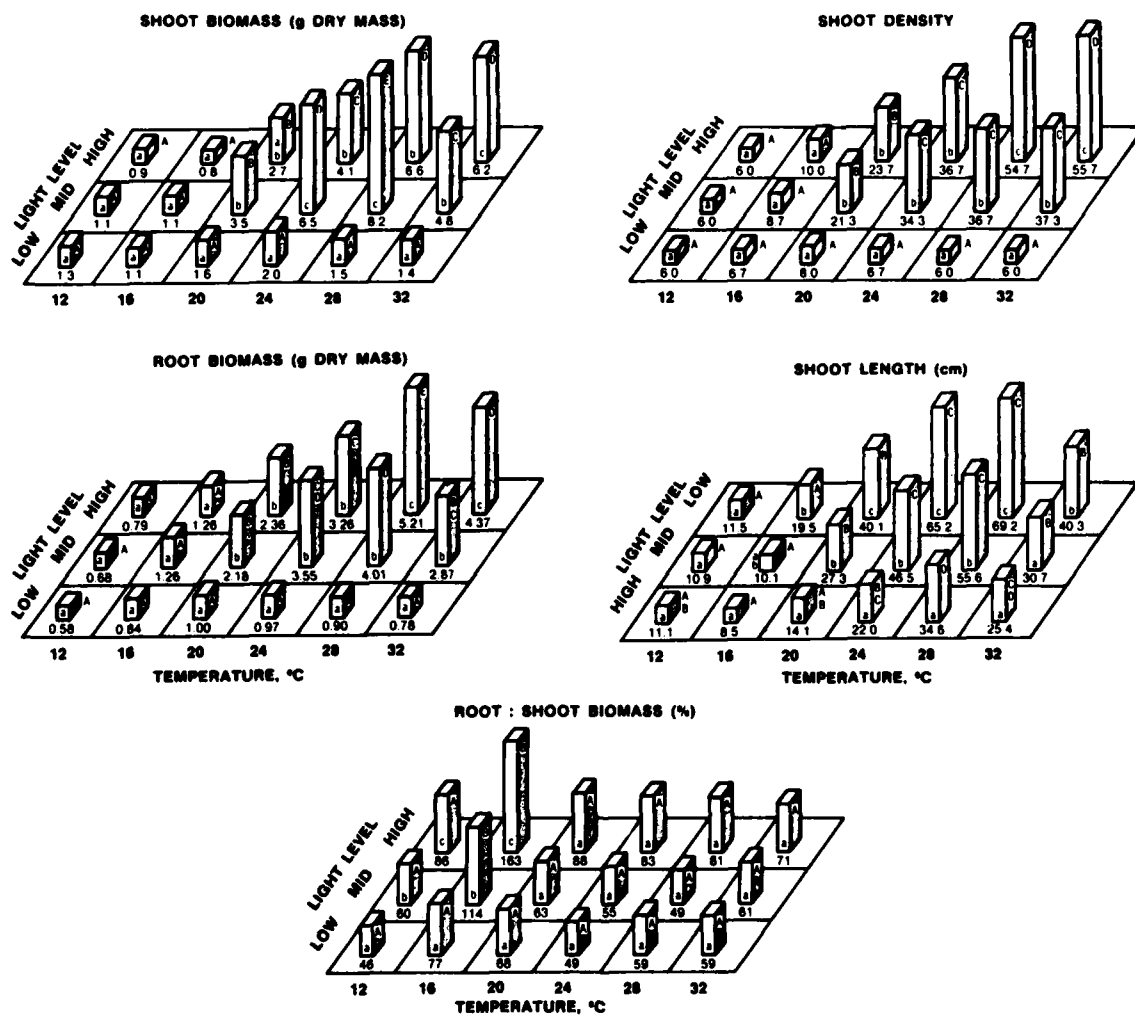


Figure 3. Growth and shoot morphology in *Vallisneria*. Within each subfigure, numerical values printed at the base of bars sharing the same letter (upper case among temperature levels and lower case among light levels) do not differ significantly from each other. The order of presenting light levels in the shoot length subfigure is reversed in comparison with the order used in the other subfigures

increasing light at 12° and 16°C, but were unresponsive to either light or temperature at the greater temperature levels. The production of roots and rhizomes (root biomass) represented a substantial fraction of overall biomass production in *Vallisneria*.

Leaf morphology in
Potamogeton and *Vallisneria*

16. In the submersed leaves of *Potamogeton*, surface area and, to a lesser extent, L:B ratio increased with decreasing temperature below 24°C (Figure 4). With the exception of a moderate increase in surface area with increasing light at temperatures between 12° and 20°C, the form of submersed *Potamogeton* leaves was unaffected by light. Floating leaves of *Potamogeton* were formed only at temperatures between 20° and 32°C and increased in number with both increasing temperature and increasing light (data not presented). Variations in the form of these floating leaves due to the effects of either light or temperature were minor and demonstrated no clearly consistent patterns. Both surface area and L:B ratio in leaves of *Vallisneria* increased with increasing temperature up to 28°C. Leaf form in *Vallisneria* was unaffected by light at 12° and 16°C, but at the higher temperature levels both surface area and L:B ratio increased with decreasing light.

17. In both leaf types of *Potamogeton* and in the leaves of *Vallisneria* the responses of leaf surface area and L:B ratio were roughly similar to one another (Figure 4). Patterns of response among these leaf variables primarily reflected differences in leaf length, which varied over a much broader range than leaf width in this investigation (data not presented). Temperature affected a greater range of response in length than did light. This is generally evident in the response of the leaf variables considered herein because of their high correlations with leaf length (Table 3). The somewhat lower correlations obtained in considering floating leaves of *Potamogeton* (Table 3) reflect their more ovate form (shorter and wider) and the consequently greater sensitivity of surface area and L:B calculations to variations in width.

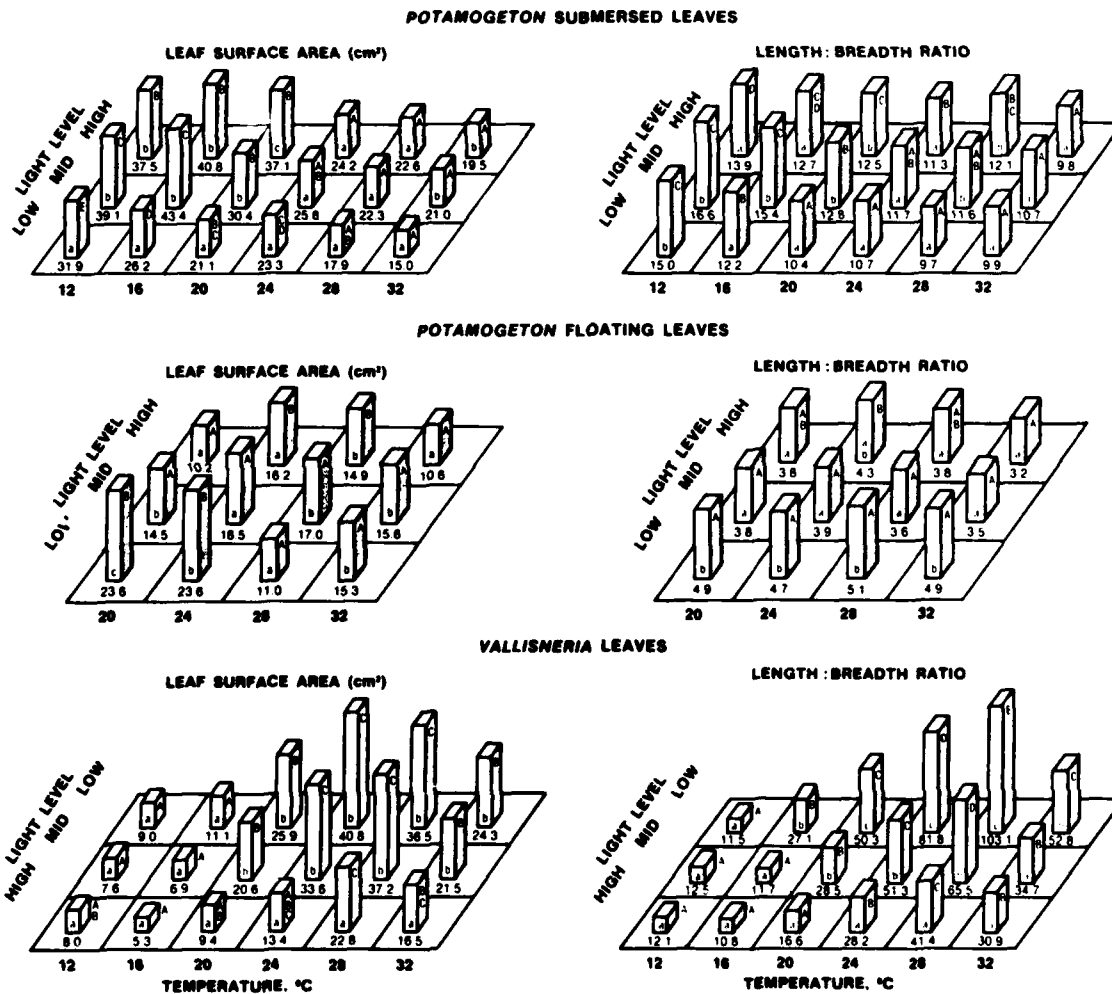


Figure 4. Leaf morphology in *Potamogeton* and *Vallisneria*. Within each subfigure, numerical values printed at the base of bars sharing the same letter (upper case among temperature levels and lower case among light levels) do not differ significantly from each other. The order of presenting light levels in the *Vallisneria* subfigures is reversed in comparison with the order used in the other subfigures

Table 3
Correlations of Leaf Surface Area and L:B Ratio with Leaf Length in
Potamogeton and Vallisneria

<u>Leaf</u>	<u>R² Values*</u>	
	<u>Area</u>	<u>L:B</u>
<i>Potamogeton</i> floating leaves	0.87	0.54
<i>Potamogeton</i> submersed leaves	0.93	0.81
<i>Vallisneria</i> leaves	0.95	0.96

* Correlations considered here are all statistically significant at the 1-percent level or less.

Discussion

18. Over the broad ranges provided, both light and temperature were equally important in affecting growth and morphology in the submersed macrophytes examined. This is generally consistent with results reported earlier for several other submersed macrophytes investigated by Barko and Smart (1981a). However, compared to the earlier investigation, the much broader range of light/temperature combinations provided herein allowed better discrimination of interactive relationships between these two factors. In this connection, it is notable that the level of one factor (either light or temperature) generally influenced macrophyte response to the other factor in the current investigation. In a general sense, these species were most responsive to differences in light at optimal temperature levels (28° and 32°C) and to differences in temperature at optimal light levels (mid and high). The growth of algae has been demonstrated to be affected by the interaction between temperature and light also (see for example Morgan and Kalff 1979). In a recent review considering photosynthetic response and adaptation to temperature in higher terrestrial plants, Berry and Bjorkman (1980) caution that meaningful comparisons of temperature-related growth curves require that the dependence on light intensity be known because of the interactive relationship between these two factors. This caution appears to be

applicable to submersed freshwater macrophytes as well.

19. Among the various morphological response variables considered herein, shoot density in each species best correlates with shoot biomass when comparisons are made across all experimental conditions. In the same context, correlations between shoot biomass and shoot length are very weak because increasing light and temperature elicit opposing shoot length responses. Shoot elongation with increasing temperature can be considered as a growth-related response, but shoot elongation with decreasing light may or may not have involved growth (as biomass production) in this investigation. In both the present investigation and in that of Barko and Smart (1981a), shoot elongation at low light was ineffective in promoting increased availability of light for biomass production because of the vertically uniform conditions of irradiance provided in the experimental tanks.

20. Several investigations involving a variety of submersed freshwater macrophyte species have indicated an inverse relationship between shoot length and total PAR (Barko and Smart 1981a; Spence 1976, Spence and Dale 1978; Stross 1979). Variations in shoot length effected by irradiance reflect differential internode elongation, which can apparently be influenced by temperature as well (noted here and in Barko and Smart 1981a). It has been suggested by Spence (1976) that shoot length and the extent of internode elongation may vary in response to red light or to changes in endogenous ethylene levels. Since water depth and pressure did not vary in this investigation, it is doubtful that ethylene affected shoot elongation unless different temperatures promoted gradients in ethylene production. Shoot elongation with decreasing light may well involve a response to red light, but this explanation is not applicable to shoot elongation as a temperature response. Aside from physiological considerations, seasonal increases in water temperature may counteract the inhibitory influence of increasing irradiance on shoot elongation in some submersed macrophytes (Barko and Smart 1981a).

21. In addition to shoot length, specific leaf area (Spence and Chrystal 1970b; Spence, Campbell, and Chrystal 1973) and leaf L:B ratio (Pearsall and Pearsall 1923, Pearsall and Hanby 1925) have also been

demonstrated to increase with depth. These variations in leaf morphology are usually associated with differences in irradiance; however, other environmental factors have also been suggested as possibly causal (Pearsall and Pearsall 1923; Pearsall and Hanby 1925; Spence and Dale 1978). In this connection, it is notable that temperature had at least an equivalent influence compared to light on leaf morphology in the current investigation.

22. There appears to be considerable variability in the morphological plasticity of leaves among different submersed macrophyte species (McMillan 1978; McMillan and Phillips 1979; Pearsall and Pearsall 1923; Spence, Campbell, and Chrystal 1973). Notably, in the present investigation, *Potamogeton* leaves were much less responsive to different light and temperature conditions than *Vallisneria* leaves. Moreover, leaf form in *Potamogeton* was essentially unresponsive to light or temperature under conditions where floating leaves were produced in large numbers. The impression gained from the investigation of Pearsall and Pearsall (1923) is that the species in the genus *Potamogeton* that most commonly form floating leaves tend to demonstrate relatively minor variations in leaf morphology, as compared with other species in this genus that are less inclined toward a heterophyllous existence.

23. The formation of floating leaves in heterophyllous species could ameliorate the necessity for leaf morphoplasticity. Apparently, the floating leaves produced by submersed macrophytes are structurally (Anderson 1978) and physiologically (Lloyd, Canvin, and Bristow 1977) similar to the leaves of terrestrial plants adapted to a high light environment. Thus, under conditions allowing maximum production of floating or aerial leaves, submersed macrophytes may concentrate photosynthesis at the water surface with lesser dependence on morphological adaptations of submersed leaves.

24. The morphological response of *Elodea* to increasing light in the current investigation was decidedly photophobic, as evidenced by its prostrate growth form at higher light levels. Yet, despite its apparent avoidance of light, *Elodea* was most productive at the higher light levels, where it grew in extremely dense aggregations. Considering the

relatively limited ability of *Elodea* to elongate to the water surface under low light conditions, this species may be disadvantaged in aquatic systems characterized by low water clarity.

25. Canopy-forming species such as *Hydrilla verticillata* and *Myriophyllum spicatum* are often particularly prominent and frequently achieve complete dominance of the littoral zone because of their extensive capabilities to elongate and concentrate photoreceptive biomass at the water surface (refer to Barko and Smart 1981a and literature cited therein). Despite the meager availability of supportive data, *Potamogeton nodosus* appears to be equally capable in this regard. In virtually any aquatic system supporting dense populations of canopy-forming species, submersed macrophytes possessing a less optimal growth form would appear to be disadvantaged because of extreme light attenuation with depth. For example, *Vallisneria*, which distributes the major portion of its shoot biomass near the sediment surface, is apparently incapable of successfully competing with *H. verticillata* in Florida (Haller and Sutton 1975) and is capable of only limited coexistence with *M. spicatum* in Lake Wingra, Wisconsin (Titus and Adams 1979).

26. Despite some physiological evidence suggesting that net photosynthesis in submersed macrophytes can be maintained at very low light levels (e.g., Van, Haller, and Bowes 1976) and the general impression that freshwater macrophytes can extend to depths receiving only 1 to 4 percent of surface irradiance (Sculthorpe 1967), the lower depth limit with some exceptions appears to more commonly occur at light levels between 5 and 10 percent of surface irradiance (Bodkin, Poluszny, and Dale 1980; Howard-Williams and Liptrot 1980). The disparity often existing between physiological estimates of light compensation point (usually obtained at near-optimal temperatures) and light determined at the lower limit of macrophyte depth distribution suggests that other factors interacting with light, particularly in clear lakes (see Sheldon and Boylen 1977), may influence macrophyte depth distribution.

27. From this investigation and other recent literature, it appears that a variety of submersed macrophyte species demonstrate increased growth with temperature up to at least 28°C. Thus, the gradient

with depth of integral seasonal temperature in lakes of temperate regions may promote depth-related differences in the growth of submersed macrophytes. In this connection, it has recently been reported that the dynamics of thermal stratification limit the growing season of *Utricularia purpurea* in a dimictic lake to 8 weeks at a depth of 6 m compared to 17 weeks at a depth of 2 m (Moeller 1980). Since mictic lakes warm and are vertically mixed at different rates and to different extents depending upon specific morphometry and localized climatic conditions (Ford and Stefan 1980), variations in the integral seasonal temperature regime could be important in promoting macrophyte growth differences among lakes even within the same geographic region. In this regard, the depth profile of integral seasonal temperature is viewed as being more important than the maximum depth of the mixed layer (epilimnion) in influencing the annual growth of submersed freshwater macrophytes. By reducing the length of the growing season, low temperatures effectively diminish the capacity of macrophytes to utilize available light in photosynthesis. This may partially account for the inability of macrophytes in some systems to colonize substrata to depths consistent with their maximum photosynthetic potential.

28. Considering the extensive morphological and/or physiological adaptability to light demonstrated by a variety of submersed macrophyte species, light may be less important than temperature in affecting the geographical distribution of submersed macrophytes. Furthermore, as suggested by reported changes in the species composition of submersed macrophyte communities subjected to thermal alterations (Allen and Gorham 1973; Anderson 1969), temperature may be as important as light in modifying competitive interactions among coexisting species. This possibility gains support from the apparent inability of submersed macrophytes to strictly acclimate to temperature, and the discrete pattern of growth and morphology demonstrated by different species in response to temperature over a broad range. In a particularly extensive investigation concerning the effect of heated effluents from power plants on seagrass communities, Thorhaug, Blakes, and Schroeder (1978) stressed that elevated temperatures only a few degrees above summer ambient in

subtropical and tropical estuaries may devastate *Thalassia* communities. In that same study, it was suggested that lower temperature limits, not upper, separate subtropical from tropical organisms. Considering the similar thermal optima (28° to 32°C) of the several submersed macrophytes investigated in the study reported herein and others conducted in this laboratory, the contention of the authors cited above may be equally applicable to the latitudinal distribution of submersed freshwater macrophyte species in North America.

29. Species that can overwinter in an active state (Boylen and Sheldon 1976) and/or are capable of rapid growth with increasing light at low temperature levels in the spring may have a competitive advantage in northern localities over species that overwinter in a dormant state and/or are incapable of growth at low temperatures. Considering the limited capacity for growth demonstrated by *Hydrilla* at low temperatures (Barko and Smart 1981a), this species is unlikely to compete effectively at northern latitudes. The ability of *M. spicatum* to extend its growing season relative to that of *Vallisneria* by photosynthesizing at low temperatures has been suggested as another important factor (refer to earlier discussion) contributing to its virtual replacement of *Vallisneria* in Lake Wingra, Wisconsin (Titus and Adams 1979). Similarly, the lack of dormancy in *Elodea canadensis* in combination with its high overwintering standing crop in ice-free areas of Lake Wabamun, Alberta, have reportedly contributed to the localized competitive success of this species (Haag and Gorham 1977). However, under snow and ice cover in the same lake, the lack of dormancy in *Elodea* apparently makes survival strongly dependent on the winter irradiance regime (Haag 1979). Thus, basic differences in life cycle mediated by seasonal light and temperature conditions appear to be important in influencing the distribution of submersed freshwater macrophytes.

Conclusions

30. Light and temperature over broad ranges appear to interact with essentially equal importance in significantly influencing the growth

and morphology of submersed freshwater macrophytes.

31. Differences in the morphological and/or physiological adaptability of macrophytes to various conditions of irradiance may partially account for the greater competitive ability of some species compared to others in aquatic systems. In this connection, species capable of concentrating photoreceptive biomass at or near the water surface in low-irradiance environments may be able to competitively displace species possessing relatively prostrate growth forms. Among the species examined in this investigation, both *Elodea* and *Vallisneria* appear to be disadvantaged in aquatic systems characterized by low water clarity because of their limited elongation potential. Conversely, *Potamogeton nodosus* possesses a significant ability to form a foliar canopy at the water surface.

32. From this investigation and recent literature, it is apparent that a variety of submersed macrophyte species demonstrate increased growth with temperature up to at least 28°. By reducing the length of the growing season, low temperatures effectively diminish the capacity of submersed macrophytes to utilize available light in photosynthesis. In this way, temperature appears to be important in defining both the depth and geographical distributions of these plants. Considering the distribution of submersed macrophytes in North America, lower temperature limits in combination with basic differences in life cycle may account for variations in the latitudinal range of many macrophyte species.

33. The potential for aquatic systems to support excessive submersed macrophyte growth generally increases from north to south in the United States because of the respectively increasing favorableness of temperature conditions. Superimposed on this latitudinal gradient, conditions of both high light and high temperature at the water surface provide a maximum-growth environment for species capable of accessing the water surface. For this reason, even in northern localities, macrophyte species that effectively concentrate biomass at the water surface are potentially more productive than other species restricted to lower positions in the water column. Considering the information reported herein, it is apparent that light and temperature conditions need to be defined

with depth on a diel basis as well as on a seasonal basis in order to assess the site-specific influence of these important factors on the growth and species composition of submersed macrophyte communities.

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