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Plant Adaptations to Saturated Soils and the Formation of Hypertrophied Lenticels and Adventitious Roots in Woody Species

Kirk J. Havens

Determining the extent of forested wetlands is a difficult task. These areas are subject to overflow and inundation of varying frequencies and durations. The frequency, timing, and duration of inundation and soil saturation are the driving forces behind the processes that affect species composition. Identifying that portion of a bottomland hardwood forest that is a wetland within the meaning of Section 404 of the Federal Water Pollution Control Act and which meets the definition of wetlands as determined by the regulating agency, U.S. Army Corps of Engineers, has been a controversial issue. The presence of certain adaptations that trees undergo to cope with flooding can provide information on the duration of flooding at a specific site. This could be valuable to resource managers by helping in the determination of the extent of forested wetland systems.

A number of plant species are known to grow in soil conditions that vary from dry upland to permanently inundated wetlands. Wetlands can be considered transitional areas that occur along a soil-moisture gradient between uplands and shallow water habitat. Hydrologic regimes associated with wetlands range from permanent inundation by shallow water to periodic soil saturation (Tiner, 1991).

Plants adapted to living in conditions of periodic saturation or inundation are called hydrophytes (Greek *hydro* = water). However, Clements'

(1920) definition of a subgroup called helophytes (Greek *helos* = marsh) may be more appropriate for species that can occur equally in both wetland and upland conditions. Clements (1920) defined helophytes as "amphibious plants rooted in water or mud."

With the advent of laws regulating the development of wetlands in the United States, a series of additional terms defining plant adaptation to wet conditions was introduced. This action effectively created five groupings of plants based on differences in the probability of occurrence in wetland versus upland habitats. These groups are termed: obligate upland, facultative upland, facultative, facultative wetland, obligate wetland. Facultative plants are defined as having an equal probability of occurring in wetland or upland habitat. The probability of occurrence in wetlands of plants in each grouping is listed in Table 1 (see page 2).

The adaptive abilities of plants allow them to survive in a broad range of physical conditions. Even though a facultative species can be found growing in upland, dry conditions, it may possess physiological or morphological adaptations that also allow it to survive in wetlands.

The flooding of soil causes a relatively rapid depletion of oxygen. Oxygen can be depleted from the soil in a few hours to a few days due to continued root oxygen demand, microbial respi-

ration, and chemical oxidation of reduced organic and inorganic compounds. Dissolved oxygen diffusion, at $1 \times 10^{-12} g \ cm^{-2} \ sec^{-1}$ into the waterlogged soil, is 10,000 times slower than in non-waterlogged soil (Armstrong, 1967) and 100 times slower than oxygen consumption (Ponnamperuma, 1972). After the loss of oxygen from the system, microbes begin using oxidized soil components in their respiration which lowers the redox potential of the system.

Wetland Indicator Category	Probability of Occurrence in Wetlands
Obligate Wetland (OBL)	>99%
Facultative Wetland (FACW)	67-99%
Facultative (FAC)	34-66%
Facultative Upland (FACU)	1-33%
Obligate Upland (UPL)	<1%

Table 1. Wetland indicator categories of plant species under natural conditions (adapted from Reed, 1988).

Redox potential (Eh) is a measure of the electron availability in chemical and biological systems. Electrons are essential reactants in inorganic, organic, and biochemical reactions. Chemical species that lose electrons become oxidized while those that gain electrons become reduced. In aqueous solutions, redox potential affects the oxidation states of oxygen, hydrogen, nitrogen, manganese, iron, copper, cobalt, sulfur, and carbon in succession (Bohn, 1971). As each of these elements is reduced it indicates the intensity of oxidation or reduction of a chemical or biological system.

Patrick and Mahapatra (1968) classified soil redox conditions into four ranges at pH 7: oxidized soils 400 mV; moderately reduced soils 400 to 100 mV; reduced soils 100 to -100 mV; and highly reduced soils -100 to -300 mV. Redox potentials for several reactions in soils of pH 7 from Bohn (1971) and Ponnamperuma (1984) are shown in Table 2.

As the system becomes more reduced, plants must cope with the increased concentrations of phytotoxins such as iron, manganese, and sulphide (Ernst, 1990) and the increased stress of being rooted in a waterlogged, anaerobic (without oxygen) environment.

Wetland plants have a number of responses and adaptations such as the formation of adventitious water roots and hypertrophied lenticels that allow them to cope with the effects of waterlogging (Figure 1). Hypertrophied lenticels are enlarged cells that allow for increased oxygen diffusion along the stem. Adventitious roots are porous roots which are more capable of oxygen uptake and generally form off the primary root or off the stem near the water line. One particularly important adaptation is the ability to transport oxygen from the stem to the roots via aerenchyma tissue (Figure 2, page 4) and the subsequent oxidation of the root zone (rhizosphere) by radial loss of oxygen from the roots.

Oxygen enters the xylem of the stem of trees through the leaves and lenticels and hypertrophied lenticels at the waterline are considered the main entry point (Armstrong, 1978; Coutts and Armstrong, 1971). Blockage of the hypertro-

Bohn (1971)	Ponnamperuma (1984)	
+225 mV Nitrate reduction	+330 mV	Disappearance of O^2
+200 mV Manganese reduction	+220 mV	Disappearance of NO_3-
+120 mV Iron reduction	+200 mV	Appearance of Mn^{2+}
+100 mV Sulfate reduction	+120 mV	Appearance of Fe^{2+}
	-150 mV	Disappearance of SO_4^{2-}
	-250 mV	Appearance of CH_4

Table 2. Redox potentials in soils of pH 7.

phied lenticels located at the waterline has been shown to reduce the oxygen status of the roots (Armstrong, 1968; Hook et al., 1971; Scholander et al., 1955). Due to the resistance to the movement of oxygen and its consumption by respiration as it moves through the stem to the root, it is believed that oxygen supplied through leaf entrance is of little importance to the roots of trees (Coutts and Armstrong, 1971). Armstrong (1968),

Hook and others (1971), and Scholander and others (1955) have demonstrated the importance of lenticels for aeration in willows, tupelos, and mangroves. In a classic experiment on mangroves, it was demonstrated that the oxygen concentration in roots submerged in anaerobic mud remained continuously high at 15-18%, but if the hypertrophied lenticels were blocked the concentration fell to 2% or less (Scholander et al., 1955).

Adenosine triphosphate (ATP) is the major energy-carrying molecule in cellular metabolism and the generation of ATP is much more efficient under aerobic conditions. Without some mechanism for ATP generation during anaerobic condi-
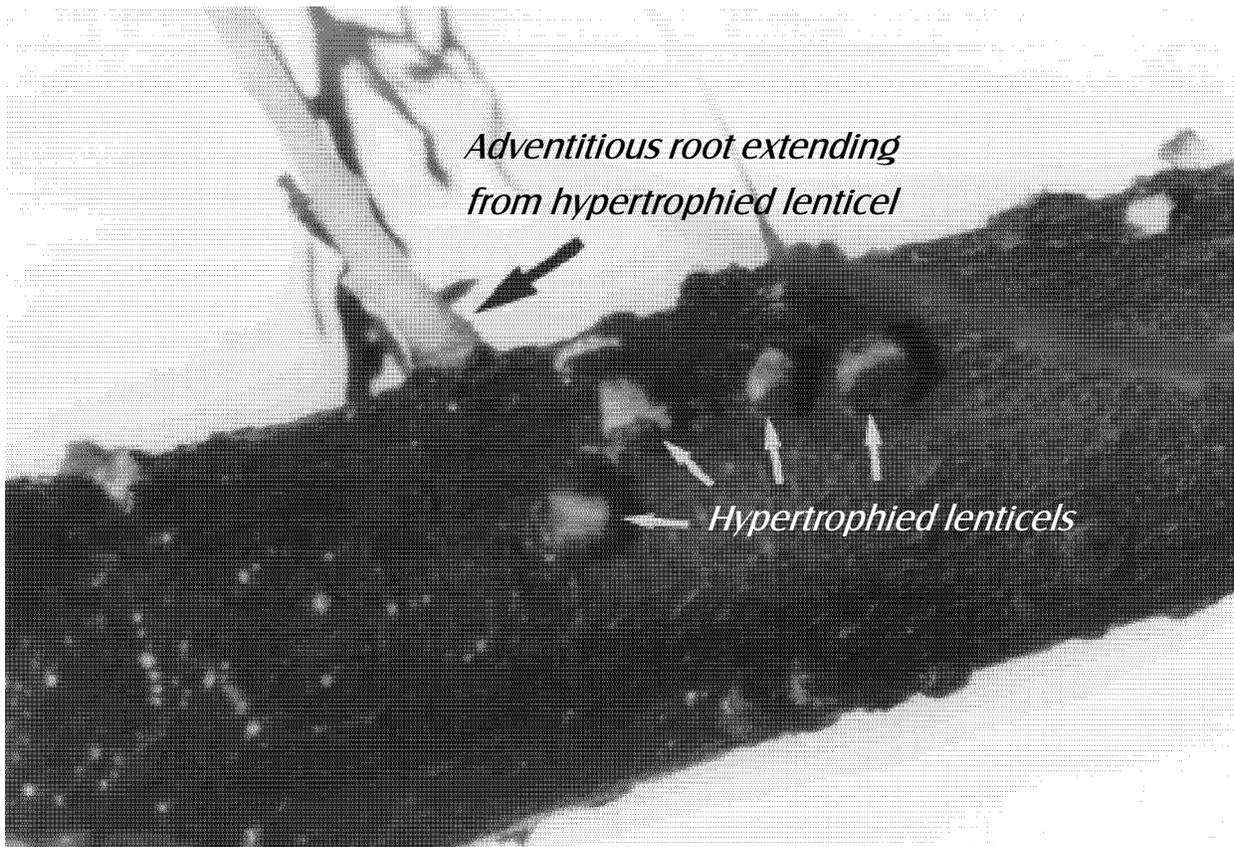

Figure 1. Hypertrophied lenticels and adventitious roots on the stem of a red maple seedling.

tions, the amount of ATP in a root cell would be sufficient for less than one minute of metabolism (Roberts et al., 1984). The diffusion of oxygen to the roots allows for continued root growth and nutrient uptake under anaerobic conditions. Radial leakage of oxygen from the root oxidizes the rhizosphere, neutralizing phytotoxins and supplying oxygen to rhizosphere microbial populations. In addition, the iron oxide plaque that forms along the roots can scavenge other metallic ions thereby decreasing their toxic effects (Crowder, 1991).
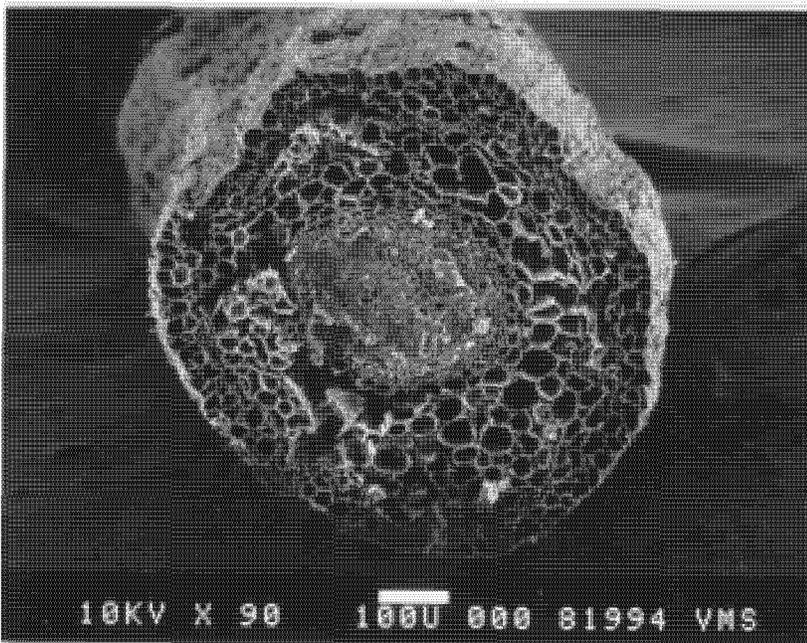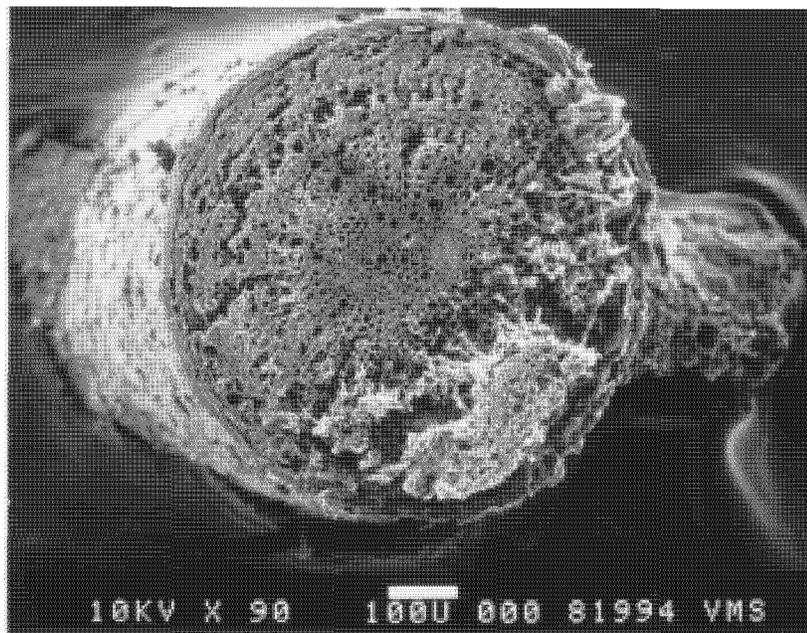
Waterlogging causes an increase in ethylene production in tissues below and immediately above the water line (Yang, 1980; Tang and Kozlowski, 1984) resulting in cellulase activity. Cellulase softens the cell walls causing stem hypertrophy (enlargement) and development of aerenchyma tissue in both the lenticels and the adventitious roots (Sena Gomes and Kozlowski, 1980; Kawase, 1981; Kozlowski, 1984). Porosity is increased due to the formation of large aerenchyma cells and the large channels in the root cortex enhance oxygen transport (Justin and Armstrong, 1987). Oxygen leakage from the aerenchyma tissue of the roots oxidizes reduced iron in the soil resulting in ferric iron (Fe^{3+}) deposits on the root and along the root channel of some plant species.

Inundation of lenticels causes hypertrophy and hypertrophied lenticels may protrude outward 2 to 3 mm from the stem (Hook and Scholtens, 1978). The proliferation of hypertrophied stem lenticels is considered an adaptation for increased oxygen exchange (Hook et al., 1970) and the aerenchyma pore space allows the diffusion of oxygen from the leaves and stem to the roots. Even though hypertro-

Figure 2. Scanning electron micrograph of the root of red maple seedling.
Top photo—parenychyma tissue of seedling from upland site;
bottom photo— aerenchyma tissue of adventitious root from inundated site.

phied lenticels collapse upon exposure to air, the large intercellular spaces and numerous breaks in the closing layers allow significant oxygen exchange (Hook et al., 1970; Hook and Brown, 1972).

Generally, adventitious stem roots emerge through hypertrophied lenticels and adventitious soil roots emerge at the point where the original root died back after flooding (Kozlowski, 1984). New adventitious roots are usually white and succulent with few branches (Sena Gomes and Kozlowski, 1980; Kozlowski, 1984). They differ from the original root by cellular structure (aerenchyma versus parenchyma tissue), rates of anaerobic respiration, and the ability to withstand high concentrations of CO_2 (Hook et al., 1972).

Pereira and Kozlowski (1977) observed the formation of hypertrophied lenticels and adventitious roots in *Salix nigra* (black willow) and *Ulmus americana* (elm) within 7 days of flooding. Adventitious roots were observed on the gums *Nyssa aquatica* and *Nyssa sylvatica* var. *biflora* after a few days of flooding (Hook and Scholtens, 1978). In the facultative wetland species *Fraxinus pennsylvanica* (green ash) hypertrophied lenticels formed after 5 days of flooding and adventitious roots after 15 days of flooding (Gomes and Kozlowski, 1980; Kozlowski and Pallardy, 1984). In a laboratory experiment on 3 month and 4 month old *Quercus macrocarpa* (oak) seedlings, Tang and Kozlowski (1982) observed hypertrophied lenticels on some seedlings after 5 days in one experiment and 11 days in another experiment and some adventitious roots after 30 days. In a separate laboratory study of ethylene production in relation to morphological responses to flooding of *Fraxinus pennsylvanica* seedlings, Tang and Kozlowski (1984) reported the presence of hypertrophied lenticels and adventitious roots between 4 and 10 days. Jackson (1990) observed a proliferation of hypertrophied lenticels and adventitious roots on a small apple tree after 4 weeks of flooding.

Red maple and sweetgum (*Liquidambar styraciflua*), both facultative species, dominate the forest community in seasonally wet areas of Virginia, especially sites subjected to logging or other disturbances (Day and Dabel, 1978). Red maple is considered an excellent colonizer of these areas due to its ability to produce adventitious roots and hypertrophied lenticels and survive different hydrologic regimes resulting in a competitive advantage over other species. Sweetgum, while it transports oxygen from aerial portions to submerged roots, does not oxidize its rhizosphere (Hook et al., 1972; Hook, 1984).

Hypertrophied lenticels and adventitious roots have been found on both continuously and intermittently flooded red maple seedlings and mature trees (Harms et al., 1980; Day, 1987). Hypertrophied lenticels and adventitious roots have been observed to form on seedlings within seven days of soil saturation and approximately three weeks of inundation, respectively (Havens, pers. obs.). Once exposed to air however, the adventitious roots will wither (Day, 1987; Havens, pers. obs.)

Seedling mortality in floodplains is extremely high and establishment is a function of flood tolerance (Jones et al., 1994). The time necessary for the formation of morphological adaptations to flooding can be essential for the survival of seedlings colonizing wetlands or floodplain areas and is probably affected by species, soil type, temperature, microbial abundance, and the type of hydrologic regime (i.e. stagnant or flowing water). The ability to rapidly form morphological adaptations, such as hypertrophied lenticels and adventitious water roots to alleviate the anaerobic stress of waterlogged conditions, gives seedlings a competitive advantage. This has important implications in seedling establishment in forest regeneration, the construction of forested wetlands as a result of compensatory mitigation, and in determining the extent of forested wetland systems.

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