

The Limnological Role of Aquatic Macrophytes and Their Relationship to Reservoir Management¹

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Abstract

Reservoir biologists often consider aquatic macrophytes an undesirable form of primary production. Techniques for controlling macrophytes have limited effectiveness. A consideration of recent research indicates that a balance between phytoplankton and macrophyte production is desirable in most reservoirs. Methods for eliminating especially troublesome macrophytes and encouraging more desirable species should be developed.

Many macrophytes produce large standing crops and are intricately involved in aquatic food webs. The nutritive value of different species varies considerably. Therefore, a distinction should be made between the quality and quantity of production. The quality of

the food is often more important than its energy content when aquatic food webs are considered.

Macrophyte communities often accumulate large quantities of inorganic nutrients early in the growing season and thereby compete with phytoplankton for nutrients. Phosphorus concentrations are apparently very important in regulating macrophyte growth. The phosphorus cycle of the littoral zone is considered in detail. In shallow, macrophyte-infested reservoirs, a considerable proportion of the phosphorus is cycled through pathways in which vascular plants are involved.

In nutrient polluted reservoirs, certain macrophyte species could be cultivated in specified areas to deny space and nutrients to nuisance species. Macrophytes could be harvested to reduce nutrient levels. The macrophyte flora of tropical reservoirs represents an important source of fodder or leaf protein that could be exploited for food.

Introduction

There has recently been much concern over the rampant growth of various species of vascular aquatic plants in natural lakes and streams, man-made

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waterways, and especially in impoundments (Holm, Weldon and Blackburn, 1969). Such plant growth frequently interferes with human activities and decreases the efficiency with which aquatic resources are utilized. As a result, control techniques involving chemical, biological, and mechanical agents have evolved. There is, however, an amazing lack of interest in the ecological relationships which cause aquatic plant infestations. Little effort has been expended to determine the causes of infestations in particular situations. Characteristically, man has attempted to eradicate what he considered a serious biological nuisance with little concern over the true nature of the ecological problem.

In the present paper, information regarding the ecology of aquatic plant infestations is introduced as a basis for encouraging the management, as opposed to the eradication, of macrophyte communities in reservoirs. At several points, previously unpublished data are presented to substantiate the discussion. Information was obtained by standard techniques which are not reported in detail in order to save space. Much of the discussion is based on general observations that I have made on many reservoirs and ponds.

The Reservoir Flora and the Origin of Aquatic Weed Problems

Obviously, any reservoir will support some type of flora. The ratio of importance between phytoplankton and macrophytes usually depends upon the morphology of the reservoir, the nature of the bottom sediments, and light conditions. Deep reservoirs with few shallow areas and very turbid reservoirs have a restricted littoral zone where light regimes are adequate for the development of a rooted flora. Dominant plants in these ecosystems are phytoplankters, although populations of emergent species may occur along the shoreline.

In warm climates, floating vascular plants such as *Eichhornia crassipes* (water hyacinth) or *Pistia stratiotes*

(water lettuce) may completely cover the surface of any reservoir. Many shallow reservoirs have very extensive littoral zones. Submersed and floating-leaved communities may dominate such situations. In most reservoirs both macrophytes and phytoplankton are important aspects of the flora. Aquatic macrophytes are therefore natural components (exotic introductions are exceptions) of the ecosystem and the balance between macrophyte and phytoplankton production in a particular reservoir will be determined by existing niches for the growth of species within the two groups.

New reservoirs undergo succession with subsequent changes in species composition and abundance as they age (Mitchell, 1969).

Most species of aquatic plants endemic to an area are capable of dispersal into a newly formed reservoir. Major environmental factors that determine establishment of a particular species at a given site in a reservoir are water depth, current, wave action, temperature, transparency, substrate characteristics, and water chemistry (Moyle, 1945; Swindale and Curtis, 1957; Spence, 1964; Seddon, 1965; Sculthorpe, 1967). Competitive interactions between phytoplankton and macrophytes (Hasler and Jones, 1940; Moore, 1950, 1952; Goulder, 1969; Fitzgerald, 1969a) and between species of macrophytes (Penfound, 1940a, 1940b; Hall, 1940; Penfound and Earle, 1948; McNaughton, 1968) are equally important in determining the development of aquatic communities.

Vegetative expansion of macrophytes from invading propagules is often rapid. *Eichhornia crassipes* can spread over many hectares in a single growing season (Holm, Weldon and Blackburn, 1969; Penfound and Earle, 1948). *Typha* (Yeo, 1964), *Nelumbo lutea* (Hall and Penfound, 1944) and *Alternanthera philoxeroides* (Penfound, 1940b) populations also expand rapidly as do many other species of macrophytes (Sculthorpe, 1967; Westlake, 1968; Holm, Weldon and Blackburn, 1969).

Many floating-leafed and emergent plants perenniate from rhizomes, e. g. *Typha*, *Saururus*, and *Nelumbo*. Such plants often produce relatively mono-specific stands that occupy a site for many years. Invasions of the stands by other species is difficult because of the well-developed root systems and the high degree of coverage by the foliage. There is evidence that chemical substances produced by *Typha latifolia* prevent invasion by other *Typha* (cattail) species (McNaughton, 1968). These substances even prevent the germination of *T. latifolia* seeds. Autotoxic mechanisms may be important in other species.

Inlets of reservoirs often contain several floating-leafed or emergent species that maintain mutually exclusive populations. Submersed species are also capable of producing dense populations that are not readily invaded by other species. However, in oligotrophic lakes, submersed plant stands comprised of coexisting assemblages of several species are frequently encountered. Dense mono-specific stands of submersed species are more common in eutrophic situations. Floating plants may cover the surface and shade out phytoplankton and submersed macrophytes.

Thus, a reservoir has a macrophytic flora determined by environmental and biological interactions with species that invade or occur in the system. Problems arise when macrophyte populations interfere with human activities. In many cases, the problem is simply the result of the reservoir having an extensive littoral zone for macrophyte growth.

The construction of reservoirs in tropical regions often produces habitat for the expansion of endemic floating plant populations. Many African reservoirs are heavily infested with *Eichhornia crassipes*, *Pistia stratiotes*, or *Salvinia rotundifolia* (Holm, Weldon and Blackburn, 1969). Serious aquatic plant problems are almost certain to occur in reservoirs in tropical and subtropical regions. These plant communities may drastically interfere with intended uses

of reservoirs, so the wisdom of constructing large impoundments in the tropics and subtropics is sometimes questionable. In more temperate climates, shallow reservoirs will probably develop extensive macrophyte colonies.

Introduction of species not endemic to an area frequently causes serious infestations. The introductions of *E. crassipes* (Penfound and Earle, 1948) and *Hydrilla verticillata* (Blackburn, Weldon, Yeo, and Taylor, 1969) into the southern United States are excellent examples. These species currently cover large areas of many lakes and streams and are serious economic problems in certain localities.

Nutrient pollution often causes macrophyte production to increase to nuisance proportions in bodies of water where native fertility levels were previously insufficient to maintain dense populations (Lind and Cottam, 1969). In other waters where pollution is not a problem, natural fertility may support nuisance growth of higher plants (Frink, 1967).

In summary, the degree of cover and production of macrophytes in a reservoir are regulated by resources, including space suitable for their growth, and a propagule source. Nuisance growths of plants are not necessarily due to human alteration of the environment. Where habitat for plant growth occurs, nothing short of removing the habitat will prevent vegetational development. Human activities and macrophyte communities should reach some compromise short of aquatic plant eradication.

Role of Macrophytes in Limnology

In addition to their role in primary production, macrophytes provide support, shelter, and oxygen to other organisms. Summaries by Wilson (1939), Hotchkiss (1941), Penfound (1956), and Sculthorpe (1967) can be consulted regarding many aspects of the biological significance of macrophytes with respect to fish production. I will primarily con-

sider macrophyte production and the nutrient relationships of these plants since much of the recent research in these areas has not been reviewed. Furthermore, the effects of nutrients on production are important in management schemes for aquatic plants.

Primary production

Most of the data on macrophyte production are for standing crops. Standing crop data are usually obtained by removing all plant material from quadrats or transects. It is rather difficult to harvest submersed plants by such techniques, and a simple optical method for determining the standing crop of underwater plants was recently developed (Owens, Learner and Maris, 1967). Grazing by herbivores, death, and losses of foliage (e.g., wave action) represent significant losses of net production in many cases (Westlake, 1966). Wetzel (1969a, 1969b) has demonstrated that large quantities of organic compounds are excreted by submersed species. Recently the carbon-14 method for measuring productivity has been adapted to macrophytes (Wetzel, 1964; Davies, 1970), and more accurate estimations of net production will hopefully be obtained.

Macrophytes are important in food webs of aquatic ecosystems. The proportion of total primary production attributed to macrophytes will vary with the suitability of the system for their growth. In most reservoirs the area and volume of water occupied by macrophytes are much less than that occupied by phytoplankton. Most macrophytes are not grazed extensively by herbivores, but when decay occurs macrophytes contribute to the organic detritus pool that is so important in aquatic food webs (Odum, 1959).

Standing crops of various species of aquatic macrophytes differ greatly. Floating-leafed and submersed species usually have standing crops less than 500 g dry wt/m² (Low and Bellrose, 1944;

Boyd, 1968; Lind and Cottam, 1969). This is much lower than values for aquatic plant communities of other types (Westlake, 1963). Emergent plants generally have much higher standing crops. Values in the range of 500 to 1,500 g/m² are commonly encountered, and occasionally standing crops in excess of 2,000 g/m² are reported (Westlake, 1963; Boyd, 1969a; Boyd and Hess, 1970; McNaughton, 1966). Floating plants such as *Lemna* (Low and Bellrose, 1944) and *Pistia* (Odum, 1957) have standing crops below 500 g/m², whereas the free floating *E. crassipes* often produces more than 1,000 g/m² (Penfound, 1956; Westlake, 1963).

Submersed, floating-leafed, and floating plants are usually less productive than emergent plants if the same body of water is considered or if data are averaged for several species within a group. However, generalization concerning the production of an individual species is difficult since standing crops of a species may differ severalfold between sites (Gorham and Pearsall, 1956; Straskraba, 1963; Boyd, 1969a; Boyd and Hess, 1970).

Data for net production are usually reported in terms of dry matter, ash-free dry matter, carbon, or energy equivalents. Such production data are usually compared directly with the consequence that all units of primary production are equated. However, the total amount of dry matter and energy consumed by a herbivore or detritus feeder gives no indication of the nutritive value of the food. Results with aquatic macrophytes (Boyd, 1968; 1970a) show that caloric content differs very little between species or within the same species at various stages of maturity or at different sites. On the other hand, levels of organic nutrients, particularly protein, were extremely variable in the samples (Boyd, 1968; 1970a).

The digestibility of macrophytes, as determined by the neutral detergent fiber technique (Van Soest and Wine, 1967), also differs greatly between

species.² In general, species that produced large standing crops contained larger proportions of fibrous supporting material and were thereby less digestible than species that had lower standing crops. The significance of a particular species in aquatic food webs does not depend entirely upon its ability to produce large quantities of dry matter. Most submersed and floating-leaved species produce small standing crops but have much higher nutritive values than highly productive emergent plants.

Nutrient relationships

Plant production at a particular site may be limited by shortages of any of the essential inorganic nutrients, including a source of inorganic carbon. However, as pointed out earlier, other environmental factors are also important in regulating growth. Light is especially important in regulating the growth of submersed plants (Peltier and Welch, 1969, 1970; Martin, Bradford and Kennedy, 1969). There are interactions between the various environmental factors affecting growth, so several factors probably regulate production.

Hutchinson (1957) and Sawyer (1966) suggested that phosphorus is probably the most important single nutrient regulating productivity since it is frequently present at levels thought to be insufficient for maximum plant production in aquatic ecosystems. Nitrogen is also thought to be a growth limiting factor in many freshwater habitats. This long accepted point of view was recently challenged. Lange (1967), Kuentzel (1969), and King (1970) attempted to relate increased production of phytoplankton to increased carbon dioxide levels. According to Kuentzel (1969), excessive plant production in polluted bodies of water results from carbon dioxide produced by microbial degradation of organic compounds which reach the system in various efflu-

ents. The same line of reasoning can be extrapolated to submersed aquatic plants. However, emergent and floating-leaved aquatic plants probably obtain most of their carbon for photosynthesis from the atmosphere.

The general application of the carbon dioxide theory proposed by Kuentzel and others is questionable. Increased carbon dioxide cannot be used for plant growth without adequate mineral nutrients, so the nutrient content of effluents is equally as important as readily degradable organic carbon unless the system already has adequate mineral nutrients to use all naturally available carbon for growth. Such may well be the case in advanced stages of artificial eutrophication. The carbon dioxide theory cannot be reconciled with data that clearly show increased phytoplankton production following inorganic fertilization of impoundments (Dendy, 1963). Phosphorus is particularly important in increasing fish production in ponds (Swingle, Gooch and Rabanal, 1963). Nutrient bioassay experiments (Goldman, 1960; Goldman and Wetzel, 1963; Polisini, Boyd and Didgeon, 1970) reveal that phosphorus and additional nutrients other than carbon dioxide frequently limit phytoplankton growth. These findings do not prove that carbon is not also limiting. The additions of nutrients merely increased the utilization of available carbon.

Submersed vascular species have lower nutrient requirements than filamentous algae or phytoplankton (Mulligan and Baranowski, 1969). Continued enrichment of reservoirs might result in the growth of larger populations of phytoplankton at the expense of submersed plants. Furthermore, bioassay experiments (Gerloff and Krombholz, 1966; Fitzgerald, 1968, 1969b; Gerloff, 1969) revealed that relatively few of the natural populations of submersed plants that were considered were actually phosphorus limited. Conversely, phosphorus is important in regulating the growth of the emergent macrophytes *Typha lati-*

² Polisini, J. M. and C. E. Boyd, unpublished data.

folia (Boyd and Hess, 1970) and *Saururus cernuus*.³

One or more nutrients may be limiting plant growth in any particular situation. I agree with Hutchinson (1957) in assuming that phosphorus is a very important limiting factor. However, carbon dioxide (or bicarbonate ion) and other nutrients may be equally important in enhancing growth in many situations.

Quantities of inorganic nutrients contained per unit area of macrophyte growth are much higher than those contained in the phytoplankton of an equal area. For example, maximum quantities of phosphorus (2.8 g/m²) and nitrogen (44.3 g/m²) in a *Justicia americana* stand were many times higher than ever encountered in phytoplankton communities. Although there are large intra and interspecific differences in the elemental composition of macrophytes (Boyd and Lawrence, 1966; Boyd, 1967, 1970b), in general, quantities of nutrients per unit area of plant stand increase with increasing dry matter standing crops when data for different species and sites are considered. Regression equations, prepared from data obtained for 24 species of macrophytes (Boyd, 1968, 1969a, unpublished), enable the calculation of g nitrogen and phosphorus per square meter (Y-variable) from standing crop data (X-variable) expressed as g dry wt/m².

$$\text{Nitrogen } Y = 0.014 + 1.587X$$

$$(r = 0.85; P < 0.01)$$

$$\text{Phosphorus } Y = 0.001 + 0.434X$$

$$(r = 0.77; P < 0.01)$$

These equations allow a rough approximation of quantities of nutrient per unit area from standing crop data of any macrophyte population or community. Whenever possible, I recommend that chemical analyses be obtained for the plant stand in question rather than that these equations be used.

Nutrients removed from water by

³ Boyd, C. E. and W. W. Walley, unpublished data.

phytoplankton are recycled rapidly. The average life of individual phytoplankters is usually two weeks or less. Macrophytes tie up net quantities of nutrients for longer periods. Several workers have used radiophosphorus to show that the turnover rate of phosphorus in aquatic vegetation is rapid (Hayes and Phillips, 1958; Rigler, 1964). However, regardless of the turnover time of individual phosphorus atoms between plants and environment, the vegetation will contain a net quantity of phosphorus that is effectively removed from circulation and availability to other organisms. The same reasoning holds for other nutrients.

Studies of nutrient uptake in natural populations of emergent macrophytes (Boyd, 1969a; 1970c; 1971) showed that some elements, particularly nitrogen, phosphorus, and potassium were absorbed early in the growing season at a proportionally greater rate than later in the season. In the southern United States, most of the total net nutrient accumulation occurs by midspring before peak dry matter standing crop is reached. Nutrients stored during early spring growth are utilized for growth at a later time. Such a pattern of nutrient absorption insures that the plants have adequate stores of nutrients when the weather is favorable for rapid growth. The nutrients are also removed from the environment early in the season, giving a macrophyte population a competitive advantage over other species of macrophytes and phytoplankton. This advantage is particularly significant in infertile waters. Stake (1967, 1968) reported a similar pattern of nutrient uptake in some submersed species.

When shoots begin to die in late summer, nutrients are leached rapidly from the foliage (Boyd, 1969a). Once emergent plants fall into the water, cations and phosphorus are lost at an even faster rate (Boyd, 1970d). Nitrogen is retained to a larger extent and there is a build-up of nitrogen (protein) during detritus formation from decaying macrophytes (Odum and de la Cruz, 1967;

Boyd, 1970d). Losses of nutrients from submersed plants are probably even more rapid since these plants have a more finely dissected structure. These findings are particularly significant to herbicide applications in reservoirs. Once vegetation is killed, a large proportion of its nutrient content will be rapidly released to the water for use by other organisms. Large increases in dissolved nutrients (including CO_2) after herbicide treatments of plant communities in plastic pools were observed by J. M. Lawrence (personal communications).

In view of the importance of phosphorus in aquatic ecosystems, the phosphorus cycle will be considered in detail. A model of the phosphorus cycle in a shallow, macrophyte infested reservoir is presented in Figure 1. Even though all species of the littoral zone are bathed by the same medium, macrohabitat differences in phosphorus concentrations and morphological characteristics of the plants determine the available phosphorus pool of respective species. Floating macrophytes and submersed species without root systems (*Ceratophyllum demersum*) likely absorb their nutrients

primarily from the water. Submersed plants with root systems are capable of absorbing nutrients from the mud (Pond, 1905; McRoy and Barsdate, 1970). Martin, Bradford, and Kennedy (1969) reported that *Najas* absorbed mineral nutrients from the mud and obtained carbon by foliar absorption of bicarbonate ion from the water.

The relative importance of the absorption of nutrients from the mud as compared to the uptake of nutrients from the water via the leaves probably varies greatly between species. The finely dissected foliage of submersed plants is considered an adaption to expose large chlorophyllous surfaces to limited light, but the large surface area also facilitates mineral nutrient, carbon dioxide, and bicarbonate absorption. Non-rooted aquatics and those without appreciable root systems are in direct competition with phytoplankton for nutrients since they are dependent upon dissolved nutrient supplies. Even submersed plants with highly developed root systems probably absorb some nutrients from the water. Floating-leaved and emergent macrophytes have well developed root systems and a comparatively small submerged foliage area. These plants probably depend largely upon nutrient supplies in the mud.

The ratio of root system to shoot system, the foliage area exposed to the water, and other morphological characteristics are only crude indices of the relative contribution of nutrients from the mud or from the water to total uptake. Nutrient uptake per unit surface area likely varies between species and plant parts.

Boyd (1967) presented evidence that rooted macrophytes have available in the anaerobic depths of the mud much higher concentrations of phosphorus than are found in aerobic water. This condition results from the high solubility of iron and aluminum phosphates at low redox potentials (Mortimer, 1941). Since aerobic conditions usually exist at the mud-water interface in the littoral zone,

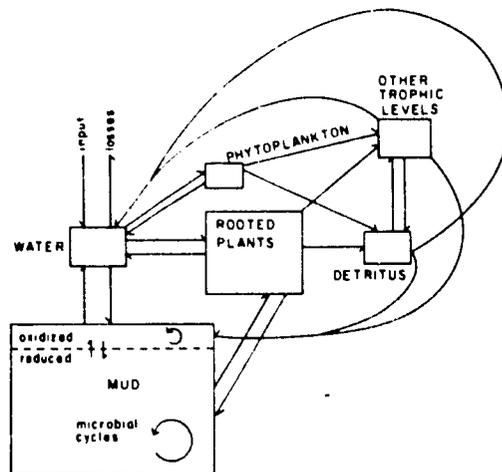


Figure 1. A qualitative model of the phosphorus cycle in a shallow, aquatic plant infested impoundment. The size of the blocks in the diagram are intended as an approximation of relative quantities of phosphorus in different phases of the system.

phosphorus moving upward from the anaerobic depths will precipitate at the interface. The solubility of phosphorus at the aerobic interface is much less than in the anaerobic layer. Rooted plants do not have to compete with phytoplankton, periphyton, or non-rooted macrophytes for the phosphorus contained in reduced muds. This phenomenon may account in part for the fact that oligotrophic lakes in the southeastern United States frequently have a well developed vascular flora.

For example, phosphorus concentrations in the waters of Par Pond, a large reservoir near Aiken, South Carolina, seldom exceed 2 ppb, and levels of other dissolved nutrients are very low. Phytoplankton productivity is relatively low (J. S. Marshall, personal communications), yet this reservoir is very productive in terms of macrophytes.

If dissolved phosphorus levels do not limit plant growth, the ability to utilize soil phosphorus is not a competitive advantage for rooted plants. In eutrophic situations, dense phytoplankton growth may shade out macrophytes if light penetration is restricted sufficiently to prevent the establishment of rooted plant communities (Dendy, 1963). Conversely, if rooted plant communities are established earlier than phytoplankton blooms occur, these macrophytes will be a dominant aspect of the littoral vegetation even in eutrophic waters.

Dissolved phosphorus rapidly equilibrates with aerobic mud (Hepper, 1958; Pomeroy, Smith and Grant, 1965; Harter, 1968). Equilibrium concentrations in the water are extremely small compared with those in the mud. Nevertheless, the mud of the littoral zone contains a reserve supply of phosphorus which is released to the water in response to displacement of the mud-water phosphorus equilibrium by foliar uptake of macrophytes or absorption by phytoplankton.

The magnitude of the reserve phosphorus capacity in an aerobic mud is illustrated in Fig. 2. A lake mud-distilled water system was shaken to phosphorus

equilibrium (30 min). The mud was centrifuged down and the water decanted. More distilled water was added to the mud and the procedure repeated 25 times. Phosphorus removal decreased rather rapidly at first and then tapered off with little difference in removal with increasing number of extractions. After 25 extractions the quantity removed per extraction was only three times less than for the initial extraction.

In a second experiment, concentrations of water soluble phosphorus (1 g soil extracted one time with 50 ml of distilled water) were determined for a series of mud samples from 29 Alabama impoundments (Boyd, 1970e). Dilute acid soluble phosphorus determinations (Jackson, 1958) were also made. Dilute acid extracts calcium phosphates and includes, based on agricultural crops, that phosphorus which is readily available for plant growth. There was a significant positive correlation between dilute acid soluble phosphorus concentrations and water soluble phosphorus ($r = 0.70$; $P < 0.05$). As expected, phosphorus rich muds deliver higher equilibrium concentrations of phosphorus to

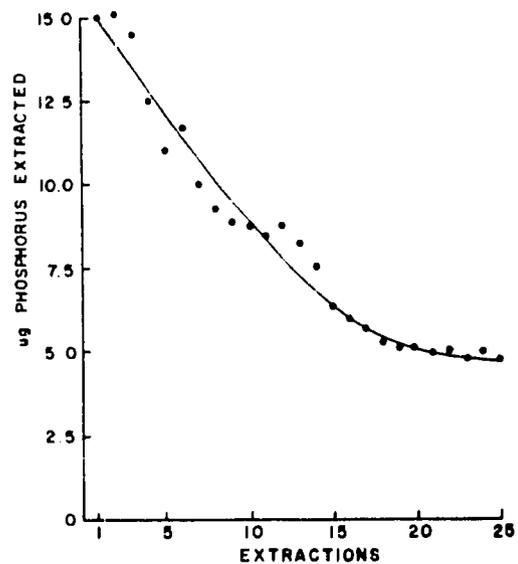


Figure 2. Quantities of phosphorus removed from a mud by consecutive extractions with phosphorus free water.

the water than muds with lower phosphorus concentrations. The reserve capacity of phosphorus in the mud explains why large standing crops of phytoplankton or macrophytes are often observed in waters with low dissolved phosphorus levels. The quantity of phosphorus in vegetation frequently exceeds that of the total water volume (Boyd, 1967).

Quantities of phosphorus that are transferred to higher trophic levels (Figure 1) are small as compared to amounts of phosphorus contained in plants. The largest proportions of phosphorus in the system are exchanged within three pathways: water and mud, mud and rooted plants, and water and rooted vegetation. There is also a possibility of a net phosphorus leak from rooted plants into the water (McRoy and Barsdate, 1970) so that rooted plants transfer phosphorus from anaerobic mud to the water. A phosphorus pump mechanism in rooted plants would be especially significant in phosphorus cycles of oligotrophic reservoirs.

In lakes without large macrophyte communities, the model will differ in that there will be much less phosphorus in the vegetation compartments. Phosphorus relationships in the hypolimnion and during overturns were omitted from Figure 1 for brevity.

Management and Utilization of Aquatic Macrophytes

Plant control

Herbicide application is the technique most frequently used for macrophyte abatement (Holm, Weldon, and Blackburn, 1969). Interest in chemical control is derived from the successful use of herbicides in agricultural operations. However, the crop plant environment is determined to a large extent by cultivation practices where the system can be altered predictably. Weeds that are competing with crop plants can be killed with herbicides so that the available resources will be used by the crop plant.

Conversely, if aquatic plants are removed by herbicide treatment, nature provides the species which will utilize the resources originally used by the pest plant.

Once aquatic plants die, space for other plants becomes available. Nutrients contained in the vegetation are quickly released to the environment for use by other species. Therefore, unless enough herbicide is added to render the environment toxic to all plant life, the original vegetation will be replaced by the same or other species. Admittedly, it may require some time for the vegetation to reach the original level and some degree of control is often obtained. However, nature will not permit a vacuum with respect to vegetation and continued control will require repeated application.

At the present state of knowledge we do not know how to predict what species will replace the species removed by herbicide treatment. Sometimes the replacement is a more desirable species, often it is the same species, and in other situations the new plant may be more offensive than the original species. In some Florida lakes, herbicide applications have upset the balance between rooted aquatics and phytoplankton, resulting in phytoplankton blooms of nuisance proportions which shaded the subsequent regrowth of rooted plants. This final result is often worse than the original situation.

Management

Although herbicide treatments of large portions of reservoirs are not recommended, localized plant stands can be controlled quite well with herbicides. Invading species can sometimes be eliminated and obstructing vegetation eradicated from specified areas. Biological agents (Holm, Weldon and Blackburn, 1969) may have potential in controlling certain species of water plants. Mechanical removal of vegetation works well in certain situations (Livermore and Wunderlich, 1969).

Where feasible, water level manipulation is one of the best control techniques

(Penfound, 1953). Water level management has been used in reservoirs of the Tennessee Valley Authority to limit the establishment of plants along shallow shorelines or to keep the plants in early developmental stages (Hess and Kiker, 1944; Penfound, Hall and Hess, 1945). The TVA workers were interested in reducing suitable areas for the breeding of anopheline mosquitoes. However, water level management can also be used for the general control of many plant species.

As pointed out above, areas of reservoirs which are suitable macrophyte habitats will produce macrophytes in spite of attempts of reservoir managers to eradicate these plants. A realization of the ecological problems involved in eradicating or reducing plant growth should bring about a reevaluation of the problem. Many aquatic plant problems can merely be accepted with the rationale that control is impossible or that the readjustment of the ecosystem following the removal of a particular pest will not lead to a significant improvement of the original situation.

The most desirable technique for coping with plant growth is to manage the littoral zone in such a way as to encourage the growth of species that are relatively innocuous to human activities to the exclusion of troublesome plants. Suitable species will vary with respect to geographic region and reservoir use. A reservoir intended primarily for waterfowl management should contain species that produce large quantities of seed. Where the fishery is most important, species with a high nutritive value that are rapidly converted into high quality detritus are desirable. In a multipurpose reservoir, particular areas might require entirely different vegetational management schemes than others.

Plant management could be effected by using chemical, biological, or mechanical techniques to remove selectively undesirable species and thus encourage coverage by less troublesome species. It will probably be necessary to resort to

plant stocking to insure that the desired species replacement occurs. The selection of species that are not competitively displaced by invading species will be important. Plant management will be fraught with difficulty and will not be feasible in many reservoirs.

The management of vegetation to control nutrient cycles also has potential in balancing macrophyte and phytoplankton growth in eutrophic lakes. In tropical regions, the cultivation of floating plants, e. g., *Eichhornia crassipes*, in selected areas of the reservoir might reduce dissolved nutrients to permit some degree of phytoplankton control. *E. crassipes* produces large standing crops. Penfound (1956) reported a standing crop of 1,276 g dry wt/m². Analyses were made on *E. crassipes* samples from 17 sites in central Florida. The means (\pm two standard deviations) were 2.39 ± 1.08 and 0.54 ± 0.40 g/100 g dry weight for nitrogen and phosphorus content, respectively. From calculations based on these data 304 kg of nitrogen and 69 kg phosphorus would be trapped per hectare of stand.

In some eutrophic lakes and reservoirs nutrient levels could probably be reduced by harvesting aquatic plants. However, the amount of plant removal required to reduce soil phosphorus levels might necessitate harvests over several years. Plants could also be used to strip nutrients from effluents prior to release into reservoirs. The subject of nutrient removal has been considered in greater detail elsewhere (Boyd, 1970f; Yount and Crossman, 1970).

Value as food

Food supplies are limited in many tropical nations, and excessive macrophyte production represents a potential food supply. Leaf protein concentrate can be prepared in satisfactory quantities from a number of macrophytes (Boyd, 1968). This protein concentrate is suitable for use in human diets (Pirie, 1966). Many other species can be dehydrated to give a fodder suitable for animal feed

(Boyd, 1968; 1969). However, macrophytes are difficult to harvest and have a high moisture content. These properties preclude direct use of macrophytes as feedstuffs in technologically advanced nations. If the plants are harvested for nutrient removal, their disposal would be a problem. Economically valuable livestock feeds could be prepared from plants harvested for purpose of nutrient removal.

Ecosystem stability

A high species diversity gives stability to ecosystems (Odum, 1969). The addition of macrophytes to a lake creates habitat not available in a system with a flora consisting entirely of phytoplankton. A high diversity of macrophytes insures a wide range of habitat for invertebrate fish food organisms, thereby increasing the diversity of these organisms. Macrophytes also serve as hiding places for small fish.

Nutritionally, an ecosystem with simple floristics does not have a wide variety of food materials, and deficiencies of specific nutrients may occur. Only herbivores or detritus feeders adapted to feeding on one or a few types of plant materials can exist. A complex flora insures the presence of species that make up for the deficiency of a nutrient that may occur in one or more other species. This condition allows for a greater diversity of faunal components and more complex food webs.

The simple versus complex floristics concept is somewhat analogous to the case of a human vegetarian. If he eats only one type of plant material, he will suffer shortages of certain amino acids. By selecting a wide variety of plants in his diet, he will usually consume a material high in a particular amino acid that will supplement food items with shortages of this amino acid, so that an adequate amino acid balance is achieved.

Therefore, when present in moderate quantities, macrophytes increase the stability of reservoir ecosystems and are beneficial to fishery interests.

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