The Concept of a Hydrophyte for Wetland Identification

Individual plants adapt to wet environments

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Wetlands have been commonly viewed as transitional habitats between deepwater aquatic systems and terrestrial systems. Although often found along rivers, lakes, ponds, and estuaries, wetlands also exist on gentle slopes or in isolated depressions surrounded by uplands. Wetlands can be considered to occur along a natural soil-moisture gradient between permanently flooded deepwater areas and dryland (Figure 1). Wetland hydrologic conditions, therefore, range from permanent inundation by shallow water or permanent soil saturation to periodic inundation or soil saturation.

The varied hydrologic regimes associated with wetlands create a diverse set of environmental conditions that require plants to tolerate different degrees of wetness. Numerous studies have been conducted in marshes, swamps, and bogs throughout the United States in an effort to better understand ecological functions and relationships. From these studies, ecologists have described certain plant species and communities as characteristic of wetlands. But recent observations reveal a more complex situation.

As soil wetness decreases along the gradient between flooded and dry areas, plant composition gradually changes from a more typical wetland community to a transitional community where wetland plants intermix

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Wetlands must be properly identified

with mesic species, making wetland identification challenging. If plant species are used as the sole criterion, distinguishing wetlands from other communities becomes somewhat arbitrary at some point. But when such an area has wetland hydrology (e.g., a seasonal high water table or standing water for prolonged periods during the growing season), it must be considered to function as a wetland, although its vegetation might not be that of a typical wetland. If a sole criterion was developed for wetland identification, it would certainly be one based on the hydrologic conditions associated with wetlands rather than on the vegetation occupying such sites. After all, wetlands hydrology is the essence of all wetlands—it is their creator.

Recent attention has focused on determining the boundaries of wetlands for regulatory purposes. Today it is critical to know the limits of wetlands on individual parcels of land, because many activities (e.g., dredging or filling) require federal or state permits before commencing work in wetlands. Because "hydrophytic vegetation" is a major determinant of federally regulated wetlands and is the chief determinant for regulation in some states (e.g., Massachusetts), it has become increasingly important to specify plants as wetland indicators. Therefore, the concept of *hydrophyte* as it relates to wetland identification and delineation is of major importance.

In this article, I give examples of species occurring in both wetlands and dry habitats, and I examine the concept of *hydrophyte* as it relatesto wetland identification and delineation. I argue that the concept should not be restricted to species but must be applied to individual plants adapted for life in water or saturated soils. This broader concept is also reflected in the recent *Federal Manual for Identifying and Delineating Jurisdictional Wetlands* (FICWD 1989), which is used for identifying wetlands in the United States. I further contend that, in many cases, plant community composition is not conclusive in differentiating wetland from nonwetland and that other factors (i.e., landscape position, soils, and hydrology) must be considered in making a determination.

Hydrophyte defined

Evolving views of the hydrophyte. *Hydrophyte* is not a new term. The prefix *hydro* suggests that the plant community is living in water or in a water-dominated environment. Although the word *hydrophyta* had appeared earlier in a report on plant geography (Schouw 1822), the word did not receive widespread usage until the 1900s. In the first plant ecology text, Dutch plant ecologist Eugenius Warming (1909) used *hydrophyte* along with other terms to describe various habitat forms (e.g., *halophyte, mesophyte*, and *xerophyte*).

Hemlock (*Tsuga canadensis*) swamp in Richland (Oswego County), New York. This type of facultative upland–dominated wetland is relatively common in parts of the northeastern United States. Landscape position, microtopography (pit and mound relief), and the presence of water-stained leaves in depressions aid in recognizing these plant communities as wetlands.

Hydrophytic vegetation criterion from federal wetland delineation manual

An area has hydrophytic vegetation when, under normal circumstances:

- more than 50 percent of the composition of the dominant species from all strata are obligate wetland (OBL), facultative wetland (FACW), and/or facultative (FAC) species, or
- a frequency analysis of all species within the community yields a prevalence index value of less than 3.0 (where OBL = 1.0, FACW = 2.0, FAC = 3.0, FACU = 4.0, and UPL = 5.0).

Caution: When a plant community has less than or equal to 50% of the dominant species from all strata represented by OBL, FACW, and/or FAC species, or a frequency analysis of all species within the community yields a prevalence index value of greater than or equal to 3.0, *and* hydric soils and wetland hydrology are present, the area also has hydrophytic vegetation. (Note: These areas are considered problem area wetlands.)

FICWD 1989

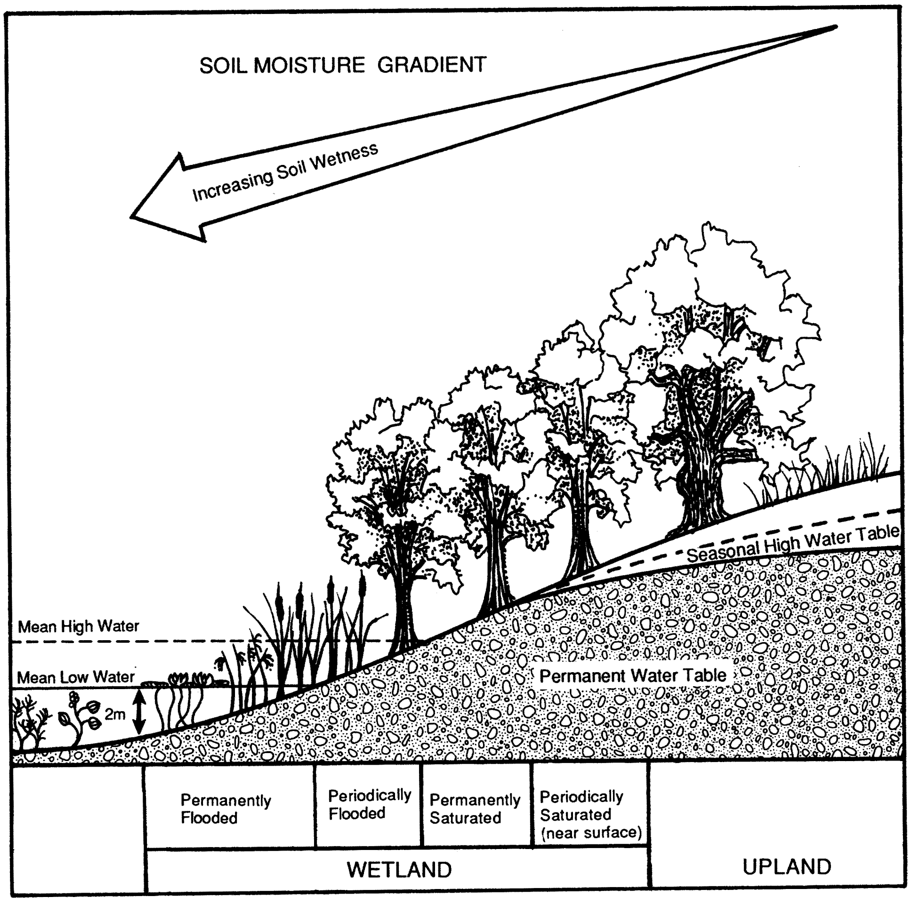

Figure 1. The general location of wetlands along the soil moisture gradient. The seasonal high water table represents the average height of the water table for a significant period during the wet part of the growing season in most years.

The term *hydrophyte* originally referred to plants growing in water or very wet soil, and these species were largely herbaceous. Today, any plant living in water or on a substrate that is at least periodically anaerobic due to excess water is defined as a hydrophyte. Consequently, more species (woody plants and herbs) have come to be considered hydrophytes.

A variety of technical definitions of *hydrophyte*, developed by scientists familiar with aquatic or wetland plant ecology, have been published in scientific journals, limnology books, wetland plant field guides, wetland identification and delineation manuals, and wetland classification reports. One general definition—plants growing only in water—is much too restrictive to be meaningful in defining wetlands, because most marshes, swamps, and bogs are not permanently flooded. A second definition of a hydrophyte—a plant growing in water or on wet soil—is more applicable for wetland identification.

Only in water. The definition of hydrophytes as plants growing only in water was used in various plant-habitat or life-form classifications (e.g., Braun-Blanquet 1932, Raunkiaer 1934, Warming 1909). This view emphasized that the perennating organs of hydrophytes are submerged in water during the cold winter or the hot, dry summer, so that these plants can survive such unfavorable times.

Warming (1909) identified two "oecological" classes associated with "very wet" soil: hydrophytes (plants with submerged organs growing in water) and helophytes (marsh plants with foliage growing above the water surface or in wet soil). He stated that "there is no sharp limit between marsh-plants and land plants" (p. 185). He recognized that the "boundary" zone of wet land (with plants living an amphibious existence) represents a gradual transition from terrestrial to aquatic conditions and that in some forested areas, "it is impossible to establish any sharp distinction between swamp-forests and forests on dry land" (p. 192).

In water or on wet soil

Clements (1920) also recognized helophytes (which he defined as amphibious plants rooted in water or mud), but he included them as a subgroup of hydrophytes. In their classic textbook on plant ecology, Weaver and Clements (1929) stated that "typical hydrophytes grow in water, in soil covered by water, or in soil that is usually saturated" (p. 336). They divided hydrophytes into three groups: submerged, floating (including floating-leaved), and amphibious. They noted that "amphibious plants have a wide range of adjustment and may grow for a time as mesophytes or partially submerged" and that they are the "least specialized of water plants" (p. 343). This remark suggests that the distinction between certain hydrophytes and mesophytes is not necessarily clear.

Daubenmire (1947) included, as hydrophytes, aquatics growing in water and "swamp and bog plants which inhabit soils containing a quantity of water that would prove supraoptional for the average plant" (p. 148). He divided hydrophytes into five "morphoecologic" groups: floating, suspended (e.g., phytoplankton), submerged anchored, floating-leaved anchored, and emergent anchored. In the last group, Daubenmire included bald cypress and mangroves (*Rhizophora* and *Avicennia*) and stated that "many sedges and willows, etc. are transitional between this group and mesophytes in that they grow in wet soil where the water table is close to the surface" (p. 152).

The modern hydrophyte. Today, the most widely used definitions of *hydrophyte* come from federal manuals used to delineate wetland boundaries for regulatory purposes or to inventory US wetland resources. These definitions are essentially that of Daubenmire (1968): plants that grow in water or in substrates that are, at least periodically, anaerobic due to excess water. This concept of hydrophyte was consistently presented in written material among the federal agencies even before the development of the *Federal Manual for Identifying and Delineating Jurisdictional Wetlands* (FICWD 1989).

Today's concept is similar to the earliest concepts of Warming and Clements, if one combines their categories of helophyte and hydrophyte, and includes plants on periodically saturated soils as well as in water or mud. These early plant ecologists recognized the similarities between certain hydrophytes and mesophytes or terrestrial plants and the limitations of using plants to separate wetlands from nonwetlands.

Categorizing plants

Plants growing only in water (e.g., lakes, ponds, rivers, and coastal wa-

Figure 2. White water lily (*Nymphaea odorata*) and other plants growing only in water are commonly called aquatic plants. They are hydrophytes by all definitions.

Recent definitions of *hydrophyte*

Any macrophyte that grows in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content; plants typically found in wetlands and other aquatic habitats.

Federal Manual For Identifying and Delineating Jurisdictional Wetlands
FICWD 1989

Large plants (macrophytes), such as aquatic mosses, liverworts, nonmicroscopic algae and vascular plants, that grow in permanent water or on a substrate that is at least periodically deficient of oxygen as a result of excessive water content. This term includes both aquatic plants and wetland plants.

EPA Wetland Identification and Delineation Manual
Sipple 1988

Any macrophyte that grows in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content; plants typically found in wet habitats.

Corps of Engineers Wetlands Delineation Manual
Environmental Laboratory 1987

Any plant growing in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content.

FWS *Classification of Wetlands and Deepwater Habitats of the United States*
Cowardin et al. 1979

Any plant growing in a soil that is at least periodically deficient in oxygen as a result of excessive water content.

Plant Communities: A Textbook of Plant Synecology
Daubenmire 1968

Figure 3. Examples of some morphological and other adaptations that may be used to recognize hydrophytes: (**a**) buttressed trunk and pneumatophores ("knees") of bald cypress (*Taxodium distichum*)—trees growing in wetlands subject to prolonged inundation may show signs of buttressing; (**b**) prop roots of red mangrove (*Rhizophora mangle*); (**c**) shallow root system of Oregon ash (*Fraxinus latifolia*), a common trait in many wetland plants; (**d**) aerenchymous stem of a hydrophytic form of rattlebush (*Sesbania drummondii*) growing on an exposed pond shore (compare this with a terrestrial form lacking aerenchyma, on left with roots exposed, that was growing just 15 feet away); and (**e**) oxidized rhizosphere along root (note the dark staining, actually reddish brown, of the soil along the root), evidence of a plant living under, at least periodically, anaerobic conditions.

ters) are unquestionably hydrophytes and are often called aquatic plants (Figure 2). These plants usually cannot live outside of water for any significant period of time because most desiccate rapidly on exposure to air. They include nonvascular plants (e.g., marine algae, freshwater algae, and aquatic mosses and liverworts) and vascular aquatic plants (e.g., water lilies, pondweeds, and naiads). Wetlands contain many aquatic species.

Most plants in wetlands are self-supporting vascular plants that emerge from shallow water or grow in periodically flooded or saturated soils. Some common species that only occur in wetlands and water are presented in Table 1. Periodically inundated or saturated soils also include many other species that grow to varying degrees in both wetlands and nonwetlands.

Because vegetation is considered a characteristic feature of wetlands, the federal government has compiled a national list of vascular plant species that occur in wetlands (Reed 1988). The list contains four "wetland indicator categories" (Table 2) based on differences in expected frequency of occurrence of a plant in wetlands: obligate wetland (OBL), facultative wetland (FACW), facultative (FAC), and facultative upland (FACU).

Most wetland scientists recognize both OBL and FACW species as indicators of wetlands, because these species are more often associated with wetlands than nonwetlands. In some regions, however, a plant species may not be as good an indicator as it is in others (Table 3). To reflect this variation, the national list contains regional indicators for 13 different regions. Intraregional differences exist in some species, but such assessment was beyond the scope of the original effort.

The national list of wetland plants contains 6728 species out of a total of approximately 22,500 vascular plant species that exist within all habitats in the United States and its territories and possessions (Reed 1988). Only 27% of the national wetland plant list is represented by OBL species.[1] The majority of listed species, therefore, grow in both wetlands and nonwetlands to different extents. Of the nation's flora, 31% of the species occur often enough in wetlands to be on the list; the majority of US plant species are virtually intolerant of flooding or prolonged soil saturation during the growing season.

The disagreement over what is or is not a wetland plant, or hydrophyte, begins with FAC species. These species, by definition, have a broad ecological amplitude with no affinity for wetlands or nonwetlands and, therefore, are not indicative of either. The controversy is centered on how these species should be used in applying the so-called "50% rule" for determining whether a given plant community is hydrophytic (i.e., is more than 50% of the community or the dominants represented by hydrophytic species?). The federal wetland delineation manual considers FAC species as potential hydrophytes; a predominance of these plants does not alone establish an area as wetland but requires examination of the soil and hydrology. A wetland definition based on three elements—hydrophytic vegetation, hydric soil, and wetland hydrology—is valuable because it recognizes the transitional nature of plant composition along the soil moisture gradient and requires that other features be evaluated.

The greatest difference in opinion on what species are hydrophytes involves the FACU, and not the FAC, species. Many wetland specialists may have an initial aversion to accepting FACU species as hydrophytes, because these species are much more common on nonwetlands. However, a particular subset of these species occurs in wetlands and may even be a dominant plant in a wetland community. Plants did not evolve to become indicator species; this designation is a human attempt to use plants to designate wetlands.

Table 1. Examples of obligate hydrophytes that are widespread or common in certain wetland types in the United States. Genera listed contain all or mostly obligates.

Life form	Species	Common name
Aquatics	*Azolla* spp.	Mosquito ferns
	Brasenia schreberi	Water-shield
	Elodea spp.	Waterweeds
	Isoetes spp.	Quillworts
	Lemna spp.	Duckweeds
	Myriophyllum spp.	Water-milfoils
	Najas spp.	Naiads
	Nuphar spp.	Pond lilies
	Nymphaea spp.	Water lilies
	Potamogeton spp.	Pondweeds
	Proserpinaca spp.	Mermaid-weeds
	Ruppia maritima	Widgeon-grass
	Thalassia testudinum	Turtle-grass
	Utricularia spp.	Bladderworts
	Vallisneria americana	Wild celery
	Zannichellia palustris spp.	Horned pondweed
	Zostera marina	Eelgrass
Emergents (herbs)	*Alisma* spp.	Water plantains
	Calla palustris	Wild calla
	Caltha palustris	Marsh marigold
	Carex aquatilis	Water sedge
	Carex stricta	Tussock sedge
	Cicuta maculata	Water hemlock
	Decodon verticillatus	Water-willow
	Drosera spp.	Sundews
	Dulichium arundinaceum	Three-way sedge
	Eleocharis spp.	Spike-rushes
	Eriophorum spp.	Cotton-grasses
	Glyceria spp.	Manna grasses
	Iris versicolor	Blue flag
	Juncus canadensis	Canada rush
	Juncus roemerianus	Black needlerush
	Leersia oryzoides	Rice cutgrass
	Lindernia dubia	Water pimpernel
	Osmunda regalis	Royal fern
	Peltandra virginica	Arrow arum
	Polygonum hydropiperoides	Water pepper

Wetland ecotypes

Most of the plants that grow in wetlands do not grow strictly in water or water-inundated soils, but also grow in terrestrial habitats. Many of these species are more common on the latter sites, but some of their populations tolerate varying degrees of soil wetness. Because these populations may not display morphological differences, often individuals of these wetland populations can only be recognized as hydrophytes when associated with more typical hydrophytic species or after identification of hydric soils (i.e., anaerobic soils due to excessive wetness) and wetland hydrology at a given location.

Swedish botanist Gote Turesson (Turesson 1922a,b, 1925) demonstrated that a given plant species may include ecotypes—populations or groups of populations having certain genetically based morphological and/or physiological characters but usually prevented from natural interbreeding by ecological barriers (Barbour et al. 1980). The scientific literature is replete with examples of ecotypes adapted to specific environmental conditions differing from the habitat of the typical species. Therefore, it is possible to envision a subset of the continental population of a FACU species that is typically adapted for life in waterlogged soils.

Table 3 lists plant species having

[1]P. B. Reed, 1988, personal communication. US Fish and Wildlife Service, St. Petersburg, FL.

Table 1. Continued

Life form	Species	Common name
Emergents (herbs)	*Polygonum sagittatum*	*Arrow-leaved tearthumb*
	Pontederia cordata	*Pickerelweed*
	Sagittaria spp.	*Arrowheads*
	Salicornia virginica	*Perennial glasswort*
	Scirpus americanus	*Olney's three-square*
	Scirpus atrovirens	*Green bulrush*
	Scirpus validus	*Soft-stemmed bulrush*
	Sium suave	*Water parsnip*
	Solidago patula	*Rough-leaved goldenrod*
	Solidago uliginosa	*Bog goldenrod*
	Sparganium spp.	*Bur-reeds*
	Spartina alterniflora	*Smooth cordgrass*
	Symplocarpus foetidus	*Skunk cabbage*
	Triglochin spp.	*Arrow-grasses*
	Typha spp.	*Cattails*
	Woodwardia virginica	*Virginia chain fern*
	Xyris spp.	*Yellow-eyed grasses*
	Zizania aquatica	*Wild rice*
Shrubs	*Andromeda polifolia*	*Big laurel*
	Betula pumila	*Bog birch*
	Cephalanthus occidentalis	*Buttonbush*
	Forestiera acuminata	*Swamp privet*
	Lonicera oblongifolia	*Swamp fly-honeysuckle*
	Myrica gale	*Sweet gale*
	Rhizophora mangle	*Red mangrove*
	Rosa palustris	*Swamp rose*
	Salix sericea	*Silky willow*
	Vaccinium macrocarpon	*Large cranberry*
Trees	*Carya aquatica*	*Water hickory*
	Chamaecyparis thyoides	*Atlantic white cedar*
	Fraxinus profunda	*Pumpkin ash*
	Gleditsia aquatica	*Water locust*
	Nyssa aquatica	*Water gum*
	Planera aquatica	*Planer tree*
	Quercus lyrata	*Overcup oak*
	Taxodium distichum	*Bald cypress*

recognized subspecies or varieties, recognized by specific morphological traits, that are found in different habitats or that have differently restricted distributions. In some cases, these varieties have been given a different indicator status, especially when their habitats are wetter than the typical species. Because of their morphological differences, they can be useful for identifying wetlands.

Besides the known difference in varietal habitat preferences, individuals of species growing in wetlands can be examined for morphological, physiological, and/or other types of adaptation to flooding or soil saturation (Table 4; Figure 3). Such study may reveal wetland ecotypes.

Responses of woody and herbaceous plants to flooding and soil saturation have received considerable attention (Crawford 1983, Gill 1970, Hook 1984, Hook and Scholtens 1978, Hook et al. 1988, Jackson and Drew 1984, Kozlowski 1984, Teskey and Hinckley 1978, Whitlow and Harris 1979). A plant's response to flooding may be quite different from its response to waterlogging. For example, red ash (*Fraxinus pennsylvanica*) was determined to be more flood-tolerant than eastern cottonwood (*Populus deltoides*; Hosner 1958), yet the latter was more tolerant of soil saturation (Hosner 1959). Caution must therefore be exercised from extrapolating results of flood tolerance studies and concluding that one species is more water-tolerant than another.

Gill (1970), in his review of flood tolerance of woody plants, alluded to the possibility of distinct populations with genotypic or phenotypic differences in flooding tolerance. These differences have been demonstrated for some herbaceous species (Crawford and Tyler 1969). Keeley (1979) recognized upland, swamp, and floodplain phenotypes of black gum (*Nyssa sylvatica*) in the Southeast. The upland plants were intolerant of flooding, the swamp plants highly flood-tolerant, and the floodplain plants had intermediate tolerances. Researchers investigating flooding and waterlogging tolerances of species, therefore, should be cognizant of potential ecotypes.

Kramer (1949) gave an interesting example of red maple's ability to thrive on both wet and dry sites. Red maple (*Acer rubrum*) has an adaptable root system. In swamps, it develops numerous shallow lateral roots to help avoid anaerobic stress, whereas in dry uplands a deep taproot is formed. Consequently, this species occurs with nearly equal frequency in both wetlands and nonwetlands. Shallow root systems in other plant species also help them survive and prosper in wetlands. This variation may be an individual plant's response to a wet environment. Timing of germination and subsequent environmental conditions may be crucial to the development of this adaptation.

Examples of FACU species as hydrophytes

All FACU species have been observed in wetlands. The national list of wet-

Table 2. Wetland indicator categories of plant species under natural conditions (after Reed 1988).

Wetland indicator category	Estimated probability of occurrence in wetlands	Estimated probability of occurrence in nonwetlands
Obligate wetland (OBL)	>99%	<1%
Facultative wetland (FACW)	67–99%	1–33%
Facultative (FAC)	34–66%	34–66%
Facultative upland (FACU)	1–33%	67–99%
(Upland (UPL)	<1%	>99%)

Table 3. Examples of species with recognized varieties occurring in different habitats. Range in wetland indicator status in its US distribution based on Reed (1988).* Habitat data from Fernald (1950) and Gleason and Cronquist (1963).

Species (common name)	Variety	National range of indicator status	Habitat
Acer rubrum			
(Red maple)	*rubrum*	FAC	Swamps, alluvial soils, and moist soils
(Swamp red maple)	*drummondii*	OBL to FACW	Deep swamps
(Trident-leaved red maple)	*trilobum*	OBL to FACW+	Forested wetlands
Andropogon virginicus			
(Broom sedge)	*virginicus*	FACU to FAC	Dry open soils, thin woods, etc.
	glaucus	Not designated	Dry sandy pine barrens
	tetrastachyus	Not designated	Dry sands, rocks, and pinelands
	glaucopsis	Not designated	Savannas, wet pinelands, and swamps
	hirsutior	Not designated	River-swamps, savannas, and marshes
Celtis laevigata			
(Sugarberry)	*laevigata*	FACW to UPL	Bottomlands and low woods
	smallii	Not designated	Bottomlands and low woods
	texana	Not designated	Bluffs, rocky slopes, dry woods, etc.
Fagus grandifolia			
(American beech)	*grandifolia*	FACU	Rich upland soils
	caroliniana†	FAC+	Moist or wet lowland soils, especially on or near the coastal plain
Nyssa sylvatica			
(Black gum)	*sylvatica*	FAC	Low-acid woods, swamps, and shores
(Swamp tupelo)	*biflora*	OBL to FACW+	Inundated swamps and damp sands
	caroliniana	Not designated	Chiefly uplands of the interior
Panicum virgatum			
(Switchgrass)	*virgatum*	FACW to FAC	Dry or moist sandy soils, and shores
	spissum	Not designated	Gravelly or sandy fresh to brackish shores and swamps
Quercus falcata			
(Southern red oak)	*falcata*	FACU to FACU−	Moist to dry woods
(Cherrybark oak)	*pagodaefolia*	FACW to FAC+	Chiefly bottomlands or near streams

*Plus after the category (e.g., FAC+) indicates that the species occurs in the higher portion of the range in wetlands (e.g., 51–66% of the time), whereas minus (e.g., FAC−) indicates the lower portion of the range (e.g., 49–34%).
†Designated as FAC+ only in the Northeast, although this variety also occurs in the Southeast, Midwest, and South Plains (Texas and Oklahoma).

Figure 4. Hydrophytic white pines (*Pinus strobus*) growing with broad-leaved cattail (*Typha latifolia*) in a Vermont swamp.

land plant species includes about 1400 FACU species (21% of the list).[2] Some prominent examples of these species that characterize certain wetlands in various regions of the United States follow. They illustrate that individuals of species more characteristic of uplands can successfully adapt to and thrive in wetland environments (Figure 4).

Evergreen woody plants. Numerous FACU evergreens occur across a wide range of moisture conditions. They include various pines, spruces, firs, and hemlocks (Table 5). Several species noted in Table 5 were observed to have hypertrophied lenticels on roots in saturated soils (Hahn et al. 1920).

[2]P. B. Reed, 1990, personal communication. US Fish and Wildlife Service, St. Petersburg, FL.

Figure 5. Pitch pine (*Pinus rigida*) growing with highbush blueberry (*Vaccinium corymbosum*) and bur-reed (*Sparganium* sp.) in a seasonal pond in southern New Jersey.

Table 4. Plant adaptations or responses to flooding and waterlogging.

Morphological
- Stem hypertrophy (e.g., buttressed tree trunks)
- Large air-filled cavities in center (stele) of roots and stems
- Aerenchyma tissue in roots and other plant parts
- Hollow stems
- Shallow root systems
- Adventitious roots
- Pneumatophores (e.g., cypress knees)
- Swollen, loosely packed root nodules
- Lignification and suberization (thickening) of roots
- Soil water roots
- Succulent roots
- Aerial root-tips
- Hypertrophied (enlarged) lenticels
- Relatively pervious cambium (in woody species)
- Heterophylly (e.g., submerged versus emergent leaves on same plant)
- Succulent leaves

Physiological
- Transport of oxygen to roots from lenticels and/or leaves (as often evidenced by oxidized rhizospheres)
- Anaerobic respiration
- Increased ethylene production
- Reduction of nitrate to nitrous oxide and nitrogen gas
- Malate production and accumulation
- Reoxidation of NADH
- Metabolic adaptations

Other
- Seed germination under water
- Viviparous seeds
- Root regeneration (e.g., adventitious roots)
- Growth dormancy (during flooding)
- Elongation of stem or petioles
- Root elongation
- Additional cell wall structures in epidermis or cortex
- Root mycorrhizae near upper soil surface
- Expansion of coleoptiles (in grasses)
- Change in direction of root or stem growth (horizontal or upward)
- Long-lived seeds
- Breaking of dormancy of stem buds (may produce multiple stems or trunks)

Lodgepole pine, Sitka spruce, and western hemlock were observed with adventitious roots in areas subject to flooding (Gill 1970).

Pitch pine (*Pinus rigida*) has a remarkable range in wet and dry tolerances, growing on excessively drained to poorly drained sands and gravels as well as on the mucks of swamps in the Northeast (Figure 5; Illick and Aughanbaugh 1930, Ledig and Little 1979, Little 1959). Pitch pine dominates many wetlands in the Pine Barrens of southern New Jersey (Tiner 1985a). Ledig and Little (1979) noted genetic variations in New Jersey's pitch pine, with a dwarf or pygmy form (less than 4 m tall) occurring on the Pine Plains (upland) and the tallest pines (30 m) found on seasonally wet sites. They concluded that genetic effects are confounded by environmental effects and that variation can occur at several levels in a species—among individuals within stands, among stands within regions, and among physiographic regions.

Eastern white pine (*Pinus strobus*) has been commonly found in forested wetlands in the glaciated northern areas of the eastern and central United States (Crum 1988, Curtis 1959, Huenneke 1982, Tiner 1989). Curtis (1959) found that 37% of the tamarack or black spruce bogs had white pine and discovered several stands in northern Wisconsin where it was the dominant species on peaty soils greater than 3 m thick. He remarked, "It is not known whether the trees [*P. strobus*] of organic swamps represent distinct ecotypes or not" (p. 205).

Dachnowski (1912) identified white pine as a "climax stage" in the Great Lakes forest that succeeded bog vegetation. Numerous forested wetlands in Rhode Island and elsewhere in New England are dominated or co-dominated by white pine (Tiner 1989), and both white and pitch pines are present in shrub bogs in this region. Studies of stand productivity in Massachusetts and southeastern New Hampshire have demonstrated that white pine grows best on poorly drained soils (Mader 1976, Husch and Lyford 1956).

In the upper Midwest, jack pine (*Pinus banksiana*) grows in a wide range of habitats from dry sandy or gravelly areas, where few other plants survive, to bogs. In the former habitat, it would be viewed as a xerophyte and in the latter as a hydrophyte. Yet jack pine grows best on well-drained loamy sands where the midsummer water table is 1.2–1.8 m below the soil surface (Fowells 1965); here it would be considered a mesophyte. Curtis (1959) identified jack pine as an important component of black spruce and tamarack swamps and as a dominant species in certain Wisconsin bogs. Similar findings were reported for Michigan by Crum (1988), who also listed white spruce (*Picea glauca*), another FACU species, as a characteristic plant of peatlands.

Figure 6. This lodgepole pine (*Pinus contorta* var. *contorta*) was codominant with alpine bog laurel (*Kalmia microphylla*) and labrador tea (*Ledum groelandicum*) in a Washington peat bog.

In the Cascade Mountains of Oregon and Washington and the Sierra Nevadas of California, lodgepole pine (*Pinus contorta*) mainly occurs in wet flats and poorly drained soils. Its

Table 5. FACU evergreen tree species that occur as common or dominant plants in wetlands (Curtis 1959, Fowells 1965, Tiner 1989, US Forest Service 1979, 1983a,b, 1986).

Species	Common name
Abies amabilis	Pacific silver fir
Abies concolor	White fir
Abies lasiocarpa	Subalpine fir
Picea engelmannii	Englemann's spruce
**Picea rubens*	Red spruce
Picea sitchensis	Sitka spruce
Pinus contorta	Lodgepole pine
**Pinus banksiana*	Jack pine
**Pinus monticola*	Western white pine
Pinus palustris	Longleaf pine
**Pinus ponderosa*	Pondersosa pine
**Pinus resinosa*	Red pine
**Pinus rigida*	Pitch pine
**Pinus strobus*	Eastern white pine
**Tsuga canadensis*	Eastern hemlock
Tsuga heterophylla	Western hemlock

*Hypertrophied lenticels on roots when growing in saturated soils (Hahn et al. 1920).

scrubby form (*P. contorta contorta*) grows in peat bogs and muskegs from Puget Sound north to southwest Alaska along the coast (Figure 6), but further south it occurs on dry sandy and gravelly coastal sites (Fowells 1965). The wetland indicator category of *P. contorta* changes from FAC in the Pacific Northwest, California, and Alaska to FACU in the Rocky Mountains and Western Plains. These regional differences may be the result of habitat preferences of different varieties: *P. contorta contorta* is a coastal scrubby form, but *P. contorta latifolia* is a tree of the interior.

Eastern hemlock (*Tsuga canadensis*) dominates certain wetlands and may be common in other swamps in the Northeast (Huenneke 1982, Niering 1953, Tiner 1989). It is highly adaptable to a wide range of soil conditions, including shallow rocky soils, upland podzols, groundwater (hydric) podzols, and peats and mucks (Fowells 1965). Eastern hemlock is a relatively shallow-rooted plant, making it well suited for a wetland existence. Other shallow-rooted tree species may also be well suited for wetlands.

Saw palmetto (*Serenoa repens*) grows mostly on dry sites (pine flatwoods, longleaf pine-scrub oak ridges, sand pine-oak scrubs, and coastal dunes) on the southeastern coastal plain, but it also occurs in seasonally wet pine flatwoods (Godfrey and Wooten 1979). Wells (1942) listed saw palmetto among the community dominants of southeastern shrub bogs, and Eleuterius (1980) reported it along the upper edge of Mississippi salt marshes. In the wettest sites, saw palmetto has an upright, often branched stem, whereas drier site plants have horizontal, mostly underground stems.[3] This morphological trait facilitates recognition of the wetland ecotype.

Deciduous woody plants. Deciduous woody FACU species may also be common or dominant in wetlands. Sugar maple (*Acer saccharum*) and paper birch (*Betula papyrifera*), common upland forest species in New England and the north-central United States, also grow in wetlands. Curtis (1959) stated that sugar maple had a prominent position on organic soils in some northern Wisconsin swamps. Sugar maple occurs in Michigan spruce bogs, but it never persists, according to Crum (1988). However, sugar maple has been observed as a dominant species on drier bogs in Michigan's Upper Peninsula.[4] Paper birch has been reported in Wisconsin (Curtis 1959) and Michigan (Crum 1988) swamps, and I have observed paper birch in northern Vermont swamps and Minnesota bogs (Figure 7). Fowells (1965) reported that it is common "even on bog and peat soils."

Figure 7. Saplings of paper birch (*Betula papyrifera*) growing with cottongrasses (*Eriophorum* sp.) and other bog plants in northern Minnesota.

White ash (*Fraxinus americana*) and tulip poplar (*Liriodendron tulipifera*) may grow in forested wetlands in greater abundance than expected. White ash is FACU throughout the United States. It is best developed on moderately well-drained soils and rarely found in swamps, according to Fowells (1965), yet it has been reported as common or dominant in forested wetlands in the Northeast (Golet et al. in press, Magee 1981, Tiner 1985a). Tulip poplar is FACU in the northern United States but is FAC in the Southeast. Often cited as a flood-intolerant species (Hosner 1960) it occurs in isolated depressional wetlands and floodplain wetlands from New Jersey to Virginia (Niering 1953, Tiner 1985a,b, 1988). It is also common in forested wetlands throughout the Southeast. Tulip poplar can develop buttressed trunks in wetlands as observed in the Dismal Swamp of Virginia and North Carolina.[5]

Gill (1970) reported adventitious roots on both tulip poplar and white ash growing in areas subject to flooding. This evidence indicates an individualistic response to wetlands.

Human interference

The occurrence of a plant species on the landscape can be drastically changed by human disturbance. The distribution and abundance of many plants have been significantly affected by forestry practices, agricultural activities, urban development, drainage projects, pollution, and other human actions.

Eastern white pine is an excellent example. At the time of U.S. settlement in southern New England, white pine, because of its susceptibility to fire, was probably only abundant in swamps and moist sandy flats and on exposed ridges (Bromley 1935). Today, with silvicultural plantings and the suppression of forest fires, the species grows on many better-drained sites. Consequently, the current distribution of eastern white pine is largely a result of human activities. Without

[3] J. Hefner, 1989, personal communication. US Fish and Wildlife Service, Atlanta, GA.

[4] L. Berndt, 1990, personal communication. USDA Soil Conservation Service, Michigan.

[5] B. Sipple, 1989, personal communication. US Environmental Protection Agency, Washington, DC.

knowing something about the history of this pine and human intervention, wetland delineators might think that it was always more abundant on uplands and misjudge the species' ecological significance. The twentieth-century landscape can be a confounding ecological message to decipher.

Individualistic concept of a hydrophyte

In *Field Guide to Nontidal Wetland Identification* (Tiner 1988), I defined a hydrophyte as "an individual plant adapted for life in water or periodically flooded and/or saturated soils (hydric soils) and growing in wetlands and deepwater habitats; may represent the entire population of a species or only a subset of individuals so adapted" (p. 265). This definition recognizes the potential for any individual plant to adapt to a wetland environment.

The individualistic concept of a hydrophyte recognizes that plant species may exhibit considerable plasticity or ecological amplitude in their adaptations to wet environments. The development of shallow root systems, for example, may be an individualistic response to anaerobic, saturated soils and one that is common to most wetland plants. Moreover, the success of a single individual seedling from a mesophytic or xerophytic population in growing in a neighboring wetland may mark the beginning of the evolution of a distinct ecotype or may simply be the result of favorable environmental conditions during its early life stage. Morphological, physiological, and genetic differences are known to develop between adjacent populations (Liu and Godt 1983), and these differences may even occur in microhabitats less than 3 m × 5 m in size (Hamrick and Holden 1979).

Conclusions

> Plant ecologists would like to use species as deductive tools, as rather precise indicators of certain levels of environmental factors. This may not be a realistic objective for two reasons. First, plants respond to a complex of climatic, edaphic, and biotic factors, and the impact of single factors is difficult to isolate. Second, taxonomic species, whether recognized on morphological, biological, or statistical grounds, are partially artifacts of the human desire to classify.
>
> Barbour et al. 1980, p. 51.

Although Linnaean species would be convenient markers of the precise limits of wetlands, many species growing in and even dominating wetland communities can also grow in nonwetlands. Braun-Blanquet (1932) qualified his observation that the species taxa have been regarded as conspicuous indicators of certain conditions of life when he added that the "most exact indicators are often, indeed, not the 'good Linnaean species' but rather the elementary species or races, the 'ecotypes' of Turesson" (p. 21).

During the past 25 years, the use of plant species to identify wetlands has evolved from one approach, where vegetation (plant species) was the chief determinant of wetland and its boundaries, to the current approach, where vegetation is used in concert with soil and hydrologic characteristics to identify and delineate wetlands. The former approach may still be useful for identifying the wettest wetlands (e.g., salt marshes, inland marshes, shrub bogs, and cypress-tupelo swamps) and areas where sharp topographic breaks occur, but a more broad-based approach is required to define accurately the limits of the variety of wetlands found throughout the United States along the soil moisture gradient.

The existence of wetland ecotypes lacking distinguishing morphological characteristics to separate them from the typical species and the broad ecological amplitude or wide wetness tolerance of many species make it difficult to rely solely on plant community composition to identify many wetlands and delineate their boundaries. Consequently, evaluation of soil properties and other hydrologic characteristics are essential to accurate identification and delineation of wetlands.

In the early days of wetland regulation, government regulators may have been more willing to rely solely on vegetation to identify wetlands for two reasons. First, certain wetlands are well-expressed by their vegetation, which eventually led to a common misconception that a predominance of species that were considered wetland plants would always result in an accurate wetland delineation. Second, most wetland regulators lacked knowledge of hydric soil properties and their strong correlation with flooded or saturated soil conditions.

Today, with increased appreciation of the role of wetlands in such functions as water quality enhancement, the accurate identification and delineation of these resources is vital to maintaining the wealth of wetland values for ourselves and future generations. It is not only the vegetation that makes wetlands important; their soils, hydrology, and landscape position facilitate, for example, the interception of flood water and surface water runoff and the assimilation of nutrients and pollutants to improve water quality. Consequently, these wetlands must be properly identified to regulate effectively alternative uses. Examination of vegetation, soils, and hydrology is now the standard procedure of the federal government, and many states have adopted it. Thus, although hydrophytic vegetation is still important for identifying and delineating wetlands, it is no longer the sole criterion.

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