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CHAPTER 5

Wetland Vegetation

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INTRODUCTION

Natural wetlands have been used to treat wastewater with varying efficiency. Concern over environmental impacts on natural systems^{2,3} and the need for an empirically based wetlands wastewater treatment technology led to emphasis on constructed wetlands. These systems treat a variety of wastewater types; however, any one artificial wetland type may be unable to treat all contaminants.

Wetlands have individual and group characteristics related to plant species present and their adaptations to specific hydrologic, nutrient, and substrate conditions. Because of this, a variety of plant species are used in constructed systems (Table 1). However, few sources describe life history characteristics of wetland species that would facilitate selecting appropriate species for use in this technology. We are only beginning to understand wetland plant adaptations to their environment and more important, their effects on the environment.

In this chapter, we (1) discuss major categories of wetland vegetation and morphological and physiological adaptations to environmental gradients and (2) examine the abilities of plants to affect their environment and transform wastewaters.

CLASSIFICATION

Natural wetlands are populated by different plant types adapted for growth in water or saturated soil. Organization into clear-cut groups is difficult because of ambiguous definitions and the unwieldliness and complexity of the classification schemes. Consequently, we have many terms referring to plants growing along the gradient from terrestrial to aquatic habitats: hydrophyte, aquatic macrophyte, vascular hydrophyte, aquatic plant, and vascular aquatic plant.

One difficulty derives from previous distinctions between aquatic and wet-

Table 1. Plant Species Tested for Use in Constructed Wetlands for Wastewater Treatment

EMERGENT Scirpus robustus Scirpus lacustris Schoenoplectus lacustris Phragmites australis Phalaris arundinacea Typha domingensis Typha latifolia Canna flaccida Iris pseudacorus Scirpus validus

Scirpus pungens

Glyceria maxima Eleocharis dulcis Eleocharis sphacelata Typha orientalis Zantedeschia aethiopica Colocasia esculenta

SUBMERGED

Egeria densa Ceratophyllum demersum Elodea nuttallii Myriophyllum aquaticum

FLOATING Lagorosiphon major Salvinia rotundifolia Spirodela polyrhiza Pistia stratiotes Lemna minor Eichhornia crassipes Wolffia arrhiza Azolla caroliniana Hydrocotyle umbellata Lemna gibba

Lemna spp.

land plants. Penfound⁴ recognized two plant groups adapted to water saturated habitats: wetland species found in saturated soils and aquatic species present where soils are covered with water. This distinction reflects the diverse evolutionary origin of the different groups and their adaptations to these transitional habitats. In reality we commonly find both aquatic species and wetland species growing together in these habitats, and in this chapter we use the terms interchangeably.

There is general agreement about the origins of aquatic plants although relationships of many of the families are poorly understood. They are clearly derived from terrestrial ancestors. Most possess such terrestrial features as nonmotile sperm and emergent flowers. In some groups, various terrestrial structures have degenerated (loss of secondary thickening), become simplified (leaf structure), or lost their function (stomates). Many primitive monocot families are aquatic, suggesting early adaptive radiation of monocots into aquatic habitats. Aquatic members of otherwise terrestrial monocot, dicot, and pteridophyte families are probably of more recent origin and have arisen by convergent evolution from diverse backgrounds.

Classification schemes for aquatic plants are based either on morphological and physiological features, e.g., types of foliage or inflorescence, or phytosociologic criteria based on life and growth form, or growth in relation to the water surface. 7.8 Conversely, wetlands and their characteristic vegetation are classified by flooding regime, substrate material, and life form. 9 The life form concept links wetland classification and the classification of aquatic plants.

Aquatic plants are divided into free floating and rooted forms. The rooted class is then subdivided into emergent, floating, and submerged classes. Hutchinson⁸ recognized 26 subdivisions based on ecological growth forms that combined taxa with similar morphological adaptations to specific habitats. However, his classification omits woody vegetation characteristic in many seasonally flooded wetlands, including willows, mangroves, ericaceous shrubs, ashes, gums, cypress, and water oaks. These woody species have all evolved adaptations for persistence in at least seasonally waterlogged soils.

ADAPTATIONS OF PLANTS TO THE AQUATIC ENVIRONMENT

Wetland plants have evolved many structural and physiological adaptations for survival in water-dominated environments. A flooded anaerobic environment reduces oxygen available for respiration; light energy penetration for photosynthesis; and carbon dioxide and mineral nutrient availability for metabolism. Many useful reviews of the various ecological adaptations of aquatic and wetland plants are available. 7,8,10-15 Plants invading water-dominated environments did not evolve new and novel structures for dealing with that environment. Instead, existing structures were modified in evolving similar solutions to common problems among unrelated plant groups. The emergents are the least modified of the nonwoody wetland plants. The trend from emergent to floating to submerged plants reflects a gradual loss of many structural and functional terrestrial characteristics and modification of others. Among emergent plants, the monocots tend to have erect linear leaves that facilitate light penetration into the canopy. Dicots have erect leafy stems that also maximize reception of light for photosynthesis.

Formation of lacunae and/or aerenchyma tissue is a characteristic feature of nonwoody wetland plants. Lacunae function as nonliving support structures, reducing metabolic costs and providing for movement and storage of gases. Woody species rarely have lacunae, but many possess specialized structures to cope with periodic flooding. Lenticels, knees, adventitious roots, prop roots, and butt swellings are examples of the better-known adaptations that allow gas exchange with the atmosphere.

Adaptations of floating and submerged species reflect conservation of form and structure. Submerged plants have little need for elaborate support structure, and these tissues are absent or reduced. Instead, leaves are thin and pliable, with aerenchyma tissue and gas-filled lacunae providing buoyancy. Many of the adaptations found in shaded terrestrial leaves are also found in the submerged species, including a thin cuticle, chloroplasts in the epidermis, and thin leaves. These adaptations reflect the reduction in light intensity resulting from the relatively rapid extinction of light downward through the water column. Similarly, submerged species have maximized leaf surface-to-volume ratios. Their leaves are either long and thin or deeply dissected along the margins, or the leaf blades are separated into leaflets.

Despite diverse evolutionary lineages, floating leaved plants are morphologically similar. Few options exist for leaf development in a spatially restricted two-dimensional environment. They are adapted to existing at the air-water interface, where their distinct dorsoventral structure exposes the upper surface to air and the lower surface to water. Most species have circular leaves with entire margins that reduce tearing and a tough, leathery texture with a hydrophobic upper surface that prevents excessive wetting. Unlike most terrestrial plants, stomata are found on the upper surface. Their long, flexible petioles allow leaf blades to spread out on the water surface and reduce wave stress.

Among free-floating plants, water hyacinth (Eichhornia crassipes) leaves

form supported rosettes, vegetative parts of duckweeds (*Lemna* spp.) are reduced in structure and float on the water surface, while the salvinids (e.g., *Salvinia*) have sessile leaves. Free-floating rosette plants have root systems that comprise 20-50% of the biomass. However, the salvinids and some lemnids have lost their roots, and nutrients are absorbed through modified leaves.

PRODUCTION AND GROWTH

Plants in wastewater systems have been viewed as storage compartments for nutrients where nutrient uptake is related to plant growth and production. Plants absorb nutrients and excrete or lose small amounts during the growing season but release a large percentage at senescence. Harvesting before senescence may permanently remove nutrients from the system. Alternatively, nutrients tied up in litter and, eventually, sediments represent semipermanent storage.

Productivity varies widely among wetland plants, 10,16-18 reflecting the availability of resources, environmental stress, and adaptations to their environment. Emergent plants, with long erect linear leaves, reduce self-shading while creating a high leaf area index and favorable microclimates for photosynthesis. Many emergents have high light saturation levels (e.g., *Typha* and *Sparganium*) and high temperature optima for photosynthesis. These plants also have high transpiration rates 19,20 with high stomatal water loss that increases with rising temperature and light intensity until photosynthesis stops.

Some species possess the C4 high-efficiency photosynthetic metabolic pathway for CO₂ fixation. Terrestrial plants with this photosynthetic pathway are found in hot, sunny areas where water is scarce. Water is rarely limiting in wetlands, but some emergent freshwater and salt marsh species also possess this pathway. It may have evolved in certain salt marsh species in response to metabolic drought from salinity stress and in some freshwater species in reducing transpiration to decrease the harmful effects of ferrous iron on roots while maintaining optimal rates of carbon fixation. 17,21,22

The productivity of floating and free-floating aquatic plants is as high or higher than emergents. 10,16 In addition to common favorable environmental conditions, floating leaved species have less respiratory tissue and possess air-filled spaces which may enable them to utilize photorespired CO_2 .

Production of submerged aquatic plants is generally low because of low light intensities under water and the low diffusion of CO₂ in water. Maximum photosynthesis usually occurs at light levels of 15–30% of full sunlight²³ although plants can photosynthesize at high temperatures.²⁴

Submerged plants can utilize carbon dioxide from alternative sources. In alkaline environments, some species may utilize $HCO_3^-, ^{25,26}$ although evidence for the general use of this ion is ambiguous. ²⁷ Other adaptations by submerged plants to the restricted availability of carbon dioxide include (1) the CAM metabolic pathway for carbon fixation, ²⁸ (2) refixation of respired CO_2 , ^{29,30}

and (3) the use of gaseous sediment carbon collected by roots and moved via the lacunae system to the leaves, where it is used in photosynthesis.

NUTRIENT UPTAKE

Few generalizations can be made about mineral uptake by wetland plants. Emergent plants utilize their roots to obtain sufficient nutrients from the interstitial water. Free-floating species have roots with numerous root hairs and can successfully obtain nutrients from the water column. Submerged plants use nutrients from both the water column and substrate.

It is unclear which source of nutrients is used by submerged aquatic plants.^{31,32} The morphology and anatomy of submerged plants seems adapted for nutrient uptake from the water column. And, in fact, materials may pass through the leaves.³¹ However, several studies³³⁻³⁵ have demonstrated preferential uptake from the sediments. In water lilies (*Nuphar luteum*), phosphorus was preferentially taken up by roots, then submersed leaves, and then floating leaves.³⁶ Leaf uptake is probably related to relative nutrient concentration in the water and substrate.

Mineral element concentrations of aquatic plants differ among species at single sites and between sites for a single species.^{37,38} Differences in nutrient composition may be environmentally induced or genetically determined. Cultivars of certain species exist that are adapted to specific nutritional environments. However, nutritional adaptations need not be advantageous in wastewater systems. Some wetland plants adapted to slow growth in nutritionally poor sites³⁹ cannot respond to increased nutrients by increasing growth.

Aquatic plants can accumulate nutrients against a concentration gradient, serving as indicators of nutrient availability in aquatic environments^{8,37,40} and also of heavy metals and rare earth elements.⁴⁰⁻⁴² High K/Ca ratios occur in various wetland grasses and graminoid plants (including *Typha angustifolia*, *Sparganium erectum*, and *Glyceria maxima*).⁴⁰

Many wetland plants use ammonia as a nitrogen source and are nitrogen limited (except see Barko⁴³). Adequate amounts of ammonia in wastewater systems will alleviate this limitation, enhancing other nutrient uptake functions. Species of *Typha*, *Azolla*, and *Glyceria* support nitrogen-fixing microbes in their rhizosphere.¹³ Without nitrogen limitation, these plants grow rapidly and are able to assimilate larger quantities of phosphorus. Some wetland species are also associated with mycorrhiza⁴⁴ implicated in nutrient uptake.

Generally, plants from nutrient-rich habitats accumulate more nutrients than plants typical of nutrient-poor habitats.³⁹ Plants in fertile habitats have high relative growth rates and increase growth with added nutrients, thereby increasing nutrient uptake. However, trade-offs are associated with life in high nutrient environments. Root absorptive capacities are sensitive to high photosynthetic rates and require high rates of root respiration that can be affected

by environmental stress. Rapid growth also results in rapid leaf and root turnover with substantial nutrient loss from senescent tissue. In these plants, nutrient uptake and recovery efficiencies decrease and plants rely more on current uptake than nutrient recycling from belowground to aboveground tissues.⁴⁵

ADAPTATIONS TO ANAEROBIC CONDITIONS

Wetland plants often grow in oxygen-poor substrates. Despite their ability for short-term anaerobic respiration, they grow best when oxygen is available for respiration. Most wetland plants possess an extensive internal lacunal system that may occupy up to 70% of the total plant volume. ^{10,12} This led Armstrong to theorize that wetland plants can satisfy their oxygen requirements through oxygen transport in the lacunal system. Pressurized flow through the lacunae transports oxygen to the roots in yellow water lily (*Nuphar luteum*)^{46,47} and similar systems may be widespread in other wetland plants. ⁴⁸ In addition, gas flux from roots and rhizomes also carries carbon dioxide that can be fixed photosynthetically in the leaves. Dacey and Klug⁴⁹ also measured significant quantities of methane leaving water lilies. Methane generated through anaerobic decomposition in sediments moved into water lily roots and rhizomes and escaped to the atmosphere as part of the pressurized flow.

Crawford⁵⁰ emphasized the metabolic adaptations to anoxia. Even in well-aerated plants oxygen concentrations are critically low in root meristematic regions. Lower metabolic rates and anaerobic metabolites acting as electron acceptors are common.⁵² However, anaerobic respiration can produce toxic levels of ethanol, although some wetland species can excrete ethanol and others accumulate nontoxic metabolic end products such as malate.

Few woody species survive in permanently flooded soil. Those that do survive have adaptations for circulating air to belowground structures, including gas flow through lenticels in the stem and other specialized structures as well as some metabolic adaptations.^{53–55}

Response to waterlogging in sweet gum (*Nyssa sylvatica*) involves both metabolic and morphological adaptations.⁵⁶ At the onset of flooding, anaerobic metabolism increases to support root metabolism. Later, new root systems with aerenchyma are produced that support aerobic metabolism. Mendelsohm et al.⁵⁷ also demonstrated that a combination of metabolic and morphological adaptations to anaerobic conditions is possible. The presence of *Spartina alterniflora* response zones corresponding to differences in substrate reduction suggested that the degree of substrate reduction induced the type of response to anoxia.

Hook and Scholtens⁵⁸ proposed that flood tolerance and the degree to which different adaptations take effect is a function of both site factors and the type of flood water introduced. Soils with low organic matter content have lower oxygen demand than highly organic soils. Stagnant waters have lower oxygen

concentrations than moving water. These considerations are important in wastewater treatment system operations.

FACTORS LIMITING PLANT GROWTH

What factors limit wetland plant growth? Water depth influences species distribution, although secondary factors or correlated changes may be mechanistically responsible. Increased water depth correlates with the onset of anaerobic conditions and reduced light availability. For submerged species, suspended sediments influence the quantity and quality of light and substrate composition.

Water flow rate can have profound effects on plant development as well as oxygen and nutrient availability and wetland substrates. ^{59,60} Variation in leaf form of wetland species with depth and velocity ^{7,61} is probably an adaptation to mechanical stress. Keough ⁶² demonstrated experimentally that the allocation of structural material in an emergent plant (*Scirpus validus*) varied in relation to water depth and velocity. Growth declined with increased depth and more biomass was allocated to roots as velocity increased in shallow water.

Nutrient availability is related to hydrology through renewal of nutrient-depleted waters, improved substrate aeration, and the water source. 63,64 Cypress tree (*Taxodium distichum*) production has been correlated to water flow, which increases nutrient renewal or aerates the substrate. 65 Nutrient depletion has also been associated with the growth of plants in dense submerged macrophyte beds. 66,67 Water movement can eliminate the boundary layer surrounding submerged plants and replenish nutrients needed for growth and photosynthesis. 68,69

Increased flow rates are also implicated in the amelioration of the effect of toxic substances in the substrate.^{54,70,71} Increased water flow raised oxygen levels and lowered the concentration of certain toxic metal forms in the peat substrate of several Canadian wetlands.⁷¹

Substrate effects on growth are tied to nutrient availability, but substrate composition may have other consequences. Sediment texture can affect the rooting depth of plants.⁶⁰ Highly organic soils can become quite anaerobic, and metals may shift to soluble toxic forms (e.g., iron and manganese).

Air and water temperature affects biochemical reactions and inhibits growth if thermal tolerances are exceeded. Many subtropical species, such as water hyacinth (*Eichhornia crassipes*), cannot tolerate low temperatures. Optimal growth of temperate submerged plants occurs at 28–32°C.⁷² In general, higher temperatures within thermal tolerances promote increased production. However, warm water discharge to wetlands throughout the winter can lead to changes in species composition as perennial species deplete their carbohydrate stores to maintain higher respiration rates and die.⁷³

Davis and Brinson⁷⁴ ranked submerged vegetation tolerance to ecosystem alteration. Species normally dominant in disturbed sites included *Ceratophy*-

llum demersum, Najas guadalupensis, Potamogeton perfoliatus, Vallisneria americana, and adventive species such as Myriophyllum spicatum and Potamogeton crispus.

Wetzel and Hough⁷⁵ portrayed hypothetical changes in primary productivity in aquatic plant communities along a gradient of increasing fertility. Submerged macrophytes do well at intermediate levels but decrease in abundance because of shading by algae and other epiphytes. Floating leaved plant productivity increases until they become crowded and occupy all available surface space. Emergent macrophyte productivity increases but occurrence in highly eutrophic waters may be limited by organic matter accumulation.

VEGETATION INTERACTIONS WITH WASTEWATER

Adaptations of wetland vegetation to water-dominated environments are the basis for their use in wastewater treatment systems. We use these species because they help transform wastewater constituents in such a way that various state and federal regulations for disposal or reuse are met. Our understanding of environmental effects on macrophytes and the effect wetland plants have on their environment are the keys to determining which types of vegetation to use in treatment systems.

Emergent wetlands have been proposed as sites for wastewater treatment because they appear to assimilate inorganic and organic constituents of wastewater. Plants with high growth rates and large standing crops can temporarily store various mineral nutrients, but long-term nutrient removal may be limited.

Emergent plants growing on organic soils incorporate only a small percentage of added nutrients into biomass. ⁷⁶⁻⁷⁹ However, growth of emergent vegetation on gravel substrates has led to significant reductions in substrate mineral nutrient concentrations. ⁸⁰⁻⁸³ Water hyacinth and other free floating wetland plants also sequester significant amounts of nutrients and heavy metals. ⁸⁴⁻⁸⁷

Oxygen transported to belowground tissues of wetland plants can leak out of roots and oxidize the surrounding substrate. ^{12,88} Substrate oxidation supports aerobic microbial populations in the rhizosphere that modify nutrients, metallic ions, and trace organics. ⁸⁹ Aerobic microbial metabolism also detoxifies substances potentially hazardous to plants. Metals such as iron and manganese are oxidized and immobilized. ⁸⁸ Altered pH and oxidation-reduction potential affect trace and toxic metal solubility and uptake in salt and brackish marshes. ^{90,91} Increased oxidation of the substrate may result in decreased sulfide concentrations increasing metal solubility. ⁹²

Oxygen changes can also occur in the water column. 93-95 Oxygen deficiencies occur under mats of floating leaved wetland plants such as water hyacinth. 96 In general, floating leaved macrophytes do not oxygenate the water as well as submersed plants. 97

Wetland vegetation can influence water movement.98 Weiler99 modeled sig-

nificant flow reduction in beds of the submerged species *Myriophyllum spicatum*. Changes in plant density and life form can affect the ability of macrophytes to retard water flow, causing significant reductions in suspended solids. ¹⁰⁰ Emergents can substantially lower the water level because of their high transpiration rates. ¹⁰

SUMMARY AND RECOMMENDATIONS

Only a few taxa of wetland plants are used in wastewater treatment studies (Table 1). Sculthorpe⁷ lists over 1000 species found entirely in aquatic families. If we include aquatic species in otherwise terrestrial families and woody species found in forested wetlands, less than 1% of the available taxa have actually been tried.

Many early wastewater treatment designs used emergent wetlands (both woody and herbaceous) for wastewater treatment (partial lists in Nichols¹ Guntenspergen and Stearns,² and Heliotis¹o¹). Analysis of these systems suggested that the vegetation acted as a temporary storage pool, with most pollutant transformations and sequestering processes occurring in the substrate.¹ Emergent plants are often grown in gravel beds to stimulate uptake and create suitable conditions for the oxidation of the substrate, thereby improving the ability of the system to treat wastewater.

Emergent and floating leaved species have been preferentially used in pilot studies of constructed wetlands. Floating leaved species have been used because of their high growth rates, large standing crops, and ability to strip nutrients directly from the water column.^{84-87,102,103} Their roots provide sites for filtration and adsorption of suspended solids and the growth of microbial communities that sequester nutrients from the water column.

Potentially useful emergent species include many members of the cattail, reed, rush, sedge, and grass families. *Phalaris, Spartina, Carex*, and *Juncus* all have potentially high uptake and production rates. They are widespread, able to tolerate a range of environmental conditions, and can alter their environment in ways suitable for wastewater treatment. Rhizosphere processes are largely unknown but presumably have positive impacts (e.g., through oxygenation) and should demand further investigation.

Submerged aquatic plants do not appear to have attributes that would be useful in wastewater treatment. They have low production rates and many species are intolerant of eutrophic conditions and/or have detrimental interactions with algae in the water column. However, some species do possess large leaf surface areas, oxygenate the rhizosphere, and are adapted to eutrophic disturbed systems. Alone, submergents may be unsuitable, but they may have a role to play in conjunction with other species in a wastewater treatment system. However, adventive or exotic species that are known nuisances (e.g., Myriophyllum spicatum) should be avoided.

Our knowledge of wetland species autecology is incomplete with the avail-

able information scattered throughout the literature. Stephenson et al.¹⁰⁴ reviewed the uptake of specific substances by emergent, floating, and submerged plant species. Compilations of biological indicators of polluted waters or surveys of plants associated with heavy metals may also assist in selecting species. However, in addition to tolerance to wastewater, we must consider how wetland plants affect their environment beyond their influence on wastewater alteration. Although many aquatic plants have potential for affecting wastewater quality, certain species may be inappropriate: (1) nuisance plants well-adapted for use in wastewater treatment systems that may escape and cause serious problems in natural wetlands and (2) plants that produce undesirable environmental change.

Universal criteria to determine wetland species suitability for wastewater treatment are not possible because different facilities have different objectives and standards. Municipal wastewater treatment requires modification of organics and nutrients; storm water runoff carries heavy metals and refractory organic substances; and mine drainage has metals and low pH. One species or set of species will not be applicable for all cases. However, only a few species are used now, so it is reasonable to suspect that many other species may be useful. Cooperative screening studies on the ecology and physiology of candidate species should be implemented.

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CHAPTER 6

Wetlands Microbiology: Form, Function, Processes

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INTRODUCTION

The number of organic compounds introduced into the environment by humans has increased dramatically in recent years. The environmental fate of xenobiotic (man-made) compounds—pesticides, polycyclic aromatic hydrocarbons, and domestic wastes—is an important issue. Disappearance, persistence, and/or partial transformation and potential hazardous effects are particular concerns. While many compounds are readily biodegradable, others persist in soil and water.

Recent research on the biochemistry and genetics of xenobiotic-degrading microorganisms, the newer biotechnology literature, and older literature on industrial microbiology describe processes in which microbial cultures play an important role.² Although some microbes can cause adverse effects, most adverse effects are controllable. Most species are benign, functioning in beneficial ways, and only a few species are pathogenic. Microorganisms have a substantial role in transformation of organic and inorganic substances critical to all life on earth, such as the transforming of free nitrogen molecules in the air for use by plants.

This chapter provides an overview of microbial processes of importance to constructed wetlands for wastewater treatment. Bacterial processes are the primary focus of discussion because more information is available. However, fungal and actinomycetous contributions, equally important, are also discussed. Information will be presented on microbial transformation processes, fate of anthropogenic organics, metals metabolism, and habitat for optimal microbial enzymology in a constructed wetland.