INTRODUCTION

Thousands of plants have adapted to life in water or wetlands, with a significant proportion of them occurring only in wetlands and shallow water. Many wetlands are readily identified by vegetation and traditional methods relied on plants for wetland identification and delineation (Chapter 6). Plants also serve as a basis for wetland classification (Chapter 8). Yet, despite the value of using plants for these purposes, all wetlands are not simply recognized by vegetation alone. Identifying the point on the gradient at which wetland begins and upland (dryland) ends can be straightforward in areas of high relief or extremely difficult in relatively flat terrain. In the former situations, plants may be used as boundary delineators, but in the latter, soil properties tend to be more indicative of prolonged saturation at or near the surface (Chapter 5). As wetland hydrologic conditions vary from permanent wetness (inundation and/or soil saturation) to periodic or seasonal waterlogging and soil wetness decreases, plant composition changes from a more typical and predictable wetland community to a transitional (ecotonal) community where wetland species intermix with mesic species, making wetland identification challenging and, by plants alone, most difficult and somewhat arbitrary. A multitude of hydrologic regimes associated with wetlands create a diverse set of environmental conditions that requires different degrees of adaptation or tolerance of wetness by colonizing plants. This chapter reviews environmental conditions induced by prolonged wetness, describes plant adaptations for living in wetlands (focusing on morphological properties that are important for wetland recognition) and the concept of a hydrophyte, and discusses how plants can be used to identify wetlands and as indicators of associated environmental conditions. Hundreds of articles and several books have been written about plant response to wetness because many plants experiencing flooding and soil saturation are economically important (e.g., rice, pines, and Atlantic white cedar). Some of the classic texts on the subject include works by Kramer (1949), Hook and Crawford (1978), Kozlowski (1984c), and Crawford (1987, 1989), while Mancuso and Shabala (2010) offer a more recent treatment. Special issues of two journals address recent research on responses of plants to flooding stress: Volume 96 of Annals of Botany (Jackson and Colmer, 2005), and Volume 190 of New Phytologist (Perata et al., 2011). Kozlowski (2002) provides a summary of physiological and ecological impacts of flooding on riparian forests. Readers are encouraged to consult these and other sources for more detailed discussions, especially regarding physiological adaptations.

The focus of this chapter is on the impacts of excess water on plants and their morphological and anatomical responses, with an emphasis on North American species. It must be recognized that many other factors also influence plant distributions including salinity, pH, nutrients, soil type, drought, light availability (e.g., light-demanding vs. shade-tolerant species), sedimentation, turbidity, competition, fire, ice, disease, herbivory, and human actions. They are not subjects for this book (see other references for discussion of these factors such as Cronk and Fennessy, 2001, and Tiner, 2013, for wetland plants or ecology texts like Gurevitch et al., 2006, and Kozlowski et al., 1991). Also, the distribution of plants along environmental gradients is not discussed in any detail; readers are referred to books and numerous scientific papers on specific wetland types (e.g., for bogs, Crum, 1988; Rydin and Jeglum, 2006; northern forested wetlands, Trettin et al., 1996; southern swamps, Messina and Conner, 1998; floodplain wetlands, Middleton, 2002; freshwater marshes, van der Valk, 2012; prairie potholes, van der Valk, 1989; Murkin et al., 2000; playas, Smith, 2003; mangroves, Hogarth, 2007; Spalding et al., 2010; tidal marshes, Tiner, 2013; Amazonian tropical
Wetland Indicators

158

ENVIRONMENTAL CHANGES DUE TO FLOODING AND WATERLOGGING

Prolonged flooding or waterlogging restricts oxygen movement from the atmosphere to the soil. Diffusion can occur but it is 10,000 times slower in saturated soils than it is in aerated soils (Greenwood, 1961). Upon flooding, respiration by aerobic bacteria and other organisms (aerobes) consume the oxygen remaining in the soil within hours to days (Turner and Patrick, 1968; Pezeshki, 1994). Evans and Scott (1955) found that in just 75 minutes, the concentration of oxygen in a saturated soil dropped to 1/100th of its initial value. The only free oxygen present thereafter is at the soil–water interface—a thin layer (a few millimeters thick) at the soil surface. With free oxygen virtually absent from the soil, facultative and obligate anaerobes multiply in number and utilize oxygen bonded to various soil elements, thereby promoting denitrification and transforming nontoxic (oxidized) forms of manganese, iron, sulfate, and other elements to toxic forms (e.g., manganous, ferrous iron, and hydrogen sulfide). The end result is a reduced soil with low redox potential and the appearance of other potentially toxic compounds including ethanol, lactic acid, acetaldehyde, and acetic and formic acid (Striker, 2012). Anaerobic substrates or soils can develop within a few days in most soils and redox potential values* as low as −250 mV can be attained within 2 weeks in soils low in nitrate and manganic and ferric oxides (Ponnamperuma, 1972, 1984). In a flooding experiment with 5-week-old seedlings of sessile oak (*Quercus petraea*), Folzer et al. (2006) measured the oxygen content in the soil around the roots and found that after 10 days oxygen content reached its low point. Besides flooding, demand for oxygen in the sediments by plant roots and microbes also affect oxygen content of soil (Pezeshki, 2001; Laskov et al., 2008; Reddy and DeLaune, 2008). Figure 3.1 illustrates the response of oxygen and redox potential (Eh) to changes in water levels in the soil.

Soil oxygen deficiency (partial, hypoxia; complete, anoxia) poses the main ecological problem for plant growth as it affects plant functions such as stomatal opening, photosynthesis, water and mineral uptake, and hormonal balance (Kozlowski, 1984b). Studies have shown that the effects of submergence can be relieved if air or 100% oxygen is supplied to the water (Larqué-Saaavedra et al., 1975; MacDonald and Gordon, 1978). This is further supported by the practice of hydroponics where flood-intolerant plants like tomatoes can be grown in an aerated, enriched aqueous solution. In nature, however, most aquatic plants are living in continuously oxygen-deficient substrates. In contrast, most wetland plants grow in a dynamic environment of alternating wet and dry conditions (i.e., frequency, duration, and depth of flooding and saturation are important variables—Chapter 2). Significant stresses accompanying anaerobiosis during wet periods are following by drier periods when aerobic conditions are present, allowing for recovery. For example, southern bottomland hardwood wetlands may be oxidized throughout their root zone for 60%–80% of the growing season (Faulkner and Patrick, 1992). The diversity of wetlands makes for a seemingly endless combination of anaerobic/aerobic conditions, with the drier-end wetlands placing the least demand on plants and the wettest ones (permanent water) requiring the greatest adaptations. In permanently saturated wetlands, oxygenated water associated with snowmelt, thawing soils, and early spring rains may provide similar relief from oxygen deficiency. Jackson and Drew (1984) speculated that early-season flush of freshwater may provide a temporal well-oxygenated environment for root growth of bog species and that such conditions are vital to the survival of these species.

Wetland environments also are affected by the type of water flooding them. Wetlands saturated with moving, partly oxygenated waters are more favorable habitats than ones with stagnant water, for the flowing water allows root development and penetration into the substrate, whereas in the latter,

*Redox potential is a measure of the oxidation–reduction status of the soil, and the values correspond with changes in the status of various elements (e.g., when iron changes from a stable, oxidized form to an unstable, reduced one at around +100 mV).

Cool water dissolves oxygen better than warm water. Flooding by salt water inflicts great hardships on plants beyond anaerobiosis that freshwater wetland plants endure. These stresses include increased water stress, chloride toxicity, hydrogen sulfide toxicity, and salt uptake (Wainwright, 1984).

Flooding and soil saturation also cause changes in the soil environment that affect plant growth and survival. Soil temperature is lower in flooded soils than in well-drained soils. Bonneau (1982) found that the average difference was 6°C in the surface layer. Lower temperatures may influence soil chemistry, nutrient release, phytotoxin production, organic matter decomposition, and plant growth (Ponnamperuma, 1976). When saturated, soil structure changes as soil colloids expand, especially in soils with high clay content. Swelling is usually completed within 1–3 days (Ponnamperuma, 1984). Salty soils swell more than calcareous or acid soils. This swelling may cause soils with low permeability to become impermeable, resulting in ponding of water on the surface for significant periods after rainfall events. Alternate flooding and drying may cause significant cracking in clayey soils. Such activity may affect root growth and restrict root penetration. Flooding also alters the pH of the soil. Acid soils attain a higher pH status when flooded, while flooded alkaline soils decrease in pH (Ponnamperuma, 1984).

Salt marshes offer some rather unique conditions for plant growth due to variable tidal flooding, duration of exposure, and salinity (Tiner, 2013). Armstrong et al. (1985) observed three general elevation zones with differing soil aeration. The first zone was the lower margin of the salt marsh. Here, reducing conditions persisted regardless of the length of exposure, with oxidation occurring only near the surface (within 2 in. or 5 cm) and at neap tides. The second zone was on the creek

**FIGURE 3.1** Changes in water levels affect soil oxygen and redox potential (Eh). Anaerobic conditions occur when the redox potential of the soil reaches +300 to +350 mV (DeLaune and Pezeshki, 1991; Faulkner and Patrick, 1992) as little oxygen diffusion occurs below this value. Aerobic conditions have values usually from +350 to +700 mV and higher. Note that a flooded soil may be aerated if little organic matter is present or no energy source (e.g., soil microbes) exists to consume the oxygen or when temperatures are cold (below biological zero). (Reprinted from Reddy, K.R. and DeLaune, R.D., \textit{Biogeochemistry of Wetlands: Science and Applications}, CRC Press, Boca Raton, FL, 2008. With permission.)
bank and on other better drained areas where low redox potentials (below 200 mV) only happened monthly in the upper soil during high spring tides. Wetter years and winter rainfall may lower soil aeration more frequently than in summer. The third zone was the mid and high marsh where the upper soil was aerated most of the summer (even to a depth of 12 in. or 30 cm in July). Reduction took place in the upper soil upon flooding by spring tides but was present below 8 in. (20 cm) for most of the summer. While flooding caused an almost instantaneous 300–400 mV fall in redox potentials within the upper 4 in. (10 cm), the rise in redox potential upon natural drainage took several days to happen. Salinity and duration of flooding also are affected by marsh elevation. Plant zonation in salt marshes is well documented (e.g., Miller and Egler, 1950; Adams, 1963; Tiner, 1987, 1993, 2013).

Given rising sea levels associated with climate change, tidal oligohaline and freshwater wetlands and coastal hammocks are becoming increasingly exposed to increased salinity and saltwater intrusion and, on the short term, from hurricane storm surges. Many studies have focused on the effect of flooding and salinity on these wetlands (McKee and Mendelsohn, 1989; Allen et al., 1996; McCarron et al., 1998; Howard and Mendelsohn, 2000; Desantis et al., 2007; Krauss et al., 2007; Spalding and Hester, 2007; Saha et al., 2011; Neubauer et al., 2013; Sutter et al., 2014; Raabe and Stumpf, 2016). Coastal bottomland forests were also being flooded by rising water levels due to sea-level changes combined with coastal subsidence (Denslow and Battaglia, 2002).

The quality of water entering wetlands may be affected by climatic conditions. In arid, semiarid, and subhumid regions, groundwater brought to the surface through capillary action due to high evaporation brings with it various salts (e.g., sodium chloride, calcium carbonate, and magnesium sulfate) that become concentrated upon drying. These evaporites exert salt stress on plants that dramatically affects plant growth; some areas are so salty that they are devoid of vascular plants. Irrigation projects have accelerated the buildup of salts in many areas of the world (Wainwright, 1984). In some cases, lethal concentrations of arsenic, boron, selenium, and other toxics collect in inflow wetlands (Lico, 1992). Salt tolerance plays an important role in the success of the invasive saltcedar (Tamarix ramosissima) along rivers in the southwestern United States (Shafroth et al., 1995; Smith et al., 1998).

Finally, there are also other effects of flooding, namely, deposition of sediments and scouring, that are important factors regulating plant distribution in riparian communities. Plants growing in flood-prone areas must be adapted to these conditions as well. Both of these factors are limiting to seedling establishment and survival. While few mature trees are killed by deposition during floods (Sigafoos, 1964), burial of seedlings should be more detrimental. The impact of sedimentation on germination was secondary to flooding (duration) for swamp chestnut oak (Quercus michauxii) and overcup oak (Q. lyrata) (Pierce and King, 2007). A study by Gage and Cooper (2004) of park willow (Salix monticola) establishment on Rocky Mountain point bars indicated that both soil water availability and scour by spring floods affected both willow seedling survival and distribution. Abandoned channel reaches may be better sites than active point bars because the former have more fine-textured sediments and lower stream energy than the latter (high-energy and coarse-textured soils/substrates). Cottonwoods (Populus spp.) are dominant floodplain trees across the country; erosion and deposition from major floods create bare areas suitable for their establishment (Braatne et al., 1996; Rood et al., 1998). Their seedlings require a continuously moist soil during the first week or more of growth and after the first growing season can then survive drastic declines in the water table of 3.3 ft (1 m) or more (Moss, 1938; Segelquist et al., 1993). Cottonwood seedling establishment is also greatly influenced by spring flooding and ice scouring as well as by human water-use and land-use practices (including damming of watercourses), shading by trees, and grazing. Along the Missouri River (Montana), researchers found some cottonwood trees in the annual flooding zone, but most of the mature trees of plains cottonwood (P. deltoides ssp. monilifera) occurred well above this zone (Auble and Scott, 1998). The latter's seedlings established under conditions of infrequent high flows (e.g., >9–10-year return flow) that provided moist exposed banks above the more frequently flooded zone where ice scouring annually occurs and seedling mortality is correspondingly very high. Greenhouse studies where increments of sediment were added to the
seed bank from a *Calamagrostis angustifolia* wetland community found that deposition of 0.2 in. (0.5 cm) of sediment significantly decreased species richness and seedling emergence (Wang et al., 2014). Species response differed with addition of more sediment; some species germinated after deposition of 0.4–0.8 in. (1–2 cm) of sediment (*Sagittaria trifolia*, *Alisma orientale*, and *Salix* spp.), whereas others decreased with less than 0.1 in. (0.25 cm) of sediment added (*C. angustifolia* and *Typha orientalis*). Gleason et al. (2003) examined the effects of sedimentation on seedling emergence from soil seed banks collected from seasonal and semipermanent prairie pothole marshes. They found that a 0.2 in. (0.5 cm) layer of sediment reduced seedling emergence by 91.7%. Only two species (*Scirpus acutus/validus* and *Sparganium eurycarpum*) were tolerant of 0.8 in. (2 cm) of sediment, whereas 7 taxa emerged from the 0.4 in. (1 cm) treatment, 11 from the 0.2 in. (0.5 cm) treatment, and 40 species from no sediment deposition.

### PLANT ADAPTATIONS TO FLOODING AND WATERLOGGING

Life in permanently or periodically anaerobic soils or substrates is more difficult than living in mesic soils due to oxygen deficiency, the nature of a highly reduced environment (low redox potential, Eh) with soluble phytotoxins, and other conditions. Most vascular plants cannot cope with anaerobiosis resulting from extended flooding or waterlogging. For example, intolerant herbs may quickly succumb to flooding for more than a few days, after passing through a series of worsening symptoms—from a yellowing of their leaves (chlorosis) and/or wilting to shedding their leaves. Grable (1966) reviewed the effect of soil aeration on plant growth, while Armstrong et al. (1994) and Pucciariello and Perata (2012) described mechanisms of plant tolerance to flooding. Maricle et al. (2014) suggested that flood tolerance may be related to ethanol tolerance. Perata and Alpi (1993) addressed plant responses to anaerobiosis. The journal *Annals of Botany* devoted at least two entire issues (January 2009 and October 2003) to the latter topic (e.g., Visser et al., 2003; Jackson et al., 2009). Braendle and Crawford (1999) listed three requirements for surviving oxygen deprivation: (1) sufficient energy reserves for cell maintenance, (2) prevention of cytoplasmic acidosis from anoxia, and (3) anaerobic mobilization of starch reserves; they also described mechanisms need to facilitate reentry to an aerobic environment.

Prolonged flooding typically kills most woody species, with seedlings being most vulnerable (e.g., Hosner, 1958, 1960; Malecki et al., 1983; Hueneke and Sharitz, 1986; Streng et al., 1989; Conner, 1994; Yamamoto et al., 1995; Jones and Sharitz, 1998; Battaglia et al., 2000; Sakio, 2005; Anderson et al., 2009). A study of seedlings of 10 forest species by Loucks and Keen (1973) found that all survived 2 weeks of flooding but longer flooding had significant negative effects on most of the species. Complete submergence poses a larger problem for seedlings than partial submergence. Hosner (1960) found that floodplain seedlings could survive longer inundation as long as the crowns were not flooded; this allows gas exchange to occur. Experiments with cuttings of Goodding’s willow (*Salix gooddingii*) and saltcedar (*T. ramosissima*) showed similar responses to complete submergence of shoots (Tallent-Halsell and Walker, 2002). Most mature trees die within 3 years of continuous flooding, as they are apparently unable to regenerate vital absorbing roots that they typically need to do every 2 years (Crawford, 1983). Old trees and young saplings of all tree species on a Mississippi floodplain died after being inundated for 5–6 years by a dam, yet rapidly growing young trees were more resistant (Yeager, 1949). More tolerant species may survive longer, up to 8 years (e.g., white ash *Fraxinus americana* reported by Yeager, 1949). In studying a Florida floodplain forested wetland subjected to increased flooding from impoundment, Brown and Lugo (1982) found that a mean water depth of 2 ft (60 cm) seemed to be the threshold at which the swamp would survive as deeper water brought about mortality. Wildlife managers use greentree reservoirs (floodings of leveed bottomland forests from late fall to early spring) to make habitat and food (largely acorns) available for migrating and overwintering waterfowl. Species with comparable flood tolerances may have different tolerances to soil saturation. For example, although willow oak (*Quercus phellos*), overcup oak (*Q. lyrata*), and green ash (*Fraxinus pennsylvanica*) had similar flood tolerances,
willow oak seedlings were more tolerant of saturated conditions that persisted after flooding at Noxubee National Wildlife Refuge in Mississippi (Young et al., 1995). Tree seedlings of temperate and boreal species are more sensitive to flooding than those of many tropical species that withstand submergence for up to 7 months on Amazon floodplains (Lucas et al., 2013).

Plant tolerance of flooding and soil saturation also is affected by the time of year, with increased tolerance in winter and early in the growing season. Prolonged flooding during the growing season is more stressful for plants than inundation during the dormant period, although winter flooding brings a different set of problems to affected plants, requiring other physiological adaptations (Crawford, 2003). When the plant is active, photosynthesis, respiration, and other metabolic processes are underway, and since oxygen is a necessary ingredient for these processes, reduced oxygen availability from flooding is a major problem. Coder (1994, p. 3) offers the following general explanation: “The higher the temperature, the faster and deeper the oxygen shortage will be felt, and the more the top of the tree will dehydrate. After only 2 weeks of inundated or saturated conditions the root crown areas began to have many problems that can lead to decline and death. Flooding during the warm growing season periods magnify flood damage because of respiration needs and foliage water loss.” As mentioned earlier, seedlings are likely to be the most vulnerable life stage. For example, up to 16 weeks of saturation had no effect on budbreak or initial stem growth of sycamore, sweet gum, and Nuttall oak seedlings when this occurred early in the growing season, but 10–12 weeks of saturation thereafter (when temperatures were warm and active growth commenced) caused severe reduction in height, root, and stem-diameter growth (Bonner, 1966). While flooding during the growing season is expected to have the greatest negative impact on seedlings, a study of the response of 1-year-old seedlings of saltcedar (T. ramosissima) and plains cottonwood (Populus deltoides ssp. monilifera) to spring and fall flooding found that survival of both species was drastically reduced by fall flooding, despite practically all seedlings surviving spring flooding (Gladwin and Roelle, 1998); nearly all saltcedar seedlings perished (0.8% mean survival), with 21% mean survival in the cottonwood. Based on an early investigation of the effect of submergence on loblolly pine (P. taeda) seedlings by Williston (1962), Schultz (1997) reported that 1-year-old potted seedlings will survive up to 12 days of inundation during the growing season, with 50% survival expected after 21 days of flooding. Moreover nearly all seedlings will die after 1 month of submergence during the growing season, yet most loblolly seedlings can survive up to 1 month of flooding during the dormant season (Williston, 1962). In the tropics with a year-round growing season, some floodplain shrubs (Coccoloba pichuna, Eugenia inundata, and E. tenuifolia) can withstand inundation up to 10 m for 280 days (Junk 1989), while Amazonian trees grow in areas flooded with up to 14 m of water for up to 270 days (Ferreira, 2000). For herbaceous plants, different life stages may also have varied tolerances, making them more susceptible to anaerobiosis and submergence at certain times (Van der Sman et al., 1988). For example, experiments with cogongrass (Imperata cylindrica), an invasive species in wet pine flatwoods, have shown that seeds and very small transplants were more susceptible to flooding than larger transplants—seed germination was reduced 74% by inundation, yet medium and large transplants showed no difference in growth under flooded or saturated conditions (King and Grace, 2000). Furthermore, most of the larger plants extended some of their leaves above the water surface within 2 weeks and developed adventitious roots.

Water temperature of floodwaters influences plant response, with higher temperatures producing higher metabolic rates. Relatively high water temperatures caused an increase in shoot length in two docks (Rumex palustris and R. maritimus), while low temperatures led to better preservation of biomass and greater survival after submergence, likely due to lower metabolism (Van der Sman et al., 1993). Study plants were more tolerant of prolonged inundation (i.e., 28 days) in early summer than midsummer flooding. In midsummer, only those plants that were able to extend their shoots above water survived, while rosettes of R. palustris survived in early summer (Van der Sman et al., 1993).

Aquatic plants are the best adapted and most specialized of the wetland plants, since they spend their entire lives in water. Such an existence necessitated development of a host of adaptations ranging from morphological structures for support, waterproofing, buoyancy, and overwinter survival to
reproductive adaptations for pollination and germination to physiological mechanisms. Many aquatic species are stimulated by flooding and send their shoots above the flood level (Ridge and Ararnsinghe, 1981; Jackson and Drew, 1984; Blom et al., 1996). The adaptations of aquatic plants for life in water are well documented (see Arber, 1920; Gessner, 1955, 1959; Sculthorpe, 1967; Hutchinson, 1975).

Responses of woody and herbaceous plants to flooding and soil saturation have received considerable attention (e.g., Hosner, 1960; Gill, 1970; Teskey and Hinckley, 1977, 1978a,b; Hook and Scholtens, 1978; Armstrong, 1979; Bell and Morley, 1979; Whitlow and Harris, 1979; Tang and Kozlowski, 1982, 1983, 1984a,b; Crawford, 1983; Hook, 1984a,b; Jackson and Drew, 1984; Kozlowski, 1984a,b; Hook et al., 1988; Pezeshki, 1994; McKevein et al., 1998; Braendle and Crawford, 1999; Kozlowski, 2002; Crawford, 2003; Colmer and Voeselek, 2009; Jackson et al., 2009; Ladig et al., 2009; Bailey-Serres and Voeselek, 2010; Striker, 2012). Braendle and Crawford (1999) liken aquatic and wetland plants to amphibians, having to deal with the challenges of life in alternating wet and dry environments (inundation and oxygen deprivation then lowered of water tables and exposure to air plus the lack of physical support provided by flooding). Flood tolerance differs by age of plant, with seedlings usually being more vulnerable than mature individuals as mentioned earlier. Once established, some trees can withstand permanent flooding, such as baldcypress and water gum in southern swamps and impoundments (e.g., Keeland et al., 1997). Theriot (1993) developed flood tolerance indices for 312 species in relatively undisturbed southeastern bottomland forests, whereas Whitlow and Harris (1979) also rated the flood tolerance of many floodplain species in the Southeast. Despite the wealth of information in these publications, our knowledge is far from complete on this subject, especially in regard to a plant’s ability to live under conditions of prolonged waterlogging. Niinemets and Valladares (2006) offer an interesting examination of waterlogging tolerance in trees and shrubs of the temperate Northern Hemisphere; few species were found to be polytolerant (to waterlogging, shade, and/or drought). Among the 806 species reviewed, three species were tolerant to all three stresses (Amelanchier laevis, Rhododendron periclymenoides, and R. viscosum); there are clearly trade-offs when it comes to tolerating multiple stresses at least for temperate species. Lucas et al. (2013) did not detect any apparent trade-offs in stress tolerance among 10 woody species common to Amazonian floodplain forests.

A plant’s response to flooding may be quite different than its response to waterlogging. For example, green ash (F. 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 in extrapolating results of such studies and concluding that one species is more water tolerant than another because the two situations (flooding and waterlogging) impose some different stresses on plants; also other factors may also affect plant distribution on periodically flooded lands (Battaglia et al., 2004).

Another problem in interpreting the results of flood or waterlogging tolerance studies is that distinct populations with genotypic or phenotypic differences in flooding tolerance undoubtedly exist (Crawford and Tyler, 1969; Gill, 1970; Tiner, 1991) and in all likelihood, the researchers did not pay attention to this important detail. For example, several studies identified tulip poplar (Liriodendron tulipifera) as a flood-intolerant species (e.g., Hosner, 1960), yet this species has been frequently observed in floodplain wetlands (Tiner, 1985a,b, 1988; Shear et al., 1997; Rheinhardt et al., 1998) and was reported growing in a red maple-yellow birch swamp in northern New Jersey (Niering, 1953). Tulip poplar with buttressed trunks has been observed in Virginia’s Dismal Swamp (Bill Sipple, personal communication, 1990). These findings suggest possible ecotypes in this species. Gill (1975) commented on the paradoxical occurrence of tulip poplar on stream banks and swamp margins (subject to periodic flooding), despite a reported flood intolerance in the literature. Keeley (1979) demonstrated the significance of considering ecotypes in flood tolerance studies by experimenting with three phenotypes of black gum (Nyssa sylvatica)—upland, swamp, and floodplain. Keeley found that the upland seedlings were very intolerant of flooding and the swamp seedlings highly flood tolerant, while the floodplain seedlings had intermediate tolerances. These results provide proof of the potential pitfalls brought about by considering only the species level
for determining what constitutes a wetland plant (see the wetland ecotypes discussion later in this chapter). Researchers must be particularly mindful of the habitat from which the seeds/seedlings come, as this may affect their response to flood/saturation tolerances and study findings.

A wide range of adaptations make it possible for plants to grow in water or wetlands. These adaptations include physiological responses, morphological adaptations, behavioral responses, reproductive strategies, and others (Table 3.1; see Ernst, 1990, for a review of physiological mechanisms). These features and processes also affect the flood or saturation tolerance of species, thereby influencing the distribution of plants within wetlands. The least adapted species possess only minor adaptations and consequently are typically restricted to the margins or the highest elevations (e.g., hummocks in pit and mound topography). Some species growing in wetlands may only be found on hummocks since they apparently cannot tolerate wetter conditions (e.g., Gaultheria procumbens and Lycopodium obscurum), while even seedlings of wet-tolerant woody species also find these sites more favorable for survival than swales (Blood and Titus, 2010). The distribution of Virginia sweetspire (Itea virginica) in the understory of southern cypress–tupelo swamps appears related to seedling flood tolerance—it is restricted to hummocks (Anderson et al., 2009). Species with the most effective adaptations are found in the wettest conditions, while those least adapted are typically found on higher ground; the zonation of tree communities on floodplains offers an excellent example. Leitman et al. (1984) described the distribution pattern of five forest types along Florida’s Apalachicola River floodplain: (1) water tupelo–baldeycress, (2) water tupelo–swamp tupelo, (3) water tupelo–Ogeeechee tupelo–baldeycress, (4) water hickory–green ash–overcup oak–diamondleaf oak, and (5) sweet gum–sugarberry–water oak. The first three communities were permanently saturated and flooded for 50%–90% of the time, while the other two communities occurred on higher ground (including levees) and were saturated or flooded only 5%–25% of the time.

Besides coping with at least recurrent prolonged anaerobic soil conditions, the presence of soluble toxins (e.g., reduced forms of iron and aluminum, plus hydrogen sulfide), and, for many species, living in water, wetland plants also must adapt to other environmental conditions, including salinity (ocean-derived or inland salts), pH (acidic to alkaline), nutrient availability, substrate types (sand, clay, or other mineral soils), sedimentation (especially in floodplains), soil temperature, climatic factors, and biological competition plus human-induced stressors (e.g., pollution). Despite the emphasis on anaerobiosis, the combination of all of these factors influences plant distribution. For example, light availability and an ability to allocate light energy to photochemistry during flooding have been suggested as factors affecting flood tolerance of plants (Hall and Harcombe, 1998; Caudle and Maricle, 2012).

**Morphological Adaptations**

Wetland plants exhibit a wide range of morphological features developed in response to frequent prolonged flooding and waterlogging (Table 3.1). These structures have long been recognized as Warming (1909) makes reference to adventitious roots, internal air-containing spaces, aerenchyma, and pneumatophores.* Morphological adaptations are likely manifestations of physiological responses as a flood-induced increase in ethylene production has been linked to the formation of stem hypertrophy (Drew et al., 1979; Tang and Kozlowski, 1984a), hypertrophied lenticels (Tang and Kozlowski, 1982, 1984a,b; Angeles et al., 1986; Topa and McLeod, 1988), aerenchyma (Drew et al., 1979; Hook, 1984b; Jackson et al., 1985; Topa and McLeod, 1988), and adventitious roots (Drew et al., 1979; Tsukahara and Kozlowski, 1985; Voesenek et al., 1996). Consequently, these features should represent reliable surrogates that confirm physiological adaptations in the species and the best morphological indicators of tolerance of prolonged anaerobiosis. Some morphological

---

*Extinct trees of the late Carboniferous swamps (330 million years ago) had platform-like flared bases, rhizophores (a meter in diameter), adventitious roots, and aerating tissue (Ingrouille, 1992).
### TABLE 3.1

**Plant Adaptations or Responses to Flooding and Waterlogging**

**Morphological adaptations/responses**
- Stem hypertrophy
- Buttressed 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 (e.g., water roots)
- Pneumatophores (e.g., cypress knees)
- Swollen, loosely packed root nodules
- Lignification and suberization (thickening) of root
- Soil water roots
- Succulent roots
- Aerial root tips
- Hypertrophied (enlarged) lenticels
- Relatively pervious cambium (in woody species)
- Heterophylly (e.g., submerged vs. emergent leaves on same plant)
- Succulent leaves

**Physiological adaptations/responses**
- Transport of oxygen to roots from lenticels and/or leaves (as often evidenced by oxidized rhizospheres)
- Anaerobic respiration
- Increased production of ethylene and abscisic acid
- Reduction of nitrate to nitrous oxide and nitrogen gas
- Malate production and accumulation
- Control of glycolysis
- Reoxidation of nicotinamide adenine dinucleotide hydride (NADH)
- Synthesis of adenosine triphosphate (ATP)
- Reduction of gibberellins and cytokinins

**Metabolic adaptations**
- Storage of more carbohydrate in roots during preflood period

**Other adaptations/responses**
- Seed germination under water
- Viviparous seeds
- Buoyant seeds
- Hydrochory (seed dispersal by water)
- 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)
- Chlorotic leaves
- Leaf abscission

adaptations like shallow root systems also may be induced by other environmental conditions (e.g., rocky or clayey soils) and may not by themselves be highly reliable wetland indicators.

For wetland identification, morphological adaptations are emphasized over other adaptations, since they may be readily observed, while physiological mechanisms are not because they require laboratory testing or elaborate field assessments beyond the means of most wetland delineators. The following discussion is mostly an overview of morphological adaptations by wetland plants to prolonged flooding and waterlogging, focusing on emergent plants (trees, shrubs, and herbs) and should give readers a better understanding of the validity of using these features as indicators of hydrophytes or of wetland hydrology. It is not an exhaustive review of these plant adaptations; readers wanting more in-depth analysis should consult Mancuso and Shabala (2010), Kozlowski (1984c), Crawford (1983), and Hook and Crawford (1978). For reviews of adaptations of the true aquatic plants found in waters in and contiguous to wetlands, consult Sculthorpe (1967) and Hutchinson (1975). Many wetland plants are halophytic and possess unique adaptations for life in salt-stressed environments (e.g., coastal salt marshes and inland wet saline or alkaline soils); their features are not discussed but are listed in Table 3.2 (see Waisel, 1972; Reimold and Queen, 1974; Albert, 1975; Wainwright, 1984; Tiner, 2013, for more information).

### Hypertrophied Stems Including Buttressed Trunks

Some wetland species growing under extended flooding conditions exhibit a noticeable swelling of the lower stem or possess conspicuous woody tabs or wings (buttresses) where shallow roots join the trunks of trees. For the former, the diameter of the stem from the ground surface to some distance above is greatly expanded. Such swelling increases the surface area and often is coupled with the presence of hypertrophied (enlarged) lenticels that collectively improve gas exchange (Hook et al., 1970). This may also be true for the added surface area created by the buttresses. Stem hypertrophy, especially the soft, spongy aerenchyma, should help eliminate toxins such as ethylene as well as improve root aeration; it is a stress avoidance mechanism (Blake and Reid, 1981).

In herbs, the enlargement of the cortex and collapse of some cells create air-filled spaces (aerenchyma) that lead to an expansion of the stem (Kawase, 1981). Spongy inflated stems have been observed in water willow (*Decodon verticillatus*), water purslanes (*Ludwigia* spp.), and rattlesbush

### Table 3.2

<table>
<thead>
<tr>
<th>Some Plant Adaptations to Salt Stress</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Morphological</strong></td>
</tr>
<tr>
<td>Salt-secretion glands (to eliminate excess salt)</td>
</tr>
<tr>
<td>Succulent stems and leaves (increased water retention to maintain internal salt balance)</td>
</tr>
<tr>
<td>Waxy leaf coatings (to minimize contact with salt water)</td>
</tr>
<tr>
<td>Salt concentration in specialized hairs</td>
</tr>
<tr>
<td>Reduced leaves (to minimize exposure to salt and evapotranspiration)</td>
</tr>
<tr>
<td><strong>Physiological</strong></td>
</tr>
<tr>
<td>Salt exclusion (reduced salt uptake by roots)</td>
</tr>
<tr>
<td>High ion uptake (lowers osmotic potential of cell sap)</td>
</tr>
<tr>
<td>Dilution of salts</td>
</tr>
<tr>
<td>Accumulation of salts in cell vacuoles</td>
</tr>
<tr>
<td><strong>Others</strong></td>
</tr>
<tr>
<td>Stress avoidance (by occupying higher levels of salt marsh or in seepage areas)</td>
</tr>
<tr>
<td>Periodic shedding of salt-saturated organs</td>
</tr>
</tbody>
</table>

Plant Indicators of Wetlands and Their Characteristics

(Sesbania drummondii) (personal observations) (Figure 3.2). In water willow, these spongy stems may aid in buoyancy (Sculthorpe, 1967) as they do in many aquatic plants (e.g., alligatorweed, Alternanthera philoxeroides). An herbaceous vine—climbing hempweed (Mikania scandens)—is well adapted for life in flooded soils due to its ability to produce aerenchyma in both its roots and stems; the latter produced a swollen stem just above the water line in a greenhouse experiment (Moon et al., 1993).

In trees and shrubs, the swelling is not due to aerenchyma (air-filled tissue) but to larger cells and lower density wood (Penfound, 1934; Kawase, 1981; Hook, 1984a). In studying the effect of prolonged waterlogging on seedlings of loblolly pine, McKevlin et al. (1987) found that hypertrophied stems developed after 3 weeks of flooding. Ethylene production during anaerobiosis may be responsible for this formation (Kozlowski, 1982). Good and Patrick (1987) noted basal swelling in green ash seedlings after 1–2 weeks of flooding. Other species possessing these features include red maple (Acer rubrum), white ash (F. americana), pond cypress, water gum (N. aquatica), swamp black gum (N. biflora), and slash pine (Pinus elliottii) (Hook, 1984a; Lewty, 1990). Slight stem hypertrophy was observed in overcup oak (Quercus lyrata) and laurel oak (Q. laurifolia) under waterlogging conditions (Gardiner and Hodges, 1993). Kurz and Demaree (1934) show examples of three types of buttressing in pond cypress (Taxodium ascendens): (1) shallow buttress (of shallow nonalluvial swamps), (2) cone buttress (of shallow lakes and ponds), and (3) bottle buttress (of deeper waters of lakes and ponds). A study of stem form in baldcypresses along a floodplain gradient (compared with others cultivated on upland) suggests that there may be a relationship between the extent of buttressing and inundation history (Varnell, 1998). Other studies reporting stem hypertrophy include Yamamoto et al. (1987) and Gardiner (1994).

From my perspective, when dealing with tree morphology, there should be a distinction made between hypertrophied trunks and buttressing. Hypertrophied trunks should be used to describe

FIGURE 3.2 Hypertrophied stems in herbaceous plants: (a) rattlebush (Sesbania drummondii), note swollen stem on specimen rooted in the pond mud and compare with an upland individual [on left] having a taproot and lacking stem hypertrophy; and (b) water-willow (Decodon verticillatus). Note that in both species the hypertrophied stems are composed of soft, spongy tissue.
trunks with an exaggerated swelling at their bases (Figure 3.3a,b), whereas buttressing should be used to describe such trunks that are flared where woody tabs or triangular platelike wings radiate from the base of the trunk connecting the trunk to the roots (Figure 3.3c through f). The latter have been referred to as “lateral flanges joining the roots and the trunk” (Clair et al., 2003). They may form on one side of the tree or around the entire tree. Woodcock et al. (2000) found as many as 20 buttresses evenly spaced around trees of *Elaeocarpus angustifolius* in Hawaii. *Fluted trunks*
are something in between buttressed trunks and hypertrophied trunks with the circumference of
the hypertrophied stem being characterized by a series of semicircular, shallow ridges that appear
flutelike in cross section. This feature is common in baldcypress (Figure 3.3c).

The earliest swamp trees on Earth (e.g., from the late Carboniferous period, 330 million years
ago) exhibited buttressed trunks (e.g., platform-like flared bases), as an adaptation for growing in

FIGURE 3.3 (Continued) Compared to buttressed trunks in (e) baldcypress, (f) laurel oak (Quercus lauri-
folia), (g) black gum (Nyssa sylvatica), and (h) overcup oak (Q. lyrata). Trunks of baldcypress can be hyper-
trophied and/or buttressed (c vs. e).
mud and other unstable substrates subject to fluctuating water levels (Darrah, 1960; Kangas, 1990; Ingrouille, 1992). While this is also the function of buttresses in contemporary wetland trees, these features stabilize shallow-rooted trees in tropical forests (e.g., Jenik, 1978; Lewis, 1988). Buttressing can be found in wetland and dryland species (e.g., Ruslandi et al., 2015). It has been suggested that buttressing is almost exclusively tropical and is found in 12%–35% of tropical tree species (ter Steege et al., 1997; Chapman et al., 1998, as reported in Woodcock et al., 2000). Ennos (1993) and Chapman et al. (1998) discussed the function and formation of buttresses. Trees appear to produce more wood in areas of mechanical stress; forces acting to topple the tree exert pressure and stress on the junction between the trunk and the lateral roots promoting the formation of a buttress (Mattheck, 1991; Ennos 1993; Mattheck et al., 1997). Buttress size increases with size and age of the tree. While buttressing is common in tropical trees, there is considerable variability in the extent of buttressing within species (i.e., some individuals may have buttresses while others do not). In a study of 29 tree species in a Uganda moist evergreen forest, Chapman et al. (1998) found that while nine species had some form of buttress, only two species typically had buttresses (Olea welwitschii, Oleaceae; Celtis durandii, Ulmaceae). They concluded that their findings support the notion that “buttresses are mechanical adaptations to counter episodic asymmetric loads, and that buttresses persist after the need for a mechanical support has disappeared” (p. 341).

Many trees exhibit what might be interpreted as buttressed trunks where the roots meet the base of the tree. However, in some temperate wetland trees, these buttresses extend higher up on the trunk and may be more conspicuously narrow in width (Figure 3.3d), whereas in dryland trees these buttresses are shallow and wider. Elongation and thinning of the buttresses also may create more surface for production of hypertrophied lenticels during periods of prolonged flooding. American elm (Ulmus americana), sugarberry (Celtis laevigata), red maple, green ash, and oaks in general, especially pin oak (Quercus palustris), cherrybark oak (Q. falcata var. pagodifolia), and overcup oak, naturally have buttressed trunks, but buttressing is more exaggerated under periodically flooded conditions (personal observations of the author and Donald Leopold).

Hollow and Adaptable Stems

Many wetland herbs possess hollow or chambered stems that favor growth in wetlands. Such stems are typical of grasses and also are present in many rushes and sedges (Crawford, 1983). Hollow or chambered stems may improve aeration to the roots as well as accumulate carbon dioxide important for photosynthesis (Billings and Godfrey, 1967, as reported by Crawford, 1983). The dead stalks of common reed (Phragmites australis) provide a means of ventilation for submerged roots—wind blowing across the broken stems creates a pressure differential that brings air to the flooded roots via Venturi convection (Colmer, 2003; Crawford, 2003). This process also facilitates oxidation of the rhizosphere (Armstrong et al., 1992). Increased photosynthetic activity will produce a corresponding increase in oxygen available for diffusion to the roots. The presence of hollow stems in graminoids might help explain why they are often dominant in wetlands. Hollow stems clearly facilitate gas movement. For example, air can also enter through leaf sheath stomata and flow down to the roots and out through a dead broken stem. This has been reported in common reed, spatterdock, and other aquatic and emergent plants (Colmer, 2003). Some graminoids like rushes (Juncus effusus and J. conglomeratus) have green tissue in their basal shoots through winter that ensures a supply of oxygen to their roots (Crawford, 2003). Wetland herbs may be able to survive inundation by having fast-growing stems. For example, maidencane (Panicum hemitomon) and southern cutgrass (Leersia hexandra) can extend their stems through 3.3 ft/1 m of water, thereby maintaining shoot and root aeration (Kirkman and Sharitz, 1993).

Buttercups (Ranunculus spp.) are known to produce stem tissue of different strengths in varied habitats. Those growing in aquatic habitats have more flexible stems (less strengthening tissue) than buttercups growing on land (Usherwood et al., 1997).
Plant Indicators of Wetlands and Their Characteristics

Shallow Root Systems

High water tables and accompanying anaerobic conditions significantly influence root growth. With few exceptions, plant roots do not grow in anoxic soils or substrates, although once established, the roots can survive such conditions for days or months depending on the species and whether the root is woody or not (Crawford, 1982). Since oxygen is the prime limiting factor in wetlands, the anaerobic environment essentially forces plants to seek oxygen near the surface and thereby also avoid phytotoxins present in the subsoil.* As a result, plant roots for most wetland species grow horizontally (diageotropic) or upwardly (negatively geotropic) to form extensive root systems near the surface.

The development of shallow roots is perhaps the most widespread morphological adaptation among wetland species. This is relatively easy for herbaceous plants since many tend to be shallow rooted at least in moist or humid climates; drought-tolerant species have much deeper roots for obvious reasons. Sweet flag (*Acorus calamus*) and yellow flag (*Iris pseudacorus*) grow in marshes that are flooded for months, especially in winter; their rhizomes (located as the water–soil interface) can survive anoxic conditions for up to 70 and 60 days, respectively (Schlüter and Crawford, 2001). A salt marsh plant, English cordgrass (*Spartina anglica*), can survive anoxia for more than 28 days (Crawford, 1989). On the other hand, trees grow much taller and need support for such growth, so life in anaerobic conditions is quite challenging. Wetland trees typically develop a dense system of shallow lateral roots that can help stabilize them in wet soils, but it also makes them more susceptible to windthrows than upland trees that are better anchored in the soil by deeper roots (Figure 3.4). Some plant species are typically shallow rooted wherever they grow, while others have adaptable root systems. Both responses favor establishment in wetlands. Mangroves dominate many tropical wetlands and they owe their predominance, in part, to their ability to grow in wet, often saline, soils. Their shallow root systems plus specialized roots (knees and pneumatophores; see following subsection) make this possible. In some species (e.g., cannonball mangrove, *Xylocarpus granatum*; looking-glass mangrove, *Heritiera littoralis*), the shallow roots (*plank roots*) extend aboveground and appear ribbonlike and extend far from the trunk in a curving pattern; they are part of the buttress structure (Figure 3.5; Lovelock, 1993; Duke, 2006). In tropical rainforests, plank roots can be taller than a person and may aid in nutrient cycling as the soils tend to be poor in nutrients. American elm growing in wet southern U.S. swamps may exhibit roots resembling plank roots (although clearly not as tall; Figure 3.3). Swamp black gum and American holly (*Ilex opaca*) also can produce a dense system of shallow exposed roots in these types of swamps (Figure 3.4). Eastern hemlock (*Tsuga canadensis*) is an example of a shallow-rooted species (Fowells, 1965) that occurs mostly on upland but has successfully colonized temperate wetlands due in part to a shallow root system (Niering, 1953; Huenneke, 1982; Tiner, 1989, 1998). Consequently, it can grow equally well on organic soils that are saturated year-round and better drained shallow soils and rocky soils. In contrast, red maple 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 (Kramer, 1949). This ability may be responsible for red maple’s even distribution in both wetlands and nonwetlands. Sweet gum (*Liquidambar styraciflua*) also has this capability (Kormanik, 1990). Development of shallow root systems may be an individual plant’s response to a wet environment or a species trait. In the former, timing of germination and the environmental conditions that follow may be crucial to the development of this adaptation. Another dominant wetland tree that occurs equally in both wetland and upland, loblolly pine (*P. taeda*), also has an adaptable root system (Baker and Langdon, 1990). Development of its roots is strongly influenced by the soil environment and probably aids the species in growing in variable soils from wet organic soils to heavy clays to dry sands (Schultz, 1997). This pine initially

---

* In marine, estuarine, and inland saline wetland ecosystems, salinity is also a major plant stressor; the combined effect of anaerobiosis and salinity restrict plant growth and distribution (Tiner, 2013).
forms a short taproot that typically stops growing to channel energy to build an extensive lateral root system, hence its dominance of flatwoods along the Atlantic coastal plain. However, in deep sandy or loamy soils, it forms a deep taproot (to 6.5 ft; Baker and Langdon, 1990). Even plants

![Shallow roots](image1)

**FIGURE 3.4** Shallow roots above the surface were observed in a Virginia swamp in swamp black gum and American holly (a); windthrow of swamp white oak (*Quercus bicolor*) in Massachusetts (b).

* Examination of loblolly pine roots in a 31-year-old natural stand in North Carolina found that the majority of the feeder roots less than 0.1 in. in diameter were located in the A-horizon (6 in. deep) and virtually no lateral roots occurred below 6–21 in. deep (reported in Baker and Langdon, 1990).
characteristic of dry sites can develop shallow root systems when the seeds germinate in wetlands. In the New Jersey Pine Barrens, scrub oak (*Quercus ilicifolia*), a typical dry-site species with deep penetrating roots, grows occasionally in wetlands (with seasonal water tables within 1–2 ft/30–60 cm) where it develops a shallow root system within 6–8 in. (15–20 cm) of the surface (Laycock, 1967). Shallow roots also can form for other reasons, for example, impenetrable rocky substrates or dense clayey soils. So when considering this feature as a wetland adaptation, existing environmental conditions need to be assessed.

Tussock sedge (*Carex stricta*) has two sets of roots: deep roots below its tussock and one root at the top of the tussock. When the plant is flooded, the upper root performs typical functions of water and nutrient uptake (Costello, 1936). This adaptation allows the plant to overcome anaerobiosis during periods of extended inundation or soil saturation.

A tropical tree fern (*Cyathea sternbergii*) is abundant on poorly drained floodplain soils in Brazil’s wetlands (Guilherme et al., 2012). It reportedly produces stolons (e.g., horizontal shoots that produce roots at their nodes) that favor vegetative reproduction (cloning)—a feature that may explain its clustered spatial distribution. Moreover, such adaptation may enhance its ability to colonize poorly drained soils.

While most wetland plants develop shallow roots, some species can produce fairly deep roots, sending their roots 8–20 in. (20–50 cm) below the water table (e.g., *Typha latifolia*, *Sagittaria latifolia*, *Scirpus validus*, and *Eriophorum*) (Emerson, 1921). For other wetland plants, deeper root penetration may occur during dry periods or when soils are otherwise less reduced, allowing the plant to tap nutrients from the subsoil. Once in this zone, metabolic mechanisms and accompanying anatomical structures (e.g., aerenchyma) permit survival when strongly reducing conditions resume. Fisher and Stone (1990) found that tap and sinker roots of slash pine (*P. elliottii*) could withstand weeks or months of saturated, anoxic soils and reported that such roots may penetrate about 3 ft into the seasonal low water table. Roots of sheep laurel (*Kalmia angustifolia*) may penetrate more than 1 ft into the water table in New Jersey’s pitch pine lowlands (Laycock, 1967).
This portion of the roots had much aerenchyma as evidenced by their lightweight and corky texture (after drying).

**Pneumatophores**

A few tree species develop pneumatophores on their roots (Figure 3.6). Among the most well known of these structures are the *knees* of baldcypress. Knees form in areas subjected to prolonged inundation; cypress trees cultivated in upland parks do not produce them. The taller the knees, the higher the water level. Knees may grow as tall as 10 ft high and in numbers reaching 100 for a single tree (Wilson, 1889). Cypress knees form along the upper roots where increased aeration stimulates cambium activity (Kramer and Kozlowski, 1979). A number of theories have been proposed in an attempt to explain their function, including aeration, nutrient storage, methane emission, mechanical support, and carbohydrate storage, but their function still remains unknown (Briand, 2000).* Since tree roots typically extend well beyond the canopy, cypress knees may occur

---

* In my observations, the knees appear to form in only areas subject to inundation and not in neighboring saturated or better drained soils—a response to inundation with an undetermined function.

---

**FIGURE 3.6** Pneumatophores: (a) baldcypress knees, (b) black mangrove (*Avicennia germinans*) covering the ground, (c) black mangrove (close-up). Hypertrophied lenticels are evident on the black mangrove (c).
at considerable distance from the trunk of an individual tree.* A few other trees have knees: pond pine (in Georgia; Wilson, 1889) and tropical mangroves including orange mangroves (Bruguiera), black mangroves (Lumnitzera), and yellow mangroves (Ceriops) (Lovelock, 1993; Duke, 2006).

Other woody plants with pencilike or peg-like pneumatophores include black mangrove, white mangrove, and many other tropical mangroves (e.g., mangrove apples or apple mangroves, Sonneratia spp.; grey mangrove, Avicennia marina; and cedar mangrove, Xylocarpus moluccensis; Lovelock, 1993; Duke, 2006). Those of the black mangrove (Avicennia germinans) are pencilike projections that extend from the soil up to a foot (30 cm) high, while those of some other tropical mangroves (e.g., Sonneratia) may grow much taller (Dahdouh-Guebas et al., 2007). These pneumatophores, covered with hypertrophied lenticels, help improve aeration within the plant, allowing this mangrove to colonize anoxic soils. Scholander et al. (1955) demonstrated this for both the red mangrove (Rhizophora mangle) and black mangrove (A. germinans). Longman and Jenik (1974) described a variety of these pneumorhizae structures found in tropical trees, including lateral knee roots, serial knee roots, root knees, peg roots, stilted peg roots, and pneumathodes (reported in Lugo et al., 1990). Densities of peg (pencilike) roots can be very high—one study of grey mangrove (A. marina) in Kenya reported 2500 pneumatophores per square meter (Dahdouh-Guebas et al., 2007).

**Looping Roots**

Resembling knees, a few trees produce _looping roots_ in wetlands. The roots form where the root rises above the ground surface then loops downward into the soil. Among the species that do this are baldcypress, water tupelo, red maple, and some mangroves (Briand, 2000; Figure 3.7).

**Water Roots**

Floating aquatic plants have their primary roots in the water column to absorb water and nutrients. These roots can be considered _water roots_ since they occur in the water column. Plants exhibiting these roots include duckweeds (Spirodela and Lemna), water hyacinth (Eichhornia crassipes), Canadian waterweed (Elodea canadensis), mosquito fern (Azolla caroliniana), alligatorweed (A. philoxeroides), American frog-bit (Limnobium spongia), water purslane (Ludwigia palustris), and water pennywort (Hydrocotyle ranunculoides). Many of these species form dense beds or floating mats in shallow water. For self-supporting plants (emergents, shrubs, and trees), another type of _water roots_ may form in the water column when the plant is flooded; these are adventitious roots.

**Adventitious Roots**

Adventitious roots are roots that form from branches or stems, usually aboveground.† They are common in many tropical/subtropical species in both wetland and nonwetland situations (rainforests)‡ as well as on certain wetland species in temperate and boreal climates. Extended inundation causes some plants to develop adventitious roots (_water roots_) at or just below the water line (close to the air–water interface) where water and oxygen are available; when the water levels decline, these roots appear above the ground surface (Figure 3.8). Water roots usually form as the original root system dies back due to anoxia and the new roots are needed to aid in survival and recovery (Jackson and Drew, 1984). The presence of aerenchyma in these roots makes them more porous than normal roots (Kozlowski, 1982). These roots replace the function of the lost roots in absorbing water and nutrients, vital for plant functions, and are positively correlated with the degree of flood tolerance within certain genera (Kozlowski, 1984a; Islam and Macdonald, 2004). Herbs, like common reed, water purslanes (Ludwigia spp.), purple loosestrife (Lythrum salicaria), docks (Rumex spp.), corn

---

* On a recent trip, I observed knees about twice the distance of the canopy from a baldcypress along a pond margin at the New Orleans Botanical Garden.
† Plants with underground stems (tubers, bulbs, and corms) produce adventitious roots below ground.
‡ Figs (Ficus spp.) are particularly noteworthy for producing these features, with the banyan tree (Ficus benghalensis) being the most well-known example.
Wetland Indicators

(Zea mays), sunflower (Helianthus annuus), rice (Oryza sativa), and tomato (Lycopersicon esculentum), typically display this adaptation when subjected to these conditions. Adventitious roots in corn seemed important in allowing it to survive flooding for up to 13 days (Wenkert et al., 1981). Van der Sman et al. (1988) found that within 5 days of waterlogging, adventitious roots began growing in golden dock (R. maritimus), while Wenkert et al. (1981) found that such roots developed in corn within 4 days (Smolders et al., 1990). After these roots formed, the plants recovered their relative growth and transpiration rates. Rich et al. (2012) observed water roots in many wetland

FIGURE 3.7 Looping root in baldcypress (a) and water tupelo (b).
herbs in southwestern Australia and conducted experiments on two species (*Cotula coronopifolia* and *Meionectes brownii*). After 28 days of partial or full submergence, both species produced >100 water roots (“aquatic roots”).

Some woody plants also have the ability to produce adventitious roots. In areas subject to permanent or prolonged inundation, water roots form in the water column—willows are well noted for their...
ability to do this (Figure 3.8). After an English fen was flooded for nearly an entire year, Compton (1916) noted and took pictures of massive adventitious roots in white and crack willows (Salix alba and S. fragilis). Basket willow or common osier (Salix viminalis) develops adventitious roots that help aerate the upper soil when inundated, while the deeper roots simply tolerate the anaerobic conditions (Jackson and Attwood, 1996). In studying 18-month-old seedling response of black spruce (Picea mariana) and tamarack (Larix laricina) to flooding, Islam and Macdonald (2004) found that after 16 days, tamarack began to develop adventitious roots while the spruce did not; the latter’s needles also showed signs of chlorosis and necrosis, while tamarack did not. Bergman (1920) described the formation of adventitious roots in swamp plants. Gill (1970, 1975) reported the formation of adventitious roots in several species—buttonbush (Cephalanthus occidentalis), false indigo-bush (Amorpha fruticosa), European alder (Alnus glutinosa), red alder (A. rubra), lodgepole pine (Pinus contorta), Sitka spruce (Picea sitchensis), western hemlock (Tsuga heterophylla), white ash, green ash, black willow (Salix nigra), crack willow, Hooker willow (S. hookeriana), white willow, tulip poplar (L. tulipifera), eastern cottonwood, black cottonwood (Populus trichocarpa), redwood (Sequoia sempervirens), baldcypress, and American elm. Hook (1984a) also found adventitious roots in water gum, swamp black gum, western red cedar (Thuja plicata), black poplar (P. nigra), and paperbark (Melaleuca quinquenervia). In swamp black gum, adventitious roots may be stimulated by flowing water, but not by stagnant water (Hook, 1984a). Hook speculated that such roots also may serve to trap debris and soil from floodwaters and thereby promote the formation of a hummock around the base of the trunk.

The ability to produce adventitious roots may be critical for survival of long-term flooding as reported for baldcypress (Pezeshki, 1991). Topa and McLeod (1986b) observed an abundance of adventitious roots in wet-site loblolly and pond pine (P. serotina) seedlings subjected to 30 days of anaerobic conditions. In examining the ecological significance of adventitious rooting in European alder, Gill (1975) found that such roots can be produced within 2–5 days after budburst (depending on temperature) in flooded plants, but they do not form during the dormant season. Also experimentally, he found that even when only the lower stem was flooded (and not the roots), this alder produced some adventitious roots, yet not as many as when the roots were saturated as well.

Evergreen conifers that grow in northern or high-elevation bogs (saturated soils) have the ability to develop adventitious roots from their branches and lower stem (just above the root crown). This layering ability has long been considered a form of vegetative propagation (Fuller, 1913). Among the many evergreens displaying this ability are Norway spruce (Picea abies), Engelmann spruce (Picea engelmannii), black spruce (P. mariana), alpine fir (Abies lasiocarpa), balsam fir (Abies balsamea), Canada yew (Taxus canadensis), and eastern hemlock (T. canadensis) (Schweingruber, 2007). In bogs, roots easily grow from lower branches of black spruce. As a large black spruce sinks in the wet organic soil, when the lower branches contact peat mosses, apical growth accelerates and the tips of the branches point upward, later becoming a ring of small trees around the parent tree that often dies due to anaerobic conditions from saturation.

Prop roots are a type of adventitious root that provides more support for the plant in unstable soils.* They also promote vertical accretion in mangrove swamps through sediment trapping, which is vital for the survival of these swamps given accelerating sea-level rise (Krauss et al., 2003). In the United States, the best examples of these are found in the red mangrove (R. mangle; Figure 3.9). The roots grow downward from branches and the trunk. Multiple layers of these prop roots (rhizophores) provide a network of structural support that allows these shallow-rooted mangroves to dominate the canopy of saltwater swamps (Méndez-Alonzo et al., 2015). In addition, these rhizophores are filled with aerenchyma and covered with hypertrophied lenticels allowing necessary gas exchange for red mangrove’s colonization of and growth in anaerobic soils. Other tropical mangroves developing prop roots include stilt mangroves (e.g., Rhizophora apiculata, R. mucronata, and R. stylosa), grey mangrove (Avicennia marina), and holly mangrove (A. ilicifolius) (Lovelock, 1993).

*There is some disagreement whether these prop roots are stems that bear adventitious roots or roots in their entirety (see De Menezes, 2006 for discussion).
Soil Water Roots

Prolonged flooding often causes the primary root system of plants to die back and some plants develop a secondary set of roots below ground (soil water roots) that aid in oxidizing the rhizosphere. Based on studies of dock species (*Rumex*), Blom (1990) described three root responses to these conditions: (1) an increase in root branching, (2) the formation of adventitious roots, and (3) an altered vertical distribution of lateral roots, with more roots concentrated in the upper layers of soil. In studies of dock species, primary root growth ceased when anaerobic conditions developed in the flooded soil medium, and new lateral roots began forming after 125–200 h of submergence (Laan et al., 1991a). These roots were unbranched and thicker (twice as wide in *R. maritimus*) than the typical roots. The latter was due to the formation of aerenchyma (see discussion that follows). After 2 weeks of flooding, curly dock (*R. crispus*) and golden dock (*R. maritimus*) produced about 16 and 24 m of new lateral roots, thereby replacing 32% and 23% of their original root length, respectively (Laan et al., 1989). During this same study period, clustered dock (*R. conglomeratus*) generated 43 m of new roots—a 44% replacement of its original root system (Laan et al., 1989). Voesenek et al. (1989) described two types of roots forming on the upper part of the taproot of flooded *Rumex*: (1) strongly branched, thin, superficially growing roots and (2) thick, white, poorly branched roots that penetrated into the waterlogged soils. The former roots exhibited diageotropism (a tendency for horizontal growth) that allowed them to take advantage of oxygen present in the air–water interface.

Soil water roots have been reported for baldcypress and swamp black gum (Harms et al., 1980). Flood tolerance in woody species may be attributed in part to this ability as stomatal reopening has been correlated with production of adventitious roots (Hook and Brown, 1973; Sena Gomes and Kozlowski, 1980; Kozlowski, 1982). These roots differ from typical roots by being more fleshy, almost clear, and relatively unbranched. Armstrong and Boatman (1967) described superficial rooting in bog plants.

Aerenchyma

The presence of aerenchyma (air-filled) tissue and lacunae in many wetland herbs, especially marsh plants, helps these plants grow in anaerobic or anoxic soils (Figure 3.10). An internal system of large air spaces is needed to transport atmospheric oxygen to the roots, thereby creating an oxidized environment around the roots (oxidized rhizosphere). This reduces resistance to oxygen movement for respiring cells, decreases the amount of respiring tissue, facilitates diffusion of oxygen-containing...
air to organs lacking oxygen, and still provides sufficient structural support (DeLaune and Pezeshki, 1991; Voesenek and van der Veen, 1994). It also aids in releasing carbon dioxide and methane to the atmosphere (Wetzel, 1990). If the link to the atmosphere provided by this internal aeration system is eliminated, anoxic conditions quickly result in plant death as demonstrated in cattails (Typha spp.) by Sale and Wetzel (1983). Aerenchyma tissue occurs in aquatic, wetland, and nonwetland plants. Jung et al. (2008) studied this tissue in 110 species and found this tissue to be more developed in aquatic plants than in wetland species, with patterns stable at the genus level and more consistent in roots than in shoots. In roots, aerenchyma tissue increases with age, so this tissue forms at a short
distance from the root tip, for example, around 1.6 in./4 cm in *Spartina alterniflora* and *S. anglica* (Maricle and Lee, 2002; Reddy and DeLaune, 2008).

Differences in flood tolerances may be caused by differences in internal aeration and the use of aerial and photosynthetic oxygen in root respiration (Blom, 1990). Flood-intolerant *Rumex* plants did not exhibit any internal aeration, whereas flood-tolerant plants did and showed oxygen loss around their roots (Laan et al., 1989). Diffusion of aerial oxygen to roots through aerenchyma tissue accounted for 40%–50% of root respiration in curly dock and golden dock (Blom, 1990).

Some studies of *Carex* species provide some interesting results. In examining several species of *Carex* from different habitats (nonflooded soil to stagnant flooded soil), Visser et al. (2000) found that all tested species increased aerenchyma in roots when grown in anaerobic ajar. They surmised that this response plus an increase in root diameter improved internal aeration of roots. Submergence and partial flooding produced varied effects among the species—those with less aerenchyma performed poorly when flooded, while partial submergence even affected species with a considerable amount of root aerenchyma. Moog (2007) studied root anatomy response of three species (flood intolerant to flood tolerant) to both aerobic and anaerobic conditions. *Carex pseudocyperus* from permanently flooded sites developed the same root anatomy under either scenario as did *C. extensa* (flood intolerant); it developed a typical *Carex* root pattern. However, *C. remota* (from periodically flooded sites) varied its structure with changed conditions. Average root porosities were >20% for the flood-tolerant species.

Smirnoff and Crawford (1983) reported that 10% root porosity was the dividing line between flood-tolerant and flood-intolerant species. Justin and Armstrong (1987) stated that most nonwetland plants have porosities less than 7% but noted that some wetland species do not produce aerenchyma.

A study of the effect of flooding on aerenchyma formation in a wetland vine (*M. scandens*) produced some interesting findings. After individuals of this species were subjected to flooded (0.8–1.2 in./2–3 cm of water) or drained (watered as needed) conditions for 6 weeks, Moon et al. (1993) found that individuals (regardless of initial size) from the flooded group have three times the amount of aerenchyma in their roots than those from the drained group (Figure 3.10). After the first week of the experiment, all flooded individuals had larger stem diameters (hypertrophied stems). At the end of the study, small individuals (<1.6 in./4 cm at the start of the study) showed a 2.5× increase in stem height compared to drained group. The flooded plants also developed new stomata on their stems while the drained ones did not; this may further facilitate aeration in anaerobic soils. Climbing hempweed showed evidence of multiple morphological adaptations to flooding.

Aerenchyma also promotes root extension into anaerobic soils in some species like rice (Armstrong, 1979). Studies of slash pine (*P. elliottii*), perhaps the wettest of the southern pines, found that it extends its roots into the anaerobic zone of waterlogged soils (as much as 3 ft or more below the seasonal low water table) (Schultz, 1972, 1973). This pine can withstand inundation for several months or a few years because its woody root tissue is aerenchymous—with 48%–69% air content versus about 15%–22% in its stemwood (Fisher and Stone, 1990). This tissue likely provides a reservoir of oxygen that permits gas exchange between the atmosphere and the oxygen-depleted root tissues.

Root porosity may differ between flood-tolerant and flood-intolerant species of the same genus. *Rumex maritimus* (flood tolerant) had a root porosity of 20% compared with 8% in *R. thrysiflora* (flood intolerant) (Laan et al., 1991b). This has a positive effect on internal aeration.

Many studies have demonstrated an increase in aerenchyma in plants subjected to flooding and to stronger anaerobiosis (Seliskar, 1988; Burdick and Mendelsohn, 1990; Moon et al., 1993; Kludze and DeLaune, 1994, 1996; Kludze et al., 1994; Pezeshki et al., 1998; Striker et al., 2008). This is a common and expected response of wet-tolerant species. It is not certain whether the formation of aerenchyma is induced by oxygen deficiency or by accumulation of anaerobiosis-caused phytotoxins and gaseous decomposition products (Klundze and DeLaune, 1996). In some species, increased ethylene production during anaerobiosis enhances aerenchyma development (Drew et al., 1979). Aerenchyma development may be genetically controlled by some species. Rice, wild rice (*Zizania aquatica*), docks, black willow, and baldeyypress grown in well-oxygened environments formed aerenchyma in their roots (Jackson and Drew, 1984; Laan et al., 1989; Kludze et al., 1994; Pezeshki et al., 1998).
Aerenchyma formation takes weeks or months to completely modify root anatomy (Das and Jat, 1977; Keeley and Franz, 1979; Burdick, 1989; Evans 2004). The process begins soon after flooding, for example, Folzer et al. (2006) found clear evidence of intercellular space—the initiation of aerenchyma formation—in the roots of sessile oak (Q. petraea) seedlings after just 7 days of flooding. Aerenchyma tissue is formed from either cell water separation and collapse (lysigeny) or by cell separation without collapse (schizogeny) (Laan et al., 1989). Even with as much as 50% of the internal tissue being aerenchyma, salt hay grass (Spartina patens) was unable to provide enough oxygen to the roots for complete aerobic respiration to occur under long-term waterlogging (Burdick and Mendelsohn, 1990). If the roots do not receive an adequate supply of oxygen to maintain aerobic respiration, then they will switch to an anaerobic pathway (Pezeshki, 1991). It appears that both anatomical and metabolic responses are important for plant survival. It must be realized, however, that not all wetland plants produce aerenchyma (Smirnoff and Crawford, 1983).

Spatterdock (Nuphar luteum) has an interesting internal gas transport system. Dacey (1981) found a pressurized flow system where air enters young emergent leaves then moves by diffusion through lacunae to the roots, while older leaves serve to release pressure, thereby moving carbon dioxide and methane from the plant to the atmosphere (Figure 3.11—“thermo-osmosis”). About 60% of the elongate leaf stalks and up to 40% of the roots and rhizome are filled with air spaces (Dacey, 1979). Coutts and Philipson (1978a,b) found more aerenchyma tissue in the roots of lodgepole pines grown in waterlogged soil than in the roots from ones grown in freely drained soils. Sand-Jensen et al. (1982) found that water lobelia (Lobelia dortmanna) had about 50% of its leaves and stems represented by lacunae and a continuous lacunae connection from the leaves to the roots. They believed that this probably led to its high oxygen release from its roots during illumination (more than two times that of the other aquatics, which included Potamogeton and Sparganium). The authors speculated that the function of these anatomical adaptations was to bring in carbon dioxide rather than release oxygen to the anoxic soil. Root porosities in cuttings of black willow varied with experimental treatment, beginning at 33% (control), increasing to 37%–39% with partial flooding, and decreasing to 29% with continuous flooding over a 28-day period (Li et al., 2006). The lower porosities in continuously flooded cuttings may have been caused, in part, by a number of factors including relatively high temperatures used in the experiment and more oxygen stress on internal root conditions leading to a failure to stimulate aerenchyma.

![Figure 3.11](image-url)
Hypertrophied Lenticels

Lenticels are the external organs in woody plants that permit gas exchange between the internal parts of the plant and the atmosphere. When flooded, some trees and shrubs develop expanded or enlarged lenticels (with large intercellular spaces) below the water level to a point just above the water line or on exposed roots (Figure 3.12). These hypertrophied lenticels form in a relatively short time from 5 to 10 days after flooding (Kozlowski, 1984a; Good and Patrick, 1987; Folzer et al., 2006). These organs increase the surface area available for gas exchange, enhance internal aeration, and allow the plant to keep functioning while subjected to anaerobiosis (Gill, 1970; Hook,

![Hypertrophied lenticels](image-url)
1984a; Jackson and Drew, 1984; Tsukahara and Kozlowski, 1985; DeLaune and Pezeshki, 1991). Lenticles are the major entry point for oxygen diffusion to the rhizosphere in some woody plants (Armstrong, 1968; Hook et al., 1970, 1971). In some species, hypertrophied lenticels also provide an exit for releasing toxins produced by anaerobiosis (e.g., ethanol, acetaldehyde, and ethylene) (Kozlowski, 1984a).

In studying conifer root morphology in relation to soil moisture and aeration, Hahn et al. (1920) found that 17 species developed hypertrophied lenticels when grown in saturated soils. These species included red spruce (Picea rubens), jack pine (Pinus banksiana), western white pine (P. monticola), ponderosa pine (P. ponderosa), red pine (P. resinosa), pitch pine (P. rigida), eastern white pine (P. strobus), and eastern hemlock (T. canadensis). An abundance of hypertrophied lenticels formed in pine seedlings after 3 weeks of flooding (Topa and McLeod, 1986b; McKevlin et al., 1987; Figure 3.13). Other species exhibiting these adaptations were green ash, black willow, cottonwood, American elm, swamp black gum, bur oak (Quercus macrocarpa), and sycamore (Platanus occidentalis) (several sources as reported in Kozlowski, 1984a; Hook et al., 1970). Black willow cuttings experimentally grown under continuous inundation for 3 months (late February–May) developed hypertrophied lenticels as well as water roots (in the water column) and aerenchyma in roots (over 30% air space) (Pezeshki et al., 1998); similar findings had been reported by Donovan et al. (1988). Under both waterlogged and flooded conditions, cuttings of Virginia sweetspire (I. virginica) produced more hypertrophied lenticels than seedlings, while seedlings produced more adventitious roots that were more abundant in waterlogged seedlings than in flooded ones (Anderson et al., 2009). The ability of mango (Mangifera indica), a moderately flood-tolerant species, to survive prolonged inundation has been largely attributed to the production of hypertrophied lenticels above the water line (Schaffer 1998). Mango trees with lenticels that hypertrophied within 4–10 days survived flooding, while trees without lenticel hypertrophy died (Larson et al., 1991, 1993).

**Oxidized Rhizospheres**

While not a morphological property of the plant, an oxidized soil layer around living roots is a feature that can be recognized during wetland delineation (see Figure 2.58a) and is positive evidence of plant growth under anaerobic conditions. In order to survive such conditions, some plants release oxygen from their roots to the surrounding reduced, anaerobic soils. This radial oxygen loss (ROL) is believed to be important to detoxify this environment by oxidizing otherwise harmful reduced forms of iron and manganese plus hydrogen sulfide and to increase nutrient uptake (Armstrong, 1979). It may also promote mycorrhizae establishment important for nutrient uptake, whereas anaerobic conditions typically inhibit them (Hook, 1984a). Mendelssohn (1993) provided a literature review and annotated bibliography of oxidized root channel formation, while Neubauer et al. (2008) described the role of microbes in the oxidation and reduction of iron in the root zone.

Oxidation of the rhizosphere may be the most important mechanism in many plants adapting to an anaerobic environment, since it allows aerobic root respiration that is vital for nutrient uptake and other processes. Leakage of oxygen from roots (root ROL) occurs when more oxygen is supplied than required for root respiration, thereby forming oxidized rhizospheres (Figure 3.14). This zone further aids the plant in oxidizing toxic materials (e.g., fermented organic compounds and hydrogen sulfide) and facilitates the nitrification–denitrification process (oxidizing ammonium to nitrate), which is a vital wetland function. Sand-Jensen et al. (1982) suggest that a shifting zone may occur in the root–soil interface, where aerobic processes dominate by day (due to active oxidation of the rhizosphere) and anaerobic processes by night (no oxidation). This might favor oxygen consumption, mineralization, and nitrification–denitrification rates. Similarly, in coastal marshes, the alternating tides also create oscillating soil conditions, with hightide boosting soil anaerobiosis (highly reduced environment) and low-tide increasing soil aeration (oxidized condition). This fluctuation promotes plant survivability by allowing time to recover from oxygen deficiency (Pezeshki and DeLaune, 1996). In addition, oxygen diffusion to the roots of some salt marsh plants promotes
the oxidation of sulfides in the rhizosphere, which is considered a major factor contributing to high sulfide tolerance (Teal and Kanwisher, 1966). This has significant implications on plant distribution and productivity (DeLaune and Pezeshki, 1991).

Oxidized pore linings, root channels, or rhizospheres (Figure 3.14) develop when oxygen comes in contact with reduced iron (ferrous iron, Fe$^{2+}$), thereby precipitating iron oxide (ferric iron, Fe$^{3+}$) in the form of iron oxyhydroxide (FeOOH) coatings, also called iron plaque, and increasing the redox potential. These linings may develop in 4–8 weeks of ponding or saturation as observed in
Texas by Griffin et al. (1996). In rice fields, oxidized rhizospheres were observed after just 7 days of flooding (Chen et al., 1980). Mendelssohn (1993) and Mendelssohn et al. (1995) reviewed factors controlling their formation. These factors include low redox potential, pH, organic matter, and texture (mineral fines), plus the amount of available iron in the soil. The presence of aerenchyma tissue in roots facilitates the formation of oxidized rhizospheres. The buildup of iron plaque is not always related to the amount of ROL from roots (Mendelssohn, 1993). For example, Laan et al. (1989) found that the species with the least ROL had the most iron plaque among three species of dock studied.

Most, if not all, aquatic species and marsh herbs are capable of moving oxygen to their roots (Bartlett, 1961; Armstrong, 1964, 1979; Bacha and Hossner, 1977; Joshi and Hollis, 1977; Sand-Jensen et al., 1982; Taylor et al., 1984; Jaynes and Carpenter, 1986; Kemp and Murray, 1986; Mendelssohn et al., 1995, among others). Yet, according to Mendelssohn (1993), very few species have been shown to produce oxidized rhizospheres—rice, broad-leaved cattail (T. latifolia), common reed, aster (Aster tripolium), smooth cordgrass (S. alterniflora), cordgrass (S. maritima), purple moor grass (Molinia caerulea), buckbean (Menyanthes trifoliata), asphodel (Narthecium sp.), beaked sedge (Carex rostrata), sweet gale (Myrica gale), and pondweed (Potamogeton polygonifolius).
The brevity of this list, however, is probably due to lack of study, as oxidized rhizospheres are frequently observed in wetlands, especially in wet meadows (personal observations). While many wetland plants show evidence of the release of oxygen to the anaerobic substrate around the roots by their oxidized pore linings, this is not a universal adaptation possessed by all wetland species.

Nonwoody roots of lodgepole, slash, and loblolly pines have large air spaces (lacunae) that oxidize the rhizosphere only under anaerobic conditions (Coutts and Philipson, 1978b; Philipson and Coutts, 1978; Hook and McKevein, 1988; Fisher and Stone, 1990). Aerenchyma in the primary root tips makes this possible. Lobolllly pine seedlings grown under flooded, anaerobic conditions developed an internal aeration system composed of aerenchyma, whereas seedlings grown under drained conditions did not (McKevein et al., 1987). Fisher and Stone (1991) described the oxidized rhizosphere of slash pine and listed references to other species reported to have these manifestations including white oak (*Quercus alba*), water gum, baldcypress, swamp black gum, lobolly pine, lodgepole pine, black spruce (*P. mariana*), and red spruce (*P. rubens*). Other trees oxidizing their rhizospheres include green ash, crack willow, Sitka spruce, and lodgepole pine (*Armstrong, 1968; Chirkova, 1968; Coutts and Philipson, 1978a; Sena Gomes and Kozlowski, 1980). Dionigi et al. (1985) found that black willow’s greater ability to oxidize waterlogged soils allowed it to colonize lower elevations along the Atchafalaya River in Louisiana, while sandbar willow (*S. exigua*) occupied higher sites. Studies of Irish wetland tree species found three species oxidizing their rhizospheres at different levels—willow (*S. cinerea* ssp. *oleifolia* or *S. atrocinerea*), ash (*F. excelsior*), and European alder, which positively affected their tolerance of waterlogging (Iremonger and Kelly, 1988). Red and black mangroves also oxidize their rhizospheres. McKee et al. (1988) found that soil around the aerial roots of red mangrove was more oxidized than soil not associated with such roots. Good et al. (1986) concluded that the presence of oxidized rhizospheres in green ash was different enough on wet versus mesic sites to serve as a useful indicator of site wetness, while Mendelsohn (1993) concluded that they indicated “soil saturation for a sufficient period to produce anaerobic soil conditions” and are a “relatively good indicator of wetland hydrologic conditions.”

**Life-form or Habit Changes**

Flood-induced breaking of stem bud dormancy leads to the formation of multiple trunks in some woody species, while flood damage to some trees results in multiple trunks sprouting from root crowns (Yanosky, 1982). Flood damage to the tops of trees and shrubs destroys the growing tips of the plants (apical dominance), which then results in the growth of lateral buds and formation of one or more sprouts; growth of adventitious buds may also be stimulated to produce more stems (Sigafoos, 1964). Sprouting is a common physiological response to damage by fire, floods, or other disturbances (e.g., logging). Even broken branches buried in the ground can sprout new shoots (e.g., a form of asexual reproduction in cottonwoods, *Populus* spp.; Braatne et al., 1996). Crawford (1983, 1989) reported that the European alder developed a *bush* form (polycormic growth form) in frequently flooded wetlands, in contrast to a *pole* form on well-drained sites. Flooding stimulates basal buds to develop forming multiple trunks. The advantage of this adaptation is improved ventilation above the flood level as there is more lenticel-containing bark at the bottom of the stems. This adaptation may also occur with other adaptations (e.g., adventitious roots and shallow roots) to provide an adequate supply of oxygen to roots growing in waterlogged soils (Crawford, 2003). Increased stem density with increasing wetness in European alder was also detected by Rodríguez-González et al. (2010). Sprouting may occur in other species as speckled alder (*A. rugosa*), red maple, silver maple, black willow, box elder (*Acer negundo*), river birch (*Betula nigra*), sycamore (*P. occidentalis*), swamp privet (*Forestiera acuminata*), and Ogeechee gum (*Nyssa ogeche*) have been observed with multiple trunks in periodically flooded wetlands (personal observations; Wistendahl, 1958; Environmental Laboratory, 1987). In Jean Lafitte National Park (LA), red maple had two different growth forms—a single-stemmed canopy tree on the natural levees and a multistemmed tree in...
the frequently flooded backswamp (Denslow and Battaglia, 2002). McLeod et al. (1988) testing the response of four woody species to flooding with high-temperature water found that buttonbush produced several basal stems in lieu of stem hypertrophy. They believed that this mechanism allowed for an increase in the area of stem tissue for potential gas exchange with the atmosphere (the same purpose of stem hypertrophy).

Saw palmetto (*Serenoa repens*) is a southern palm that grows mostly on dry sandy sites such as pine flatwoods, longleaf pine–scrub oak ridges, sand pine–oak scrubs, and coastal dunes. Yet it is also common in seasonally wet pine flatwoods (Godfrey and Wooten, 1979). Wells (1942) listed it as one of the community dominants of southeastern shrub bogs. On dry soils, the saw palmetto sends up its palm leaves from a horizontal, usually underground, rhizome. On seasonally flooded sites, however, it develops an upright, often branched stem (Figure 3.15). Godfrey and Wooten (1979) recognized this different growth form and included this species in their book on aquatic and wetland plants of the Southeast.

**Seed Adaptations**

Colonization of flooded soils, if done through reproduction, requires that seeds be adapted to aquatic conditions. Hydrochory—dispersal of seeds/propagules by water—is a common strategy for wetland plants in shallow water and on floodplains (e.g., Schneider and Sharitz, 1988; Nilsson et al., 1991; Huiskes et al., 1995; Middleton, 2000; Lopez, 2001), whereas seed persistence is an alternative strategy for hydrophytic plants in regions with cyclical precipitation patterns (e.g., van der Valk and Davis, 1978). For those species using hydrochory, floatable seeds are important for dispersal, and as

![Figure 3.15](image-url)
expected, seed floatability differs among species. In a study of some common freshwater tidal species, Parker and Leck (1985) found that the floatability of seeds from two smartweeds (Polygonum arifolium and P. punctatum) benefitted from attached flowers (i.e., P. arifolium did not float without their perianth, while P. punctatum floated longer), whereas seeds of jewelweed (Impatiens capensis) and bur marigold (Bidens laevis) may stay afloat for very long periods—after 30 days at least 25% of the seeds were still floating (Parker and Leck, 1985). A study of seed buoyancy and germination of 55 wetland species provides some interesting insights (van den Broek et al., 2005). Seeds from plants in more aquatic habitats (i.e., reed beds characterized by P. australis) tended to remain buoyant longer than those from species inhabiting less flooded fens and saturated wet meadows. Species with higher buoyancy seed may have lower longevity than the others, suggesting a trade-off between dispersal and seed persistence. The former may have longer or flatter seeds that are not likely to be buried as round seeds. The seeds of some plants may have structures to aid floatation (e.g., the marginal floats in the seeds of laceflower—Ptilimnium nuttallii; Baskin et al., 1999). In the Amazon, during the flood season, nonbuoyant seeds drop to the bottom of the submerged ground where they await the drawdown phase for germination (Junk et al., 2010).

**Germination and Seedling Survival**

Most seeds have a limited ability to germinate under anaerobic conditions and many wetland plants, especially those incapable of germinating underwater, delay germination until the floodwater recedes and the likelihood of more flooding has passed (Crawford, 2003). The combination of changes in light and fluctuating temperatures from reduced flood levels stimulates germination in many wetland species, including water horehound (Lycopus europaeus), purple loosestrife (L. salicaria), and fragrant flatsedge (Cyperus odoratus) (Baskin and Baskin, 2014). Flooding can stimulate annual species, like those colonizing mudflats in summer, to break dormancy. Crawford (2003) provides several examples of the physiological problems of seed germination in a variety of seasonal flooding circumstances and different strategies for responding to these issues.

The seeds of most plants lose viability when inundated for long periods. Some floodplain species have demonstrated increased germination rates and success with longer submergence, with an Amazon tree (Crataeva benthamii) reaching peak percent germination (98%) after 6 weeks (Lucas et al., 2012). In contrast, seeds of marsh and aquatic species have prolonged dormancy and remain viable for many years (Leck, 1989). Scientists claim to have germinated a 1200-year-old lotus seed from China (The Boston Globe, November 14, 1995, p. 3). While some wetland plants are noted for their persistent in seed banks, others are short-lived (e.g., Tatar, 2010). Seed banks in the soil are important for wetland restoration efforts as they may harbor species that are not present in the existing aboveground community. In studying California vernal pools, Faist et al. (2013) found more rare and native species in the seed bank than in the existing vegetation; the seed bank better reflected the 2003–2006 plant community than the current one (2007–2010). When favorable conditions occur, seeds in the banks can germinate. Seed banks in drained wetlands in agricultural regions may, however, have limited native species (Seabloom and van der Valk, 2003; Nabity and Hoagland, 2006). Seeds need some level of oxygen to germinate, with few exceptions, two being rice (O. sativa) and barnyard grass (Echinochloa crus-galli) (Kennedy et al., 1980; Benvenuti and Macchia, 1995; Magneschi and Perata, 2009). Rice is undoubtedly the most studied wetland plant due to its economic importance—the staple for millions of people around the globe—with particular emphasis on its tolerance of flooding and waterlogging (Colmer et al., 2014). Once rice germinates, its coleoptile (first shoot) grows upward (even when roots and leaves fail to grow), increasing its length by 30% hourly, and upon reaching the water’s surface (contact with the atmosphere), roots and leaves begin to grow (Atwell, 2010). Only certain genotypes of rice can actually do this fast enough to do this under field conditions (Ismail et al., 2009). Miro and Ismail (2013) review some major physiological processes involved in rice tolerance of flooding during germination, while Baskin and Baskin (2014) provide a treatise on seed ecology, germination, and dormancy, with some attention to aquatic species.
Many wetland plants can germinate underwater. Among these exceptional species, Hook (1984a) listed several wetland plants (including *Peltandra virginica*, *Alisma plantago-aquatica*, *T. latifolia*, *C. occidentalis*, *U. americana*, *S. nigra*, and *P. deltoides*), plus cultivated species (*Phleum pratense*, *Lactuca sativa*, *O. sativa*, *Petunia* spp., and *Dianthus* spp.) as good germinators and others as poor submerged germinators (e.g., *Nyssa* spp., *T. distichum*, *L. styraciflua*, *F. pennsylvanica*, *F. caroliana*, *P. occidentalis*, *Z. mays*, *Lolium perenne*, and *Festuca pratensis*). The latter rely on natural drawdown conditions in wetlands for germination, so characteristic southern deepwater swamp species like baldcypress and water gum regenerate at low water accompanying extended droughts. Rapid growth of seedlings allows these species to get their foliage above water, thereby enhancing survival of the species. A germination study of six helophytes (*I. pseudacorus*, *Phalaris arundinacea*, *P. australis*, *Scirpus lacustris*, *T. latifolia*, and *T. angustifolia*) found that all the species, except *I. pseudacorus*, could germinate under flooded or saturated conditions, although *Phragmites* had poor success under those conditions (Coops and van der Velde, 1995). *Typha* spp. experienced poor germination under moist conditions. This experiment also investigated seedling growth after flooding and dewatering—growth of *Phragmites* and *Phalaris* ceased upon flooding but resumed upon drainage, and growth of *Typha* and *Scirpus* was unaffected by flooding, while *Iris* seedlings grew slowly when submerged but responded quickly upon drainage. Interestingly, seedlings of all species survived 7 weeks of inundation (Coops and van der Velde, 1995). The seeds of wetland species that germinate in fall may have physiological adaptations that prevent their germination in spring during high water conditions. For example, the annual dormancy/nondormancy cycle of laceflower (*P. nuttallii*), a winter annual of southeastern wetlands, may help it avoid high water that could prevent seedling establishment (Baskin et al., 1999).

Work by Kramer (1949) identified that soil wetness during the first year or two was critical for seedling survival of shallow-rooted species, specifically baldcypress and yellow birch (*Betula alleghaniensis*). Experimental studies of germination and seedling survival in lodgepole pine and ponderosa pine (*P. ponderosa*) by Cochran (1972) in Oregon found significant germination in both species when water tables were below 15 cm and only a few germinants when soil was saturated to the surface, no mortality of seedlings of either species when in saturated soils (duration of 130 days), and most of the seedlings of both species survived 52 weeks of saturation. The conclusion was that the predominance of lodgepole pine (a FAC species in Oregon) over ponderosa pine (a FACU species) on wet soils must be related to other factors—possibly the former is a better competitor in sites with grasses and forbs. Tolerance of saturated conditions may change with age, as in loblolly pine; tolerance to oxygen deficiency was found to increase with age (Grable, 1966, Leyton and Rousseau, 1958, as reported in Hu and Linnartz, 1972).

**ACCELERATED STEM AND OTHER GROWTH**

Flooding stimulates ethylene production in many aquatic plants, which then promotes shoot elongation, allowing some of them to get their shoots or leaf tips above the flood level and thereby continue exchange of gases (mainly through stomata), photosynthesis, and other life processes (Ku et al., 1970; Crawford, 1992; Blom et al., 1996). In some species, adventitious root formation may begin after emergence (Van der Sman et al., 1993). While many aquatic and marsh plants have this adaptive response to flooding, some terrestrial species, including corn (*Z. mays*), also have evolved this mechanism to escape minor submergence (Kozlowski, 1984a; Jackson et al., 1985; Crawford, 1987; Jackson, 1988; Blom, 1990; Laan and Blom, 1990; Voesenek and Van der Veen, 1994). Stem growth can be extremely rapid. This can happen in less than 20 min (Jackson, 1971). Blom (1990) found that certain docks (*Rumex*) increased their petioles 100%–120% within 4 days of flooding, with one species growing as much as 40 cm within a few days. Variations in plant responsiveness of stem elongation help explain plant distribution at different levels on floodplains (Blom et al., 1996).

McKevlin et al. (1995) suspect that rapid height growth in seedlings of water tupelo during occasional dry periods facilitates their survival when such sites are reflooded. This species is a dominant
species of semipermanently flooded and intermittently exposed wetlands, yet does not germinate underwater. Instead it germinates during drawdowns late in the growing season or during dry years. This late germination also may require rapid stem growth to guarantee that the terminal shoot is above the winter flood level.

In a study of the response of dallisgrass (*Paspalum dilatatum*) and narrowleaf trefoil (*Lotus tenuis*) to flooding with or without defoliation, Striker et al. (2008) documented morphological and anatomical responses in both of these wet-tolerant species. Dallisgrass grew taller when flooded for 15 days compared to nonflooded plants, while there was no noticeable height difference in the trefoil. The flooded dallisgrass also produced more tillers above the water level, which according to some sources increases the possibility of oxygen capture (Laan et al., 1990; Grimoldi et al., 1999), and increased root porosity by 42% (from 28% to 40%). The trefoil produced more shoots above the water and its root porosity increased by 61%.

**WETLAND PLANTS: HYDROPHYTES**

Plants growing in wetlands and water are technically called “hydrophytes.” Most wetland plants do not grow strictly in water or very wet soils, but also grow in terrestrial habitats, especially under mesic soil conditions (e.g., the species of Wisconsin’s wet-mesic prairies or forests according to Curtis, 1959). Many of these species are more common on the latter sites but have populations that tolerate varying degrees of soil wetness. Unfortunately, due to the lack of distinctive morphological differences, 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., periodically anaerobic soils due to excessive wetness) and other reliable signs of wetland hydrology at a given location.

**Evolving Concept of a Hydrophyte**

Today’s usage of the term “hydrophyte” is different than its original use. In the 1800s and the early 1900s, it was used to define aquatic plants that were plants growing in water (Schouw, 1822, as reported in Warming, 1909) or plants with perennating buds beneath the water (Raunkiaer, 1905, 1934). Warming and Raunkiaer were among the earliest of the plant ecologists to use the term “hydrophyte.” Hydrophytes were distinguished from helophytes, which included various wetland plants depending on whose definition was used.

Raunkiaer’s life-forms were based on a plant’s adaptation to the critical season (e.g., winter), mainly the degree of protection possessed by the dormant buds (Smith, 1913). According to this system, hydrophytes (plants with perennating rhizomes or winter buds) and helophytes (plants with buds at the bottom of the water or in the underlying soil) were the two types of cryptophytes (plants with dormant parts below ground), while other wetland plants were included in other life-forms, such as phanerophytes (trees and shrubs) (Smith, 1913). Raunkiaer’s helophytes did not include all typical marsh species.

Warming (1909) was probably the first ecologist to arrange plant communities by the degree of soil wetness. He recognized aquatic plants (water plants) that spend their entire life submerged or with leaves floating at the surface and terrestrial plants that are mostly exposed to air, including marsh plants. Vegetation was then separated into numerous “ecological classes” based principally on soil properties. The first of the groupings was for soil that was very wet and two classes were listed: class 1, hydrophytes (formations in water), and class 2, helophytes (formations in marsh). His concept of helophyte was much broader than Raunkiaer’s, including plants with their roots under water or in “soaking” soil with emergent foliage (herbs, shrubs, and trees). The distinction between hydrophytes and helophytes had ecological merit in that the truly aquatic plants (hydrophytes) were separated from those that grow on anaerobic saturated soils (helophytes). This distinction is still made by some authors as Cook (1990) in this *Aquatic Plant Book* (a guide to the world’s aquatic plants) defined hydrophytes as “plants physiologically bound to water, at least part of the generative
cycle takes place in or on the surface of water” and helophytes as “essentially terrestrial plants whose photosynthetically active parts tolerate long periods submerged or floating” (p. 2). In describing marsh and fen vegetation of an English lake, Pearsall (1917) referred to the plants of marshes (near the water) and fens (on peaty or sedimentary soils) as “terrestrial hydrophytic vegetation.”

Following the lead of Warming, Clements (1920) also used soil wetness to separate plants into different groupings. He might have been the first ecologist to expand the definition of hydrophyte to include helophytes (“amphibious, rooted in water or mud”) as a type of hydrophyte (along with emophytes, submerged plants, and plotophytes, floating plants, at least floating-leaved). Later in 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.” They divided hydrophytes into three groups: (1) submerged, (2) floating (including floating-leaved rooted species), and (3) amphibious—“the least specialized of the water plants…many…may grow for a time as mesophytes or partially submerged.” Weaver and Clements (1929, pp. 347–348) offered an interesting commentary about mesophytes (moist-site plants): “Mesophytes stand midway between hydrophytes and xerophytes. For this reason, they pass, on the one hand, into dry land plants, and, on the other hand, into amphibious plants. Various xerophytes and hydrophytes have, moreover, often found themselves in conditions that changed them to mesophytes.” One interpretation of the latter statement is that classifying a plant species as a hydrophyte or a mesophyte is not necessarily an easy task.

Daubenmire (1947) identified five “morphoecologic” groups of hydrophytes: (1) floating, (2) suspended (e.g., phytoplankton), (3) submerged anchored, (4) floating-leaved anchored, and (5) emergent anchored. Included in the last group are “swamp and bog plants which inhabit soils containing a quantity of water that would prove supraoptimal for the average plant.” His hydrophyte definition (“any plant growing in a soil that is at least periodically deficient in oxygen as a result of excessive water content”) has been used in various U.S. government wetland delineation manuals and the official federal wetland classification system (Daubenmire, 1968).

While Daubenmire’s definition relates to an individual plant, the need to use plant species as indicators of wetlands led to the development of national and regional lists of indicator species for the United States (see “Wetland Plant Lists” discussion). The lists included many typical upland species that had wetland ecotypes or broad ecological amplitudes and were typically adapted for life in wetlands. Recognizing the significance and potential confusion of using wetland ecotypes of common upland species as wetland indicators prompted Tiner (1988) to refine the definition of a hydrophyte in his Field Guide to Nontidal Wetland Identification 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.” This definition embodies the individualistic concept of a hydrophyte, recognizing that plant species may exhibit considerable plasticity or ecological amplitude in their adaptations to wet environments. This concept is not bound to the species level in plant taxonomy, but allows, for example, wetland variants of mostly dry-site species to be classified as hydrophytes. Tiner (1991) provides a detailed review of the concept of a hydrophyte as applied to wetland delineation. The EPA wetland delineation manual and interagency federal manual embraced this concept (Sipple, 1988; Federal Interagency Committee for Wetland Delineation, 1989).

In 2007, the U.S. Army Corps of Engineers (Corps) established the National Technical Committee for Wetland Vegetation (NTCWV) to provide technical assistance to the agency in the use of plants and their ecology for wetland identification and delineation. One of the committee’s first assignments was to review the concept of a hydrophyte and prepare a definition that conforms with the use of hydrophytic vegetation for wetland delineation (Tiner, 2012). The NTCWV published the following definition: “Hydrophytes grow in water or on a substrate that is saturated at a frequency and duration during the growing period sufficient to affect plant occurrence.” This definition recognizes that hydrophytes are not restricted to anaerobic environments, but occur in wet-stressed environments whether anaerobic or not (Tiner, 2012). It recognizes that recurrent, prolonged wetness during periods of plant growth has a major influence on plant colonization, survival, and reproduction.
The definition excludes plant species that only colonize wetlands during dry periods (i.e., draw-down) when soils are aerated, at least in the upper part, and perish when wet conditions return. The phrase “growing period” was included instead of “growing season” since the latter has many definitions. Growing period focuses on the growth of root, shoot, and other plant parts by native species. Finally, the definition does not restrict hydrophytes to soils recognizing that they also grow on nonsoils, such as rocks and riverwash (gravel bars), so the term “substrate” is more appropriate.

**PLANT SPECIFICITY**

While a couple of thousand species grow exclusively in U.S. wetlands, thousands of others are more wide-ranging. Some of the latter occur mostly but not always in wetlands, whereas others display no particular affinity for wetlands and still others are actually more common in uplands. When the plants are growing under wetland hydrologic conditions, they are hydrophytes regardless of where the majority of individuals of their species occur. The best plant indicators of wetland are clearly those species with the highest affinity for wetlands (see Table 3.3 for common examples).

The affinity of certain species may vary with latitude or, in mountainous areas, with altitude. For example, in the Northeast, Labrador tea (*Ledum groenlandicum*) is restricted to wetlands, mainly bogs. Yet in Labrador and Newfoundland, this species also occurs in dry heaths and woods (Ryan, 1989). Mountain holly (*Nemopanthus mucronata*), an exclusive wetland species in most of its U.S. range, occurs in uplands and wetlands in coastal eastern Maine. Presumably the combination of low evapotranspiration, cold climate, moderate frequency of fogs, and cool, moist air (maritime influence) creates favorable conditions on drier soils. The colder climates, especially along the coast, may permit some excellent wetland indicator plants to be less reliable indicators locally.

Most plants growing in wetlands have a broad ecological amplitude and are tolerant or adaptable to many environmental conditions (e.g., wet, moist, and sometimes dry). Such species are not particularly useful indicators of any environment, unless they possess morphological adaptations developed in response to prolonged flooding or waterlogging. A flood tolerance study of red maple (*A. rubrum*) seedlings from wet sites and from dry sites by Will et al. (1995) demonstrated that this species is highly adaptable regardless of its original habitat. As mentioned earlier, red maple was reported to have a highly adaptable root system (Kramer, 1949). It is a good example of a species demonstrating ecological plasticity. Another example of a plastic species is water smartweed (*Polygonum amphibium*)—plants growing on land (dry soil) have hairy, rough stems and leaves, yet those in water possess stems and leaves that are quite smooth throughout (Weaver and Clements, 1929). While many species are quite adaptable, some have populations of individuals that are better adapted to one set of environmental conditions than other populations of the same species. These populations have been referred to as “ecotypes.” The existence of ecotypes is well established in the literature.

**WETLAND ECOTYPES**

While the definition of *species* is useful for taxonomic reasons and to discuss ecological relationships, it is not without problems. Merrell (1981) commented that up to half of all species of flowering plants are believed to be allopolyploids—the product of hybridization between species plus complications due to asexuality, introgression, geographic variation, and combinations of these factors. Recognizing the varied responses to different habitats, Clements et al. (1950) simply concluded that the typical *species* is the form that occupies the most extensive area. This clearly reveals the possibility for less habitat specificity than the nonscientist might expect from a given plant species.

At the species level, plants do not have exactly the same environmental requirements and individual populations may differ in their tolerance of degrees of waterlogging or flooding. It has long been recognized that a given plant species may include ecotypes—a population or group of populations having certain genetically based morphological and/or physiological characters—but usually prevented from natural interbreeding by ecological barriers (Turesson, 1922a,b, 1925; Barbour et al., 1980).
TABLE 3.3
Examples of Obligate Hydrophytes That Are Widespread or Particularly
Common in Certain Wetland Types in the United States

<table>
<thead>
<tr>
<th>Aquatics</th>
<th>Emergents (herbs)</th>
<th>Shrubs</th>
<th>Trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Azolla spp. (mosquito ferns)</td>
<td>Potamogeton spp. (pondweeds)</td>
<td>Osmunda regalis (royal fern)</td>
<td>Carya aquatica (water hickory)</td>
</tr>
<tr>
<td>Brasenia schreberi (water shield)</td>
<td>Proserpinaca spp. (mermaid weeds)</td>
<td>Pelantra virginica (arrow arum)</td>
<td>Myrica gale (sweet gale)</td>
</tr>
<tr>
<td>Elodea spp. (waterweeds)</td>
<td>Ruppia maritima (widgeon grass)</td>
<td>Polygonum hydropiperoides (water pepper)</td>
<td>Rhizophora mangle (red mangrove)</td>
</tr>
<tr>
<td>Isoetes spp. (quillworts)</td>
<td>Thalassia testudinum (turtle grass)</td>
<td>Polygonum sagittatum (arrow-leaved tearthumb)</td>
<td>Rosa palustris (swamp rose)</td>
</tr>
<tr>
<td>Lemma spp. (duckweeds)</td>
<td>Utricularia spp. (bladderworts)</td>
<td>Pontederia cordata (pickerelweed)</td>
<td>Salix sericea (silky willow)</td>
</tr>
<tr>
<td>Myriophyllum spp. (water milfoils)</td>
<td>Vallisneria americana (wild celery)</td>
<td>Sagittaria spp. (arrowheads)</td>
<td>Vaccinium macrocarpon (large cranberry)</td>
</tr>
<tr>
<td>Najas spp. (naiads)</td>
<td>Zannichellia palustris (horned pondweed)</td>
<td>Scirpus americanus (Olney’s three-square)</td>
<td>Nyssa aquatica (water gum)</td>
</tr>
<tr>
<td>Nuphar spp. (pond lilies)</td>
<td>Zostera marina (eelgrass)</td>
<td>Scirpus atrovirens (green bulrush)</td>
<td>Nyssa aquatica (water gum)</td>
</tr>
<tr>
<td>Nymphaea spp. (water lilies)</td>
<td></td>
<td>Scirpus tabernaemontani (soft-stemmed bulrush)</td>
<td>Planera aquatica (planer tree)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Shrubs</th>
<th>Trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andromeda polifolia (bog laurel)</td>
<td>Carya aquatica (water hickory)</td>
</tr>
<tr>
<td>Betula pumila (bog birch)</td>
<td>Nyssa aquatica (water gum)</td>
</tr>
<tr>
<td>Cephalanthus occidentalis (buttonbush)</td>
<td>Chamaecyparis thyoides (Atlantic white cedar)</td>
</tr>
<tr>
<td>Forestiera acuminata (swamp privet)</td>
<td>Fraxinus profunda (pumpkin ash)</td>
</tr>
<tr>
<td>Lonicera oblongifolia (swamp fly-honeysuckle)</td>
<td>Gleditsia aquatica (water locust)</td>
</tr>
</tbody>
</table>

Source: Tiner, R.W., BioScience, 41, 236, 1991; nomenclature has not been updated.
Note: Genera listed contain all or mostly obligates.
Daubenmire (1968) in his classical treatise on plant communities pointed out that “each habitat type is a distinctive combination of environmental factors, so the different selection pressures in contiguous habitats tend to develop special ecotypes that are homozygous for at least the adaptive characteristics.” Ecotypes are better fit for occupying a certain habitat than individuals from other populations of the species. The significance of ecotypes must not be overlooked for, as noted by Braun-Blanquet (1932), “the most exact indicators are often, indeed, not the ‘good Linnaean species’ but rather the elementary species or races, the ‘ecotypes’ of Turesson (1925)” for “these forms require more narrowly circumscribed life conditions and, therefore, are socially more sharply specialized.” Recognizing the existence of wetland ecotypes, races, varieties, subspecies, and other variants or simply acknowledging wide wetness tolerances of plant species is vital to understanding how to use plants as indicators of wetlands.

For some plant species, subspecies or varieties that are found in different habitats or with a restricted distribution are morphologically distinguishable (Table 3.4). In some cases, these varieties have been assigned a different indicator status on national and regional wetland plant lists (see following section for discussion), especially when their habitats are wetter than the typical

<table>
<thead>
<tr>
<th>Species (Common Name)</th>
<th>Subspecies or Variety</th>
<th>Nat'l Range of Indicator Status</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum (Red maple)</td>
<td><strong>rubrum</strong></td>
<td>FAC</td>
<td>Swamps, alluvial soils, and moist soil</td>
</tr>
<tr>
<td>(Drummond’s red maple)</td>
<td><strong>drummondii</strong></td>
<td>Not designated</td>
<td>Deep swamps</td>
</tr>
<tr>
<td>(Trident-leaved red maple)</td>
<td><strong>trilobum</strong></td>
<td>Not designated</td>
<td>Forested wetlands</td>
</tr>
<tr>
<td>Celtis laevigata (Sugarberry)</td>
<td><strong>laevigata</strong></td>
<td>FACW to UPL</td>
<td>Bottomlands and low woods</td>
</tr>
<tr>
<td></td>
<td><strong>smallii</strong></td>
<td>Not designated</td>
<td>Bottomlands and low woods</td>
</tr>
<tr>
<td></td>
<td><strong>texana</strong></td>
<td>Not designated</td>
<td>Bluffs, rocky slopes, dry woods, etc.</td>
</tr>
<tr>
<td>Fagus grandifolia (American beech)</td>
<td><strong>grandifolia</strong></td>
<td>FACU</td>
<td>Rich upland soils</td>
</tr>
<tr>
<td></td>
<td><strong>caroliniana</strong></td>
<td>Not designated</td>
<td>Moist or wet lowland soils, especially on or near the coastal plain</td>
</tr>
<tr>
<td>Nyssa sylvatica (Black gum)</td>
<td><strong>sylvatica</strong></td>
<td>FAC</td>
<td>Low acid woods, swamps, and shores</td>
</tr>
<tr>
<td></td>
<td><strong>caroliniana</strong></td>
<td>Not designated</td>
<td>Chiefly on uplands of the interior</td>
</tr>
<tr>
<td>Panicum virgatum (Switchgrass)</td>
<td><strong>virgatum</strong></td>
<td>FACW to FAC</td>
<td>Dry or moist sandy soils, and shores</td>
</tr>
<tr>
<td></td>
<td><strong>spissum</strong></td>
<td>Not designated</td>
<td>Gravelly or sandy fresh to brackish shores and swamps</td>
</tr>
<tr>
<td>Toxicodendron radicans (Poison ivy)</td>
<td><strong>radicans</strong></td>
<td>FAC to PACU</td>
<td>Thickets, open woods, sandy or rocky places, and fencerows</td>
</tr>
<tr>
<td></td>
<td><strong>vulgaris</strong></td>
<td>Not designated</td>
<td>Wooded swamps and bottomlands</td>
</tr>
</tbody>
</table>


Notes: See discussion of “Wetland Plant Lists” for definitions of wetland indicator statuses.

Since the original version of this book was published, certain subspecies have been recognized as separate species: *Andropogon virginicus glaucopis* is now *A. glaucopis* (FACW); *A. virginicus hirsutior* is now *A. hirsutior* (FACW); *Nyssa sylvatica biflora* is now *N. biflora* (OBL to FACW); *Quercus stellata paludosa* is *Q. similis* (FACW); *Quercus falcata pagodaefolia* is *Q. pagoda* (FACW to FAC).

* Not recognized as a separate subspecies on the national wetland plant list.
Wetland indicators evolve due to differences in environmental conditions that reproductively isolate wet-site individuals from dry-site individuals. Timing of flowering may be different, thereby limiting cross-fertilization. In their study of ecotypic variation in western white pine (Pinus monticola), Squillace and Bingham (1958) found that seedbed moisture served as an ecological barrier to gene flow from contiguous populations. Genetically distinct populations can be created wherever there is a steep gradient in microhabitats, even when gene flow is strong (Liu and Godt, 1983). In the case of western white pine, seedlings from dry-site populations failed to survive wet conditions, while wet-site seedlings could not grow in dry beds (Squillace and Bingham, 1958). Examination of the physiological responses of eight red maple provenances (four each from wet and dry sites) to soil water availability led researchers to conclude that red maple (A. rubrum) has evolved into physiologically distinct wet- and dry-site ecotypes (Bauerle et al., 2003). Cultivars of nursery plants and cropped species may be more tolerant to flooding than others. Seedlings of the “Golden Star” cultivar of a starfruit (Averrhoa carambola) could survive up to 36 days of inundation, while another cultivar could not (Joyner and Schaffer, 1989; Ismail and Noor, 1996, as reported in Schaffer, 1998). Anella and Whitlow (1999) subjected fully leafed-out saplings of 7 red maple cultivars, 4 Freeman maple (A. freemanii) cultivars, and 1-year-old saplings grown from seeds collected from red maples along the James River (i.e., representing the wet extreme of red maple’s range) to 45 days of flooding—4 were rated as having high flood tolerance, 5 as intermediate, and 3 as low. The James River saplings and cultivars rated as high tolerance had longer hypertrophied lenticels than the other cultivars. The authors were surprised at the poor development of adventitious roots, especially in the James River saplings as their other work found extensive adventitious roots in such saplings.

In summarizing literature on plant adaptations to saltwater flooding, Wainwright (1984) mentioned the presence of salt-tolerant ecotypes of creeping bentgrass (Agrostis stolonifera), red fescue (Festuca rubra), and several other typically nonsaline species in salt marshes. Individuals of these two species from salt marsh populations did not grow as vigorously as individuals from inland populations when grown under freshwater conditions (Hannon and Bradshaw, 1968; Tiku and Snaydon, 1971). Intraspecific variation in salt tolerance has also been detected in many common salt marsh plants (S. alterniflora, S. foliosa, S. patens, Sporobolus virginicus, and Juncus roemeri-anus) (Nestler, 1977; Cain and Harvey, 1983; Eleutrius, 1989; Blits and Gallagher, 1991; Pezeshki and DeLaune, 1995; Hester et al., 1996). Salt hay grass occurs in dunes, interdunal swales, salt marshes, and brackish marshes, and these stocks showed different responses to salinity (Silander and Antonovics, 1979; Pezeshki and DeLaune, 1991).

Different populations of species have shown unlike responses to flooding and waterlogging. Lessmann et al. (1997) detected intraspecific variations in three species (S. alterniflora, S. patens, and P. hemitomon) and suggested that the more flood-tolerant stocks be used in wetland creation and restoration. Lynn and Waldren (2003) compared the flood response of creeping buttercup (Ranunculus repens) seedlings from two different habitats (turlough, wet; ruderal, damp); there was no difference in aerenchyma formation or in response to saturation, but submergence produced leaf decay and
blackening of root tissue in the ruderal seedlings but not in those from the turlough. An interesting side note for the experiment was that the ruderal seedlings extended their petioles upward when submerged, while no such response was made by the turlough seedlings; in their natural habitat the latter are often covered by many feet (several meters) of water for months (e.g., Skeffington et al., 2006), so they are adapted to endure submergence and there is no need for petiole elongation. Foresters have long recognized different site types to maximize timber production from variable sites. Forestry researchers often use wet-site and dry-site seed sources when studying the responses of seedlings to anaerobic conditions as Topa and McLeod (1986a) did when evaluating such responses in loblolly pine and other pines. In searching for more waterlogging-tolerant genotypes of loblolly pine for forestry improvement, Shear and Hook (1988) subjected seedlings from 11 sources (“families”) to 3 winter waterlogging regimes (waterlogging from 0 to 15 cm, 0 to 30 cm, and 0 to 45 cm) and found significantly different intraspecific responses to the wettest treatments. Gill (1975) noted several examples of intraspecific and intravarietal differences in possessing the ability to produce adventitious roots. Several researchers observed that flood tolerance varied in *Eucalyptus* among ecotypes and provenances (Karschon and Zohar, 1972; Ladiges and Kelso, 1977, as reported in Kozlowski, 1984a). Sahrawat et al. (1996) evaluated numerous rice cultivars and found significantly different responses to iron toxicity tolerance, which could help boost rice production in irrigated and lowland rice paddies. When seaside goldenrod (*Solidago sempervirens*) from a Florida population was grown in New York, it grew poorly, while the New York populations clearly had no trouble growing there (Clausen and Hiesey, 1958). Yellow monkeyflower (*Mimulus guttatus*) has many ecological races related to climatic, altitudinal, and other factors. Even when the distributions of habitats overlap, the races may remain separate due to ecological conditions, with only minor hybridization (Clausen et al., 1941). Darlington (1973) referred to such hybrids as “misfits.”

Many species seem to exhibit ecological plasticity—the ability to successfully colonize a wide range of habitats, even within a single geographic region. These are highly adaptive and opportunistic species. An example is pitch pine, the characteristic plant of the New Jersey Pine Barrens, predominating both wetlands and uplands. It grows across a broad continuum of soil moisture from the driest sites (e.g., sand dunes) to the wettest (mucky soils and seasonally ponded sites). Ledig and Little (1979) noted genetic variations in pitch pine, with the dwarf or pygmy form (<4 m tall) occurring on dry sand sites in the New Jersey Pine Barrens and the tallest form (30 m) growing on seasonally wet sites. They admitted that genetic effects are confounded by environmental effects and that genetic variation can occur at several levels in a species—among individuals within stands, among stands within regions, and among physiographic regions.

Persimmon (*Diospyros virginiana*) occurs in permanently flooded sites on the Delmarva Peninsula (Delaware, Maryland, Virginia) and on sand dunes. It coexists with buttonbush (*C. occidentalis*) in Delmarva bay or pothole wetlands. Titus (1990) also found this species growing in a Florida hardwood swamp at low elevations, with its mean elevation between that of baldcypress and American elm (*U. americana*). It is likely that a wetland ecotype for persimmon exists.

On the West Coast, lodgepole pine occupies a similarly broad range of habitats (Fowells, 1965), with varietal habitat preferences. The shrubby coastal form (var. contorta) grows in peat bogs and muskegs from Puget Sound north but occupies dry sandy and gravelly sites in the southern part of its range. The inland variety (var. latifolia) is typically an upland plant of the interior (e.g., Rocky Mountains).

It is also important to recognize that a portion of the world’s vascular (flowering) plants have successfully made the transition back to a fully aquatic existence, despite the origin of land plants from aquatic algae over 400 million years ago (Davy et al., 1990). The evolution from land to water (a terrestrial existence to an aquatic one) by vascular plants may have happened over 200 times (Jackson et al., 2009). Cattails and bur reeds evolved from terrestrial plants (Cronquist, 1968). Curiously, some terrestrial monocots were derived from aquatic ancestors only to return to a watery life as hydrophytes (Crawford, 1983). The first trees on Earth grew in Carboniferous swamps about 250 million years ago, so these swamps are the ancestors of terrestrial vegetation (Kangas, 1990).
Interestingly, Jackson et al. (2009) claim that “all but the most basic attributes of flooding tolerance (e.g., the anaerobic respiratory pathways) seemingly involved an adaptive return to aquatic competence by land-dwelling plants.” They cite water lilies as one of the oldest-diverging lineages, having existed for ~120 million years, first appearing when angiosperms were developing. Evolution is still occurring and land plants are continuing to adapt to life in wetlands and water.

Traditionally, plant ecologists have attempted to use certain plants as indicators of specific environmental conditions (e.g., hydrophytes, halophytes, and calciphiles). In seeking to identify wetlands, there are many species that can serve as useful indicators for various wetland types especially the seasonally flooded and wetter types. However, given the transitional nature of many wetlands or portions of wetlands (e.g., ecotonal wetlands between wetter wetlands and mesic uplands), caution must be exercised in deciding what species are used as indicators of either wetlands or uplands. Species in the drier-end wetlands are not likely to be reliable indicators of either wetlands or uplands, so plants may not be useful for identifying wetland boundaries under these conditions. Barbour et al. (1980) summarized the problem aptly, “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” (p. 51). While many botanists and ecologists would like to use the Linnaean species to determine precise limits of wetlands, it must be understood that most wetlands, especially the drier-end ones, cannot be simply identified by plant species alone. The existence of wetland ecotypes of species that are typically on drier sites has confounded the situation. Moreover, unless morphological adaptations are present, the only way to recognize these hydrophytic ecotypes is through verifying the presence of undrained hydric soils.

**USING PLANTS TO IDENTIFY WETLANDS**

Since the beginning of plant ecology as a modern science, botanists have found certain plant species and communities to be characteristic of wetlands. They have been interested in describing plant communities and explaining the reasons for their establishment. They were not concerned about determining the exact boundaries between the communities as they collected data from representative sites or sites that typified the overall plant community. Typically, a plant ecologist would not select a sample plot in the interface between two communities unless he or she was interested in this transitional area. Certain aspects of wetlands have baffled plant ecologists for some time as witnessed by the following quotations:

... there is no sharp limit between marsh-plants and land-plants.” ... “Thus this zone [fresh-water swamp] represents a very gradual transition from terrestrial to lacustral conditions.” ... “It is impossible to establish any sharp distinction between swamp-forests and forests on dry land …

_**Warming**_  
(1909, _Oecology of Plants: An Introduction to the Study of Plant-Communities_)

The vascular species of this group [amphibious plants] are closely related to mesophytes and are the least specialized of water plants. Owing to their frequent occurrence at the water’s edge, many amphibious plants have a wide range of adjustment and may grow for a time as mesophytes or partially submerged.

_**Weaver and Clements**_  
(1929, _Plant Ecology_)

Many sedges and willows, etc. are transitional between this group [emergent anchored hydrophytes] and mesophytes in that they grow in wet soil where the water table is close to the surface.

_**Daubenmire**_  
(1947, _Plants and Environment: A Textbook of Plant Autecology_)
Today, there is great interest in both identification and delineation of wetlands due to passage of laws and promulgation of regulations to protect wetlands or to curtail unnecessary wetland destruction. Consequently, attention is focused on determining the boundaries of wetlands. For the first time in history, it is critical to know the limits of wetlands on individual parcels of land, since many activities (e.g., dredging or filling) require federal or state permits before commencing work. Vegetation plays a major role in wetland identification and delineation, so it is important to know which plants or groups of plants (plant communities) are wetland indicators (see Chapter 9 for examples of U.S. wetland plant communities).

**Wetland Plant Lists**

To aid in using plants to identify wetlands, a national list of vascular plant species that occur in wetlands has been prepared and updated by the federal government. Initially prepared by the U.S. Fish and Wildlife Service with cooperation from the Army Corps of Engineers, Environmental Protection Agency, and Natural Resources Conservation Service (Reed, 1988, 1997), the list is now compiled by the U.S. Army Corps of Engineers (Lichvar et al., 2014).

The list was originally developed for use in defining hydrophytes or plants that occurred in wetlands to help interpret the U.S. Fish and Wildlife Service’s wetland definition (Chapter 1). In reviewing the scientific literature, thousands of species of plants were reported growing in U.S. wetlands. Rather than compiling a simple list of these species, it was realized that the affinity for wetlands varies considerably among plant species and in some cases across regions. Consequently, species were assigned to one of four *wetland indicator categories* based on differences in expected frequency of occurrence in wetlands: (1) obligate wetland (OBL), (2) facultative wetland (FACW), (3) facultative (FAC), and (4) facultative upland (FACU). Plants not found in wetlands are considered upland plants (UPL). The definitions of these categories have slightly changed over time. The categories were initially defined with an expected value of their probability of occurrence in wetlands and/or nonwetlands to give reviewers as well as readers a sense of the expected occurrence of the species in each habitat type (Reed, 1988).

<table>
<thead>
<tr>
<th>Category</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obligate wetland (OBL)</td>
<td>“Occur almost always (estimated probability &gt;99%) under natural conditions in wetlands”</td>
</tr>
<tr>
<td>Facultative wetland (FACW)</td>
<td>“Usually occur in wetlands (estimated probability 67%–99%), but occasionally found in nonwetlands”</td>
</tr>
<tr>
<td>Facultative</td>
<td>“Equally likely to occur in wetlands or nonwetlands (estimated probability 34%–66%)”</td>
</tr>
<tr>
<td>Facultative upland (FACU)</td>
<td>“Usually occur in nonwetlands (estimated probability 67%–99%), but occasionally found in wetlands (estimated probability 1%–33%)”</td>
</tr>
<tr>
<td>Obligate upland (UPL)</td>
<td>“Occur almost always (estimated probability &gt;99%), under natural conditions in nonwetlands”</td>
</tr>
</tbody>
</table>

Draft lists were subject to peer review by wetland specialists and plant ecologists across the country. Since all reviewers did not concur with a single indicator status, pluses and minuses were also assigned to species within the three facultative categories (e.g., FACW+, FAC+, FAC−, and FACU−); these assignments help build consensus. Given that a plant’s indicator status may vary across the country, 13 regional lists were initially developed. The national list (Reed, 1988) represented a compilation of regional lists. The regions were still quite broad and further subdivisions could make the list even more sensitive to species habitat requirements. The proposed 1997 list (Reed, 1997) was the first attempt to address some significant intraregional differences.

The 1988 national list of wetland plants contained 6,728 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). Although the list is lengthy, it did not contain the majority of U.S. plant species, which are virtually intolerant of flooding or prolonged soil saturation during the growing season. Only 31% of the nation’s flora occurred often enough in wetlands to be on this list. Roughly one quarter (27%) of the species on the 1988 national wetland plant list was represented by OBL species (Tiner, 1991; see Tiner, 2006, for regional breakdown). The majority of listed species,
therefore, grow in both wetlands and nonwetlands to at least some extent, which is quite expected for habitats that are, in many ways, transitional between land and water.

In December 2006, maintenance and updating of the list was transferred from the U.S. Fish and Wildlife Service to the Corps, given their extensive use of the list for regulatory purposes.* In assuming responsibility for the list, the Corps provided further review of the wetland ratings. An important step in this review was eliminating the pluses (+) and minuses (−) and a focused reevaluation of species previously designated as FAC− (Lichvar and Minkin, 2008). The Corps also slightly redefined the definitions of the categories to remove the percentages of expected occurrence in wetlands and nonwetlands and redefined regions of interest (Lichvar and Minkin, 2008; Lichvar and Gillrich, 2011; Lichvar et al., 2012). The Corps felt that the inclusion of percentages in the definitions gave users the impression that the assignment to a particular category was based on analysis of statistical sampling data, which clearly was not the case; the assignments were based on a review of botanical literature (e.g., regional floras) and peer review by regional botanists and wetland ecologists. The revised definitions emphasized the general concept of each indicator status as follows and provided examples of the types of plants in each category (Lichvar et al., 2012).

<table>
<thead>
<tr>
<th>Obligate wetland (OBL)</th>
<th>“Almost always occur in wetlands. With few exceptions, these plants (herbaceous or woody) are found in standing water or seasonally saturated soils (14 or more consecutive days) near the surface.”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Facultative wetland (FACW)</td>
<td>“Usually occur in wetlands, but may occur in non-wetlands. These plants predominately occur with hydric soils, often in geomorphic settings where water saturates the soils or floods the soil surface at least seasonally.”</td>
</tr>
<tr>
<td>Facultative (FAC)</td>
<td>“Occur in wetlands and non-wetlands. These plants can grow in hydric, mesic, or xeric habitats. The occurrence of these plants in different habitats represents responses to a variety of environmental variables other than just hydrology, such as shade tolerance, soil pH, and elevation, and they have a wide tolerance of soil moisture conditions.”</td>
</tr>
<tr>
<td>Facultative upland (FACU)</td>
<td>“Usually occur in non-wetlands, but may occur in wetlands. These plants predominately occur on drier or more mesic sites in geomorphic settings where water rarely saturates the soils or floods the soil surface seasonally.”</td>
</tr>
<tr>
<td>Upland (UPL)</td>
<td>“Almost never occur in wetlands. These plants occupy mesic to xeric non-wetland habitats. They almost never occur in standing water or saturated soils. Typical growth forms include herbaceous, shrubs, woody vines, and trees.”</td>
</tr>
</tbody>
</table>

The regions of interest for the wetland plant lists were revised to correspond with the 10 ecologically based regions used for their recently published regional supplements to the Corps wetland delineation manual (Figure 3.16). This required further peer review of the lists and wetland ratings. The Corps also established a process for updating the list annually—one that allowed the public, in addition to state and federal agencies, to suggest additions, deletions, and modifications of the wetland ratings. The 2016 list contained 8085 species, up from 7828 in 2012, 7937 in 2013, and 8061 in 2014 (Lichvar et al., 2014, 2016). National, regional, and state lists are available for downloading at the national wetland plant list website (http://wetland_plants.usace.army.mil). Figure 3.17 shows the number of the listed species for each region by wetland indicator status based on the 2016 list.

While most states are adopting the state-relevant species and corresponding indicators from the national list for their programs, at least one state may take the state list one step further. Scientists in California have expressed interest in dividing the state into more regions and further regionalizing the list of wetland plants for California (San Francisco Estuary Institute, 2011).

---

* Transfer was done through a memorandum of agreement between the four agencies responsible for compiling the list: U.S. Army Corps of Engineers, USDA Natural Resources Conservation Service, U.S. EPA, and U.S. Fish and Wildlife Service (December 12, 2006).
FIGURE 3.16  Map showing regions used to identify wetland indicator status of U.S. plant species; regions are those used to prepare regional supplements for wetland delineation. (Courtesy of U.S. Army Corps of Engineers, Washington, DC.)

FIGURE 3.17  Number of listed species by wetland indicator status for each region (2016). Codes: AGCP, Atlantic-Gulf Coastal Plain; AW, Arid West; CB, Caribbean; EMP, Eastern Mountains and Piedmont; GP, Great Plains; HI, Hawaii; MW, Midwest; NCNE, Northcentral/Northeast; WMVC, Western Mountains, Valley, and Coast; and AK, Alaska. OBL, obligate wetland; FACW, facultative wetland; FAC, facultative; FACU, facultative upland; and UPL, upland. Note: The only UPL species included on the regional lists were those rated as FACU or wetter in at least one region. (Compiled from data by Lichvar, R.W. et al., Phytoneuron, 2016-30, 1, 2016.)
FIELD INDICATORS OF HYDROPHYTIC VEGETATION

Interpretation of plants as wetland indicators varies according to the approach taken for wetland delineation. To date, the federal government has generally embraced a three-factor approach for identifying regulated wetlands (Environmental Laboratory, 1987, and regional supplements; Federal Interagency Committee for Wetland Delineation, 1989). This approach tends to define hydrophytic vegetation in broad terms (including FAC-dominated communities) because hydric soils and signs of wetland hydrology are usually required to help make the final wetland determination. Another approach used to identify wetlands for inventories and mapping projects—the primary indicators method (PRIMET; Tiner, 1993)—focuses on plant and other indicators that are unique to wetlands for positive wetland identification. This type of approach has gained acceptance for regulatory purposes in some states. For example, state agencies that traditionally used vegetation to identify wetlands, mainly a predominance of FACW and OBL species as positive indicators of hydrophytic vegetation and wetlands, now recognize other plant communities as hydrophytic upon verification of hydrology or hydric soils (see Chapter 6). Table 3.5 outlines field indicators of hydrophytic vegetation used by several sources. Most methods focus on dominant species (i.e., the most abundant plants in a given community), yet the presence of obligate species, in more than extremely limited amounts (i.e., materially present), should be an excellent indicator of wetland.

The best vegetation indicators of wetlands are the genera, species, or subspecies (varieties) that are unique to wetlands—the obligate hydrophytes (see Table 3.3). Whenever these species are common or abundant in an area, the area should be easily recognized as a wetland by vegetation alone. The FACW species also are fairly reliable indicators as they are found mostly in wetlands.

Since the Corps regional supplements are now the basis for determining hydrophytic vegetation for regulatory purposes across the United States, a table highlighting their indicators is provided (Table 3.6). Five hydrophytic vegetation indicators are given; one addressing bryophytes pertains only to the Western Mountains, Valleys, and Coast Region (see preceding table for brief description). For wetland identification, the investigator starts with the first one on the list, then if it is not satisfied, goes to the next one, and so forth. The use of the prevalence index and the morphological adaptations indicators requires that hydric soils and sufficient wetland hydrology indicators are present (see Chapter 6). It should also be recognized that there are provisions in the regional supplements to address “problematic vegetation situations” where the vegetation may not meet the typical hydrophytic vegetation indicators (see Chapter 7 for further discussion).

CONCERNS INTERPRETING FAC AND FACU SPECIES AS HYDROPHYTES

While both OBL and FACW species are universally recognized as useful indicators of wetlands, FAC and FACU species are not reliable wetland indicators and their use in wetland delineation has been contentious (see 56 Federal Register 40446–40480, August 14, 1991). Since they occur in wetlands with some frequency and may even dominate certain types, they have the potential to be hydrophytes (Chapter 6). Hydrophytic members of these species can be recognized in four ways:

1. When associated with OBL and FACW species
2. When they possess certain morphological adaptations
3. After verification of undrained hydric soils
4. By their occurrence in areas with documented wetland hydrology

FAC species, by definition, have essentially no affinity for wetlands or nonwetlands and, therefore, are not indicative of either. This has led to the development of the so-called FAC-neutral rule for determining the presence of hydrophytic vegetation (Environmental Laboratory, 1987)—a rule that is no longer used for that purpose (Williams, 1992), but instead is now used as a wetland hydrology indicator (e.g., the “FAC-neutral test”—U.S. Army Corps of Engineers, 2012). This test does not
Table 3.5

Field Indicators of Hydrophytic Vegetation from Various Sources

<table>
<thead>
<tr>
<th>Indicator</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;50% dominants are OBL, FACW, and/or FAC (the dominance test)</td>
<td>CE, CE-R, FI, WI</td>
</tr>
<tr>
<td>All dominants are OBL and/or FACW (the rapid test)</td>
<td>CE-R</td>
</tr>
<tr>
<td>Prevalence index of 3.0 or less</td>
<td>CE-R</td>
</tr>
<tr>
<td>Prevalence index less than 3.0</td>
<td>FI, FSA</td>
</tr>
<tr>
<td>OBL + FACW species &gt; FACU + UPL species (FAC-neutral test)</td>
<td>CE, FI, FSA</td>
</tr>
<tr>
<td>OBL + FACW species (excluding exotics, vines, and aquatic plants)</td>
<td>FL</td>
</tr>
<tr>
<td>&gt;50% of dominants are FACW and/or OBL species and no FACU or UPL species are dominant#</td>
<td>NY</td>
</tr>
<tr>
<td>FAC and wetter species (excluding FAC species)</td>
<td>MA</td>
</tr>
<tr>
<td>One or more OBL dominants* #</td>
<td>EPA, PRIMET</td>
</tr>
<tr>
<td>OBL perennial species have 10% cover and are evenly distributed throughout the community#</td>
<td>PRIMET, NY</td>
</tr>
<tr>
<td>Any plant community dominated by FACU and wetter species occurring on undrained hydric soils (EPA needs hydrology indicator plus no UPL species, except on microsites)</td>
<td>EPA, FI, PRIMET, MA</td>
</tr>
<tr>
<td>Dominant species with certain morphological adaptations#</td>
<td>CE, FI, EPA, PRIMET, MA, NY</td>
</tr>
<tr>
<td>Communities that meet the &gt;50% dominance test or have a PI ≤3.0 when more than 50% of the FACU individuals (in the wet site) have certain morphological adaptations that are not found in the same species on neighboring upland sites</td>
<td>CE-R</td>
</tr>
<tr>
<td>Plants observed growing in areas flooded or saturated for 10% or more of the growing season</td>
<td>CE</td>
</tr>
<tr>
<td>Plants with known physiological adaptations for life in saturated soils</td>
<td>CE, EPA</td>
</tr>
<tr>
<td>Plants with known reproductive adaptations for life in wetlands</td>
<td>CE, EPA</td>
</tr>
<tr>
<td>Plants reported in the literature growing in wetlands</td>
<td>CE</td>
</tr>
<tr>
<td>Patches (expanses) of peat moss (<em>Sphagnum</em> spp.)</td>
<td>PRIMET, RI, NY</td>
</tr>
<tr>
<td>More than 50% of the total cover of bryophytes consists of species known to be highly associated with wetlands (<em>Chiloscyphus pallescens</em>, <em>Eurhynchium praelongum</em>, <em>Rhizomnium glabrescens</em>, <em>R. magnifolium</em>, <em>Riccardia latifrons</em>, <em>Sphagnum angustifolium</em>, and <em>S. palustre</em>; designed for use in coastal OR and WA but may be applicable elsewhere in the region)</td>
<td>CE-R-W</td>
</tr>
<tr>
<td>Plants listed in the wetland protection act</td>
<td>FL, MA, NY, RI</td>
</tr>
<tr>
<td>FACW, FAC, and/or FACU species with other indicators of wetland hydrology</td>
<td>RI</td>
</tr>
</tbody>
</table>

Sources: Federal interagency manual (FI; Federal Interagency Committee for Wetland Delineation, 1989); Corps manual (CE; Environmental Laboratory, 1987); Corps manual regional supplements (CE-R; e.g., U.S. Army Corps of Engineers, 2012), Corps regional supplement for Western Mountains, Valleys, and Coast Region (CE-R-W; U.S. Army Corps of Engineers, 2010); Food Security Act manual (FSA; USDA Natural Resources Conservation Service, 1994); EPA manual (EPA; Sipple, 1988); Primary indicators method (PRIMET; Tiner, 1993); Florida manual (FL; Florida Dept. of Environmental Protection et al., 1995); Massachusetts manual (MA; Jackson, 1995); New York manual (NY; Browne et al., 1996); Rhode Island procedures (RI; Rhode Island Dept. of Environmental Management, 1994); Wisconsin procedures (WI; Wisconsin Coastal Management Program, 1995).

Notes: An asterisk (*) denotes applicability of indicator in the absence of significant drainage. A pound sign (#) means that the indicator is also used to verify the presence of wetland under PRIMET or NY procedures.

utilize FAC species, but weighs the abundance of OBL and FACW species against the abundance of FACU and UPL species. According to the Corps regional supplements, a positive test (OBL + FACW > FACU + UPL) may be used as a secondary indicator of wetland hydrology.

While FAC species may not be reliable indicators of wetlands (due to their equal occurrence in wetlands and uplands), they dominate many forested wetlands across the country. Examples of
TABLE 3.6
Applicable Indicators of Hydrophytic Vegetation across Regions of the United States according to the Regional Supplements to the Corps Wetlands Delineation Manual

<table>
<thead>
<tr>
<th>Code</th>
<th>Indicator</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Alaska</td>
</tr>
<tr>
<td>1</td>
<td>Rapid test</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>Dominance test</td>
<td>X</td>
</tr>
<tr>
<td>3</td>
<td>Prevalence index</td>
<td>X</td>
</tr>
<tr>
<td>4</td>
<td>Morphological adaptations</td>
<td>X</td>
</tr>
<tr>
<td>5</td>
<td>Wetland non-vascular plants</td>
<td>—</td>
</tr>
</tbody>
</table>

Sources: Courtesy of Jacob Berkowitz, U.S. Army Corps of Engineers, Washington, DC.

Note the earliest regional supplements (Alaska, 2007; Arid West, 2008) did not include the rapid test; it was developed later and included in the other supplements.

Rapid test—all dominants are OBL and/or FACW based on a visual assessment.
Dominance test—>50% of the dominant species are FAC or wetter.
Prevalence index (PI)—PI ≤ 3.0 (weighted average test).
Morphological adaptations—used these properties to identify FACU species as hydrophytes.
Wetland non-vascular plants—more than 50% of the total coverage of bryophytes consists of species highly associated with wetlands (list provided in supplement).
See Chapter 4 for examples of tests.
some dominant hydrophytic FAC trees include red maple, black gum, sweet gum, eastern cottonwood, balsam fir (A. balsamea), yellow birch, water oak (Quercus nigra), loblolly pine, ironwood (Carpinus caroliniana), quaking aspen (Populus tremuloides), Engelmann spruce (P. engelmannii), and western red cedar (T. plicata).* FAC species are well adapted to wetlands. For example, loblolly pine’s ability to withstand waterlogging is well known among foresters due to its commercial significance. McKevlin et al. (1987) described seedling adaptations including stem hypertrophy, hypertrophied lenticels (on stem and roots), soil water roots, aerenchyma (large lacunae), and an internal aeration system. Loblolly pine is tolerant of prolonged anaerobic conditions extending from winter through early spring and achieves some of its best growth under these circumstances. In studying several Louisiana stands, Hu and Linnartz (1972) found that the wettest sites had the highest loblolly pine site index values (most productive sites). The availability of water early in the growing season may be more important for plant growth than an adequate oxygen level in the soil.

FACU species (plants that are typically found in nonwetlands) are more contentious as wetland species, since by definition they occur more in uplands than in wetlands. Some species are quite common in wetlands and when growing under such conditions are hydrophytic. In his monograph on the development of the vegetation of New York state, Bray (1930) reported two FACU species, white pine (Pinus strobus) and eastern hemlock (T. canadensis), as common forested wetland species, commenting that “the fact that very big trees of pine and hemlock do occur in typical swamp forest seems to me noteworthy and to be deserving of special study.” Eastern hemlock typifies certain familiar wetland types called hemlock swamps in the Northeast (Niering, 1953; Hueneke, 1982; Tiner, 1989, 1998). In another classic vegetation study, Curtis (1959) reported that white pine occurred in 37% of the tamarack or black spruce bogs in Wisconsin and even dominated some northern stands on more than 10 ft (3 m) of peat. He also found two other FACU species to be common in wetlands—jack pine (P. banksiana) in similar situations and sugar maple (Acer saccharum) in some wet-mesic forests dominated by northern white cedar (Thuja occidentalis; FACW) and balsam fir (FAC). Crum (1988) observed white pine and jack pine in Michigan bogs, along with beech (Fagus grandifolia; FACU) and sugar maple (A. saccharum; FACU) seedlings that failed to persist. He felt that the first two were examples of broad tolerances, while the latter two were freak occurrences. He also noted that white spruce (Picea glauca; FACU) was a characteristic peatland species and that some rather large red pines (P. resinosa; FACU) were found in Michigan bogs. Pitch pine (P. rigida) is a FACU species with a remarkable range in wet and dry tolerances, growing on excessively drained soils to poorly drained sands and gravels, mucks, and peats (Illick and Augustnau, 1930; Little, 1959; Ledig and Little, 1979; personal observations). Subalpine fir (A. lasiocarpa) dominates many western forested wetlands (see Table 9.8). These types of plants demonstrate considerable ecological plasticity and create a serious perception problem when attempting to depict these plant species as hydrophytes or wetland plants. While the general public may have some difficulty understanding that FACU species can be hydrophytes, wetland ecologists should not, recognizing the ecological amplitude of and the possibility of ecotypes for many species. Moreover, the problem with FACU species is an artifact of our attempt to use the species level to identify wetland indicators. The individual FACU plants growing in wetlands are well adapted to a wetland existence. Individual plants are continually adapting to varied environmental conditions in the pursuit of life and survival of the species.

For wetland identification purposes following the Corps regional supplements (e.g., U.S. Army Corps of Engineers, 2010, 2012), FACU species can be recognized as hydrophytic when the plants grow on a site with verified hydric soils and sufficient signs of wetland hydrology. More than 50% of the individuals must, however, have morphological adaptations for life in wetlands (e.g., adventitious roots, hypertrophied lenticels, multistemmed trunks, and shallow root systems), and such features are not common on the plants of the same species growing on adjacent nonhydric soils.

* Some of these species have drier or wetter statuses in some regions.
**HUMAN EFFECTS ON WETLAND PLANT DISTRIBUTION**

The occurrence of a plant species on the landscape can be drastically changed by human disturbance or interference. This further complicates the potential use of plants to identify wetlands. Specifically, the distribution and abundance of many plants have been significantly impacted by forestry practices, agricultural activities, urban development, drainage projects, water diversion, pollution, and other human-induced actions. Planted crops, either agricultural or silvicultural, provide little information on the types of plants that would naturally grow in an area. Also human society’s suppression of fires on the landscape has created more favorable conditions for fire-intolerant plants. At the time of this country’s settlement, in southern New England white pine was probably only abundant in swamps and moist sandy flats and on exposed ridges due to its susceptibility to fire (Bromley, 1935); today it is found across the landscape. In Louisiana and probably elsewhere in the Southeast, many dry flatwoods were originally dominated by longleaf pine, whereas loblolly pine and hardwoods characterized the wetter ones (Hu and Linnartz, 1972). In precolonial times, loblolly pine was a minor species in both uplands and river bottomlands and swamps, being an important species of moist forests that were not subject to burning, especially those along the coastal plain* (Schultz, 1997). Given loblolly’s limited tolerance to fire, the occurrence of most pure stands of this pine was likely found in areas recently opened by hurricanes, fire, or clearing by Native Americans. Changing environmental conditions greatly affected its distribution. Now loblolly pine and hardwoods or loblolly pine plantations probably occupy the bulk of the flatwoods in much of the Southeast. Forestry practices and the suppression of forest fires have significantly altered the composition of many, if not most, forests in much of the conterminous United States. Many species now grow on better drained sites where they probably were not particularly abundant before. Consequently, the present-day abundance and distribution of eastern white pine and loblolly pine may be largely attributed to human intervention.

Areas that are annually tilled and planted with row crops offer only limited information on the current wetness of the site. The success of exotic annual weeds associated with agriculture has further complicated the interpretation of vegetation as indicators of wetland. The effects of past drainage on wetlands once used for agriculture but now abandoned create a sometimes confusing pattern of vegetation to interpret. Recovery of wetland vegetation may take some time in these cases and the present community may be a mixture of drier-site species and a few typical wetland species and may gradually move toward becoming more typically hydrophytic.

Nonnative species, sometimes associated with agriculture (e.g., planted as row crops or for hayfields, timber, or as windbreaks, or unintentionally introduced), horticulture (e.g., escapes from gardens or nurseries), or accidentally introduced in harbors on ballast, have invaded and altered native plant communities including wetlands (e.g., Zedler and Kercher, 2004). In general, many of these invasive species were rated as FAC or wetter species that do not affect hydrophytic vegetation determinations, yet some are FACU species. Table 3.7 lists some invasive species common to wetlands, with FACU species noted.

Wetland delineators must be particularly mindful of the situations mentioned earlier or else risk misjudging a plant species’ ecological significance. The twentieth-century landscape can be a most confounding ecological expression to decipher due to the great impact of urban development, agricultural and grazing practices, hydrologic alteration, and natural resource management.

**USING PLANTS TO PREDICT ENVIRONMENTAL CONDITIONS IN WETLANDS**

Besides their use in wetland identification, plants also may be used as indicators of other environmental conditions associated with certain types of wetlands. Plants with low tolerances or narrow

---

* The name “loblolly” was probably attributed to this pine because in colonial times it was commonly found in low, wet spots called “loblollies”; another common name “oldfield pine” relates to the plant’s rapid colonization of abandoned farm fields (Schultz, 1997, who provides a comprehensive treatment of the ecology and culture of *P. taeda*).
### TABLE 3.7
Some Common Invasive Species in Eastern and Midwestern U.S. Wetlands

<table>
<thead>
<tr>
<th>Life-Form</th>
<th>Species</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic</td>
<td>Alternanthera philoxeroides (alligatorweed)</td>
<td>Southeast</td>
</tr>
<tr>
<td></td>
<td>Eichhornia crassipes (water hyacinth)</td>
<td>Southeast</td>
</tr>
<tr>
<td></td>
<td>Hydrilla verticillata (hydrilla)</td>
<td>Northeast, Southeast</td>
</tr>
<tr>
<td></td>
<td>Trapa natans (water chestnut)</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Myriophyllum spicatum (Eurasian water milfoil)</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Myriophyllum aquaticum (parrotfeather)</td>
<td>Northeast, Southeast</td>
</tr>
<tr>
<td></td>
<td>Salvia minima (common salvia)</td>
<td>Southeast</td>
</tr>
<tr>
<td></td>
<td>Salvia molesta (giant salvia)</td>
<td>Midwest, Southeast</td>
</tr>
<tr>
<td></td>
<td>Pistia stratiotes (water lettuce)</td>
<td>Southeast</td>
</tr>
<tr>
<td>Emergent herb</td>
<td>Phragmites australis (common reed)</td>
<td>Northeast</td>
</tr>
<tr>
<td></td>
<td>Phalaris arundinacea (reed canary grass)</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Lythrum salicaria (purple loosestrife)</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Microstegium vimineum (Japanese stilt-grass)</td>
<td>Northeast, Midwest, Southeast</td>
</tr>
<tr>
<td></td>
<td>Polygonum perfoliatum (mile-a-minute weed)</td>
<td>Northeast</td>
</tr>
<tr>
<td></td>
<td>Iris pseudacorus (yellow flag)</td>
<td>Northeast</td>
</tr>
<tr>
<td></td>
<td>Alliaria petiolata (garlic mustard)*</td>
<td>Midwest</td>
</tr>
<tr>
<td></td>
<td>Polygonum cuspidatum (Japanese knotweed)*</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Typha × glauca (hybrid cattail)</td>
<td>Northeast, Midwest, Southeast</td>
</tr>
<tr>
<td></td>
<td>Typha angustifolia (narrow-leaved cattail)</td>
<td>Midwest</td>
</tr>
<tr>
<td></td>
<td>Lysimachia nummularia (moneywort)</td>
<td>Midwest</td>
</tr>
<tr>
<td></td>
<td>Panicum repens (torpedo grass)</td>
<td>Florida</td>
</tr>
<tr>
<td></td>
<td>Urochloa mutica (pará grass)</td>
<td>Florida</td>
</tr>
<tr>
<td>Shrub</td>
<td>Frangula alnus (glossy or European buckthorn)</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Rhamnus cathartica (common buckthorn)</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Rosa multiflora (multiflora rose)*</td>
<td>Northeast, Midwest</td>
</tr>
<tr>
<td></td>
<td>Lonicera morrowii and L. tatarica (bush honeysuckles)*</td>
<td>Northeast, Midwest, Southeast</td>
</tr>
<tr>
<td></td>
<td>Schinus terebinthifolius (Brazilian pepper)</td>
<td>Florida</td>
</tr>
<tr>
<td>Tree</td>
<td>Triadica sebifera (Chinese tallow)</td>
<td>Southeast</td>
</tr>
<tr>
<td></td>
<td>Melaleuca quinquenervia (punktree)</td>
<td>Florida</td>
</tr>
</tbody>
</table>


* Designates FACU species; others are FAC or wetter. Species listed may also be invasive in regions not noted. Also there are many other common invasive aquatics; only a few are listed here.
ranges of occurrence are reliable indicators of conditions such as hydrology, water chemistry, and other situations. Knowing the sensitivity of various plants to these conditions may help with attempts to classify wetlands. While certain species of plants may be universally useful predictors of certain environmental conditions, other species may vary in their distribution locally and may have only limited application for indicating a particular environmental condition. An introduction to how plants can be used in this regard follows.

**PLANTS AS HYDROLOGY INDICATORS**

Aquatic plants and many other species occur within a fairly narrow range of hydrologic conditions. These species can be used to distinguish different water regimes in coastal and inland wetlands (Table 3.8). In some cases, their vigor or robustness may be indicative of certain conditions such as the tall form of smooth cordgrass (*S. alterniflora*) for daily tidal inundation and the short form for less flooded areas where salt concentration buildup and soils are more reduced (producing the stunted form).

Many other plants have a wide range of tolerance for wetness ranging from swamps to neighboring uplands (e.g., red maple and loblolly pine). Certain species, although widely distributed in wetlands, may occur in greater abundance in wetter or drier circumstances. Busch et al. (1998) found Gulf Coast spike rush (*Eleocharis cellulosa*) in higher densities in the wettest marshes of the southern Everglades where it was the only species positively correlated with water depth, while the density of sawgrass (*Cladium jamaicense*) was inversely correlated with water depth—being more common at higher elevations with shorter hydroperiods.

Relationships between plant species and plant communities and water depth during the growing season have been reported by numerous researchers (e.g., Hall et al., 1946, Stewart and Kantrud, 1972, Thomas and Stewart, 1969, Shipley et al., 1991, Ferreira, 2000, Seabloom et al., 2001, Sorrell and Hawes, 2010, Strayer and Findlay, 2010). The collective works of Allen-Diaz (1991), Ratliff (1985), Dwire et al. (2006), Castelli et al. (2000), Chambers and Miller (2004), and Cooper (1990) describe these relationships for montane meadows in the western United States. In Nevada, Castelli et al. found Nebraska sedge (*Carex nebrascensis*) to be the most reliable indicator of shallow water table, as it occurred consistently at water tables of 0–12 in. (0–30 cm) below the surface.

Numerous studies have been conducted on the flood tolerance of plants (e.g., Broadfoot and Williston, 1973; Theriot, 1993). While such studies did not likely take into account the existence of ecotypes, the studies do provide some useful information on the likelihood of occurrence of certain species in flood-prone areas.

Other species may be frequently associated with disturbance and their presence may indicate alterations of hydrology (e.g., common reed in tidally restricted wetlands, cattails in lakes with now stabilized water levels such as Lake Ontario, and black cherry [*Prunus serotina*] in partly drained eastern forested wetlands) (Wilcox, 1995; personal observations).

**PLANTS AS INDICATORS OF WATER SOURCES**

Attempts to use plants to locate water go back to ancient times. A government report “Plants as Indicators of Ground Water” by Meinzer (1927) offers an interesting account of how certain plants in arid regions may be used to indicate groundwater conditions. Meinzer* quotes Vitruvius, a Roman architect/engineer, who he claims to be the first writer to advocate the modern theory of the origin of groundwater (p. 8):

Besides these there are other indications of places where water can be found namely, the presence of small rushes, willows which are not planted, alder trees, vitex, reeds, ivy, and all other such plants

---

* Meinzer may have created the term “phreatophyte,” which addresses plants growing in dry places where they must extend their roots deep into the soil to obtain “a perennial and secure supply of water” from the water table or capillary fringe; he used it in a 1923 U.S. Geological Survey Water-Supply Paper 494 (p. 55).
### TABLE 3.8
Examples of Potential Indicator Species for Certain Water Regimes in Different Parts of the United States

<table>
<thead>
<tr>
<th>Region</th>
<th>Water Regime</th>
<th>Indicator Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>East</td>
<td>Permanently flooded</td>
<td><em>Nymphaea odorata, Brasenia schreberi, Nuphar luteum, Potamogeton spp., Ceratophyllum, Najas, Myriophyllum</em></td>
</tr>
<tr>
<td></td>
<td>Semipermanently flooded</td>
<td><em>Scirpus validus, S. acutus, Sparganium eurycarpum, Pontederia cordata, Sagittaria latifolia, Decodon verticillata, Cephalanthus occidentalis</em></td>
</tr>
<tr>
<td></td>
<td>Seasonally flooded</td>
<td><em>Saussurea cerna, Leersia oryzoides, Acorus calamus, Carex crinita, Thelypteris thelypteroides, Woodwertia areolata, Polygonum sagittatum, Asclepias incarnata, Eupatorium perfoliatum, Chelone glabra, Senecio aureus, Symphocarpus foetidus, Glyceria striata, Rhododendron viscosum,  Ilex verticillata, Itea virginica, Magnolia virginiana, Salix nigra, Chamomorapis thyoides, Nyssa sylvatica biflora, Populus heterophylla, Mikania scandens</em></td>
</tr>
<tr>
<td></td>
<td>Temporarily flooded</td>
<td><em>Geum canadense, Cryptotaenia canadensis, Polygonum virginicum, Allaria petiolata, Leersia virginica, Laportea canadensis, Asimina triloba, Platanus occidentalis, Populus deltoides, Carya cordiformis, Acer negundo, Acer saccharinum, Ilex opaca</em></td>
</tr>
<tr>
<td></td>
<td>Continuously saturated</td>
<td><em>Sarracenia purpurea, Drosera rotundifolia, Rhynchospora alba, Ledum groenlandicum, Vaccinium macrocarpon, Andromeda glaucophylla, Kalma polifolia, Empetrum nigrum, Carex exilis</em></td>
</tr>
<tr>
<td>Interior West</td>
<td>Semipermanently flooded</td>
<td><em>Scirpus acutus, S. maritimus, S. validus, S. heterocharaetus, S. fluviatilis, Typha latifolia, T. glauca, T. angustifolia</em></td>
</tr>
<tr>
<td></td>
<td>Seasonally flooded</td>
<td><em>Eleocharis palustris, Scirpus americanus, Sium suave, Alisma spp., Beckmannia syzigachne, Carex atherodes, Polygonum coccineum, Sparganium eurycarpum, Allopecurus aequalis, Glyceria grandis, Glyceria striata, Schoenoclaa festucacea, Sagittaria cuneata</em></td>
</tr>
<tr>
<td></td>
<td>Temporarily flooded</td>
<td><em>Distichlis spicata, Hordeum jubatum, Poa palustris, Juncus balticus, Spartina pectinata, Calamagrostis inexpansa, C. canadensis, Carex sartwellii, C. lanuginosa, C. praegracilis, Agronzyron repens, Echinocloa cras-galli, Polygonum lapathifolium, Aster simplex, Bidens frondosa</em></td>
</tr>
<tr>
<td></td>
<td>Continuously saturated</td>
<td><em>Calamagrostis inexpansa, Pedicularis groenlandica, Caltha leptosepala</em></td>
</tr>
<tr>
<td>Alaska</td>
<td>Permanently flooded</td>
<td><em>Arctophila fulva, Hippuris vulgaris</em></td>
</tr>
<tr>
<td></td>
<td>Semipermanently flooded</td>
<td><em>Carex aquatilis, Equisetum fluviatile</em></td>
</tr>
<tr>
<td></td>
<td>Seasonally flooded</td>
<td><em>Eriophorum angustifolium, Carex stichensis</em></td>
</tr>
<tr>
<td></td>
<td>Temporarily flooded</td>
<td><em>Populus balsamifera, Equisetum arvense</em></td>
</tr>
<tr>
<td></td>
<td>Continuously saturated</td>
<td><em>Betula nana, Picea mariana, Eriophorum vaginatum</em></td>
</tr>
<tr>
<td>East Coast</td>
<td>Regularly flooded*</td>
<td><em>Spartina alterniflora (tall form), Amaranthus cannabinus, Nuphar luteum, Pontederia cordata, Petalandra virginica, Scirpus validus, Zizania aquatica, Crassula aquatica, Heterethera reniformis, Alternanthera philoxeroides, Orontium aquaticum, Isoetes riparia, Sparganium americanum, Limosella subulata, Decodon verticillatus, Aspogodium nodosum, Fucus vesiculosus, Ulva lactuca</em></td>
</tr>
<tr>
<td></td>
<td>Irregularly flooded*</td>
<td><em>Spartina patens, S. cynosuroides, S. pectinata, S. alterniflora (short form), Distichilis spicata, Juncus gerardii, J. balticus, Iva frutescens, Scirpus maritimus, S. robustus, Solidago sempervirens, Aster tenuifolius, Lythrum lineare, Cladium mariscoides, Hibiscus moscheutos, Kosteletzkya virginica, Rosa palustris, Juncus roemerianus (in salt marsh)</em></td>
</tr>
</tbody>
</table>

(Continued)
TABLE 3.8 (Continued)
Examples of Potential Indicator Species for Certain Water Regimes in Different Parts of the United States

<table>
<thead>
<tr>
<th>Region</th>
<th>Water Regime</th>
<th>Indicator Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Florida</td>
<td>Regularly flooded*</td>
<td>Spartina alterniflora (tall form)</td>
</tr>
<tr>
<td></td>
<td>Irregularly flooded*</td>
<td>Batis maritima, Borrichia frutescens, Salicornia virginica, Conocarpus erectus, Monanthochloa littoralis</td>
</tr>
<tr>
<td>West Coast</td>
<td>Regularly flooded*</td>
<td>Monanthochloa littoralis, Frankenia grandifolia, Distichlis spicata, Cressa truxillensis, Cuscuta salina, Salicornia virginica, Jaumea carnosa, Triglochin maritimum, Limonium californicum</td>
</tr>
<tr>
<td>Alaska</td>
<td>Regularly flooded*</td>
<td>Triglochin maritimum, Salicornia europaea</td>
</tr>
<tr>
<td></td>
<td>Irregularly flooded*</td>
<td>Carex subspathacea, C. ramenski, Potentilla anserina, Elymus arenarius</td>
</tr>
</tbody>
</table>


Notes: Tidal regimes are marked by an asterisk (*); these species include both estuarine and tidal freshwater plants. Species listed may generally be used to predict water regimes, especially when common or dominant. Some of these species may also occur in other situations but usually in lesser abundance. Scientific names for some species have changed.

which occur and thrive only in places where there is water. One must not rely on these plants, however, if they occur in marshes, where being lower than the surrounding country, receive and collect and for some time retain rain waters that fall on the near-by fields in winter; but if these plants occur naturally in places that are not marshes, one can seek for water in these places.

These statements suggest that if you are not in a marsh, but find these types of plants growing naturally, that place may be wet and you can look for water (groundwater) there. Meinzer also provided a short list of plants that occur where water is seasonally at or near the surface in the desert, many of which are phreatophytes and extend their roots deep into the soil. Among the listed species were rushes, sedges, common reed, giant wild rye (Elymus condensatus), salt grass (Distichlis spicata), pickleweed (Allenrolfea occidentalis), and willows.

With more of a focus on predicting water source in humid regions, Goslee et al. (1997) have attempted to use plant species to determine whether a wetland is groundwater fed or surface water driven. After examining 379 plots in 28 wetlands in central Pennsylvania and comparing vegetation with hydrologic data, they found some species highly correlated with a particular water source, while others showed no preference. Among the indicators of groundwater were yellow birch, black gum, eastern hemlock, rosebay rhododendron (Rhododendron maximum), silky dogwood (Corylus amomum), marsh St. John’s-wort (Triadenum virginicum), goldthread (Coptis groenlandica), marsh fern (Thelypteris palustris), swamp dewberry (Rubus hispidus), and sedges (Carex emoryi, C. folliculata, and C. intumescens). Species associated with seasonal surface water included many drier-site species such as timothy (P. pratense), multiflora rose (Rosa multiflora), stinging nettle (Urtica dioica), and dandelion (Taraxacum officinale), plus poison ivy (Toxicodendron radicans). Skunk cabbage (Symplocarpus foetidus) also was listed as a surface water indicator, while elsewhere in
the Northeast it also seems to be widely associated with groundwater seepage (personal observations). The authors did, however, caution readers that the list of indicators needs to be developed on a regional basis. Such regions may actually be more local areas having similar geology and soils. Other studies examining the relationship between vegetation and water sources include Grootjans et al. (1988), Vostokova (1965), and Wassen et al. (1989).

In mineral-poor wetlands that receive input of groundwater, there may be a shift in the plant community at and near the source of the minerotrophic water. At the source, more minerotrophic species may be found, whereas further from the groundwater source, oligotrophic species typical of mineral-poor wetlands predominate. Daniel (1981) described this condition for Carolina bay wetlands and the Great Dismal Swamp (Virginia/North Carolina) where minerotrophic forested wetlands dominate the edges and oligotrophic bog-type species abound in the bay interior. This situation also is common in northern peatlands where a nutrient-poor bog is surrounded by a narrow marginal band of fen or swamp species indicative of minerotrophic conditions (the “lagg” - Howie and Tromp-van Meerveld, 2011). Groundwater and surface runoff from adjacent lands introduce more nutrients to the edge of the complex.

**Plants as Water Chemistry Indicators**

Water chemistry also can be predicted by the existence of certain species. It may be possible to interpret the average salinity of a given wetland or the general pH level (acid, neutral, alkaline) by noting the occurrence of particular species or groups of species. It is usually best to use a group of species, since most species have some degree of latitude in tolerance. However, those species with rather narrow ranges can by themselves be useful indicators of water chemistry conditions.

Many wetlands are subjected to salt stress due to flooding by salt-laden tides in coastal regions and by high evaporation in subhumid, semiarid, and arid regions. In coastal areas, tidal waters with ocean-derived salts, mainly sodium chloride, induce this stress. With increasing mixing with freshwater as one moves upstream in tidally influenced rivers, salt stress is reduced and vegetation composition changes. Tidal wetlands have salinities ranging from above sea strength, which is roughly 35 parts per thousand (ppt) of salt to fresh (<0.5 ppt). The U.S. federal wetland classification system has six categories for salinity—hyperhaline (>40 ppt), euhaline (30–40 ppt), mixohaline (0.5–30 ppt), polyhaline (18–30 ppt), mesohaline (5–18 ppt), oligohaline (0.5–5 ppt), and fresh (Cowardin et al., 1979). Soil salinity is quite dynamic due to tidal fluctuations, freshwater inflows, and rainfall. It seems that species occurrence in an area then may be related to its maximum tolerance with the most salt-tolerant species in the pannes (depressions) of salt marshes and the least salt-tolerant along the upland edges of salt marshes and in brackish marshes where more dilution occurs. Some examples of common tidal halophytes that may serve as useful predictors of salinity regimes are listed in Table 3.9. Common reed may be an indicator of reduced salinity (degraded salt marshes) in the Northeast since it often supplants typical salt marsh species where tidal flow is severely reduced or eliminated.

In dry climates, high evaporation of groundwater in the capillary fringe results in a buildup of four major cations (calcium, magnesium, sodium, and potassium) and three major anions (bicarbonate, sulfate, and chloride) that affect plant distribution. Salinity for inland areas is measured by specific conductance reported in microsiemens per centimeter at 25°C (µS/cm), microhoms (Mhos), or parts per million (ppm). The official U.S. federal wetland classification system identified six categories: hypersaline (>60,000 µS/cm), eusaline (45,000–60,000 µS/cm), polysaline (30,000–45,000 µS/cm), mesosaline (8,000–30,000 µS/cm), oligosaline (800–8,000 µS/cm), and fresh (<800 µS/cm) (Cowardin et al., 1979; LaBaugh, 1989). In the pothole region of North America, Stewart and Kantrud (1972) and Millar (1976) have described vegetation associated with different degrees of salinity. Like their coastal counterparts, inland saline wetlands experience variable levels of salt stress during the year, but they also endure significant annual changes during the course of the wet–dry hydrologic cycle (Lieffers and Shay, 1983). Mesosaline indicator species may include red saltwort (*Salicornia rubra*), Pursh seepweed (*Suaeda depressa*), three-square (*Schoenoplectus americanus*),
Nuttall’s alkali grass (Puccinellia nuttalliana), seaside arrowgrass (Triglochin maritimum), cordgrass (Spartina gracilis), and alkali muhly (Muhlenbergia asperifolia) (Kantrud et al., 1989). Oligosaline indicators in the prairies are whitetop (Scolochloa festucacea), silverweed (Potentilla anserina), and biennial wormwood (Artemisia biennis), while freshwater indicators include slender bulrush (Schoenoplectus heterochaetus), soft-stemmed bulrush (Schoenoplectus tabernaemontani), reed meadowgrass (Glyceria maxima), reed canary grass (P. arundinacea), and short-awn foxtail (Alopecurus aequalis). Some salinity indicator species for western wetlands also are associated with particular water regimes and therefore may be useful predictors of both salinity and water regime (see Kantrud et al., 1989, for a more complete listing of species and their maximum, minimum, and mean specific conductance tolerances).

Another important set of water chemistry variables is pH or hydrogen ion concentration. It is used to separate acidic (pH < 5.5) from circumneutral (pH 5.5–7.4) from alkaline (pH > 7.4) wetlands. Many plants may be sensitive to differences in pH and therefore may be useful for recognizing calcareous conditions of minerotrophic fens or nutrient-poor acidic wetlands (Table 3.10). Gorham and Janssens (1992) examined 440 plots from North American peatlands and found that bryophytes were useful for separating bogs from fens: members of the Sphagnaceae dominated bogs with a pH mode of 4.10–4.25, whereas Amblystegiaceae were characteristic of fens with a pH mode of 6.76–7.00. In studying the vegetation of coastal wetlands along the Great Lakes, Minc and Albert (1998) used various calciphiles to distinguish the northern rich fen type from other wetlands. Key species included yellow sedge (Carex viridula) and Kalm’s lobelia (Lobelia kalmii), plus some others listed...
TABLE 3.10
Some Wetland Plant Indicators of Acid and Circumneutral to Alkaline (Calcareous) Conditions in the Glaciated Northern States

<table>
<thead>
<tr>
<th>Acidic indicators</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trees:</strong> Picea mariana</td>
</tr>
<tr>
<td><strong>Shrubs:</strong> Vaccinium vitis-idaea, Gaultheria procumbens, G. hispidula, Ledum groenlandicum, Kalmia polifolia, Vaccinium oxyccocos</td>
</tr>
<tr>
<td><strong>Herbs:</strong> Carex trisperma, C. oligosperma, C. pauciflora, Eriophorum spissum, Smilacina trifolia</td>
</tr>
<tr>
<td><strong>Mosses:</strong> Pleurozium schreberi, Dicranum sp.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Circumneutral to alkaline indicators</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Trees:</strong> Thuja occidentalis</td>
</tr>
<tr>
<td><strong>Shrubs:</strong> Potentilla fruticosa, Rhamnus alnifolia, Salix candida, S. pedicellaris, S. serissima, Lonicera oblongifolia, Rubus pubescens, Betula pumila, Toxicodendron vernix, Myrica pensylvanica</td>
</tr>
</tbody>
</table>


*Includes mostly calciphiles (calcium-loving species).*

in Table 3.10. It is interesting that some calciphiles are typical halophytes, characteristic of northeastern salt and brackish marshes, such as twig rush (*Cladium mariscoides*), silverweed (*P. anserina*), and seaside arrowgrass (*T. maritimum*). Most ericaceous shrubs are indicators of nutrient-poor conditions. They are well represented in bogs and pocosins, which are low-nutrient, acidic wetlands in the northern and southern regions, respectively. In his study of peatlands in Saskatchewan, Jeglum (1971) found good correlations between vegetation and pH and water levels. He also concluded that groups of species were the most reliable predictors of pH and water levels. Glaser (1992) summarized information on vegetation and water chemistry for Minnesota peatlands. Lagg (moat) vegetation found around many northern bogs is characterized by minerotrophic species like speckled alder and northern white cedar providing evidence of mineral-rich water at the margins in stark contrast to the ericaceous shrubs (e.g., leatherleaf, Labrador tea, and sheep laurel) of the nutrient-poor bog interior. The presence of cattails along the margins of some bogs at road and railroad crossings, for example, provides evidence of higher nutrient levels, perhaps introductions from road runoff.

Changes in water chemistry may be detected by the arrival of new species in watersheds. The best examples of this can be found where naturally acidic, nutrient-poor streams are subjected to nutrient loading from expanding development or agriculture. Significant changes in understory species of Atlantic white cedar swamps in suburbanizing watersheds were reported in the New Jersey Pine Barrens (Ehrenfeld, 1983; Ehrenfeld and Schneider, 1991, 1993). Weedy, cosmopolitan species were replacing native acidic, nutrient-poor indicators such as tussock sedge, round-leaved sundew (*Drosera rotundifolia*), golden club (*Orontium aquaticum*), bog aster (*Aster nemoralis*), swamp pink (*Helonias bullata*), cotton grass (*Eriophorum virginicum*), and bladderworts (*Utricularia* spp.). For this area, Zampella and Laidig (1997) identified numerous disturbance indicator species, with water starwort (*Callitriche heterophylla*), lurid sedge (*Carex lurida*), dye bedstraw (*Galium tinctorium*), jewelweed (*I. capensis*), water purslane (*L. palustris*), climbing hempweed (*M. scandens*), arrow-leaved tearthumb
Wetland Indicators

(*Polygonum sagittatum*), and Nepal microstegium (*Eulalia viminea*) being among the more common. The latter is an invasive exotic species that has become a dominant herb in many forested wetlands in New Jersey. Disturbance in other naturally acidic areas may be detected by the presence of minerotrophic species.

**Plants as Indicators of Pollution and Disturbance**

Changes in vegetation typically accompany water pollution and other disturbances from urban and agricultural development. When excess nutrients enter waterways and waterbodies, there is usually a vegetation response, especially when the preexisting condition was nutrient poor. An excellent example of this was briefly described earlier where development in and around the New Jersey Pine Barrens has provided opportunities for the establishment of many disturbance species (e.g., Ehrenfeld and Schneider, 1993). The occurrence of cattails in a bog is another such sign of pollution—nutrient enrichment that may also be tied to hydrologic changes. Three widespread emergents recognized as possible indicators of eutrophication are cattails, reed canary grass, and common reed; they are invasive species that replace native plants and form virtual monocultures. In agricultural areas, nutrient loading is common and readily observed in local ponds that are filled with algae and/or duckweeds (*Lemna* spp.) or by blooms of cyanobacteria breakout in lakes, reservoirs, and rivers. This is a common occurrence across the country. Various indices have been developed to evaluate water quality using algae and cyanobacteria (Nygaaard, 1949; Palmer, 1969, 1977). The U.S. EPA (2002a) has published a guidebook to using vegetation as indicators of nutrient enrichment that include, among other plant-based metrics, determination of the number of enrichment-tolerant and enrichment-intolerant species. As an example of these species for the Florida Everglades, cattail, duckweed, and leather fern (*Acrostichum danaeifolium*) are listed as enrichment-tolerant species, while bladderworts (*Utricularia* spp.) are the intolerant ones.

Disturbances such as increased sedimentation, mowing, grazing, fire, and timber harvest also can produce changes in species composition. The Corps regional supplements for the Midwest and Great Plains provide lists of some species that increase and decrease with grazing and others that are weedy species associated with farm fields (Table 3.11). The regional supplement for Alaska contains a list of bryophytes that may be used to help identify wetlands where black spruce has been removed; if the cover of these species is >50%, the vegetation is considered hydrophytic (Table 3.12).

Altered hydrology is another disturbance where less water-tolerant plants replace native species. In many cases, nonnative, invasive species tend to colonize such sites. The damming of major rivers has altered river flow around the world with significant impacts on floodplain vegetation. In the western United States, perhaps the notable example of such change is the replacement of cottonwood and willow by saltcedar, which is more tolerant to water stress (drought) and salinity and exhibits superior growth after fire (Smith et al., 1998; DeLoach et al., 2000; Birken and Cooper, 2006). Its ability to salinize the soil also gives it an edge over the native species.

**Plants as Soil Type Indicators**

Gordon (1940) used certain plant communities as indicators of forest soils in western New York. For wetland soils, he stated, “The presence of yellow birch, ironwood (blue beech), and American elm in a hemlock forest generally indicates poor internal drainage conditions … On lacustrine soils of fine texture and imperfect drainage, American elm, swamp white oak, and beech are favored … Associated dark soils are indicated by the White Pine-American Elm type with an undergrowth of hemlock, yellow birch, black ash, red maple and balsam fir.” In local areas there may be strong relationships between certain species and soil types. Wetland plants commonly associated with sandy soils include goldenpert (*Gratiola aurea*) in freshwater areas and salt marsh sand spurrey (*Spergularia marina*), silverhead (*Philoxerus vermicularis*), sea purslane
Plants Indicators of Wetlands and Their Characteristics

**TABLE 3.11**

Plant Indicators of Grazing in the Midwest Wetlands and Weedy Species Found in Wet Farm Fields

<table>
<thead>
<tr>
<th>Species That Increase</th>
<th>Species That Decrease</th>
<th>Weeds of Wet Farm Fields</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achillea millefolium</td>
<td>Andropogon gerardii</td>
<td>Alopecurus carolinianus</td>
</tr>
<tr>
<td>Agrostis alba</td>
<td>Anemone canadensis</td>
<td>Amaranthus rudis</td>
</tr>
<tr>
<td>Asclepias incarnata</td>
<td>Campanula aparinaoides</td>
<td>Ambrosia trifida</td>
</tr>
<tr>
<td>Asclepias verticillata</td>
<td>Carex stricta</td>
<td>Bidens frondosa</td>
</tr>
<tr>
<td>Cirsium arvense</td>
<td>Dalea purpurea</td>
<td>Cyperus esculentus</td>
</tr>
<tr>
<td>Lathyrus palustris</td>
<td>Erigeron strigosus</td>
<td>Cyperus strigosus</td>
</tr>
<tr>
<td>Panicum virgatum</td>
<td>Geum laciniatum</td>
<td>Echinochloa crus-galli</td>
</tr>
<tr>
<td>Tradescantia ohiensis</td>
<td>Helenium autumnale</td>
<td>Polygonum lapathifolium</td>
</tr>
<tr>
<td></td>
<td>Helianthus grosseserratus</td>
<td>Polygonum pensylvanicum</td>
</tr>
<tr>
<td></td>
<td>Physalis heterophylla</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Poa pratensis</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ribes americanum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rosa multiflora</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Solidago gigantean</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thalictrum revolutum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Verbena stricta</td>
<td></td>
</tr>
</tbody>
</table>


**TABLE 3.12**

Bryophyte Indicators of Wetlands in Disturbed Sites for Interior and Southcentral Alaska

<table>
<thead>
<tr>
<th>Species</th>
<th>Species</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aulacomnium palustre</td>
<td>Polytrichum strictum</td>
<td>Sphagnum angustifolium</td>
</tr>
<tr>
<td>Blepharostoma trichophylliuma</td>
<td>Sphagnum fuscum</td>
<td>Sphagnum papillosum</td>
</tr>
<tr>
<td>Calliergon stramineum</td>
<td></td>
<td>Sphagnum russowii</td>
</tr>
<tr>
<td>Calypogea sphagnicola</td>
<td></td>
<td>Sphagnum squarrosum</td>
</tr>
<tr>
<td>Drepanocladus spp.</td>
<td></td>
<td>Mylia anomala</td>
</tr>
<tr>
<td>Meesia triguetra</td>
<td></td>
<td>Tolynthypnum nitens</td>
</tr>
<tr>
<td>Meesia uliginosa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mylia anomala</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pohlia proligeria</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


* Denotes liverworts; the rest are mosses.

(Sesuvium portulacastrum), and common frog-fruit (Phyla nodiflora) in estuarine wetlands. Bigler and Richardson (1984) found that the presence of bulrush (Scirpus sp., now Schoenoplectus) could be used to predict soil properties in the deep marsh zone of prairie potholes. In the field, many soil scientists use plant communities coupled with landscape position to help prepare soil maps after analyzing soils in selected areas. Russian scientists have developed an entire field of science called...
“geobotany” based on using plants to indicate a variety of soil and geologic conditions (Viktorov et al., 1965, as reported in Goslee et al., 1997).

As discussed previously, plants have traditionally been used to identify wetlands since many species and certain plant communities are highly reliable indicators of wet soil conditions. Numerous studies have shown an excellent correlation between vegetation and hydric soils (e.g., Scott et al., 1989; Segelquist et al., 1990; Veneman and Tiner, 1990). The OBL and FACW species on the national wetland plant list remain useful indicators of hydric soils as sites dominated by these species are typically wetlands, whereas a predominance of UPL and FACU species typically indicates nonhydric soils (Chapter 4). Moreover, certain species (calciphiles) favoring mineral-rich sites may be used to indicate calcareous or alkaline soils, while acidophilic species can be used to predict likely acid soil conditions noted earlier.

**PLANTS AS INDICATORS OF WATER STRESS**

Plant vigor has been used as an indicator of the health of an individual plants for several applications including and probably most widely in the fields of agriculture (e.g., Silvertooth et al., 1996; Maisuria and Patel, 2009) and horticulture. For wetlands, plant vigor has been used to assess the impact of rising sea level and marine transgression on lowland forests (Feldbaum and Burdick, 2012; Tiner and Veneman, 2014), plant growth in wetlands through remote sensing (e.g., Phragmites—Artigas and Yang, 2005), and the effect of water-level management on vegetation. It has also been suggested for use in wetland delineation to aid in identifying problematic wetland plant communities in the Arid West (U.S. Army Corps of Engineers, 2008). For evaluating the effect of marine transgression (sea-level rise) on adjacent forests, Tiner and Veneman (2014) developed condition metrics based on the condition of the canopy of woody plants assessed: excellent, no sign of dieback or stress; good, no sign of die-back but some stress noted (e.g., chlorosis); fair, some sign of dieback (up to 25% dieback of canopy); somewhat poor, significant dieback (25%–50% dieback); poor (>50%–90% dieback); and extremely poor (>90% dieback, very little live woody material). The number and types of species stressed, dying, or dead trees will also be recorded. Signs of stress include wilting leaves, reduced growth, chlorophyll deficiency (chlorosis—yellowing of leaves), dying parts, dead parts, and possibly lack of normal twig growth. Stress could be related to either increased soil saturation or salt stress from more frequent tidal flooding.

Plant vigor has been especially useful for assessing the results of waterfowl habitat management practices that involve water-level manipulations, namely, greentree reservoirs. As mentioned earlier in this chapter, this management involves flooding bottomland forests from late fall to early spring to create waterfowl habitat. Managers are particularly interested in making acorns from a few oak species (e.g., Q. phellos and Q. texana) available for waterfowl. After years of management, the health of trees can be assessed to determine if the focus species are being positively or negatively impacted by the management regime. To evaluate management at an Arkansas wildlife refuge, Keeland et al. (2010) developed four vigor classes based on the percentage of tree limb loss: (1) good, <5%; (2) fair, 5%–25%; (3) poor, 26%–95%; and (4) dead, >95%. Such assessments can help wildlife managers adjust water management practices to maximize the benefits to waterfowl.

Condition of vegetation is also an important metric for water management programs. For example, water resource managers have developed a condition index to assess and monitor the effect of management actions on water-stressed river red gum (Eucalyptus camaldulensis) in South Australia (Souter et al., 2009). This index combines crown extent (i.e., the extent of the crown outline that fills the space that would be occupied by a fully foliated crown of a reference tree of similar size and shape) and crown density (defined as “the inverse of the commonly assessed measure of foliage transparency … the lower the transparency the higher the density”). Additional features to record include bark form (cracked or intact), epicormic state (active or inactive), plus trajectory (epicormic growth, reproduction [buds, flowers, and fruits], crown growth, leaf die-off, leaf damage, and mistletoe). The manual includes sketches of various combinations of crown extent and density and numerous photographs showing an array of conditions as guides. This work is built upon the work of others including Grimes (1987). For the western United States, Cooper and Merritt (2012) proposed several categories for
determining tree or shrub condition based on the canopy: critically stressed (major leaf death and/or branch dieback; >50% of canopy volume affected); significantly stressed (prominent leaf death and/or branch dieback; 20%–50% of canopy volume affected); stressed (minimal leaf death and/or branch dieback; <20% of canopy volume affected); normal (little or no sign of leaf water stress/no water stress-related leaf death); and vigorous (no sign of leaf water stress/very healthy looking canopy).

Plants as Indicators of Floristic Quality

Since European settlement, a tremendous influx of new species have become part of the U.S. flora. Many species were purposefully brought in for agricultural, forestry, or horticultural purposes, while most were simply unintentional migrants. Today, there is increasing concern about conserving and restoring native flora (autochthonous) and plant communities in wetlands and other habitats (e.g., native prairie). In determining priority areas for preservation and for assessing the need for restoration, the presence and predominance of naturalized post-settlement species (allochthonous) have become important.

Botanists interested in characterizing habitat status or condition based on plant species composition explored ways of using plants to establish a metric for expressing floristic quality or nativeness (Swink and Wilhelm, 1979, 1994). They assigned a rating of a species’ habitat specificity—coefficient of conservatism—to native species in the Chicago area (Wilhelm and Ladd, 1988). Thirteen categories were established: 0–10, plus 15 and 20. A species with a 0-rating is ubiquitous over a wide range of disturbances. The 5-value is assigned to species with a pronounced affinity for a certain type of native community. A 10-rating is given to plants that typify stable conditions and that have very specific environmental requirements. A 15-species is like a 10, but is rare, while a 20-species is locally threatened or endangered. The rating system may be useful for wetland evaluations interested in maintaining biodiversity of native species. Some examples of species in the Chicago, IL, area with different coefficients follow: 0, Acer negundo, Ambrosia trifida, Circaea quadriradiata, Echinocloa crus-galli, and Equisetum arvense; 1, Bidens frondosa, Calystegia sepium, and Cyperus esculentus; 2, Boehmeria cylindrica, Carex vulpinoidea, and Claytonia virginica; 3, Aster simplex, Calamagrostis canadensis, Carex tribuloides, Celtis occidentalis, and Equisetum hyemale intermedium; 4, Alisma triviale, Amphicarpaea bracteata, Asclepias incarnata, Aster lateriflorus, Carex lanuginosa, and Elymus canadensis; 5, Angelica purpurea, Arisaema atrorubens, Bidens comosa, Caltha palustris, Carex stricta, Cinna arundinacea, Echinocloa walteri, Eleocharis palustris, Eloedia canadensis, and Elymus virginicus; 6, Alopecurus aequalis, Aster punicicus, Betula nigra, and Cornus stolonifera; 7, Acorus calamus, Campanula aparinoides, Carya cordiformis, Cephalanthus occidentalis, and Equisetum fluviatile; 8, Alnus rugosa, Bidens connata, Carex lasiocarpa, Carpinus caroliniana, Chelone glabra, and Epilobium leptophyllum; 9, Amelanchier humilis; 10, Aster umbellatus, Carex lacustris, Carex rostrata, Carex sartwellii, and Dryopteris cristata; 15, Chamaedaphne calyculata, Deschampsia caespitosa, Drosera intermedia, and Thelypteris noveboracensis; and 20, Cyripedium calceolus (Wilhelm and Ladd, 1988). Coefficients of conservatism for other areas may be available from state natural heritage programs.

Once coefficients are established for a given area, they can be used in various equations to qualify the condition of a given area. Initially, the Chicago botanists used the coefficients to produce the Natural Area Index reflecting the nativeness of a particular area, using the following equation:

\[
NI = \frac{R}{N} \times \sqrt{N}
\]

where
- NI is the Natural Area Index
- R is the sum of coefficients of conservatism
- N is the number of native species recorded
Following this approach, a single survey during the growing season can usually provide an accurate assessment of site nativeness. This index was replaced by the Floristic Quality Index (FQI), which is derived from the following equation:

$$FQI = \bar{C} \times \sqrt{N}$$

where

- $FQI$ is the Floristic Quality Index
- $\bar{C}$ is the mean coefficient of conservatism (derived from the sum of the coefficients of all species divided by the total number of native species like was done for the Natural Area Index mentioned earlier)
- $N$ is the total number of native species in the site evaluated (Wilhelm and Masters, 1995)*

FQI and various iterations have received much attention since the 1990s (e.g., Andreas and Lichvar, 1995; Taft et al., 1997; Herman et al., 2001; Lopez and Fennessy, 2002; Cohen et al. 2004; Bourdaghs et al., 2006; Cretini et al., 2011). Some modifications have incorporated non-native species and cover/abundance into the equation (see Cretini et al., 2011, for further discussion). The index can be used to compare habitat quality from a floristic perspective for land acquisition/protection and to monitor and evaluate changes in a plant community over time (e.g., restoration projects).

**Plants as Indicators of Wetland Condition**

Many wetlands have been disturbed in various ways by such factors as hydrologic alteration (e.g., ditching, tile drainage, or damming), pollution, animal activity (e.g., grazing), invasive species, and destruction/degradation of natural vegetation buffers. With declining wetland losses in the United States, increasing attention has been given to assessing the condition of wetlands (e.g., virtually pristine to highly disturbed) by natural resource agencies.

Since the early 1990s, the federal government, mainly through the Corps of Engineers, has been actively involved developing hydrogeomorphic profiles for use in evaluating the condition of major wetland types in response to Mark Brinson’s hydrogeomorphic wetland classification (Brinson, 1993; see Chapter 8). Although such assessments are beyond the scope of this book, readers should be aware that these assessments collect and analyze vegetation, soil, hydrology, and other data from wetlands of a given type to characterize and predict the condition of the wetland (i.e., how close or far is a given wetland from the reference condition—a nearly pristine condition).

Ecological integrity has been another subject for evaluating wetland condition. This type of assessment involves looking well beyond species presence or absence or community composition and structure. For example, Adamus (1996) included algal indicators as well as vascular plant indicators, among others, for evaluating the ecological integrity of prairie wetlands. The latter included species composition, species richness (mature plants and seed bank), biomass, cover ratio, seed density, and germination rate as indicators of hydrologic stressors. He also listed indicators for changes in vegetative cover, salinity, sedimentation and turbidity, excessive nutrient loads and anoxia (e.g., a decrease in submerged plants and an increase in emergent and floating-leaved plants), and pesticide and heavy metal contamination. More recently, DeKeyser et al. (2003) developed an index for prairie wetlands—an index of plant community integrity using metrics including species richness and % of introduced and annual plants compiled from 46 seasonal wetlands to establish a 5-class rating system. The index can be used for evaluating restoration, habitat evaluation, or ecological studies. Wetland condition and biotic integrity indices have been developed by many others that also utilize

* When Wilhelm and Masters (1995) examined native versus introduced species with “wetland indicator status” (Reed, 1988), they found that natives dominated the wetland categories (OBL to FACU, with increasing proportions of introduced species, the drier the category) and that introduced species dominated the UPL category.
Plant Indicators of Wetlands and Their Characteristics

vegetation as a metric (e.g., Kantrud and Newton, 1996; Spencer et al., 1998; Helgen and Gernes, 2001; Teels and Adamus, 2001; U.S. EPA, 2002a,b; Wilcox et al., 2002; DeKeyser et al., 2003; Lane et al., 2003; Clarkson et al., 2004; Mack, 2004; Chipps et al., 2006; Reiss, 2006; Reiss et al., 2010; Deimeke et al., 2013).

For assessing the biological condition of wetlands, the U.S. Environmental Protection Agency (U.S. EPA, 2015) developed a new vegetation-based metric that combined a few other vegetation metrics into a “vegetation multimetric index” (VMMI). The VMMI consists of four metrics: a floristic quality assessment index (FQAI), relative importance of native plant species, number of plant species tolerant to disturbance, and relative cover of native monocot species. FQAI is an assessment based on a plant species sensitivity to human-caused disturbance, with each species assigned a value—coefficient of conservatism or C-value on a scale of 0–10 (see discussion on “Plants as Indicators of Floristic Quality” for details). The relative importance of native plant species metric addresses the cover and number of native species versus that of all species combined. The next metric—number of plant species tolerant to disturbance—is aimed at using the increase in tolerant species (C-value 4 or less) with increasing disturbance as an indicator of stress to disturbance-intolerant species. Relative cover of native monocot species is intended to identify relatively undisturbed wetlands. EPA also included a nonnative plant stressor indicator (relative cover, richness, and frequency of occurrence) as an indicator of biological stress on wetlands.

USEFUL GUIDES FOR IDENTIFYING WETLAND PLANTS

Following is a list of some wetland plant manuals and field guides that are useful for identifying these plants across the United States. The list is arranged by region of the country. Other regional field guides to wildflowers, trees, etc. are not listed but also will be valuable references as will regional flora (taxonomic manuals). Lichvar and Dixon (2011) provided an extensive listing of flora manuals and field guides that should be of interest to wetland delineators.

NORTHEAST

Aquatic and Wetland Plants of the Northeastern United States, by G.E. Crow and C.B. Hellquist (2000), Monocotyledons (2 volumes), University of Wisconsin Press, Madison. 2 volumes.

Field Guide to Nontidal Wetland Identification, by R.W. Tiner (1988), Maryland Department of Natural Resources, Annapolis, MD and U.S. Fish and Wildlife Service, Newton Corner, MA. (Reprint available from Institute of Wetlands & Environmental Education & Research, P.O. Box 288, Leverett, MA 01054.)

Field Guide to Tidal Wetland Plants of the Northeastern United States and Neighboring Canada, by R.W. Tiner (2009), University of Massachusetts, Amherst, MA.


Sedges of Maine, by M. Arsenault and others (2013), University of Maine Press, Orono, ME.


SOUTHEAST


Aquatic and Wetland Plants of the Southeastern United States, by R.K. Godfrey and J.W. Wooten (1979/1981), Monocotyledons and Dicotyledons (2 volumes), University of Georgia Press, Athens, GA.

* The U.S. Environmental Protection Agency (2002b) has published a guidance manual on using algae to evaluate wetland condition.
Aquatic and Wetland Plants of the Western Gulf Coast, by C.D. Stutzenbaker (2010), Texas A&M University Press, College Station, TX.
A Manual of Marsh and Aquatic Vascular Plants of North Carolina with Habitat Data, by E.O. Beal (1977), North Carolina Agricultural Experiment Station, Raleigh, NC.
Wetland Plants of the New Orleans District, by U.S. Army Corps of Engineers (1977), New Orleans District, New Orleans, LA.
A Guide to Selected Florida Wetland Plants and Communities, by U.S. Army Corps of Engineers (1988), Jacksonville District, Jacksonville, FL.
Aquatic and Wetland Plants of Missouri, by D.L. Combs and R.D. Drobney (undated), Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, MO.
Florida Wetland Plants: An Identification Manual, by J.D. Tobe et al. (1998), Florida Department of Environmental Protection, Tallahassee, FL.

MIDWEST

A Manual of Aquatic Plants, by N.C. Fassett (1966), University of Wisconsin Press, Madison, WI.
Wetland Plants and Plant Communities of Minnesota and Wisconsin, by S.D. Eggers and D.M. Reed (2014), U.S. Army Corps of Engineers, St. Paul District, St. Paul, MN.
The Aquatic and Wetland Vascular Plants of North Dakota, by G.E. Larson and W.T. Barker (1980), North Dakota Water Resources Research Institute, North Dakota State University, Fargo, ND.
Great Lakes Coastal Plants, by W.J. Hoagman (1994), Michigan State University, Tawas City, MI.
Sedges of Indiana and Adjacent States, by P.E. Rothrock (2012), Indiana University Press, Bloomington, IN.
Wildflowers and Other Plants of Iowa Wetlands, by S. Runkel and D. Roosa (2015), University of Iowa Press, Ames, IA.

INTERIOR WEST

A Handbook of Wetland Plants of the Rocky Mountain Region, by D.J. Cooper (1989), U.S. Environmental Protection Agency, Region VIII, Denver, CO.

SOUTHWEST


FAR WEST AND PACIFIC NORTHWEST

Common Wetland Plants of Coastal California, by P.M. Faber (1982), Pickleweed Press, Mill Valley, CA.
Wetland Plants of the Pacific Northwest, by F. Weinmann and others (1984), U.S. Army Corps of Engineers, Seattle District, Seattle, WA.
Flora of the Marshes of California, by H.L. Mason (1957), University of California Press, Berkeley, CA.
Wetland Plants of King County and the Puget Sound Lowlands, by V. Crawford (1981), King County, WA.
Plant Indicators of Wetlands and Their Characteristics


**HAWAII**


**ALASKA**

*The Common Plants of the Muskegs of Southeast Alaska*, by O.W. Robuck (1985), USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.


**REFERENCES**


Bray, W.L. 1930. The development of the vegetation of New York State. Technical Publication No. 29. New York State College of Forestry, Syracuse University, Syracuse, NY.
Wetland Indicators

Coder, K.D. 1994. Flood damage to trees. University of Georgia Extension Forest Resources Publication FOR94-61, Athens, GA.


Curtis, J.T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison, WI.


Gardiner, E.S. 1994. Physiological responses of four bottomland oak species to root hypoxia. PhD dissertation, Mississippi State University, Starkville, MS.


The University of the State of the New York, Albany, NY.

Gorham, E. and J.A. Janssens. 1992. Concepts of fen and bog re-examined in relation to bryophyte cover and 


Hu, S.-C. and N.E. Linnartz. 1972. Variations in oxygen content of forest soils under mature loblolly pine stands. *Bulletin No. 668*. Louisiana State University, Agricultural Experiment Station, Baton Rouge, LA.


Jackson, S. 1995. Delineating bordering vegetated wetlands under the Massachusetts Wetlands Protection Act. Massachusetts Department of Environmental Protection, Division of Wetlands and Waterways, Boston, MA.


Lichvar, R. and J. Gillrich. 2011. Final protocols for assigning wetland indicator status ratings during national wetland plant list update. ERDC/CRREL TN-11-1. U.S. Army Engineer Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.

Lichvar, R. and P. Minkin. 2008. Concepts and procedures for updating the national wetland plant list. ERDC/CRREL TN-08-03. U.S. Army Engineer Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.


Wetland Indicators


Merrell, D.J. 1981. Ecological Genetics. The University of Minnesota Press, Minneapolis, MN.


234 Wetland Indicators

Rhode Island Department of Environmental Management. 1994. Rules and regulations governing the administration and enforcement of the Freshwater Wetlands Act. Providence, RI.


Wisconsin Coastal Management Program. 1995. Basic guide to Wisconsin’s wetlands and their boundaries. State of Wisconsin, Department of Administration, Madison, WI.


