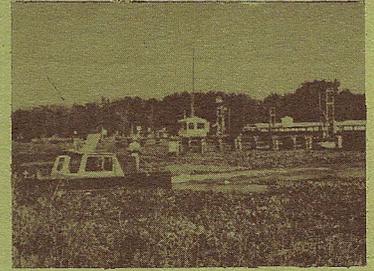
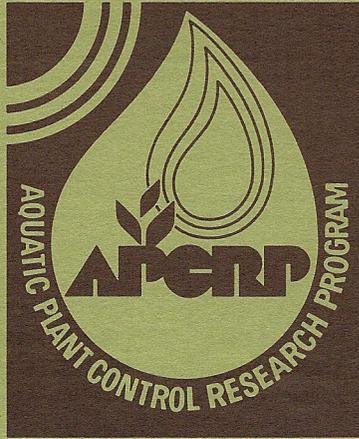
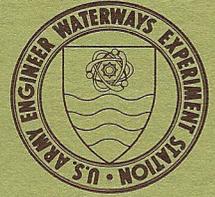
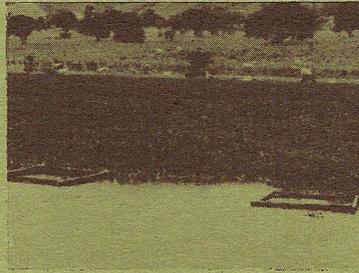
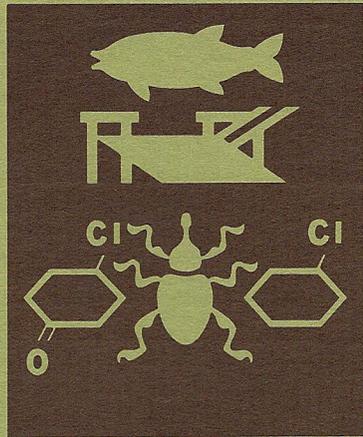


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ECOLOGY OF SUBMERSED MACROPHYTES

BY JOHN W. BARKO*

INTRODUCTION

A variety of physical, chemical, and biotic-environmental factors influence the growth of aquatic macrophytes. The strengths and weaknesses of different macrophyte species in relation to environmental conditions strongly affect specific growth rates and ultimately regulate macrophyte community composition. Whenever an ecosystem becomes disturbed, either naturally or by human activities, the competitive balance among species can be altered through associated changes in species-specific growth potentials.

Our present inability to effectively

anticipate changes in the growth and species composition of submersed macrophyte communities makes it difficult or impossible to alleviate undesirable trends. This problem is largely a consequence of an inadequate understanding of the influence of the environment on aquatic macrophytes.

This article considers some of the more important environmental factors known to regulate the growth of submersed macrophytes — light, water temperature, sediment, water chemistry, and biotic-environmental factors — and identifies some related deficiencies in available data. The information was derived primarily from experimental research conducted in the ERSD facilities (Figures 1 and 2). A large volume of literature supports the major points made herein, but citations

were excluded from the article to achieve brevity.

LIGHT

In many lakes, particularly in reservoirs, the availability of light required by submersed macrophytes in photosynthesis is limited by turbidity associated with high suspended-solids loads. In eutrophic systems, light may also be reduced by high densities of phytoplankton and epiphytic algae. Shade-tolerance and light-related morphological variability may confer competitive advantages during growth in light-limiting situations, perhaps influencing species composition in submersed macrophyte communities. For example, species possessing significant capabilities to elongate to the water surface under conditions

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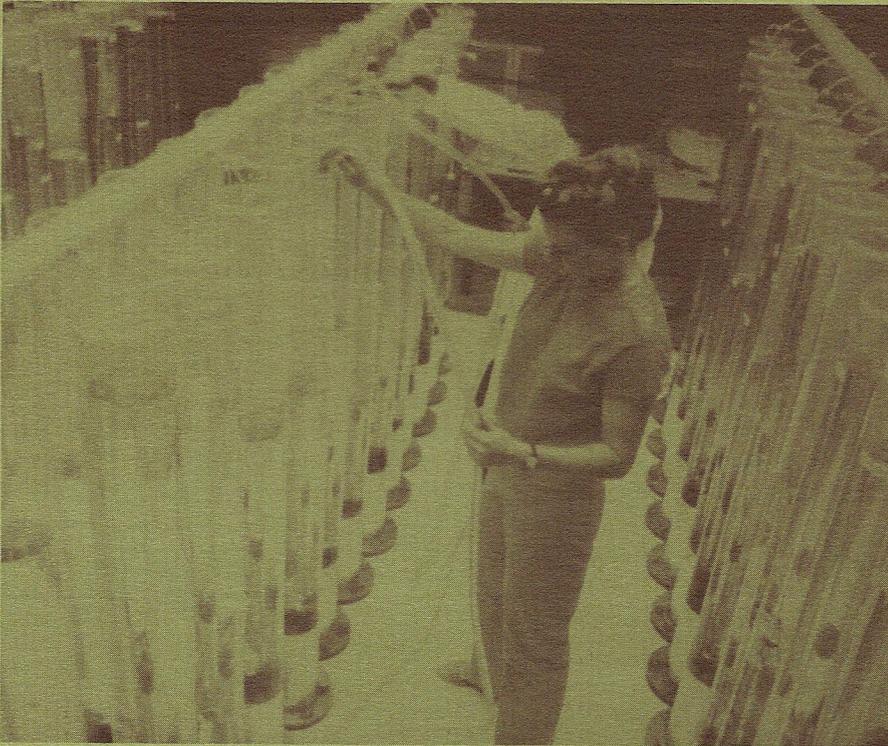


Figure 1. Controlled environment facility

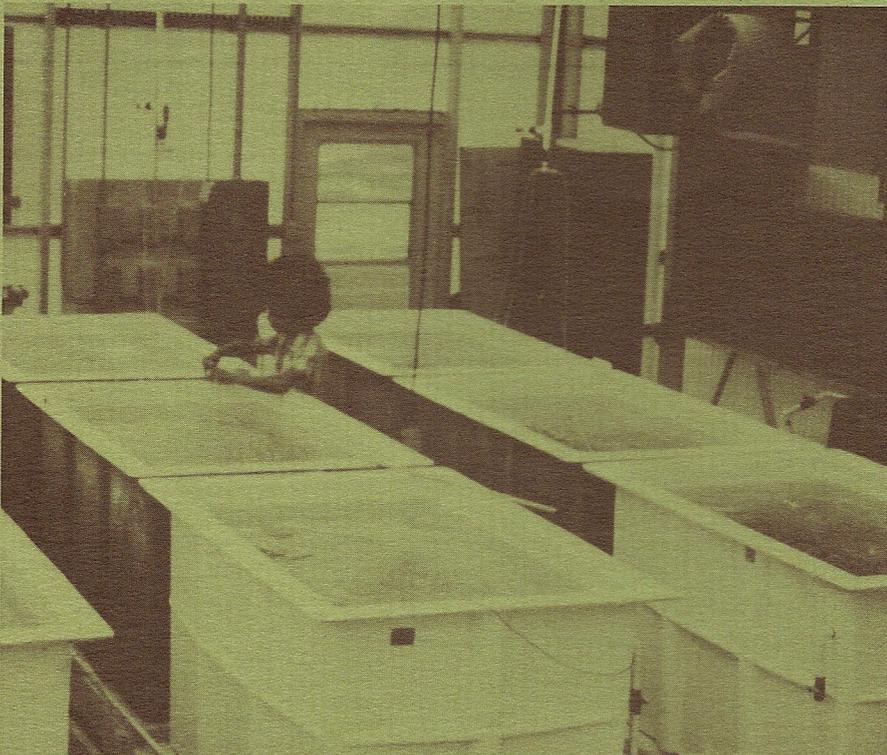


Figure 2. Greenhouse

of low light may have a competitive advantage over species with more prostrate growth forms. The availability of light is unquestionably an important factor influencing the depth distribution of submersed macrophytes.

WATER TEMPERATURE

In macrophyte-dominated lacustrine systems, vertical profiles of light and water temperature in the littoral zone roughly parallel one another. Seasonal changes in photoperiod and incident solar radiation correspond with substantial changes in water temperature in most aquatic systems. Thus, light may interact with temperature in determining the growth of submersed macrophytes.

Water temperature affects rates of various physiological processes in plants, but very little data are available to characterize either the thermal requirements or the thresholds of thermal tolerance for most submersed macrophyte species. There are some indications based on geographical distribution data and on temperature-related growth data that different species possess discrete ranges of thermal tolerance. These differences appear to affect both the productivity and geographical distribution of some submersed macrophytes in nature.

SEDIMENT

The role of sediments in the nutrition of submersed macrophytes is a subject of continuing debate. For the most part, submersed plants are considered to be capable of absorbing nutrients from either the sediment or the water depending upon relative differences in the availability of specific nutrients. Evidence suggests that the roots of submersed macrophytes are functionally similar to those of terrestrial plants. Because the availability of nutrients is usually greater in sediments than in water, sediments

represent a potentially important source of nutrition to rooted macrophytes.

Nitrogen and phosphorous (N and P) in aquatic systems appear to be readily mobilized from the sediment by submersed macrophytes. Losses of these nutrients from decaying macrophyte tissues can significantly contribute to the internal nutrient loading of aquatic systems. The generally accepted consensus regarding the P nutrition of submersed macrophytes is that most (if not all) species can obtain this element entirely from the sediment. The extent to which other elements can be mobilized from sediments by aquatic plants is less certain. For example, potassium (K) appears to be mobilized by submersed macrophytes from sediments to only a minor extent in comparison with K uptake from the open water of lakes.

Recent experimental evidence suggests that there may be a relationship between sediment organic content and the species composition of aquatic macrophyte communities, since the growth of some species can be inhibited by changes in sediment chemistry associated with the decomposition of sediment organic matter. Aquatic macrophytes modify the sediment environment by promoting increased sedimentation both through their passive reception of decaying materials from other plants and through contributions of their own decaying materials to the sediment. It is intriguing to speculate that the development of unfavorable changes in sediment chemistry due to the prolific growth of adventive macrophyte species might ultimately contribute to their own demise.

WATER CHEMISTRY

With most rooted macrophytes, water chemistry may be less important from a nutritional standpoint than sediment chemistry

(with the exceptions mentioned in the preceding paragraph). Two interrelated and important aspects of water chemistry are pH and carbon availability. As with temperature, both of these factors can specifically affect overall plant metabolism and thereby potentially influence community composition. The species composition of acidic versus alkaline environments often differs markedly, yet there is little definitive information related to the underlying causes of such observations.

In highly alkaline waters, there may be some selectivity for macrophyte species that can utilize bicarbonate sources of inorganic carbon (C) in photosynthesis. The cation composition of natural waters seems to have an important influence on bicarbonate utilization by submersed macrophytes.

In alkaline systems, macrophytes must be able to effectively withstand heavy carbonate precipitation and associated epiphyte development on their leaf surfaces. In nonalkaline (unbuffered) systems, macrophytes must be adaptable to oftentimes dramatic variations in pH associated with diel and seasonal changes in community metabolism.

To some extent, macrophyte communities themselves control water chemistry through processes of nutrient uptake, photosynthesis, and respiration. The relative strengths and weaknesses of macrophytes in relation to diel and seasonal fluctuations in water chemistry may be important in influencing the outcome of competition among species with similar environmental requirements.

BIOTIC-ENVIRONMENTAL FACTORS

One of the key interactions between phytoplankton and submersed macrophytes involves competition for light. In addition to planktonic algae, the growth of attached (epiphytic) algae on the

leaf surfaces of submersed macrophytes can substantially reduce irradiance. Dense populations of free-floating plants compete with algae for nutrients and, with algae, may competitively exclude submersed vegetation by reducing the depth of light penetration in water.

There are few data available on allelopathy (chemical interference) among aquatic macrophytes. However, the influence of extracellular metabolites on algal species succession has been demonstrated to be important in some aquatic systems. The role of allelochemical substances in the succession of aquatic macrophytes can apparently be influenced by aqueous nutrition in duckweeds and sediment nutrition in emergent macrophytes. Research on allelopathy among submersed macrophytes with emphasis on sediment chemistry may someday provide a new perspective in aquatic plant management.

CONCLUSIONS

The relative importance of individual environmental factors in determining the growth of macrophytes cannot be ranked because their influence undoubtedly varies from one aquatic system to the next and from one species to the next. However, some generalizations can be made. In most aquatic systems, nutrients supplied from both the sediment and the open water should be adequate to meet the nutritional requirements of submersed macrophytes. Light and temperature are both important in controlling the depth distribution of submersed macrophytes. In this connection, water temperature may assert greater control over the geographical distribution and seasonal growth of macrophytes than has been previously realized.

It is unlikely that carbon supply limits the seasonal growth of macrophytes, but short-term reductions in dissolved inorganic carbon or differences in its form may promote physiologically

compensatory adaptations in some species. These adaptations could be important in offsetting the competitive balance among species, particularly in systems subject to pronounced diel or seasonal variations in carbon concentrations. Specific physiological adaptations to changes in sediment chemistry during lake development may also influence macrophyte community composition.

Many methods of aquatic macrophyte control currently in use are generally cosmetic and have relatively short-term effectiveness. Changes in macrophyte community composition following the implementation of control measures have been essentially unpredictable, and the final outcome is often unfavorable when the aquatic ecosystem is considered as a whole. The development of long-term and ecologically suitable plant management procedures will require an increased understanding of the specific environmental requirements of individual macrophyte species and the related causes of their excessive growth. Such knowledge will also be valuable in bettering capabilities of predicting potential changes in the present geographical distribution of nuisance macrophyte species.

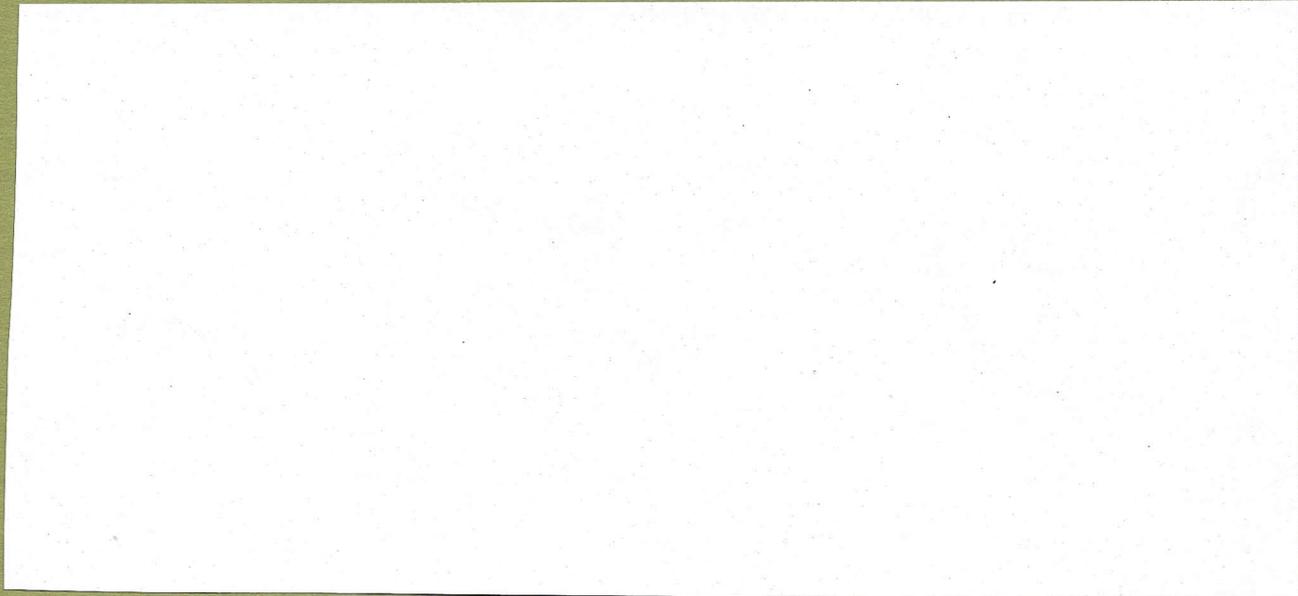
Most of the information provided in this article was derived from experimental research. Such studies provide quantitative indications of the ranges over which different environmental factors can influence the growth of aquatic macrophytes. As more of this information becomes available, it will become increasingly necessary to examine and

This bulletin is published in accordance with Army Regulation 310-2. It has been prepared and distributed as one of the information dissemination functions of the Environmental Laboratory of the Waterways Experiment Station. It is principally intended to be a forum whereby information pertaining to and resulting from the Corps of Engineers' nationwide Aquatic Plant Control Research Program (APCRP) can be rapidly and widely disseminated to Corps District and Division offices as well as other Federal agencies, State agencies, universities, research institutes, corporations, and individuals. Contributions are solicited and will be considered for publication so long as they are relevant to the management of aquatic plants as set forth in the objectives of the APCRP, which are, in general, to provide tools and techniques for the control of problem aquatic plant infestations in the Nation's waterways. These management methods must be effective, economical, and environmentally compatible. This bulletin will be issued on an irregular basis as dictated by the quantity and importance of information to be disseminated. Communications are welcomed and should be addressed to the Environmental Laboratory, ATTN: J. L. Decell, U. S. Army Engineer Waterways Experiment Station, P. O. Box 631, Vicksburg, Miss. 39180, or call 601-634-3494.



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Colonel, Corps of Engineers
Commander and Director

redefine concepts concerning the ecology of aquatic macrophytes and to apply this knowledge in developing efficacious plant management procedures.



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