Hydrophytic plants and their environment: stressors and adaptations

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INTRODUCTION

The vegetation community structure in freshwater wetlands is controlled by interactions between a wide range of environmental factors, including regional climate, hydrology, surface geology, the chemical oxidation and reduction (redox) potential, as well as the method of construction. Many of these factors change through time, both seasonally and on a yearly basis, as the wetland matures. Unique adaptations have developed in wetland plants, called hydrophytes, to deal with the stresses that occur in systems in which the soil is inundated for part or all of the growing season (Hale and Orcutt, 1987).

Soil saturation limits the amount of oxygen that is able to diffuse into soil from the atmosphere (Mitsch and Gosselink, 2000). When the available oxygen is used up through aerobic respiration, other types of chemical reactions are able to take place, this is accompanied by a lowering of electron availability in the system (Mitsch and Gosselink, 2001), measured as the redox potential (Richardson and Vepraskas, 2001). The anaerobic reactions that occur as redox potential decreases can have a large impact on nutrient availability in a system, as well as concentrations of phytotoxic chemicals (Cronk and Fennessey, 2001). Hydrophytes have developed adaptations to survive under the stresses associated with soil saturation and limited oxygen supply. These include mechanisms in which oxygen from the atmosphere is directed to the roots/rhizomes via active and passive means, as well as release of oxygen into the substrate surrounding the below ground portions of the plant. This process forms a zone of oxidized soil surrounding roots/rhizomes in otherwise anoxic soil layers (Cronk and Fennessey, 2001).

In herbaceous systems there are also stresses associated with high incident radiation; this is due to the lack of shading from a forested or shrubby canopy. High levels of incident radiation mean that photosynthetically available radiation (PAR), the portion of sunlight available for use by vegetation (400-700 nm), is also high in these environments (Fisher et al., 2003). Under conditions of high PAR photorespiration occurs, lessening the net productivity of the plant. The C_4 photosynthetic pathway is an adaptation that eliminates the occurrence of photorespiration, thereby increasing the net photosynthetic productivity of plants that use this pathway (Hale and Orcutt, 1987). The mechanisms and importance of these processes will be discussed in further detail later in this manuscript.

The ability of hydrophytic species to deal with environmental stressors is an important factor in regulating vegetation community zonation (Grace and Wetzel, 1998). Plant interactions such as inter- and intraspecific competition, as well as facilitation play an important role in regulating the zonation of hydrophytic communities. The purpose of this manuscript is to synthesize a comprehensive review of the literature that describes the environmental factors affecting vegetation community structure and zonation in herbaceous freshwater wetlands.

ENVIRONMENTAL SETTING

Various environmental factors facilitate the existence of wetlands in the landscape, such as regional climate, geomorphology, hydrology, and biogeochemistry. The specific type of wetland at a given location is dependent on the occurrence of a relatively narrow range of environmental variables (Mitsch and Gosselink, 2000). Stressors unique to the wetland environment limit the occurrence of species that are unable to survive under inundated conditions; this allows for dominance of the system by hydrophytes, species that are adapted to wetland conditions.

Climate, Geomorphology, and Hydrology

Latitude and regional geomorphic features largely determine the climatic conditions experienced at a given location. Climate in turn exerts control on the vegetation of a site through influences on hydrology (the amount of precipitation and evapotranspiration), temperature range of both air and soil, and the amount of photosynthetically active radiation (PAR) that reaches the canopy. In herbaceous wetlands the lack of shading allows for very high levels of PAR to reach the emergent vegetation.

Geologic conditions that influence wetlands include: surface relief, slope, permeability of the soil, as well as the hydrologic properties of the underlying strata (Bedford,1996). Climate, geomorphology, hydrology, and the connections between them have a strong influence on the zonation and succession of hydrophytic plant communities in wetland ecosystems.

Wetlands are often defined by the relative influence of inflows of water, such as groundwater, precipitation, and surface flow. Some of the designations include tidal or nontidal influence, riverine, palustrine, and lacustrine (Cowardin et al., 1979). The hydroperiod is the seasonal pattern of water level fluctuation unique to every system, which is controlled by the water budget (inflows and outflows), as well as physical aspects of the surrounding environment, such as soil permeability and proximity to other water bodies (Mitsch and Gosselink, 2000). The hydroperiod determines the amount of time the wetland is inundated with water during the year, and directly modifies the physiochemical factors of the system such as soil makeup, redox potential, and nutrient availability.

Biogeochemistry

The biologically and physically mediated chemical processes that occur in wetlands are largely controlled by the presence or absence of water in the substrate.

Inundation, or saturation to the soil surface, replaces the air that is normally found in the pore spaces of the soil with water.   Because the diffusion of molecular oxygen through water is 10,000 times slower than through air, as oxygen in the water is depleted through use as a terminal electron acceptor in microbial respiration, oxygen replenishment, through molecular diffusion, is not able to keep up and hypoxic or anoxic conditions develop (Mitsch and Gosselink, 2000). Anoxia in the substrate due to rapid depletion of oxygen from the pore water within the sediments is characteristic of wetland systems. This is the factor responsible for development of hydric soils as well as an important influence on nutrient cycling and availability within the system. The chemical progression of soils from an oxidized state to a reduced state can be observed through measurements of the redox potential, a measure of the electron pressure or availability in a solution, reported in millivolts (mV) (Mitsch and Gosselink, 2000). As alternate electron acceptors are used, a continual lowering of the redox potential occurs. The lowering of the redox potential continues as the length of inundation increases. If the water level falls and the soil is able to come in contact with the atmospheric oxygen the redox potential increases (Cronk and Fennessey, 2001).

The hierarchy of reduction oxidation reactions that take place with lowering redox potential can be seen in Table 1. After the depletion of oxygen, the redox potential continues to decrease and denitrification (a loss of nitrogen from the system) occurs at 250 mV; this process is the reduction of nitrate and nitrite to NH_4^+, N_2O, and N_2.

Table 1: The oxidized and reduced forms of major elements and the redox potential at which reduction reactions begin to occur, as well as the effects the reductions have on the surrounding vegetation (adapted from Cronk and Fennessy, 2001).

Element	*Oxidized Form*	*Reduced Form*	*Redox Potential (mV)*	*Effects on vegetation*
Nitrogen	NO_3^-	NH_4^+ , N_2O, N_2,	250	Removal of bioavailable N from the soil through loss to atmosphere
Manganese	Mn^{+4}	Mn^{+2}	225	High levels of reduced Mn can interfere with enzyme structure and nutrient composition
Iron	Fe^{+3}	Fe^{+2}	120	High levels of reduced Fe can interfere with Mg during chlorophyll formation; causing discolored leaves, diminished photosynthesis, and decreased root respiration
Sulfur	SO_4^{-2}	S^{-2}, HS^- , H_2S	-75 to -150	Inhibits photosynthesis and the ability of the roots to respire aerobically and anaerobically
Carbon	CO_2	CH_4	-250 to -350	Transported through gas spaces in plants and released to the atmosphere

Manganese and iron reduction occur at similar redox potentials, following the depletion of NO_3^- as an electron acceptor. Manganese reduction occurs at a redox potential of about 225 mV and is a microbially mediated process. Iron reduction, both a microbially and chemically mediated process, occurs at a redox potential of 120 mV

(Cronk and Fennessy, 2001). Both iron and manganese have a conspicuous oxidized precipitate form, which can be seen in oxic soils. Manganic oxide is black, and ferric oxide is a reddish-orange color. The reduced forms of both minerals are soluble in water. Once dissolved they leach out of the soils causing the grey soil conditions characteristic of wetlands to develop. The mechanism and outcome of this process will be discussed in more detail later.

Sulfate reduction occurs following the depletion of oxidized iron and manganese as the redox potential continues to drop. However, sulfates are generally limited in freshwater systems compared to brackish and salt marsh systems, and their redox chemistry does not typically exert a large impact on the biogeochemical environment of freshwater wetlands. However, the presence of sulfate in the soil needs to be considered when selecting a site for construction of a created wetland. This is especially important in coastal plain areas because high sulfate levels are often seen in these soils. The sulfate was deposited during times of higher sea level, and can leach out after formation of the wetland, lowering the pH and profoundly altering the chemical conditions and nutrient cycling of the system.

Methanogenesis and fermentation also occur low on the redox hierarchy; both processes use carbon as the terminal electron acceptor; methanogenesis uses CO_2 and fermentation uses simple low molecular weight organic compounds. The methane that is formed is not retained in the plants or the soils; instead it is diffused from the root zone through the gas spaces and is then released into the atmosphere (Mitsch and Gosselink, 2000, Cronk and Fennessy, 2001).

The redox potential of wetland soil has a large impact on nutrients that are directly affected by changing redox conditions as well as nutrients that do not undergo redox reactions. This is especially important for phosphorus availability, which is greatly increased in reduced conditions; even though phosphate does not under go reduction or oxidation reactions. This is due to the adsorption of phosphate to oxidized iron. The phosphate is released when the iron is reduced (Cronk and Fennessy, 2001), leading to high availability of phosphate under anoxic reduced conditions.

Morphology of hydric soils

The morphology of wetland soil is also influenced by redox chemistry. Hydric soils form when inundation and lowering of the redox potential leads to the dissolution of iron and manganese and the characteristic loss of color associated with hydric soils. The reduced forms of both iron and manganese are soluble in water and leach out of the soil under reduced conditions. When this occurs the background color of the soil's mineral matrix can then be seen, this process is called gleying, and is a distinguishing characteristic of hydric soils (Mitsch and Gosselink, 2000). When there is fluctuation in the water table, nodules of precipitated iron and manganese oxides can often be seen at the saturation horizon, where they formed in the presence of oxygen. These mottles are another characteristic used to define hydric soils. The precipitation of iron and manganese indicate reintroduction of oxygen into soil that had previously been anoxic.

Radial oxygen loss (ROL) is the process in which the soil surrounding the roots of hydrophytic plants can become saturated with oxygen due to the release of oxygen from the roots (Weiss et al., 2003). The oxygen is either actively pumped or flows freely due to diffusion from the aerial portion of the plant to the roots through aerenchymatous tissue, which is made of gas spaces called lacunae. The mechanisms of this gas transfer will be discussed later. The region of ferrous and manganous precipitation surrounding the root is called the oxidized rhizosphere, and is clearly visible against the gleyed substrate. The presence of oxidized rhizospheres is another distinguishing characteristic of hydric soils. Often the plaque of precipitated minerals that form can deprive the root of nutrients, especially phosphorus (Christensen and Wigand, 1998). Phosphorus adsorbs to oxidized iron and so is not available for uptake within the oxidized rhizosphere.

STRESSES AND ADAPTATIONS OF VEGETATION

Method of creation or restoration

In created wetlands the hydrology and geomorphology are often determined during construction. Therefore, when considering the physical characteristics of created wetlands, it is also important to keep in mind the influence of the method of creation or restoration. One method of creation is planting, in which the species composition mimics the composition of natural wetlands from the beginning. Another is salvaged marsh surface in which the soil is taken from a natural wetland and still includes a seed bank, which can be partially relied on to establish the marsh vegetation. The third approach is self organization or self design, in which it is assumed that with the correct hydrogeomorphic environment, the vegetation that needs to be there will establish itself; either from the seed bank or from propagule dispersion from adjacent sites (Whigham et al., 2002*)*. The construction techniques should also be considered; certain construction techniques have been shown to be detrimental to development of proper function. Alteration of the hydrology can occur from packing of the clay layer beneath the created wetland from use of heavy equipment; this creates a clay pan through which water is not able to penetrate.

Impact of hydrology

The effect of the hydroperiod on soil structure, chemistry and other metabolic processes, such as oxidation and reduction of nutrients and toxins is an overriding control on the vegetation community structure (Mitsch and Gosselink, 2000). Productivity is often much higher in wetlands that experience pulsing hydroperiods (Cronk and Fennessey, 2001); this allows for large nutrient inputs as well as the removal of toxins, detritus, and organic matter (Lockaby and Walbridge, 1998). Herbaceous marshes that are associated with river or stream flow experience increased inflows and outflows and generally higher productivity than depressional wetlands that are dependent purely on precipitation and groundwater for nutrient inputs (Cronk and Fennessy, 2001). The controls that the hydroperiod and the degree of fluctuation have on hydrologic and geochemical gradients also closely regulate the distribution of wetland plants (Bedford, 1996). Water depth can define niches in which tolerant species are able to take hold and excludes other species that would, under drier conditions, be dominant. Marsh species are generally able to tolerate and even thrive in flooded conditions for long periods of time. Herbaceous marshes are often dominated by vegetatively reproducing (clonal) species. Over time the clonal species are able to become dominant over species that reproduce solely with seeds. The decrease in the abundance of plants that reproduce primarily with seeds is related to the requirement of a drawdown of water depth for seed germination and establishment to occur. This phenomenon may explain why vegetatively reproducing forms, such as *Typha spp*. and *Phragmites australis*, are able to invade wetlands in which the seasonal hydroperiod fluctuations have been artificially dampened (Woo and Zedler, 2002). Short-term drawdowns of water can allow germination and establishment of rare species that are often lost from a community in which the water level is stable (Schneider, 1994).

High Light Intensity

Plants in herbaceous wetlands have the added factor of direct sunlight, the high incidence of PAR that hits the canopy of emergent herbaceous wetland vegetation can cause stress in plants that are not adapted to deal with bright light conditions. The occurrence of photoinhibition is dependent on the intensity and duration of high light exposure as well as physiologic factors of individual plant species. Photoinhibition is the destruction of the reaction center in photosystem II under conditions of high incident radiation. The process of photosynthesis causes damage to the reaction center at all levels of PAR, but the effect of photoinhibition is only observable as reduced production when the rate of damage exceeds the rate of repair (Adir et al., 2003).

C_3 Photosynthesis

The most common form of photosynthesis is called C_3 because of the three carbon organic acid, 3-phosphoglyceric acid (3-PGA) that is formed during carbon fixation. The C_3 pathway involves carboxylation of CO_2 by the enzyme rubisco. The CO_2 is combined with ribulose biphosphate (RuBP) in the mesophyll cells; this is the process that produces 3-PGA (Smith and Smith 2001). 3-PGA is then reduced to form the energy rich molecule glyceraldehyde-3-phosphate (G3P), some of which are combined to form one molecule of glucose, the net product of photosynthesis.

C_3 photosynthesis has a draw back in high light environments, as production increases with increased PAR the relative CO_2 concentration decreases within the mesophyll. When this occurs rubisco, which also acts as an oxygenase, begins to catalyze the reaction between RuBP and oxygen. This reaction results in a release of CO_2 and the reduction of the photosynthetic efficiency in the plant. Photorespiration occurs only in plants with the C_3 photosynthetic pathway (Waller and Lewis, 1979).

C_4 Photosynthesis

Photorespiration is avoided in plants that use an alternate photosynthetic pathway; the alternate pathway most often found in wetlands is the C_4 photosynthetic pathway. C_4 plants have different internal leaf anatomy than C_3 plants. In C_4 plants the vascular bundles are surrounded by tightly packed bundle sheath cells, where photosynthesis is concentrated. CO_2, brought in by diffusion through the stomata, is catalyzed by the acceptor molecule phosphoenolpyruvate (PEP) carboxylase in the mesophyll, producing oxalacetate (OAA). OAA is rapidly transformed into malic and aspartic acids, which are the four carbon molecules from which C_4 photosynthesis gets its name. These acids are then moved into the bundle sheath cells, where they are enzymatically broken down releasing pyruvic acid and CO_2. The CO_2 is then fixed within the bundle sheath cells using the C_3 pathway, and the remaining pyruvic acid diffuses back to the mesophyll where it is used to regenerate PEP. The CO_2 is concentrated in the bundle sheath cells, and the RuBP is separated from the oxygen that is present in the mesophyll; therefore the occurrence of photorespiration is greatly reduced. The C_4 pathway is generally considered to be an adaptation for arid conditions; however it is also advantageous in salt marsh environments as well as other habitats that receive high levels of incident radiation, including herbaceous freshwater wetlands. A list of Virginia wetland species known to utilize the C_4 photosynthetic pathway is given in Appendix I. The lower water intake required by C_4 plants may also be advantageous in freshwater environments because it reduces the intake of toxic dissolved forms of reduced elements that are common in freshwater wetland soils. This adaptation allows C_4 photosynthesizers to increase the rate of photosynthesis to full light intensity, photosynthesize under very low CO_2 concentrations, and use water much more efficiently.

Table 2: The photosynthetic characteristics of C_3 and C_4 plants (adapted from Mitsch and Gosselink, 2000).

Characteristic of Photosynthesis	*C_3*	*C_4*
Initial CO_2 fixation enzyme	RuBP carboxylase	PEP carboxylase
Location of final carboxylation	Mesophyll	Bundle sheath
CO_2 compensation concentration (ppm CO_2)	30-70	0-10
Transpiration ratio (g H_2O transpired/g dry weight) water use efficiency	450-950	250-350
Optimum day temperature for net CO_2 fixation (^oC)	15-25	30-47
Response of net photosynthesis to increasing light intensity	Saturation at ¼ to ½ full sunlight	Saturation at full sunlight
Maximum growth rate (g m^{-2} d^{-1})	19.5	30.3

Anoxia

Anoxic conditions in pore water are stressful because the lack of available oxygen can shut down the aerobic metabolism of the root. The reduction of metabolically mediated processes can result in the destruction of mitochondria (Mitsch and Gosselink, 2000). Plants deal with low oxygen in two ways, sequestration and tolerance. In order to get oxygen to root tissues that are deprived of oxygen, plants develop extensive systems of connected gas filled spaces called lacunae, which are surrounded by spongy aerenchymatous tissue. This system of air spaces extends from the leaves through the petioles, stems, rhizomes, and eventually to the roots. In some flood tolerant species it makes up 50 to 60% of the root volume (Smits et al., 1990). It has been reported that in *Typha latifolia* up to half the leaf volume is composed of gas spaces (Constable et al., 1990)

The development of aerenchymatous tissue is thought to be related to the concentration of ethylene in plant tissues. Hypoxic conditions caused by flooding stimulate the production of an enzyme, 1-aminocyclopropane-1-carboxylate (ACC) synthase, as well as ACC oxidase. The ACC oxidase that is produced is directly responsible for ethylene production, a process which requires oxygen. As the ACC oxidase diffuses throughout the plant it produces ethylene in areas where oxygen is present; the ethylene is not able to diffuse out of the plant if there is water surrounding it. It is hypothesized that the accumulation of ethylene in the tissues causes cell rupture and degradation of cell walls, forming gas spaces (Cronk and Fennessy, 2001)

Passive diffusion is the process that is responsible for oxygen flow to the roots in most plants. Oxygen flows down from the leaves due to a concentration gradient and carbon dioxide flows upward due to a similar gradient. Active gas transport can also occur in wetland species. Pressurized ventilation and Venturi-induced convection are two processes by which gases are moved against the concentration gradient. Pressurized ventilation occurs when air moves into the stomata of young leaves, down the stems to the rhizomes and up the stems of older leaves, where it leaks out of the stomata. The pressurized gas flow occurs because of changes in the temperature and vapor pressure inside and outside the leaves. The young leaves have smaller stomata, which lead to higher gas pressure than in the larger, more degraded, and leaky older leaves. This sets up the gas flow throughout the entire plant, allowing oxygenation of the roots and removal of carbon dioxide. This process is seen in *Typha spp*. (Armstrong and Armstrong, 1991)

Venturi induced convection creates a similar circulation of gas through the plant. However, it involves pressure differences created by the amount of wind that passes over different stems. This process is seen in stands of *Phragmites australis*, in which the old broken shoots are still connected through rhizomes to the new taller shoots. The difference in wind exposure between the old and new shoots causes an ambient pressure difference that allows movement of air from the shoots close to the ground through the rhizomes and out the taller new shoots. This type of convection is especially important in areas of high winds and when there is a high ratio of number of dead broken shoots to rhizome length (Armstrong and Armstrong, 1991).

The oxygen that is brought to the roots by active or passive gas exchange is often released through the pores in the rhizomes into the surrounding soil, creating an oxidized rhizosphere. This oxidation allows the plant to prevent the accumulation of reduced dissolved toxic compounds, like iron and manganese, which can be brought in by diffusion.

PLANT INTERACTIONS

In order for competition between different species (interspecific) and between members of the same species (intraspecific) to occur, there must be a limiting factor, such as water, light or a nutrient required for growth. Competition can be exploitative in which there is competition for the same resource and dominance is determined by the individual better able to exploit the resource. Competition can also involve active denial of access to the resource, called interference competition. This can be seen in the shading of one plant by another. This is a form of interference because the larger shading plant is able to deny the other plant access to light.

Intraspecific Competition

Self-thinning has been observed in monospecific stands in which intraspecific competitive pressure is high. This is the process in which as the number of individuals increases but the mean weight of individuals and the biomass of the total population decrease. (Cronk and Fennessy, 2001). It is related to the limitations on space and the amount of space that is required by each plant. Smaller plants need less space so more plants are able to thrive in a given location.

Interspecific Competition

Interspecific competition is often the determining factor in the species distribution and abundance in a community. In a study by Grace and Wetzel (1998), the interspecific competitive dynamics between *Typha angustifolia* and *T. latifoila* were investigated. The two species of *Typha* were often found together but were segregated by water depth, with *T. angustifolia* being found in deeper water, and *T. latifolia* in shallower water. They were able to determine that the greater leaf area of *T. latifolia* allowed it to outcompete *T. angustifolia* for light in shallow water. However, *T. angustifolia* is better adapted to deal with deep water and therefore is able to take advantage of lower elevations in which *T. latifoilia* cannot survive. The deep-water adaptations they observed in *T. angustifolia* include thinner taller leaves and smaller rhizomes. Other advantages for deeper water include a better ability to oxygenate the rhizosphere. Often emergent species that have higher gas throughflow due to pressurized ventilation, or Venturi induced gas flow, are better competitors in areas of prolonged inundation.

Facilitation

Another form of interaction seen in wetland species is the nurse species idea. It contends that actions of an earlier colonizing plant provide the conditions required for other plants to colonize (Ervin, 2005). In a study by Calloway and King (1996) it was shown that oxygenation of sediments by *T. latifolia* facilitated growth of nonaerenchymatous species. This may indicate that domination of a site, by monospecific stands of *Typha spp.* or other aerenchymatous emergent macrophytes, is a necessary step in the development of a functional plant community in an herbaceous created wetland. This will be investigated further in the future.

CONCLUSION

Hydrophytic vegetation interacts with the physiochemical environment as well as the biological community. These complex interactions determine the community that is present. Because of this relationship certain information about the physical, chemical, and hydrologic setting can be gleaned from the type of plant community that is present. It is important to have a good understanding of the interactions between plants and their environment. Based on the interactions and adaptations discussed above, the plant community that would be expected in an herbaceous freshwater wetland can be predicted. It would most likely include vegetation well adapted to high PAR and high heat; this includes C_4 plants as well as C_3 plants that are better adapted to high sunlight, such as *Typha* and *Juncus* spp. The vegetation would be arranged along gradients of water depth and hydroperiod. In the early successional stages of a created wetland the vegetation would primarily be clonally reproducing species often in monospecific stands. While these generalizations can be made about all herbaceous freshwater wetlands in a region it is still important to note that small differences in hydrology and geomorphology between sites can cause slightly different plant communities to develop. The age of a created site can also have a profound impact on the type of community that is present. Because of this variation it is important to understand as much as possible about the physical environment in a wetland when trying to understand the ecology of the plant community.

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