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EFFECTS OF WATER CHEMISTRY ON SUBMERSED
AQUATIC PLANTS: A SYNTHESIS

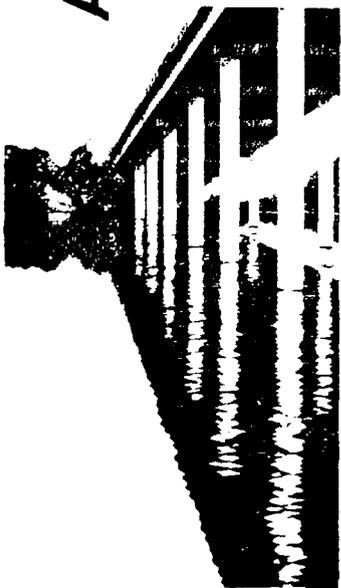
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<p>The effects of water chemistry on the growth and distribution of submersed aquatic plants are evaluated, based on review of technical literature and results of recent research conducted under the US Army Corps of Engineers Aquatic Plant Control Research Program.</p> <p>Submersed aquatic plants require a continual supply of inorganic carbon to fuel photosynthesis. However, the aquatic environment imposes limits on both the supply and availability of inorganic carbon. Several factors, including alkalinity, dissolved inorganic carbon (DIC), and pH, affect the availability of inorganic carbon. These factors are among the most important water chemistry parameters with respect to their potential effects on the growth and distribution of submersed aquatic plants.</p>					
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Many submersed plants exhibit adaptations enabling them to more readily acquire inorganic carbon from the aquatic environment. A common adaptation is the ability to use bicarbonate (usually the predominant form of DIC) in photosynthesis. Photosynthesis in bicarbonate users, typified by Eurasian watermilfoil, is roughly proportional to DIC concentration.

While photosynthesis is directly related to DIC, the relationship between plant biomass production and DIC is less clear. Factors other than DIC (such as nutrient limitation) also affect biomass production. Although inorganic carbon supply may limit growth rate, peak biomass attainment may be more likely limited by nitrogen availability. While water chemistry influences species distribution, it is unlikely that this factor is involved in limitations on biomass production.

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Preface

The studies reported herein were sponsored by the Headquarters, US Army Corps of Engineers (HQUSACE), Directorate of Civil Works, through the US Army Corps of Engineers Aquatic Plant Control Research Program (APCRP). Funds were provided under Department of the Army Appropriation No. 96X3122, Construction General. Technical Monitor for HQUSACE was Mr. James W. Wolcott. The APCRP is managed by the US Army Engineer Waterways Experiment Station (WES) under the Environmental Resources Research and Assistance Programs, Mr. J. Lewis Decell, Manager.

Principal Investigator for the studies summarized in this report was Dr. R. Michael Smart, Environmental Laboratory (EL), WES. The report was prepared by Dr. Smart. The research was conducted by Drs. Smart and John W. Barko, with technical assistance provided by Mr. Harry L. Eakin and Ms. Dwilette G. McFarland, all of the Aquatic Processes and Effects Group (APEG). The report was reviewed by Drs. Barko, Thomas L. Hart, and Kurt D. Getsinger, APEG.

This investigation was performed under the general supervision of Dr. John Harrison, Chief, EL, and Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, and under the direct supervision of Dr. Hart, Chief, APEG.

Commander and Director of WES was COL Larry B. Fulton, EN. Technical Director was Dr. Robert W. Whalin.

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EFFECTS OF WATER CHEMISTRY ON SUBMERSED AQUATIC PLANTS:

A SYNTHESIS

Introduction

1. We have known for some time that the chemical composition of water affects the growth and distribution of submersed aquatic plants. The distribution of these plants has often been related to parameters such as nutrient status, salinity (also conductivity and total dissolved solids), alkalinity, calcium (Ca) content, and pH. Many of these parameters are intercorrelated, and information on the effects of specific aspects of water chemistry on the growth of submersed aquatic plants is lacking. It is, therefore, difficult to ascribe differences in growth and distribution to specific water chemistry parameters. As a consequence, our ability to predict the likelihood of excessive growth of submersed aquatic vegetation in particular water bodies has been hindered.

2. The objective of this synthesis report is to summarize the existing information on the influence of specific water chemistry parameters on the growth and distribution of submersed aquatic plant species. In this summary, the author draws on technical literature as well as recent research conducted under the Aquatic Plant Control Research Program. In the interest of increasing readability to a broad audience, specific literature citations within the text are avoided. At the end of each section, particularly relevant works are listed to enable the interested reader easy access to additional technical information.

Background

3. It was once widely held that submersed aquatic plants, even those possessing roots, obtained their nutrients from the water and that the nutrient content of the water was an important factor affecting the distribution of these plants. Recent evidence has shown, however, that rooted submersed aquatic plants can generally obtain nitrogen (N) and phosphorus (P) as well as micronutrient metals from sediment. Potassium (K) may be generally acquired from the water, but, since most surface waters contain abundant K, this element probably does not often affect plant biomass production or

distribution. In addition to K, the nutrients Ca and magnesium (Mg) also seem to be acquired by foliar uptake from the water. The potential importance of these major cations will be examined in a subsequent section.

4. Other nutrient elements, including sodium, chlorine, and sulfur, seem to be acquired from either the water or the sediment, depending on relative availability. Since these elements are generally required in very low quantities relative to their abundance in the water, low concentrations of these are unlikely to limit either the distribution or production of submersed aquatic plant species. Plant requirements for micronutrient elements, including iron, manganese, zinc, molybdenum, and boron, are generally met by root uptake from sediment; thus, the concentration of these in the water column will unlikely affect plant growth or distribution.

5. Salinity, including conductivity and total dissolved solids, may often limit the distribution of aquatic plants in localized areas subject to marine influences or drainage from saline soils. While the effects of salinity on biomass production of submersed aquatic plants are not well known, relative salinity tolerances can be inferred by their distribution in estuarine areas. The effects of salinity on biomass production and distribution should be evaluated in view of the potential for salinity to delimit plant invasion of extensive estuaries such as the Potomac River-Chesapeake Bay system. However, the salinity of most inland waters of concern to the Corps of Engineers Aquatic Plant Control Program is within the range tolerated by the majority of submersed aquatic plant species. For this reason, salinity will not be further considered in this summary.

6. The remaining parameters--alkalinity, Ca, and pH--are important components of the carbonate system and together control the availability of inorganic carbon (C) in surface waters. Carbon is the element most required by plants and accounts for more than 40 percent of the dry weight of aquatic plants, while N and P account for only about 3 and 1 percent, respectively. Carbon dioxide (CO₂) limitation of terrestrial plant photosynthesis is common, and photosynthesis in the aquatic environment is even more likely to be limited by the supply of C.

[Barko 1982; Barko and Smart 1980, 1981a, 1986;
Huebert and Gorham 1983; Smart and Barko 1985]

Carbon availability

7. The air-water interface acts as a barrier, slowing the exchange of CO_2 between the atmosphere and the water column. Advection or mixing, which promotes the continual replenishment of CO_2 for land plants, is greatly reduced in the aquatic environment, particularly in nonflowing waters. Reduced advection and the slow rate of diffusion of CO_2 in water can result in a limited rate of supply of inorganic C to submersed aquatic plants.

8. In addition to limitations on the rate of supply of CO_2 , the actual quantity of CO_2 available for photosynthesis in most surface waters is quite low. When CO_2 dissolves in water it becomes chemically associated with the water in equilibrium with other forms of dissolved inorganic carbon (DIC). There are three forms of C in this equilibrium (Figure 1): free CO_2 (undissociated carbonic acid, H_2CO_3), bicarbonate (HCO_3^-), and carbonate (CO_3^{--}). Uptake of free CO_2 , as in photosynthesis, causes a shift in the equilibrium, resulting in increases in pH and further decreases in free CO_2 concentration. At the pH levels found in most submersed plant beds (7.5 to 10), most of the DIC is in the form of HCO_3^- . At the higher end of this range, free CO_2 is virtually nonexistent.

9. The combined effects of these constraints on CO_2 supply and availability would seem to result in a CO_2 regime that is not very favorable for the growth of submersed aquatic plants. However, as demonstrated in the following section, submersed aquatic plants are quite well adapted for obtaining inorganic C under these seemingly adverse conditions.

[Hutchinson 1957, 1975; Wetzel 1983]

Physiological adaptations to low carbon availability

10. HCO_3^- assimilation. Submersed aquatic plants have evolved a variety of strategies for coping with low C availability. Although free CO_2 is considered to be the preferred form of C for photosynthesis, many species are capable of assimilating HCO_3^- . The ability to access the generally large pool of HCO_3^- is a definite advantage in most surface waters. Species that do not possess this ability are generally confined to acidic waters, where most of the DIC exists as free CO_2 , or to flowing waters, where advection and turbulent mixing provide continual replenishment of CO_2 .

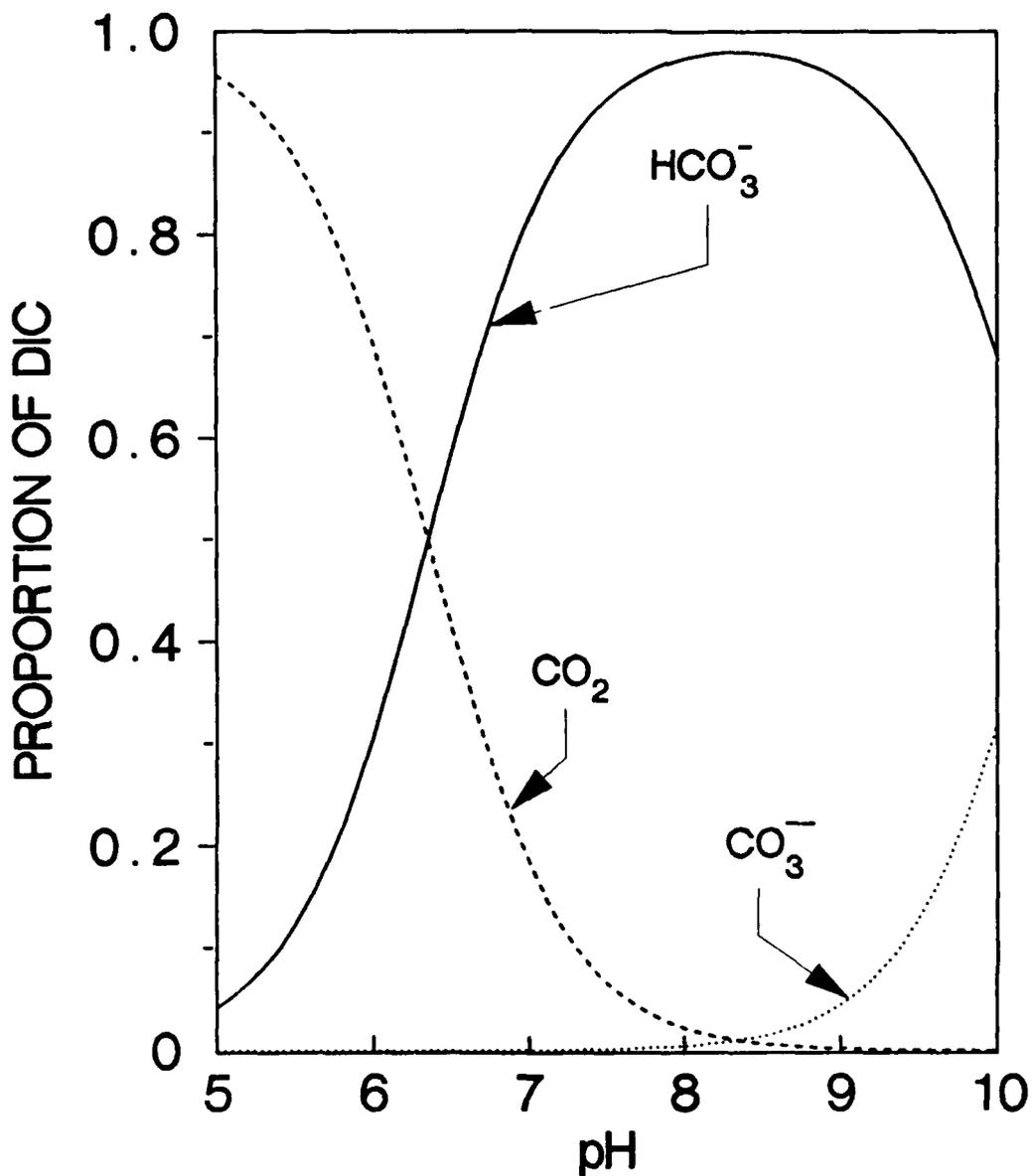


Figure 1. Proportion of DIC in different chemical forms as a function of pH

11. Although there is no consensus on details of the mechanism of HCO_3^- assimilation, HCO_3^- uptake must be balanced by extracellular hydroxyl (OH^-) production. Regions of HCO_3^- uptake and OH^- release are usually separated spatially, and many species of submersed aquatic plants possess polar leaves in which the upper and lower surfaces of the leaves are differentiated. In these species, uptake of HCO_3^- occurs on the lower leaf surface while hydroxyl efflux occurs on the upper leaf surface. The significance of this spatial separation is that OH^- efflux lessens the availability of HCO_3^- by increasing pH and shifting the equilibrium toward the formation of CO_3^{2-} . This often

results in the precipitation of calcium carbonate (CaCO_3), which can be readily observed as a white deposit, usually on the upper leaf surfaces of many submersed aquatic plants.

12. While the use of HCO_3^- does allow submersed aquatic plants to access a large supply of inorganic C, it is not without disadvantages. Bicarbonate uptake requires energy and can result in greatly elevated pH; it also promotes the formation of CaCO_3 encrustations on the leaves. Tolerance of high pH levels is generally coupled with the ability to assimilate HCO_3^- . This combination enables HCO_3^- users to competitively displace nonusers from high-alkalinity, high-pH waters.

13. Photosynthetic pathways. In the terrestrial environment, several distinct photosynthetic pathways have been identified. These include C3 photosynthesis, in which the initial products of photosynthesis are three-C compounds; C4 photosynthesis, in which the initial products are four-C compounds; and Crassulacean acid metabolism (CAM), in which C fixation can occur during the dark. The latter pathways represent adaptations for concentrating or conserving CO_2 in hot, dry environments where stomatal opening (to obtain CO_2) can result in severe water deficits. In plants exhibiting C4 photosynthesis, C is conserved by refixing photorespired CO_2 . These terrestrial adaptations have counterparts in the aquatic environment.

14. Some submersed aquatic plant species are capable of C4 photosynthesis and exhibit characteristics typical of terrestrial C4 plants, such as low photorespiration rates and low CO_2 compensation points. The advantages of this photosynthetic pathway include conservation of photorespired C and efficient C assimilation under the high dissolved oxygen and low free CO_2 concentrations common in dense submersed aquatic plant populations. The operation of C4 photosynthesis in a variety of submersed aquatic plants is induced by high temperatures, low CO_2 levels, and long day conditions. Some of these species, notably *Hydrilla*, have also been shown to accumulate malic acid during the night, thus exhibiting some of the characteristics of CAM as well.

15. Species characteristic of soft, oligotrophic waters often exhibit CAM. The environments of these species are characterized by large diurnal changes in pH and free CO_2 . These species, which apparently cannot assimilate HCO_3^- , are unable to acquire sufficient CO_2 during the day. To supplement the low daily uptake of CO_2 , these plants fix CO_2 into malic acid during the night when free CO_2 levels are highest. During the day when CO_2 availability is

low, this stored source of C can be utilized through conventional C3 photosynthesis. Species possessing CAM thus avoid the problem of acquiring C under low free CO₂ conditions and also conserve C otherwise lost through respiration at night. Since CAM is not suited for fixing large quantities of inorganic C, its utility is restricted to infertile sites of low productivity.

[Adams 1985, Bowes 1985, Sand-Jensen 1989,
Søndergaard 1988, Spence and Maberly 1985]

Morphological adaptations to low carbon

16. Many of the species common in soft, oligotrophic waters have well-developed root systems and an extensive network of intercellular air spaces (lacunae) for the transport of gases between the roots and shoots. Some of these species are capable of photosynthetically fixing CO₂ taken up by the roots and transported to the leaves.

17. Another common morphological characteristic of submersed aquatic plants is the development of finely divided leaves, resulting in a high surface area-to-volume ratio. The large contact area between the leaf and the water enhances the transfer of substances (including CO₂) between the water and the plant. Interestingly, many amphibious species (species that are capable of growing either submersed or emergent) develop finely divided submersed leaves that are quite different in appearance from the aerial, emergent leaves. That this phenomenon is related to C acquisition is indicated by the observation that bubbling CO₂ through the solution induces formation of the aerial leaf type.

18. Another morphological adaptation, common in pondweeds (*Potamogeton* species), is the development of specialized floating leaves. These leaves provide access to atmospheric CO₂. Even strictly submersed species such as *Hydrilla* and Eurasian watermilfoil (*Myriophyllum spicatum*) are morphologically adapted to access atmospheric CO₂. These species are capable of rapid elongation to reach the water surface and subsequent development of a highly branched horizontal canopy. Canopy formation at the surface allows the plant access to the rapid flux of CO₂ diffusing into the water from the atmosphere. An additional benefit for species capable of canopy formation is their increased access to solar radiation, particularly in turbid environments.

[Barko and Smart 1981b, Sculthorpe 1967]

Importance of carbon as a limiting factor

19. In view of the many varied morphological and physiological adaptations of submersed aquatic plants for enhancing C uptake and conservation, it is apparent that the problem of C acquisition in the aquatic environment has exerted a strong selection pressure on the evolution of these plants. The relatively recent introduction of large quantities of nutrients into the Nation's waterways through cultural eutrophication has increased both the likelihood and severity of C limitation. Therefore, in eutrophic environments where submersed aquatic plants are likely to grow to nuisance proportions, C availability may potentially limit biomass production. For these reasons, recent research on the effects of water chemistry on submersed aquatic plants has focused on those water chemistry parameters that affect carbon acquisition by these plants.

Research Summary

Inorganic carbon and cation effects on growth and photosynthesis

20. A series of experiments was conducted to examine the importance of DIC and cation levels in affecting the growth of submersed aquatic plants. Results of these studies revealed that growth of Eurasian watermilfoil was affected by both DIC and cations. The effects of cation levels on growth were restricted to low DIC conditions. Of the two parameters, plant growth was more affected by levels of DIC than by levels of cations. In a secondary experiment the stimulatory effect of cations was attributed primarily to Ca.

21. Since the influence of Ca on plant growth appeared to involve its role in C uptake, additional experiments focused on photosynthesis. Low levels of Ca, in combination with low levels of DIC, caused reductions in photosynthesis of Eurasian watermilfoil. However, at levels of DIC and Ca prevalent in most natural waters, Ca levels did not limit photosynthesis.

22. Since these first experiments verified the influence of inorganic C on growth of Eurasian watermilfoil, and since growth is dependent on photosynthesis, an additional experiment was conducted to determine the effects of DIC on photosynthesis. Results of this study demonstrated that photosynthesis in Eurasian watermilfoil was proportional to the concentration of DIC. These data also fit a typical first-order kinetics curve with a half-saturation constant of 24.5 mg DIC/l (Figure 2). This relationship indicates that

photosynthesis is operating at half of its maximal rate at a DIC concentration of 24.5 mg/l, and that photosynthesis will be proportional to DIC concentrations near or below this level. Since most natural freshwaters exhibit DIC concentrations of this magnitude, photosynthesis in this species is potentially limited by the level of DIC found in most natural systems.

[Smart and Barko 1986]

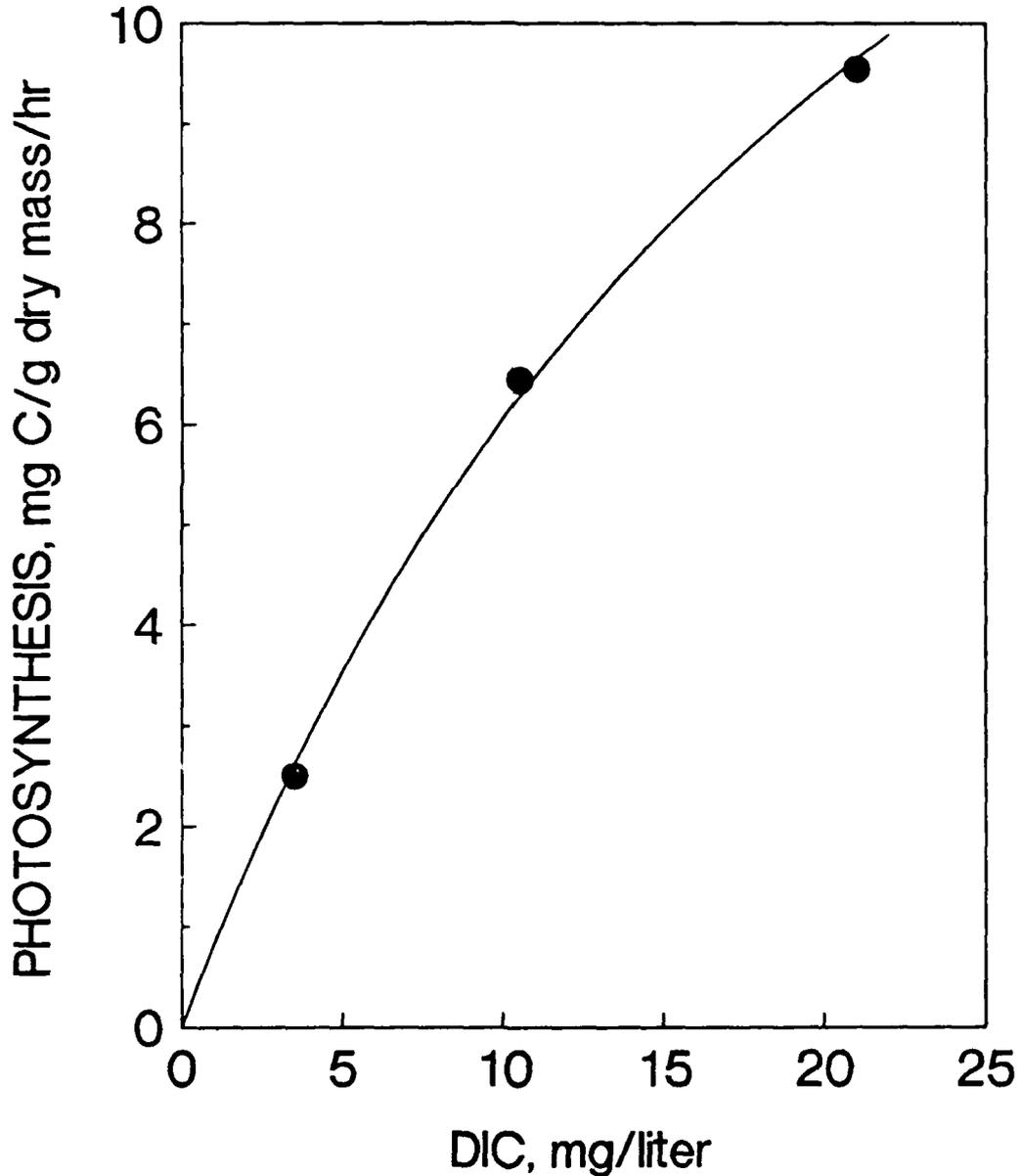


Figure 2. Photosynthesis and kinetic constants for Eurasian watermilfoil in relation to DIC

DIC depletion

23. Submersed aquatic plants rapidly deplete concentrations of DIC during growth. This depletion makes it difficult to conduct controlled studies of the growth responses of these plants to different levels of DIC. After only a few weeks growth, DIC levels can be depleted to less than half of their original concentration (Figure 3).

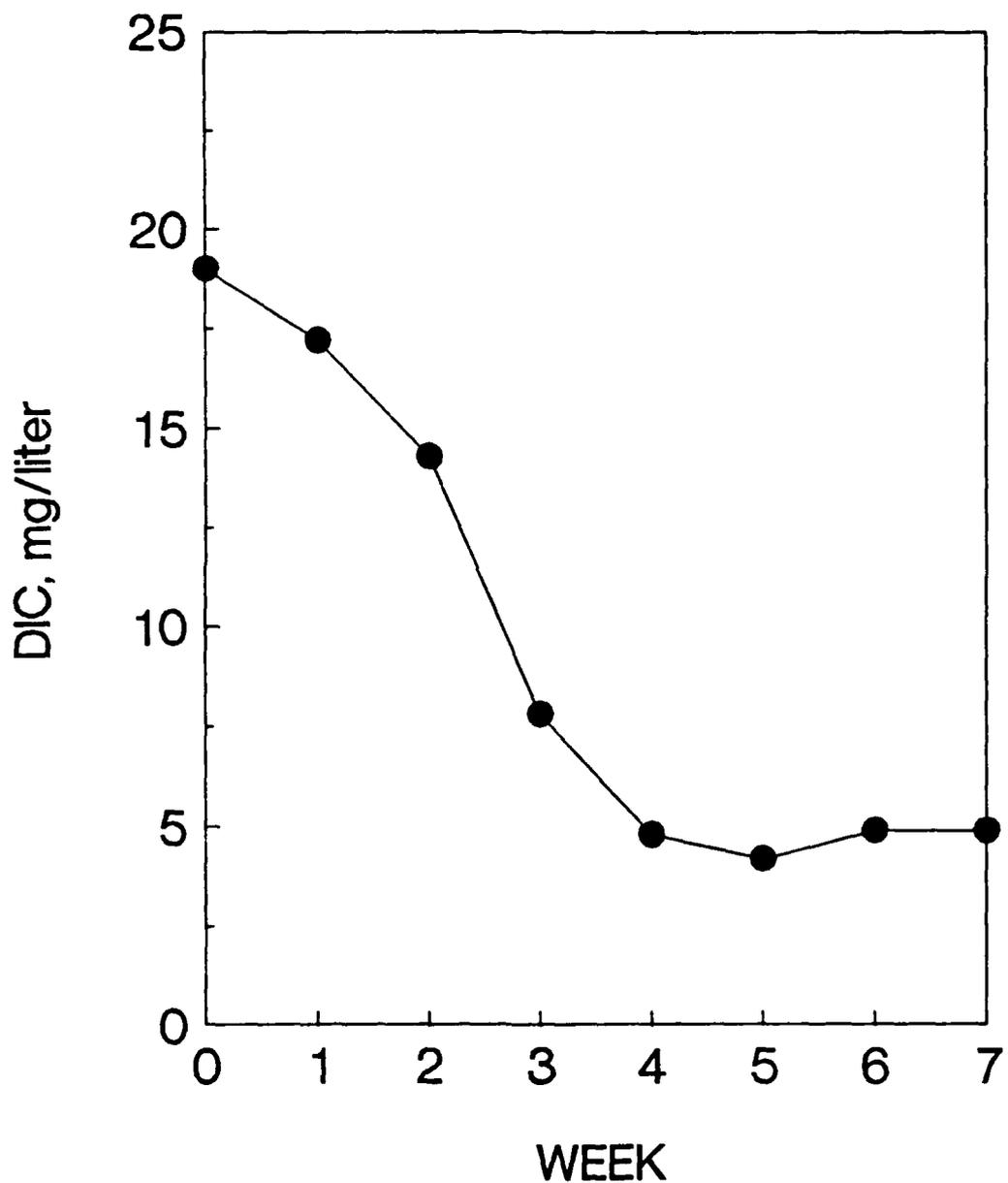


Figure 3. Dissolved inorganic carbon concentrations of water during the growth of *Hydrilla*

24. The high demand for DIC and the resultant rapid depletion of DIC observed during laboratory growth experiments suggest that similar declines in

DIC may also occur in the field. For example, a field population with a biomass level of 250 g dry mass/m², photosynthesizing at an average rate of 2 mg C/g dry mass/hr, has a daily C requirement of about 6 g C/day. In a water column 1.5 m deep with an average level of DIC (20 g/l), the total quantity of DIC in the water column is only about 30 g DIC/m². Thus, the water column contains less than a 1-week supply of inorganic C, and DIC would rapidly become depleted in the absence of other sources of inorganic C supply.

[Smart and Barko 1984, 1988]

Inorganic carbon supply

25. One source of inorganic C is the atmosphere. As solution DIC decreases, due to plant uptake of inorganic C, a gradient in the concentration of CO₂ is set up across the air-water interface. As a result of this concentration gradient, atmospheric CO₂ diffuses from the atmosphere into the water. The rate of diffusion is proportional to the gradient in CO₂ concentration between the atmosphere and the water.

26. As photosynthesis removes DIC from solution, the gradient between the solution and the atmosphere increases rapidly toward its maximal value (Figure 4). Differences in initial solution composition exert little effect on the magnitude of the gradient between the solution and the atmosphere. Differences in atmospheric CO₂ exchange between solutions of different DIC levels are thus rapidly negated by the dramatic changes in free CO₂ concentration that accompany DIC depletion (Figure 4). Since the concentration of CO₂ in the atmosphere is roughly constant at 350 μl/l, and the minimum concentration in the water is 0, the maximum gradient between the atmosphere and solution is 350 μl/l. At this concentration gradient, CO₂ exchange between the atmosphere and the solution will be maximal, regardless of the initial solution composition. Atmospheric replenishment of solution DIC thus acts to moderate differences in the potential C-supplying capacity of different solutions.

27. Other sources of inorganic C potentially regenerating the DIC pool include water column respiration, sediment respiration, and advection or mixing. Although DIC regeneration may not match photosynthetic demand, the contribution of inorganic C provided by these sources is substantial. The quantity of inorganic C provided by water and sediment respiration is also unrelated to the chemical composition of the water. Thus, respiratory, as

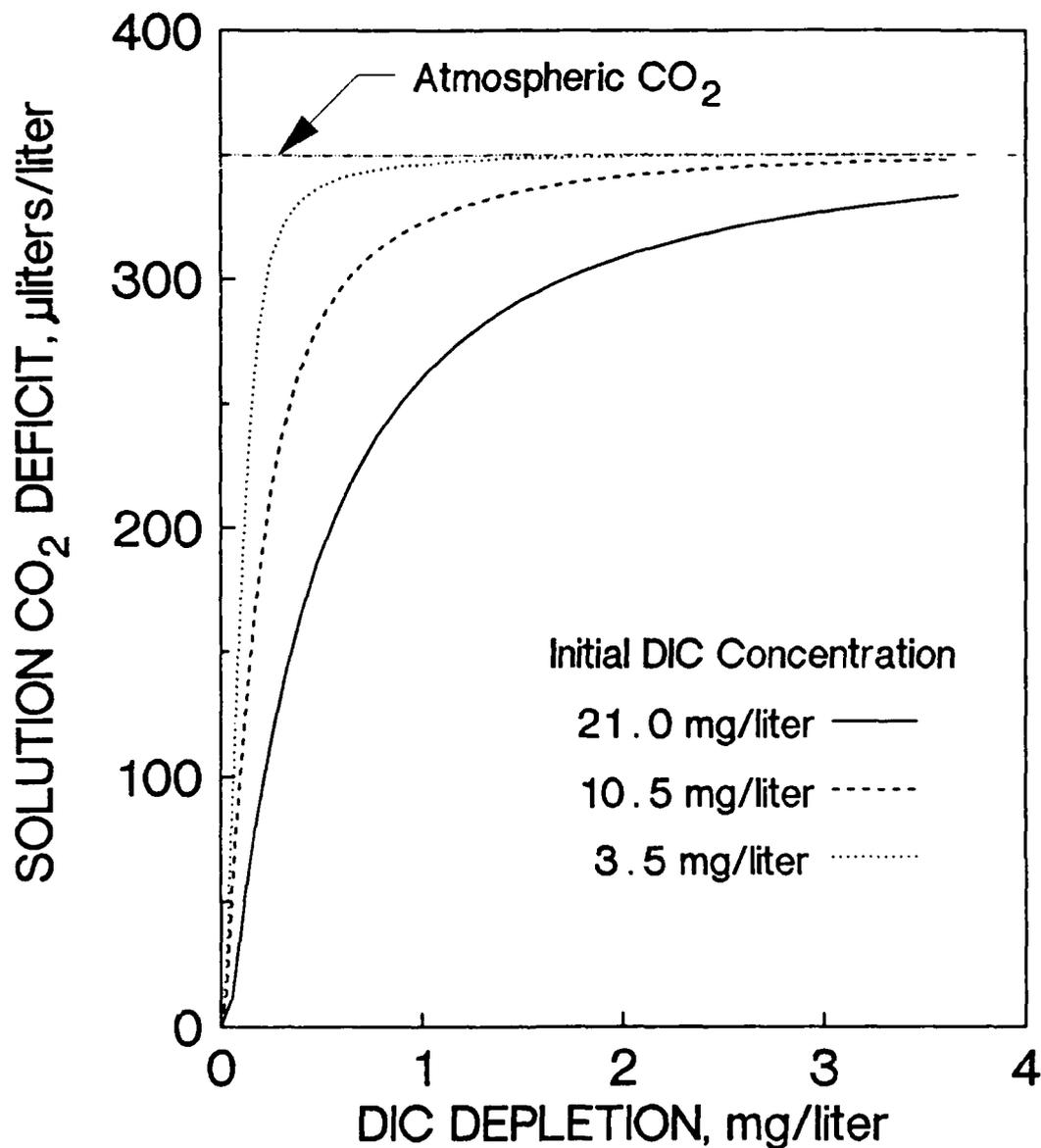


Figure 4. Relationship between the gradient in CO₂ concentration across the air-water interface and the amount of DIC depletion from three solutions differing in alkalinity and initial DIC

well as atmospheric, sources of inorganic C act to moderate any effects solution composition might exert on photosynthetic C uptake.

[Smart and Barko 1986]

Inorganic carbon-nutrient interactions

28. In a study of the effects of different levels of DIC on the growth of submersed aquatic plants, we increased the concentration of CO₂ in the aerating gas to 4x ambient levels. We reasoned that by enhancing atmospheric

exchange of CO_2 , DIC depletion might be prevented. Unfortunately, this fourfold increase in CO_2 supply was insufficient to prevent the depletion of DIC. However, we did note that at the higher levels of DIC, further increases in plant growth were precluded due to the occurrence of N limitation.

29. These results demonstrated the potential importance of sediment N availability in regulating the response of plants to inorganic C. In our most recent study we examined interactions between inorganic C supply and sediment N availability. This study employed a 10x increase in CO_2 concentration in the aerating gas and an increase in sediment N availability, both alone and in combination. Biomass production exhibited little or no response to increased supply of either C or N alone (Figure 5). However, simultaneous increases in both inorganic C supply and sediment N availability promoted dramatic increases in the growth of all species. This result suggests that maintenance of problem levels of submersed aquatic plant biomass may require high levels of both inorganic C supply and sediment N availability.

30. Increases in inorganic C supply in this study increased plant demand for sediment N and other nutrients. Likewise, increased sediment N availability increased demand for inorganic C. High levels of both of these factors stimulate increased growth, increasing the demand on the other factor, until one of them (or some other environmental factor) becomes growth-limiting. Long-term biomass production in these populations may thus be self-regulating. This reciprocal relationship between inorganic C supply and sediment N availability is an example of an interactive feedback control system that may be involved in regulating the growth of rooted submersed aquatic plants. If this control system does in fact operate in natural systems, the production of very high levels of aquatic plant biomass may require both a high rate of inorganic C supply and high sediment N availability. Reductions in either of these factors could result in reduced rates of plant growth. Indirect evidence for this occurrence is provided by the cycle of explosive growth followed by decline, which is characteristic of many species of weedy submersed aquatic plants.

31. While the demand for inorganic C fluctuates diurnally with photosynthesis, the demand for N is more seasonal. The requirement for inorganic C is also more immediate because most species of submersed aquatic plants cannot store appreciable quantities of C to be used during later periods of high demand. Submersed plants can, however, store appreciable quantities of N to meet later demands for growth. For these reasons, inorganic C supply can be

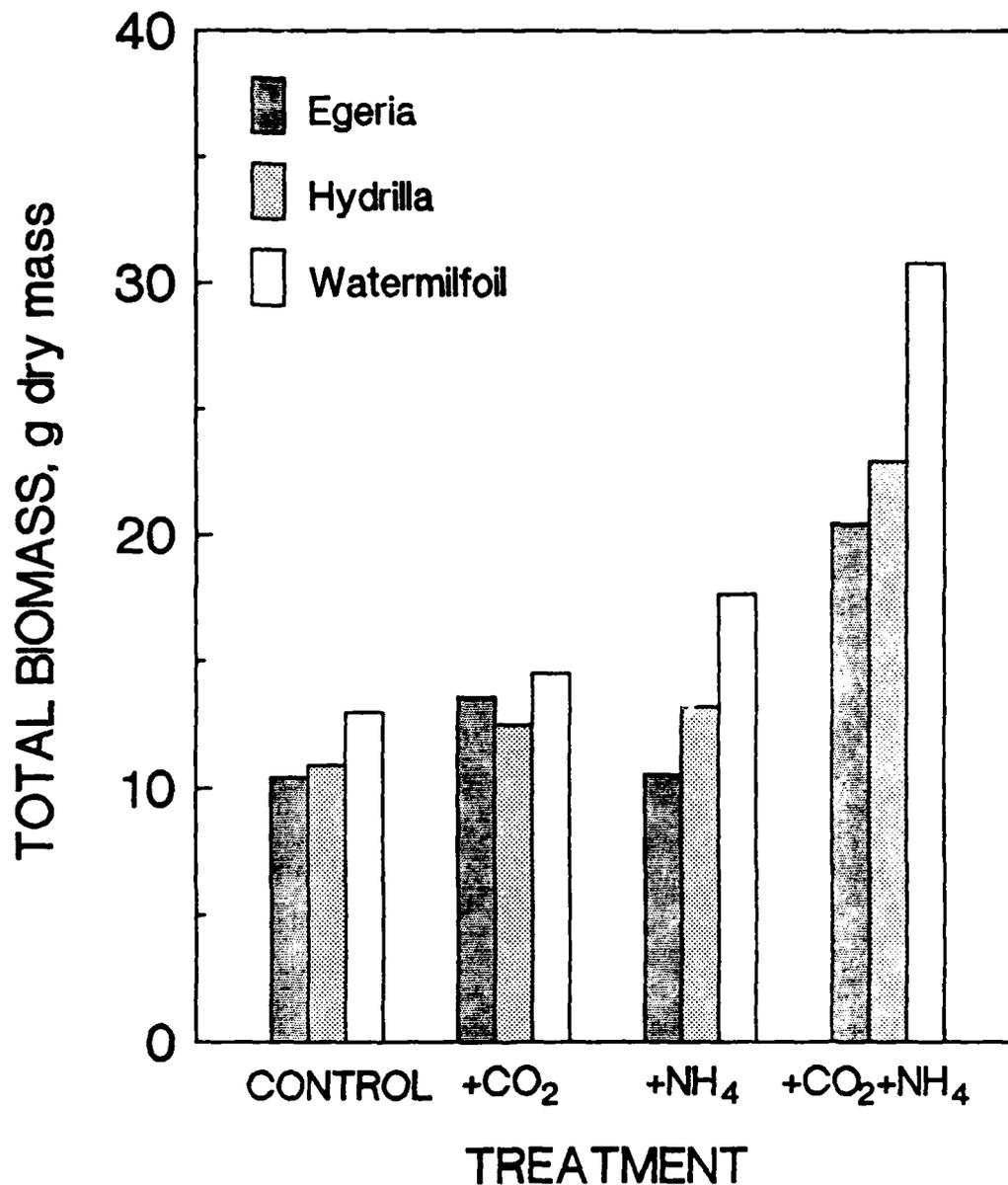


Figure 5. Biomass responses of egeria, hydrilla, and Eurasian watermilfoil to inorganic carbon supply and sediment N availability

important in regulating photosynthesis and short-term growth rates, while N availability is perhaps more important in setting upper limits on potential biomass attainment. If the supply of inorganic C is plentiful, the attainment of maximum potential biomass will be accomplished more rapidly. Thus, while the magnitude (biomass) of submersed aquatic plant problems may be more affected by N availability, the seasonal duration of the problem may be controlled by inorganic C supply.

32. Sediment N availability has been demonstrated to decrease with time due to cumulative losses of N in the senescent shoot tissues of submersed aquatic plant species. Factors increasing biomass production are thus likely to accelerate these autogenic reductions in sediment N availability. For this reason, high levels of inorganic C availability may actually accelerate the decline of submersed aquatic plant biomass as populations age, allowing ecosystem succession to proceed.

[Barko et al. 1988; Smart and Barko 1988;
Smart and Barko, in preparation]

Conclusions

33. Based on recent research and review of the technical literature, the following conclusions regarding the effects of water chemistry on plant growth and distribution can be drawn:

- a. Bicarbonate usage is prevalent among weedy aquatic plant species, allowing them access to a large portion of the DIC in natural waters.
- b. While photosynthesis is proportional to DIC, there is no simple relationship between plant growth and DIC.
- c. Inorganic C supply may often limit photosynthesis and may affect growth rates of submersed aquatic plants.
- d. Sediment N availability may limit peak biomass attained by submersed aquatic plant populations.
- e. Water chemistry influences species distribution but probably does not play a major role in limiting the peak biomass attained by submersed aquatic plants.

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