Morphological, Physiological and Reproductive Adaptation of Plant Species for Occurrence in Areas Having Anaerobic Soil Conditions

APPENDIX C

Adapted from the 1987 USACE Wetlands Delineation Manual

1. Morphological adaptations.

Many plant species exhibit recognizable physical characteristics that reflect their ability to occur in wetlands. These structural modifications most often provide the plant with increased buoyancy or support. In some cases (e.g., adventitious roots), the adaptation may facilitate the uptake of nutrients and/or gases (particularly oxygen). However, not all species occurring in areas having anaerobic soil conditions exhibit morphological adaptations for such conditions. The following is a list of morphological adaptations that a species occurring in areas having anaerobic soil conditions may possess (a partial list of species with such adaptations is presented in Figure C.1):

a. Buttressed tree trunks: Tree species *(Fraxinus pennsylvanica)* may develop enlarged trunks in response to frequent inundation. This adaptation is a strong indicator of hydrophytic vegetation in non-tropical forested areas.

b. **Pneumatophores**: These modified roots may serve as respiratory organs in species subjected to frequent inundation or soil saturation. Cypress knees are a classic example, but other species may also develop pneumatophores.

c. **Adventitious roots**: Sometimes referred to as “water roots,” adventitious roots occur on plant stems in positions where roots normally are not found. Small fibrous roots protruding from the base of trees (e.g., *Salix nigra)* or roots on stems of herbaceous plants and tree seedlings in positions immediately above the soil surface (e.g., *Ludwigia* spp.) occur in response to inundation or soil saturation. These usually develop during periods of sufficiently prolonged soil saturation to destroy most of the root system.

CAUTION: Not all adventitious roots develop as a result of inundation or soil saturation. For example, aerial roots on woody vines are not normally produced as a response to inundation or soil saturation.

d. Shallow root systems: When soils are inundated or saturated for long periods during the growing season, anaerobic conditions develop in the zone of root growth. Most species with deep root systems cannot survive in such conditions. Most species capable of growth during periods when soils are oxygenated only near the surface have shallow root systems. In forested wetlands, windthrown trees are often indicative of shallow root systems.

e. Inflated leaves, stems, or roots: Many hydrophytic species, particularly herbs (e.g., *Ludwigia* spp.) have or develop spongy (**aerenchymous**) tissues in leaves, stems, and/or roots that provide buoyancy or support and serve as a reservoir or passageway for oxygen needed for metabolic processes.

f. Polymorphic leaves: Some herbaceous species produce different types of leaves, depending on the water level at the time of leaf formation. For example, *Alisma* spp. produce strap-shaped leaves when totally submerged, but produce broader, floating leaves when plants are emergent.

CAUTION: Many upland species also produce polymorphic leaves.

g. Floating leaves: Some species (e.g., *Nymphaea* spp.) produce leaves that are uniquely adapted for floating on a water surface. These leaves have stomata primarily on the upper surface and a thick waxy cuticle that restricts water penetration. The presence of species with floating leaves is strongly indicative of hydrophytic vegetation.

h. Floating stems: A number of species (e.g., *Ludwigia spp.*) produce matted stems that have large internal air spaces when occurring in inundated areas. Such species root in shallow water and grow across the water surface into deeper areas. Species with floating stems often produce adventitious roots at leaf nodes.

i. **Hypertrophied lenticels:** Some plant species (e.g., *Acer rubrum*) produce enlarged lenticels on the stem in response to prolonged inundation or soil saturation. These are thought to increase oxygen uptake through the stem during such periods.

Morphological adaptations include:

a. Buttressed tree trunks.
b. Pneumatophores.
c. Adventitious roots.
d. Shallow root systems.
e. Inflated leaves, stems, or roots.
f. Polymorphic leaves.
g. Floating leaves.
h. Floating stems.
i. Hypertrophied lenticels.
j. Multitrunks or stooling.

j. **Multitrunks** or **stooling**: Some woody hydrophytes characteristically produce several trunks of different ages or produce new stems arising from the base of a senescing individual in response to inundation.

k. **Oxygen pathway** to roots: Some species (e.g., *Salix spp.*) have a specialized cellular arrangement that facilitates diffusion of gaseous oxygen from leaves and stems to the root

Figure C.1 - Partial List of Species with Known Morphological Adaptations for Occurrence in Wetlands*

Species	*Common Name*	*Adaptation*
Acer negundo	Box elder	Adventitious roots
Acer rubrum	Red maple	Hypertrophied lenticels
Acer saccharinum	Silver maple	Hypertrophied lenticels; adventitious roots (juveniles)
Alisma spp.	Water plantain	Polymorphic leaves
Alternanthera philoxeroides	Alligatorweed	Adventitious roots; inflated, floating stems
Avicennia nitida	Black mangrove	Pneumatophores; hypertrophied lenticels
Brasenia schreberi	Watershield	Inflated, floating leaves
Caladium mariscoides	Twig rush	Inflated stems
Cyperus spp. (most species)	Flat sedge	Inflated stems and leaves
Eleocharis spp. (most species)	Spikerush	Inflated stems and leaves
Forestiera accuminata	Swamp privet	Multi-trunk, stooling
Fraxinus pennsylvanica	Green ash	Buttressed trunks; adventitious roots
Gleditsia aquatica	Water locust	Hypertrophied lenticels
Juncus spp.	Rush	Inflated stems and leaves
Limnobium spongia	Frogbit	Inflated, floating leaves
Ludwigia spp.	Waterprimrose	Adventitious roots; inflated floating stems
Menyanthes trifoliata	Buckbean	Inflated stems (rhizome)
Myrica gale	Sweetgale	Hypertrophied lenticels
Nelumbo spp.	Lotus	Floating leaves
Nuphar spp.	Cowlily	Floating leaves
Nymphaea spp.	Waterlily	Floating leaves
Nyssa aquatica	Water tupelo	Buttressed trunks; pneumatophores; adventitious roots
Nyssa ogechee	Ogechee tupelo	Buttressed trunks; multi-trunk; stooling
Nyssa sylvatica var. biflora	Swamp blackgum	Buttressed trunks
Platanus occidentalis	Sycamore	Adventitious roots
Populus deltoides	Cottonwood	Adventitious roots
Quercus laurifolia	Laurel oak	Shallow root system
Quercus palustris	Pin oak	Adventitious roots
Rhizophora mangle	Red mangrove	Pneumatophores
Sagittaria spp.	Arrowhead	Polymorphic leaves
Salix spp.	Willow	Hypertrophied lenticels; adventitious roots; oxygen pathway to roots
Scirpus spp.	Bulrush	Inflated stems and leaves
Spartina alterniflora	Smooth cordgrass	Oxygen pathway to roots
Taxodium distichum	Bald cypress	Buttressed trunks; pneumatophores

*Many other species exhibit one or more morphological adaptations for occurrence in wetlands. However, not all individuals of a species will exhibit these adaptations under field conditions, and individuals occurring in uplands characteristically may not exhibit them.

system.

2. Physiological adaptations.

Physiological adaptations are the metabolic features of a species which result in it being better suited to its environment. Most, if not all, hydrophytic species are thought to possess physiological adaptations for occurrence in areas that have prolonged periods of anaerobic soil conditions. However, relatively few species have actually been proven to possess such adaptations, primarily due to the limited research that has been conducted. Nevertheless, several types of physiological adaptations known to occur in hydrophytic species are discussed below:

NOTE: Since it is impossible to detect these adaptations in the field, use of this indicator will be limited to observing the species in the field and checking the list in Figure C.2 to determine whether the species is known to have a physiological adaptation for occurrence in areas having anaerobic soil conditions.

a. Accumulation of malate: Malate, a nontoxic metabolite, accumulates in roots of many hydrophytic species (e.g., *Carex lasiocarpa*, *Nyssa sylvatica* var. *biflora*). Non-wetland species concentrate ethanol, a toxic byproduct of anaerobic respiration, when growing in anaerobic soil conditions. Under such conditions, many hydrophytic species produce high concentrations of malate and unchanged concentrations of ethanol, thereby avoiding accumulation of toxic materials. Thus, species having the ability to concentrate malate instead of ethanol in the root system under anaerobic soil conditions are adapted for life in such conditions, while species that concentrate ethanol are poorly adapted for life in anaerobic soil conditions.

b. Increased levels of nitrate reductase: Nitrate reductase is an enzyme involved in conversion of nitrate nitrogen to nitrite nitrogen, an intermediate step in ammonium production. Ammonium ions can accept electrons as a replacement for gaseous oxygen in some species, thereby allowing continued functioning of metabolic processes under low soil oxygen conditions. Species that produce high levels of nitrate reductase (e.g., *Larix laricina*) are adapted for life in anaerobic soil conditions.

c. Slight increases in metabolic rates: Anaerobic soil conditions effect short-term increases in metabolic rates in most species. However, the rate of metabolism often increases only slightly in wetland species, while metabolic rates increase significantly in non-wetland species. Species

Table C2 - Species Exhibiting Physiological Adaptations for Occurrence in Wetlands

Species	*Physiological Adaptation*
Alnus incana	Increased levels of nitrate reductase; Malate accumulation
Alnus rubra	Increased levels of nitrate reductase
Baccharis viminea	Ability for root growth in low oxygen tensions
Betula pubescens	Oxidizes the rhizosphere; malate accumulation
Carex arenaria	Malate accumulation
Carex flacca	Absence of ADH activity
Carex lasiocarpa	Malate accumulation
Deschampsia cespitosa	Absence of ADH activity
Filipendula ulmaria	Absence of ADH activity
Fraxinus pennsylvanica	Oxidizes the rhizosphere
Glyceria maxima	Malate accumulation; absence of ADH activity
Juncus effusus	Ability for root growth in low oxygen tensions; absence of ADH activity
Larix laricina	Slight increases in metabolic rates; increased levels of nitrate reductase
Lobelia dortmanna	Oxidizes the rhizosphere
Lythrum salicaria	Absence of ADH activity
Molinia caerulea	Oxidizes the rhizosphere
Myrica gale	Oxidizes the rhizosphere
Nuphar lutea	Organic acid production
Nyssa aquatica	Oxidizes the rhizosphere
Nyssa sylvatica var. biflora	Oxidizes the rhizosphere; malate accumulation
Phalaris arundinacea	Absence of ADH activity; ability for root growth in low oxygen tensions
Phragmites australis	Malate accumulation
Pinus contorta	Slight increases in metabolic rates; increased levels of nitrate reductase
Polygonum amphibium	Absence of ADH activity
Potentilla anserina	Absence of ADH activity; ability for root growth in low oxygen tensions
Ranunculus flammula	Malate accumulation; absence of ADH activity
Salix cinerea	Malate accumulation
Salix fragilis	Oxidizes the rhizosphere
Salix lasiolepis	Ability for root growth in low oxygen tensions
Scirpus maritimus	Ability for root growth in low oxygen tensions
Senecio vulgaris	Slight increases in metabolic rates
Spartina alterniflora	Oxidizes the rhizosphere
Trifolia subterraneum	Low ADH activity
Typha angustifolia	Ability for root growth in low oxygen tensions

exhibiting only slight increases in metabolic rates (e.g., *Larix laricina, Senecio vulgaris)* are adapted for life in anaerobic soil conditions.

d. Rhizosphere oxidation: Some hydrophytic species (e.g., *Nyssa sylvatica*, *Myrica gale*) are capable of transferring gaseous oxygen from the root system into soil pores immediately surrounding the roots. This adaptation prevents root deterioration and maintains the rates of water and nutrient absorption under anaerobic soil conditions.

e. Ability for root growth in low oxygen tensions: Some species (e.g., *Typha angustifolia*, *Juncus effusus*) have the ability to maintain root growth under soil oxygen concentrations as low as 0.5 percent. Although prolonged (>l year) exposure to soil oxygen concentrations lower than 0.5 percent generally results in the death of most individuals, this adaptation enables some species to survive extended periods of anaerobic soil conditions.

Physiological adaptations include:

a. Accumulation of malate.
b. Increased levels of nitrate reductase.
c. Slight increase in metabolic rates.
d. Rhizophere oxidation.
e. Ability for root growth in low oxygen tensions.
f. Absence of alcohol dehydrogenase (ADH) activity.

f. Absence of alcohol dehydrogenase (ADH) activity: ADH is an enzyme associated with increased ethanol production. When the enzyme is not functioning, ethanol production does not increase significantly. Some hydrophytic species (e.g., *Potentilla anserina, Polygonum amphibium*) show only slight increases in ADH activity under anaerobic soil conditions. Therefore, ethanol production occurs at a slower rate in species that have low concentrations of ADH.

3. Reproductive adaptations

Some plant species have reproductive features that enable them to become established and grow in saturated soil conditions. The following have been identified in the technical literature as **reproductive adaptations** that occur in hydrophytic species:

a. Prolonged seed viability: Some plant species produce seeds that may remain viable for 20 years or more. Exposure of these seeds to atmospheric oxygen usually triggers germination. Thus, species that grow in very wet areas may produce seeds that germinate only during infrequent periods when the soil is dewatered.

NOTE: Many upland species also have prolonged seed viability, but the trigger mechanism for germination is not exposure to atmospheric oxygen.

b. Seed germination under low oxygen concentrations: Seeds of some hydrophytic species germinate when submerged. This enables germination during periods of early-spring inundation, which may provide resulting seedlings a competitive advantage over species whose seeds germinate only when exposed to atmospheric oxygen.

c. Flood-tolerant seedlings: Seedlings of some hydrophytic species (e.g., *Fraxinus pennsylvanica)* can survive moderate periods of total or partial inundation. Seedlings of these species have a competitive advantage over seedlings of flood-intolerant species.

Reproductive adaptations include:

a. Prolonged seed viability.
b. Seed germination under low oxygen concentrations.
c. Flood-tolerant seedlings.