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**The Formation of Hypertrophied Lenticels, Adventitious  
Water Roots, and an Oxidized Rhizosphere by  
*Acer rubrum* Seedlings over Time  
Along a Hydrologic Gradient**

Kirk J. Havens

December, 1994

*Key words:* Hypertrophied lenticels, adventitious water roots, oxidized rhizosphere, ferric iron, red maple, redox potential

## Abstract

The effect of three hydrologic regimes (dry, saturated, and inundated) on red maple (*Acer rubrum*) seedlings was investigated both in the laboratory and in the field. Hypertrophied lenticel formation occurred within 7 days in the inundated site. Adventitious water root formation was observed after 3 weeks in the inundated site but only after 12 weeks in the saturated site. Hypertrophied lenticels and adventitious water roots were lacking in the seedlings grown in the dry site. Hydrophytic vegetation was shown to elevate the redox potential in the upper 15 centimeters of the soil profile and the ability of red maple seedlings to oxidize their rhizosphere was demonstrated using a leuco-methylene blue/agar medium. The visible presence of ferric iron deposits along the rhizoplane of red maple seedlings was observed after 3 weeks of inundation. Ferric iron deposits were not observed in the dry seedlings and were only observed in the saturated seedlings after the area was flooded for 6 weeks.

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## **Introduction**

A number of plant species are known to grow in soil conditions that vary from dry to permanently saturated or inundated. 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. However, Clements' (1920) definition of a subgroup called helophytes 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." Weaver and Clements (1929) later refined the definition of hydrophytes by creating three groups: submerged, floating, and amphibious. Weaver and Clements (1929) suggested that amphibious plants have a wide range of adaptations to flooding, and that differences between some hydrophytes and the less wet-adapted mesophytes are not distinct.

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 were introduced, based on differences in the probability of occurrence of a plant in wetland versus upland habitats. These terms include: obligate upland, facultative upland, facultative, facultative wetland, obligate wetland. Facultative plants are defined as having a 50% probability of occurrence in wetlands (Reed, 1988). The probability of occurrence in wetlands of the other terms is listed in Table 1. In this paper, the term facultative will be used to describe hydrophytic vegetation that has an equal probability of being found in either upland or wetland conditions.

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

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

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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.

Flooding causes a relatively rapid depletion of oxygen due to continued root oxygen demand, microbial respiration, and chemical oxidation of reduced organic and inorganic compounds. Dissolved oxygen diffusion at  $1 \times 10^{-12} \text{g cm}^{-2} \text{sec}^{-1}$  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.

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 (Bohn, 1971) and indicates the intensity of oxidation or reduction of a chemical or biological system. As the system becomes more reduced, plants must cope with the increased stress of being rooted in a waterlogged, anaerobic environment.



Wetland plants have a number of responses and adaptations that allow them to cope with the effects of waterlogging. Ernst (1990) suggested three main theories of plant resistance to waterlogging: 1) the transport of oxygen from the stem to the roots via aerenchyma tissue and the subsequent oxidation of the rhizosphere by radial loss of oxygen from the roots (Oxygen Transport Theory), 2) the ability to withstand higher concentrations of iron, manganese, and sulphide (Ion Toxicity Theory), and 3) changes in the metabolic activity to produce organic acids and avoid ethanol accumulation (Metabolic Adaptation Theory).

The Oxygen Transport Theory is considered an anoxia avoidance mechanism and the transport of oxygen to the roots is but one of many avoidance mechanisms demonstrated by flood-tolerant plants. The transport of oxygen from the shoots to the roots in flood-tolerant plants is the result of morphological changes in the root anatomy, such as the formation of aerenchyma tissue, increased root branching, formation of new adventitious roots, and formation of shallow, lateral roots in the upper soil layer (Blom et al., 1990). Oxygen leakage from the aerenchyma tissue of the roots oxidizes reduced iron in the soil resulting in ferric iron deposits on the root and along the root channel of some plant species.

Red maple and sweetgum (*Liquidambar styraciflua*), both facultative species, dominate the forest community in seasonally wet areas of Virginia (Silberhorn in prep.), 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 transports oxygen from aerial portions to submerged roots, however it does not oxidize its rhizosphere (Hook et al., 1972; Hook, 1984).

Red maple is more shade tolerant than early successional species such as poplar (*Populus* sp.) and pin cherry (*Prunus pennsylvanica*) and can exist in the understory for several years (Walters and Yawney, 1990). Jones and others (1989) demonstrated a high tolerance of one year old red maple seedlings to

competing roots. Red maple roots form horizontally in the upper 25 cm of soil and, under wet conditions, grow soil water roots upward into the more aerated soil layer (Walters and Yawney, 1990). Adventitious roots and hypertrophied lenticels have been found on both continuously and intermittently flooded red maple seedlings and mature trees (Day, 1987).

This study investigated hypertrophied lenticel and adventitious water root formation and the time required for ferric iron deposits to become materially visible in the rhizosphere of red maple (*Acer rubrum*) seedlings in an Acredale soil under both field (Virginia Beach, Virginia) and laboratory conditions.

## **Materials and Methods**

The site is located in Virginia Beach, Virginia on the Virginia Army National Guard State Military Reservation (Figure 1). The study was conducted from September 7, 1992 to December 21, 1992. Water table wells (1.5 m deep) were established at three points along a hydrologic gradient ranging from upland to permanently inundated wetland. Wells were constructed of 5.1 cm diameter PVC pipe covered with screen (lower 1.0 m). The wells were surrounded with gravel and sealed with bentonite to eliminate vertical infiltration from the surface. Water table elevations were recorded remotely (at 12 minute intervals) using a data logger and a pressure transducer sensor.

Organic matter and exchangeable iron were determined on five soil samples (15 cm depth) at each hydrologic regime after 29 days and 71 days. Soil samples ( $10 \pm 0.5$  g wet) were weighed in the field, transferred into 50 ml sealing centrifuge tubes, and purged with nitrogen gas until they could be extracted in the laboratory.

Exchangeable iron was extracted by adding 25 ml of 1N sodium acetate (adjusted to pH 2.0) to each tube, shaking for 4 hrs and centrifuging to obtain a clear supernatant (Faulkner et al., 1991). Total iron in the supernatant was determined by atomic absorption spectrometry. Organic matter was measured by loss on ignition at 450 °C and converted into percent of dry weight.

Redox potential was measured on an *Orion Model 290A Portable Meter* with a platinum electrode referenced to a calomel electrode. The platinum electrodes were constructed as follows: 1/2 inch lengths of 18 gauge platinum wire were soaked in a 1:1 solution of hydrochloric acid and nitric acid for at least four hours to remove surface contamination, rinsed with deionized water, and fused to copper wire. The copper/platinum wire junction was sealed with shrink tubing and fast-drying epoxy glue (Megonigal, per. comm.). All values were corrected for the potential of the reference electrode by adding 199 mV.

Only precious metals such as gold or platinum are used for redox electrodes because the equilibrium activities of their ions at medium redox potentials remain very low (Buhler and Baumann, 1982). During the formation of redox potential, electrons either flow from the electrode to the redox system or from the redox system to the electrode. The separation of charges causes a potential to be built up on the metallic probe surface which resists further migration of electrons. When a state of equilibrium is reached, the electrochemical force (potential) and the oxidizing and reducing forces balance each other.

Care must be taken to avoid erroneous measurement of redox potentials. Variability in redox measurements have been attributed to electrode poisoning, leakage, probe drift, epoxy breakdown at the probe joint, and microsite differences (Cogger et al., 1992). Cogger and others (1992) studied redox electrodes under various conditions and determined that generally, differences observed during the reduction cycle were due to microsite effects and not due to inherent electrode differences.

Patrick and Mahapatra (1968) classified soil redox conditions into five 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 Ponnampereuma (1984) are shown in Table 2.

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**Table 2. Redox potentials in soils of pH 7.**

<b>Bohn (1971)</b>	<b>Ponnampereuma (1984)</b>
+225 mV Nitrate reduction	+330 mV Disappearance of O <sup>2</sup>
+200 mV Manganese reduction	+220 mV Disappearance of NO <sub>3</sub>
+120 mV Iron reduction	+200 mV Appearance of Mn <sup>2+</sup>
+100 mV Sulfate reduction	+120 mV Appearance of Fe <sup>2+</sup>
	-150 mV Disappearance of SO <sub>4</sub>
	-250 mV Appearance of CH <sub>4</sub>

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Soil temperature was recorded weekly to the nearest 0.5°C. An *Orion Model 290A Portable Meter* was used to measure pH.

Soil microorganism abundance was measured by extracting 10 grams of soil from randomly collected samples within each of the hydrologic regimes. The soil was transferred aseptically to 100 ml of sterile water and blended to separate microorganisms from the soil particles. A dilution spread plate technique was used to culture microorganisms and appropriate dilutions were prepared in sterile, deionized water. Visible microorganism abundances (CFU) were estimated by colony formation on petri dishes containing 12 ml of nutrient agar.

The nutrient agar petri dishes were divided into an aerobic and anaerobic incubation. Separation into two distinct oxidation conditions allowed investigation of both active and inactive microbial abundances. It is probable that obligate anaerobic microorganisms are present but inactive during oxidized conditions and the same may hold for obligate aerobic microorganisms during anaerobic conditions. Simultaneous

sampling of both systems may allow investigation in total cultural abundance as well as shifts in community structure under differing oxidation states.

The microbial community composition was characterized by assessing morphologically distinct colony types present on the nutrient agar. Criteria for distinguishing colony types followed Jonas (1989) and consisted of colony diameter, shape, edge type, surface elevation, color, surface sheen, degree of transparency, and diffusible pigments. Each unique colony type may not represent a different species but for this study it was assumed that each unique colony type represented a distinct biotype (i.e. distinct growth type).

Radial oxygen root leakage patterns for red maple seedlings were examined using plexiglass containers and an agar solution (1% w/v) to which leuco-methylene blue solution (1%) was added (0.5-1.0 ml l<sup>-1</sup>). Nitrogen gas was bubbled through the agar solution as the solution cooled. At about 42 °C the seedling was removed from soil, rinsed, and the root system was immersed in the dye-agar mixture and, once the agar solidified, the container was filled with tap water. To reduce the effect of respiratory processes on oxygen leakage patterns, the plexiglass containers were immersed in melting ice (Smits et al., 1990). Leuco-methylene blue is colorless when reduced, but becomes blue in the presence of oxygen. Five seedlings grown in upland conditions and five seedlings grown under inundated conditions (greater than two months) were tested.

It has been shown that some wetland species can alter the oxidation state of soil by radial oxygen loss from the roots (Howes, et al., 1981). In order to investigate the possibility that existing vegetation may elevate the redox potential within the top 15 cm of the soil profile, three plots were randomly established within three different vegetated communities in the saturated regime.

The square meter plots were established within a shrub community dominated by swamp rose, *Rosa palustris*, a tree community dominated by red maple, and a herbaceous community dominated by lizard's tail, *Saururus cernuus*. Redox potentials were measured weekly for three weeks both inside and outside the plots. After three weeks, the plots were denuded of vegetation and heavy gauge plastic was trenched into at least 60 cm around each plot to prevent external root intrusion. Redox potential measurements were continued for eight weeks.

A laboratory investigation of ferric iron deposits in the rhizosphere of red maple seedlings was conducted by transplanting one year old greenhouse grown bare root seedlings to glass containers filled with Acredale soil. Red maple seedlings were chosen because of their facultative wetland indicator status (Reed, 1988), their tolerance to saturation (Hosner and Boyce, 1962; Hook and Scholtens, 1980; Theriot, 1988), and their dominant position in coastal plain bottomland hardwood areas (Silberhorn, per. comm.). Red maple has a wider range of soil types, textures, moisture, pH, and elevation than any other forest species in North America. It has a soil range that covers the following orders: Entisols, Inceptisols, Udisols, Alfisols, Spodosols, and Histosols (Walters and Yawney, 1990). Acredale soil was selected for this study because, in many cases, this soil type is located throughout the wetland transitional gradient in the coastal plain of Virginia. The soils of the Acredale series are found on inland flats of the coastal plain, are poorly drained, and formed in loamy marine and fluvial sediments (Hatch et al., 1985).

One seedling was randomly selected for each container. The roots of the seedling were displayed against the glass for ease of observation and photography. Black plastic was positioned around the containers to prevent algal production within the soil sample from light penetration through the glass sides (Figure 2).

Three test regimes were established: dry (control); saturated; and inundated. The dry system received moisture through mimicking area precipitation. The saturated system was maintained by continuous

waterlogging of all available pore space within the root zone (upper 15 cm). The inundated system was maintained with water at least 5 cm above the soil surface.

Roots adjacent to the container wall were checked weekly for the development of adventitious water roots, hypertrophied lenticels, and for visible evidence of ferric iron precipitates (reddish-brown colored concretions) along the root system. All samples displaying visible ferric iron deposits were photographed. Upon completion of the experiment, the seedlings were extracted and the root complex photographed.

Field investigation of ferric iron deposits in the rhizosphere of red maple seedlings was conducted by transplanting 300 seedlings to the field in an Acredale soil as previously described. The test plot was divided into three hydrologic regimes along a transitional gradient: dry - rarely saturated (control); saturated - temporarily flooded; and inundated - semi-permanently flooded (Figure 3). For statistical purposes, seedlings were selected at random and randomly placed in each hydrologic regime (Hurlbert, 1984).

On monthly intervals seedlings were randomly extracted from each hydrologic regime. All adventitious root sections were examined and those showing visible evidence of ferric deposits were photographed. The root of each seedling was excised at the root collar. All adventitious roots were removed. The dry weight of the primary root and the adventitious roots were compared among the different hydrologic regimes. All hypertrophied lenticels were identified and enumerated. Redox potential and soil temperature were measured weekly.

Statistical analysis of the data was conducted using the t-test for normally distributed data with equal variances, Welch's t-test for normally distributed data with unequal variances, and the Mann-Whitney U-test if nonnormality was detected.

## Results

### *Site hydrology*

The water table in the inundated zone ranged between 12 cm and 36 cm above the soil surface (Figure 4). The water table in the saturated zone ranged between 15 cm and 5 cm below the soil surface from September through the end of October but was saturated the entire period. This may be due to the presence of a capillary fringe (Gillham, 1984; Heliotis and DeWitt, 1987). In the beginning of November through the remainder of the study period the saturated zone soil was inundated with between 2.5 cm and 9 cm of water. The water table in the upland zone ranged between 2.8 m and 2.2 m below the soil surface. The pond depth fluctuated between 1.4 m and 2.0 m. During the study period the inundated zone had water above the soil surface 100% of the time. In the saturated zone the water level was above the soil surface from November 2 to December 21 or 52% of the time.

### *Organic matter and exchangeable iron*

Organic matter was significantly lower ( $p < 0.05$ ) in the upland site than in the saturated or inundated sites on the October 5, 1993 sample date. Exchangeable iron was significantly higher ( $p < 0.005$ ) in the inundated site than in the upland or saturated sites. There was no significant difference in exchangeable iron content between the upland or saturated site (Figure 5).

Forty two days later, on November 16, 1993, the differences in organic matter were essentially the same as the October sample, however, exchangeable iron was significantly higher ( $p < 0.05$ ) at the saturated and inundated sites (Figure 6).



### *Redox potential measurements*

Redox potential measurements in the inundated and saturated sites were indicative of anaerobic conditions (less than 300 mV) throughout the study period, while the upland site never measured below 300 millivolts. The redox measurements at the saturated site rarely fell below the level generally accepted for iron reduction (200 mV at pH of 6-7) while the inundated site only measured above 200 millivolts for a one week period in October (Figure 7). The drop in redox potential in the saturated zone coincided with a rise in the water level above the soil surface of approximately 5 cm (Figure 4). This period of inundation within the “saturated” zone, with the consequent barrier to oxygen diffusion, may have caused the lowering of the redox potential. The redox potential remained low until a sharp drop in temperature occurred near the end of November.

In the laboratory experiment redox potentials for the upland and inundated experiments resembled the results of the field experiment. However, the saturated experiment never reached levels below 240 mV (Figure 8). This may be a result of the diffusion of oxygen along the sides of the glass container and within the upper soil profile and a lack of organic matter to drive the microbial populations (Gotoh and Patrick, 1974; Couto et al., 1985).

### *Soil microorganism abundance*

Microbial abundance was significantly higher ( $p < 0.02$ ) in the inundated zone under both anaerobic and aerobic conditions. There was no significant difference in abundance between the saturated and upland zones under anaerobic and aerobic conditions. Under anaerobic conditions biotype diversity was greatest in the inundated and saturated zones while richness was much higher in the saturated zone. Under aerobic conditions the saturated zone had the lowest abundance, lowest diversity, and lowest richness (Table 3).

**Table 3. Microbial abundance (CFU/g), diversity, and richness for each hydrologic regime under anaerobic and aerobic culturing conditions. Biotype diversity and richness calculated using Shannon-Weaver index.**

<b>Site</b>	<b>Anaerobic</b>			<b>Aerobic</b>		
	<b>Abundance</b>	<b>Diversity</b>	<b>Richness</b>	<b>Abundance</b>	<b>Diversity</b>	<b>Richness</b>
Inundated	29.2 x 10 <sup>4</sup>	1.69	3.14	32.7 x 10 <sup>4</sup>	1.78	3.49
Saturated	20.2 x 10 <sup>4</sup>	1.70	3.84	17.5 x 10 <sup>4</sup>	1.56	3.16
Upland	19.5 x 10 <sup>4</sup>	1.62	3.38	25.3 x 10 <sup>4</sup>	1.72	3.21

*Oxygen leakage patterns*

Oxidated methylene blue could be observed around the adventitious roots and hypertrophied lenticels of the inundated seedlings (Figure 9). A time sequence for the oxidation of leuco-methylene blue was not investigated, however the oxidation process was visually observed within 16 hours. No evidence of blue coloration, indicating the presence of an oxidizing agent, was observed around the roots of the upland seedlings.

*Vegetation effect on redox potential*

The denuded test plots showed a significantly lower ( $p < 0.05$ ) redox measurement than the vegetated area in all three community types. Redox measurements became nonsignificant between denuded and vegetated plots after leaf-fall in the woody plots and senescence in the herbaceous plots (Figures 10,11,12).

*Formation of hypertrophied lenticels and adventitious roots*

Hypertrophied lenticels were observed in the laboratory on inundated and saturated red maple seedlings within 7 days. The saturated system had a significantly greater ( $p = 0.023$ ) number of hypertrophied lenticels than the inundated system after 12 weeks while no hypertrophied lenticels were observed on seedlings in the dry system (Figure 13).

In the field experiment, the inundated seedlings formed hypertrophied lenticels within 7 days and a proliferation of hypertrophied lenticels did not occur on the saturated seedlings until between 3 to 7 weeks. Hypertrophied lenticel formation was significantly greater ( $p < 0.001$ ) in the wetter sites, though after 13 weeks there was no significant difference in the number of hypertrophied lenticels between the saturated and inundated seedlings (Figure 14). There was a negative correlation between percent adventitious roots and the number of hypertrophied lenticels in both the field and laboratory seedlings ( $r_{sp} = -0.716$  and  $r_{sp} = -0.843$ , respectively) (Figure 15).

In the laboratory, adventitious water roots were observed growing through hypertrophied lenticels in the inundated systems after 4 weeks (Figure 16) with only a few, small (less than 1 cm) adventitious water roots visible in the saturated systems after 12 weeks. No adventitious water roots were observed in the dry systems. Adventitious water roots were evident on the inundated seedlings in the field experiment between 3 to 7 weeks with a few observed after 13 weeks on the saturated seedlings. Cross-sectional electron scanning micrographs of the roots of seedlings grown in the upland zone and the adventitious roots of seedlings grown in the inundated zone show the differential development of parenchyma tissue and aerenchyma tissue, respectively (Figure 17).

In the field the saturated seedlings had higher root biomass production than either the inundated or the upland seedlings after 3 weeks but after 7 weeks average root biomass of the upland seedlings was more than double the saturated and inundated plants (Figure 18). In the laboratory total root biomass was significantly less ( $p < 0.01$ ) in the inundated seedlings after 12 weeks (Figure 19).

#### *Observation of materially visible ferric iron deposits*

In the field experiment visible evidence of ferric iron deposits along and adjacent to the adventitious roots was present at 7 weeks on the inundated samples and at 13 weeks on the saturated samples. No evidence

of visible ferric iron deposits were observed on the upland samples (Table 4). Ferric iron deposits were observed in the laboratory experiment adjacent to adventitious roots at 6 weeks, however; it must be noted that this was only for the roots adjacent to the glass wall. No observations could be made of adventitious roots within the soil matrix and not visible by external examination through the glass wall. No evidence of ferric oxide deposits was observed in the upland or saturated samples.

**Table 4. Presence of hypertrophied lenticels, adventitious water roots, and visible ferric oxide deposits along roots. Hypertrophied lenticels=average number per plant, adventitious water roots=average percent of total roots (g dry wt) per plant (n=25).**

<u>Site</u>	<u>Initial</u>			<u>3 Weeks</u>		
	<u>Hypertrophied Lenticels</u>	<u>Adventitious Water Roots</u>	<u>Ferric Oxide Deposits</u>	<u>Hypertrophied Lenticels</u>	<u>Adventitious Water Roots</u>	<u>Ferric Oxide Deposits</u>
Upland	<1	0	no	0	0	no
Saturated	<1	0	no	<1	<1%	no
Inundated	<1	0	no	7	<1%	no
<u>Site</u>	<u>7 Weeks</u>			<u>13 Weeks</u>		
	<u>Hypertrophied Lenticels</u>	<u>Adventitious Water Roots</u>	<u>Ferric Oxide Deposits</u>	<u>Hypertrophied Lenticels</u>	<u>Adventitious Water Roots</u>	<u>Ferric Oxide Deposits</u>
Upland	<1	0	no	<1	0	no
Saturated	11	<1%	no	14	2%	yes
Inundated	14	23%	yes	14	48%	yes

## Discussion

### *Microbial interaction*

Flooding affects the soil environment in a number of ways. The immediate effects are the loss of soil oxygen and the transformation of microbial populations as the soil elements become more reduced.

Oxygen is depleted within a few hours after flooding, and aerobic microbial populations are replaced by facultative anaerobes. Depending on the intensity of reduction, populations of facultative anaerobes are ultimately replaced by obligate anaerobes (Yoshida, 1978). Facultative and obligate anaerobes begin using oxidized soil components and dissimilation products of organic matter as electron acceptors in their respiration, initiating a thermodynamic sequence in soil reduction.

The first process to occur following oxygen depletion is the reduction of nitrate. This process is mediated by two different groups of nitrate-reducing bacteria: nitrate-ammonifying bacteria and denitrifying bacteria. Facultatively anaerobic bacteria in the genera *Bacillus*, *Aeromonas*, and *Citrobacter* mediate nitrate ammonification (MacFarlane and Herbert, 1982) while denitrification is found in obligate aerobic bacteria in the genera *Agrobacterium*, *Alcaligenes*, *Bacillus*, *Paracoccus*, *Pseudomonas*, and *Thiobacillus* (Knowles, 1982). Work by Kuenen and Robertson (1987) provides evidence that nitrate reduction can occur in the presence of oxygen. Therefore, oxygen depletion is not a necessary precursor to nitrate reduction.

At redox potentials of approximately +220 mV to +200 mV the reduction of manganese (IV) occurs. Since sulphide and fatty acids produced by anaerobic bacteria can reduce manganese, the direct involvement of bacteria is not completely understood (Jauregui and Reisenauer, 1982). However some species of the genera *Clostridium* and *Alteromonas* have been shown to generate energy from the reduction of manganese (Francis and Dodge, 1988; Lovley et al., 1989).

Primary minerals rich in iron are among the first to weather upon exposure to water under oxidized conditions (Buol and Rebertus, 1988) and ferric iron is considered one of the most abundant electron acceptors in soils (Ponnamperuma, 1972). Bohn (1971) and Ponnamperuma (1984) showed that reduction of ferric iron to ferrous iron occurs at a redox potential of approximately +120 mV. Cogger and others

(1992) found exchangeable Fe(II) present at +200 mV and below at a pH of between 6 and 7. Vepraskas and Wilding (1983) found Fe(II) present at +250 mV and below at similar pH values. Nitrate and ferric iron are reduced by the same microorganisms. However, since microorganisms have a preference for nitrate in the reduction of organic compounds, the processes of nitrate and ferric iron reduction are essentially mutually exclusive (Laanbroek, 1990). The involvement of bacteria in the reduction of ferric iron is well established (Jones et al., 1983; Lovley and Phillips, 1986). Laanbroek (1990) describes two types of ferric iron reducing bacteria: a group of facultative and obligate anaerobic bacteria producing fermentation products, and a group of obligate anaerobic bacteria using fermentation products to generate energy.

With the addition of oxygen to soil, either following drainage or by leakage from roots, oxidation of these reduced elements will occur.

For nitrogen this occurs through the oxidation of ammonia to nitrite, and subsequently to nitrate. Obligately aerobic chemolithotrophic bacteria of the genera *Nitrosospira*, *Nitrosolobus*, and *Nitrosomonas* utilize the energy obtained from the oxidation of ammonia for growth, while facultative chemolithotrophic bacteria of the genus *Nitrobacter* use the energy obtained from the oxidation of nitrite and organic compounds for growth (MacDonald, 1986; Laanbroek, 1990).

At pH less than 7.5 manganese oxidation in soils is almost entirely dependent on microorganisms (Marshall, 1979). Bacteria that oxidize manganese include species in the genera *Arthrobacter*, *Bacillus*, *Caulobacter*, *Chromobacter*, *Cytophaga*, *Hyphomicrobium*, *Leptothrix*, *Pedomicrobium*, and *Pseudomonas*. According to Van Veen et al. (1978) some species of the genus *Leptothrix* form a manganese sheath that may serve as protection from parasites or predators, or to detoxify H<sub>2</sub>O<sub>2</sub> (Adams and Ghiorse, 1985).

At neutral pH, iron oxidation may proceed almost completely through chemical reactions, and Jones (1986) suggested that bacteria of the genera *Gallionella*, *Hyphomicrobium*, *Leptothrix*, *Metallogenium*, *Pedomicrobium*, and *Siderocapsa* produce sheaths of chemically oxidized ferric iron rather than oxidize ferrous iron directly. However in more acidic soils, as is the case with many wetlands, *Thiobacillus ferrooxidans* and *Leptosprillum ferrooxidans* have been shown to oxidize ferrous iron (Johnson et al., 1992).

The production of organic matter and the radial leakage of oxygen by roots stimulates microbial activity in waterlogged soils. Leakage of oxygen from the roots produces an oxidized microhabitat in the reduced soil. Microorganisms are a major component in redox reactions, rhizosphere oxidation and the subsequent formation of ferric iron deposits along the rhizoplane.

It has been assumed that below 5°C biological activity within soils is insignificant (Soil Survey Staff, 1975). However, in wetland soils climatic extremes are buffered by the high specific heat of water. In the present study the upland site reached 4°C at 15 cm at the beginning of December while the saturated and inundated sites never fell below 7°C. Pickering and Veneman (1984) found that soil temperatures of a very poorly drained soil in central Massachusetts were high enough during the winter for continued biological activity and significant reduction. Megonigal and others (1993), working in seasonally flooded forest soils in South Carolina, measured soil temperatures during the winter that varied from 7°C to 13°C and rarely fell below 5°C. Anaerobic and reducing conditions may continue to develop throughout the year and wetland systems, particularly forested wetland systems, may maintain a level of biological activity year-round.

The higher abundance of microorganisms in this study from the inundated zone in both the aerobic and anaerobic cultured systems may be attributed to the higher organic content of the inundated soil and the

higher clay content associated with wetland soils. Microorganisms in soil develop primarily in water films, contact rings, and capillaries between soil particles and with an ample supply of organic matter, microbial populations will flourish (Stotzky and Norman, 1961). Acredale soils are considered Typic Ochraqualfs (Hatch et al., 1985). Aqualfs generally have a higher montmorillonite content than better drained upland associates (Wilding and Rehage, 1985). Clay minerals, particularly montmorillonite and montmorillonite-like minerals, that have a high cation exchange capacity maintain the pH of the environment longer by replacing H ions produced during metabolism with basic cations from the exchange complex (Stotzky and Rem, 1966; Etherington, 1982). Clay minerals may allow for a more stable environment for microbial populations.

At low moisture levels clays with a large charge deficiency, such as montmorillonite and vermiculite, may not be completely expanded and their full cation exchange capacity will not be as available as under saturated conditions (Stotzky, 1966). Consequently, saturated and inundated systems with high organic matter and fine 2:1 type clays may be more conducive to microbial populations than dry systems with low organic content.

The higher diversity of the saturated and inundated systems cultured under anaerobic conditions may be the result of maintaining the samples under ambient conditions while suppressing the growth of obligate aerobes from the upland sample. High diversity in the upland and inundated cultures grown under aerobic conditions suggests that obligate anaerobes and obligate aerobes are absent from the saturated system due to the periodicity of flooding and drying.

#### *Vegetation effect on redox potential*

Redox potentials measured during this study in both the vegetated and nonvegetated areas of the saturated zone showed significant ( $p < 0.05$ ) differences. Redox potentials were higher at a depth of 15cm in the



vegetated areas and only became nonsignificant when leaf fall occurred in the woody plots and dieback occurred in the herbaceous plots. This suggests that hydrophytes growing in the saturated zone can cause an elevated redox potential within the root zone via rhizosphere oxidation. Similar results have been reported by other workers (Teal and Kanwisher, 1966; Anderson and Anderson, 1972; Kuenzler et al., 1980; Howes et al., 1981; Jaynes and Carpenter, 1986; Laan et al., 1989; Flessa, 1994).

Plant species that oxidize their rhizospheres can influence the redox potential of the soil (Table 5). Wium-Anderson and Anderson (1972), working with *Lobellia* and *Littorella* vegetation in similar soil types, determined that the redox profile depends on the presence or absence of vegetation. Where the vegetation was absent, the redox level was low relative to the vegetated areas.

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**Table 5. Comparison of redox potentials (mV) in vegetated soil and nonvegetated soil. Modified from Wium-Anderson and Anderson, 1972; Jaynes and Carpenter, 1986; and Laan et al., 1989.**

<u>Species</u>	<u>Eh(mV)</u>	
	<u>Vegetated Area</u>	<u>Nonvegetated Area</u>
<i>Rumex thyrsiflorus</i>	55	-183
<i>Rumex crispus</i>	173	-183
<i>Rumex maritimus</i>	183	-163
<i>Isoetes braunii</i> / <i>Myriophyllum tenellum</i>	175	-100
<i>Littorella/Lobelia</i>	400	-100
<i>Acer rubrum</i>	305	265
<i>Saururus cernus</i>	240	205
<i>Rosa palustris</i>	265	240

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Howes and others (1981) studied redox profiles of short and tall forms of the halophyte *Spartina alterniflora* in a salt marsh in Massachusetts. It has been recognized for some time that *S. alterniflora* has a high rhizosphere oxidizing capacity under waterlogged conditions (Teal and Kanwisher, 1966). In a comparison between redox profiles of vegetated and nonvegetated sediments, they observed redox

potentials of approximately -100 to +75 mV at a depth of 15cm in the vegetated sediments and approximately -150 mV in the nonvegetated sediments.

In a study of the rhizosphere of *Isoetes braunii* and *Myriophyllum tenellum*, Jaynes and Carpenter (1986) observed a rise in sediment redox potential of as much as 300 mV relative to bare sediment sites. They attributed the higher redox potential to the influence of radial oxygen loss from the roots of the test plants.

Laan and others (1989) studied the effect of radial oxygen loss from the roots of *Rumex thyrsiflorus*, *Rumex crispus*, and *Rumex maritimus* on the soil redox potential. They observed a redox potential in the rhizosphere as much as 350 mV higher than in the nonrooted soil. They also noted that while the redox potentials were higher in the vegetated areas, the levels were still indicative of mild reducing conditions though the amount of ferrous iron had decreased to lower than 0.01mM.

Flessa (1994) measured redox potential around the roots of the submerged macrophyte *Ranunculus circinatus* and showed a distinct increase around the root tips. In areas where the zone of oxidation of adjacent roots overlapped, redox potential measurements were higher than those measured around single roots.

The above studies dealt with submerged or periodically flooded macrophytes with high rhizosphere oxidizing power. Redox potentials in intermittently flooded or saturated systems would likely react differently. The periodic barrier to atmospheric oxygen diffusion resulting from inundation would lower the redox potential while during periods of saturation, oxygen diffusion to the upper soil profile may be less inhibited. Kuenzler and others (1980) working in a floodplain swamp system found increased ferrous iron concentrations during spring when standing water was present. They also observed both ferric and ferrous iron in soil samples obtained at a 15cm depth. They attributed the simultaneous presence of both the

oxidized and reduced form of iron to the complex nature of the physical characteristics and hydrology of the swamp. However, no investigation of possible rhizosphere oxidation effects was conducted.

Sand-Jensen and others (1982) made an interesting observation of radial oxygen loss from a study of eight species of submerged macrophytes. They suggested that there is a zone within the rhizosphere that, depending on the oxidizing power of the specific plant species, shifts diurnally between aerobic and anaerobic conditions corresponding to photosynthetic and respiratory activity. The extent to which red maple may follow this pattern is unknown.

#### *Formation of hypertrophied lenticels and adventitious roots*

Flooding can cause both a lowering of the redox potential by producing a more reduced condition within the soil and changes in the stem growth of specific plant species. In some flood-tolerant species flooding can stimulate stem growth (Ridge and Amarsinghe, 1981). The swelling of the stem base (stem hypertrophy) is the result of cell enlargement in the cortex and is common in flooded herbaceous species (Jackson and Drew, 1984). In some tree species it may be a mechanism to increase surface area and oxygen exchange (Hook and Brown, 1972). The proliferation of stem lenticels is also considered an adaptation for increased oxygen exchange and is found in flood-tolerant species (Hook et al., 1970). According to Kawase (1981) ethylene production is accelerated in flooded plants with a subsequent increase in cellulase activity. Cellulase softens the cell walls causing stem hypertrophy and development of aerenchyma tissue in both the lenticels and the adventitious roots (Sena Gomes and Kozłowski, 1980; Kozłowski, 1982; Kozłowski, 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).

The aerenchyma pore space in wetland-adapted plants allows the diffusion of oxygen from the leaves and stem to the roots. Diffusion is considered the primary mechanism for aeration of roots under anaerobic

conditions (Armstrong, 1978), though cytoplasmic streaming within the medullary rays may enhance the movement of dissolved oxygen (Coutts and Armstrong, 1971).

Mathematical formulas for the diffusion of oxygen through roots have been developed (Greenwood, 1967; Armstrong, 1978) however, various resistance factors such as nonuniform distribution of gas space along the root (Armstrong, 1971) and sinuous intercellular channels can change the diffusion path (Jensen et al., 1967).

It has been demonstrated that oxygen can enter the xylem of the stem of trees through the leaves and lenticels (Chirkova, 1968), however the presence of lenticels at the water line is considered the main entry point (Armstrong, 1978; Coutts and Armstrong, 1971). Blockage of the lenticels located at the water line has been shown to reduce the oxygen status of the roots (Armstrong, 1968; Hook et al., 1971; Scholander et al., 1955). Due to resistance to oxygen movement and its consumption through 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 *Salix* spp., *Nyssa sylvatica*, and *Avicennia nitida*, respectively. Scholander and others (1955), in a classic experiment on mangroves, found 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.

Without some mechanism for ATP generation during anaerobic conditions, 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 effect (Crowder, 1991).

Adventitious roots have been observed growing through the hypertrophied lenticels of a number of species (Pereira and Kozłowski, 1977; Sena Gomes and Kozłowski, 1980; Tang and Kozłowski, 1984), however the length of time of inundation necessary to form hypertrophied lenticels and subsequent adventitious roots varies between species and is probably affected by soil type, temperature, microbial abundance, and the type of hydrologic regime (i.e. stagnant or flowing water).

In this study, the formation of hypertrophied lenticels occurred within 7 days in both the field and laboratory experiments on seedlings under inundated conditions. Seedlings under saturated conditions formed hypertrophied lenticels within 7 days in the laboratory and between 3 and 7 weeks in the field. This difference may be due, in part, to the oxidation of the upper soil profile by the surrounding vegetation in the field experiment which reduces the initial anaerobic stress on these seedlings.

Adventitious water roots were observed on the inundated seedlings after 4 weeks and 3 weeks in the laboratory and field, respectively, and on the saturated seedlings only after 12 weeks and 13 weeks in the laboratory and field, respectively. This difference in the time of adventitious water root formation between inundated and saturated seedlings suggests that the additional barrier to oxygen diffusion into the soil caused by the layer of water and the subsequent increased anaerobic stress necessitates the quick formation of adventitious water roots. The negative correlation between the number of hypertrophied lenticels and percent adventitious water roots adds evidence that the increased stress of the more anaerobic condition due to inundation promotes the growth of adventitious water roots through the hypertrophied lenticels.

Pereira and Kozlowski (1977) observed the formation of hypertrophied lenticels and adventitious roots in *Salix nigra* and *Ulmus americana* within 7 days of flooding. Adventitious roots were observed on *Nyssa aquatica* and *Nyssa sylvatica* var *biflora* after a few days of flooding (Hook and Scholtens, 1980). In the facultative wetland species *Fraxinus pennsylvanica* hypertrophied lenticels formed after 5 days of flooding and adventitious roots after 15 days of flooding (Sena Gomes and Kozlowski, 1980; Kozlowski and Pallardy, 1984). In a laboratory experiment on 3 month and 4 month old *Quercus macrocarpa* seedlings Tang and Kozlowski (1982) observed hypertrophied lenticels on some seedlings after 5 days in one experiment and 11 days in another experiment. At the end of 30 days some adventitious roots were noted. 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.

In a study of five forested wetland sites in western Kentucky, Mitsch and Taylor (1991) found productivity highest in the intermittently flooded sites, intermediate in the inundated flowing water sites, and lowest in the inundated stagnant water sites. Red maple seedlings have been shown to be equally affected by both saturation and inundation with high survival and only moderate growth reduction under inundated conditions (Jones et al., 1989; Walters and Yawney, 1990). In this study total root biomass was similar between the saturated and inundated seedlings after 3 weeks but was significantly higher ( $p < 0.05$ ) in the saturated seedlings after 7 weeks and 13 weeks. This follows a pattern similar to data obtained by Day (1987) who studied red maple seedlings transplanted from a forested wetland system in Virginia. He found no significant difference between total root biomass (primary roots and adventitious water roots) of intermittently flooded seedlings and flooded seedlings until after 7 months. This suggests that the less stressful condition associated with saturation, as opposed to inundation, may allow red maple seedlings to allocate more biomass to the primary root system rather than adventitious root formation.

The lack of adventitious roots on the saturated seedlings may also be explained, in part, by the higher redox levels in the saturated zone and the absence of the “water jacket” effect associated with flooding. As the water level rises above the soil level, the inundated portion of the stem will be subject to ethylene entrapment even in aerated water (Jackson, 1990). Kawase (1981) and Tang and Kozlowski (1984) suggest the increase in ethylene content of the stems of flooded plants may be due to local stimulation of ethylene production under anaerobic conditions, blocking of ethylene escape by a water jacket effect, and by absorption and upward translocation of ethylene from the soil. Inundation 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 which is involved in cell enlargement (Kawase, 1981). Maronek and Wott (1975) studied flooding effects on 2 to 7 year old red maple trees. They found an increase in ethylene concentration in the internal atmosphere of the roots and the basal 10-inch stem segment and found that it also coincided with lenticel hypertrophy. Lenticel hypertrophy can be reproduced in non-flooded plants by supplying ethylene and inhibited in flooded plants by applying an ethylene-action inhibitor such as silver nitrate (Jackson and Palmer, 1981; Kawase, 1981).

The presence of an overlying layer of water in the inundated system acts as a barrier to oxygen diffusion into the soil. The presence of hydrophytic vegetation capable of rhizosphere oxidation may maintain elevated redox levels and reduce anaerobic stress. The additional expenditure of energy in adventitious root formation may not be necessary under this condition.

#### *Radial oxygen leakage and materially visible ferric iron deposits*

The oxidation of reduced dye solutions has been used to show root-oxidizing activity in a number of woody species including *Betula pubescens* (Huikari, 1954), *Salix atrocinerea* (Leyton and Rousseau, 1957), *Nyssa sylvatica*, *N. aquatica*, and *Fraxinus pennsylvanica* (Hook et al., 1972). The ability of red maple seedlings to oxidize their rhizosphere was demonstrated in this study by the presence of an oxidizing agent adjacent

to the adventitious roots in the leuco-methylene blue experiments. Oxygen is lost through the cell wall into the adjacent soil where iron oxyhydroxide (FeOOH) can precipitate as a reddish/orange plaque on and around the root.

The oxidized deposits are generally considered to consist of the oxyhydroxide mineral lepidocrocite ( $\gamma$ -FeOOH) (Sung and Morgan, 1980; Cornell and Schwertmann, 1991) though an extended reduction time or high carbon dioxide in the soil may favor goethite formation ( $\alpha$ -FeOOH) (Schwertmann and Taylor, 1972; Chen et al., 1980; St-Cyr et al., 1993). Some bacteria accumulate oxidized iron on their outer cellular structures which over time become visible as reddish/orange deposits (Trolldenier, 1988; St-Cyr et al., 1993). In this study redox potentials indicated only moderately reduced soil conditions and it was assumed that lepidocrocite was the dominant iron oxyhydroxide mineral.

Many studies have investigated the presence of oxidized iron in plant rhizospheres (Bartlett, 1961; Bacha and Hossner, 1977; Mendelsohn and Postek, 1982; Crowder and MacFie, 1986; Good et al., 1986; Trolldenier, 1988; Ernst, 1990). Few studies however, have investigated the time required for iron plaque formation. Chen and others (1980) reported the presence of iron plaque on rice roots after 7 days of flooding. Trolldenier (1988) showed the presence of visible ferric iron deposition on the roots of rice 11 days after transplanting to ferrous sulfide agar medium.

Generally, the reduction of ferric to ferrous iron is not initiated until all of the nitrate and manganese have been depleted (Takai and Kamura, 1966; Turner and Patrick, 1968; Gambrell and Patrick, 1978; Armstrong, 1982; Ponnampereuma, 1984). In order for radial oxygen leakage from the root to form iron oxide deposits along a root channel, significant amounts of ferrous iron must be present in the soil. In the present study, visible ferric iron deposition occurred between 3 and 7 weeks in the inundated field seedlings. Ferric iron deposits were observed proximate to the adventitious roots and hypertrophied



lenticels after 13 weeks among saturated field seedlings but only after 6 weeks for seedlings under inundation. In the laboratory, the visible presence of ferric iron deposits was observed after 4 weeks only in the inundated seedlings. This suggests that a period of inundation of at least 3 weeks, with the subsequent barrier to oxygen diffusion, may be required to lower the redox potential at the 15 cm depth sufficient enough for ferrous iron to be present. Additional time will be required for the oxidation of ferrous iron by radial oxygen leakage from the adventitious roots or hypertrophied lenticels to form visible ferric iron deposits along the rhizoplane. In red maple seedlings growing in Acredale soil this inundation requirement time is at least 3 weeks.

Turner and Patrick (1968) showed the presence of ferrous iron in a soil solution after four days of waterlogging. However, their experiment was conducted at elevated soil temperature conditions. Stoops and Eswaran (1985) suggest several consecutive days of waterlogging are necessary for the reduction of iron. McKee and Hook (1992) reported that it took 4 to 8 weeks of waterlogged conditions at ambient temperatures for ferrous iron to predominate in the soil solution, while Vepraskas and Wilding (1983) reported 6 to 197 cumulative days of saturation for redox potentials to be sufficiently low to reduce ferric compounds. In a study of the distribution of inorganic reducible substances in flooded Crowley silt loam soil, Patrick and Delaune (1972) found no iron reduction after one day and very little reduction after 7 days. Maximum reduction was reached after 8 weeks of flooding.

Depending on a number variables, including soil temperature, microbial abundance, mineral content, soil organic matter content, and time of waterlogging, some period of time will be required for the formation of adventitious roots and before ferrous iron will be prevalent enough to be precipitated as ferric iron deposits. Additional time will be required for iron precipitates along the root channel to become visible to the naked eye. Care must be taken for the proper identification of rhizosphere oxidation since iron

concretions can line large pores within soil peds (channel neoferrans) (Pickering and Veneman, 1984) and could be mistaken for root channel oxidation.

## Summary

1. Organic matter and microbial abundance was highest in the inundated zone and microbial diversity was lowest in the saturated zone.
2. Exchangeable iron was highest in the inundated zone at the first sampling with no significant difference between the saturated and the upland zones. At the second sampling, after the saturated zone had been inundated for two weeks, the inundated and saturated zones had similar exchangeable iron levels which were significantly higher ( $p < 0.05$ ) than the upland zone, suggesting that a period of inundation is necessary to reduce iron at the 15 cm depth.
3. Redox potential remained high ( $> 300\text{mV}$ ) in the upland field and upland laboratory experiments indicating aerobic conditions. The redox potential of the field saturated experiment rarely fell below  $200\text{mV}$  and only when the site became inundated. The laboratory saturated experiment never reached redox levels indicative of iron reduction. The inundated experiment in both the field and laboratory experiments maintained redox levels below that necessary for the mobilization of iron.
4. The oxidation of leuco-methylene blue adjacent to the adventitious water roots and hypertrophied lenticels of red maple seedlings grown under an inundated hydrologic regime demonstrates that radial leakage of oxygen does occur.

5. Hydrophytic vegetation that is capable of rhizosphere oxidation can elevate the redox potential at the 15cm depth in saturated soil.
6. Hypertrophied lenticels were observed on the inundated seedlings within 7 days in the field and in the laboratory. Hypertrophied lenticels were observed on the saturated seedlings within 7 days in the laboratory and after 3 weeks in the field.
7. Adventitious water roots were observed on the inundated field and laboratory seedlings after 3 and 4 weeks, respectively. The saturated field and laboratory seedlings developed adventitious water roots after 13 and 12 weeks, respectively.
8. Total root biomass was highest in the upland seedlings. Total root biomass was similar between the saturated and inundated seedlings for 7 weeks after which the inundated seedlings showed reduced growth.
9. Materially visible ferric iron deposits were observed on and adjacent to the adventitious water roots of the inundated field seedlings after 3 weeks and the inundated laboratory seedlings after 4 weeks. The saturated field seedlings had visible ferric iron along the rhizoplane only after the site was flooded for 6 weeks.

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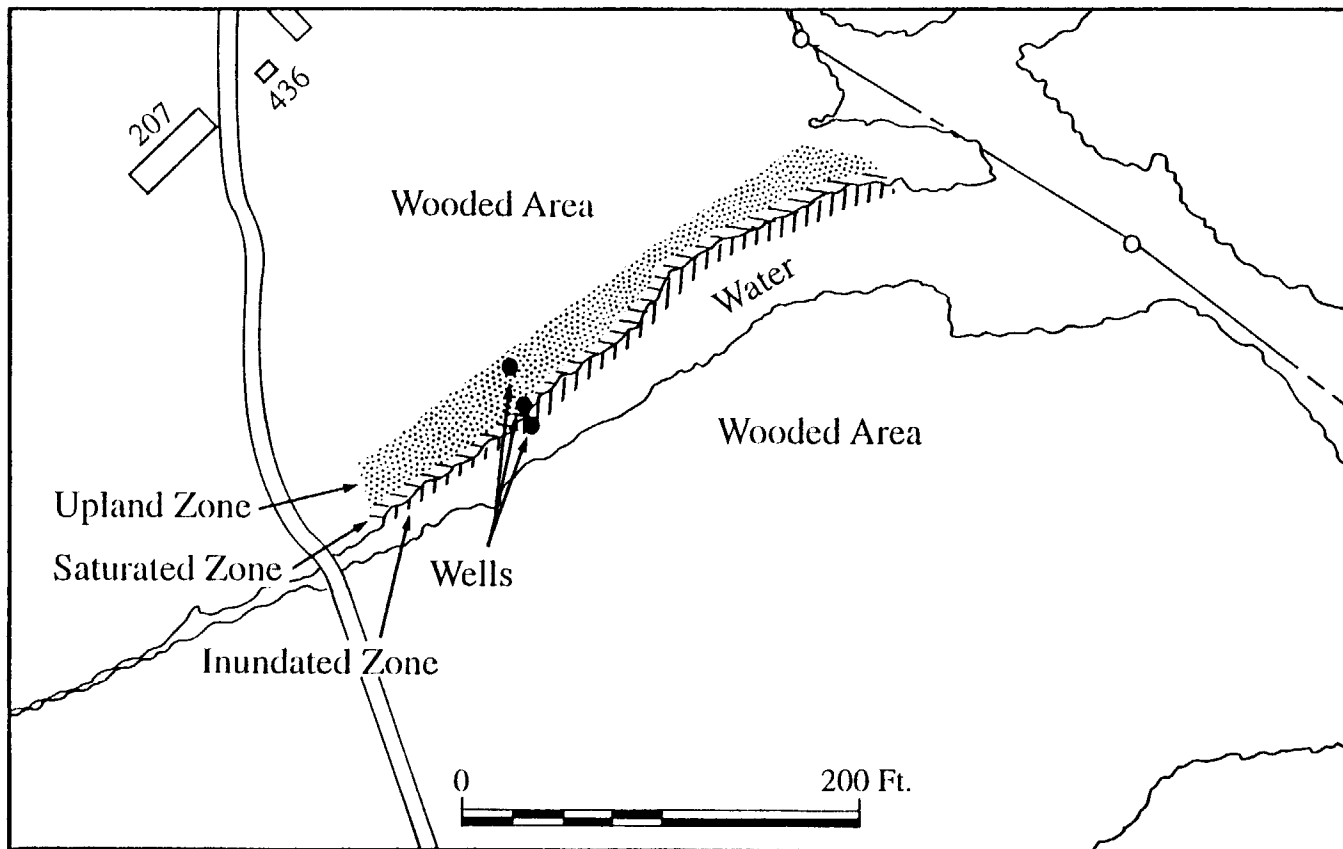


Figure 1. Field site at Camp Pendleton, Virginia Beach, Virginia, Virginia Army National Guard State Military Reservation.

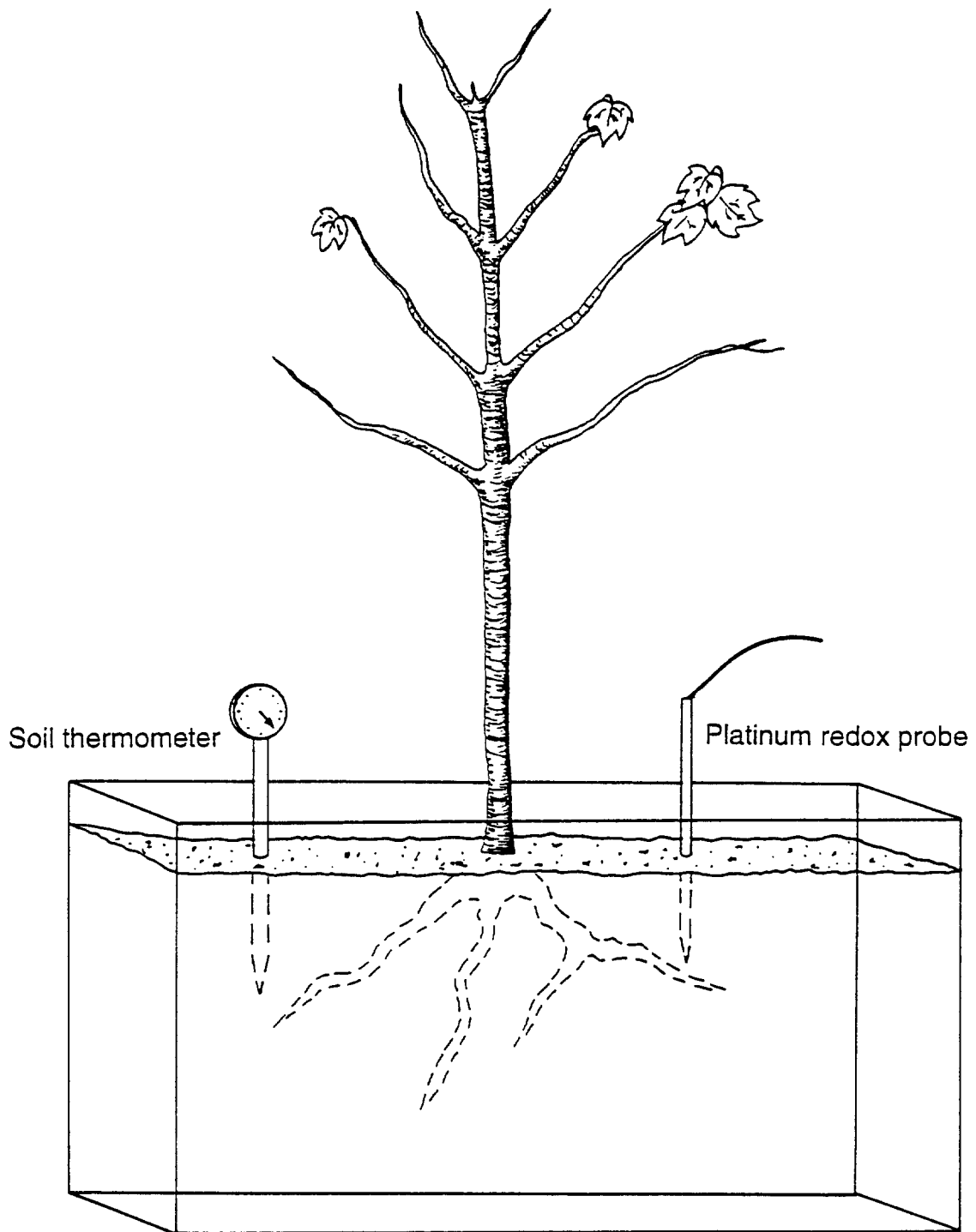


Figure 2. Schematic of *Acer rubrum* seedling laboratory experiment. One seedling per container with 7 containers per hydrologic regime.

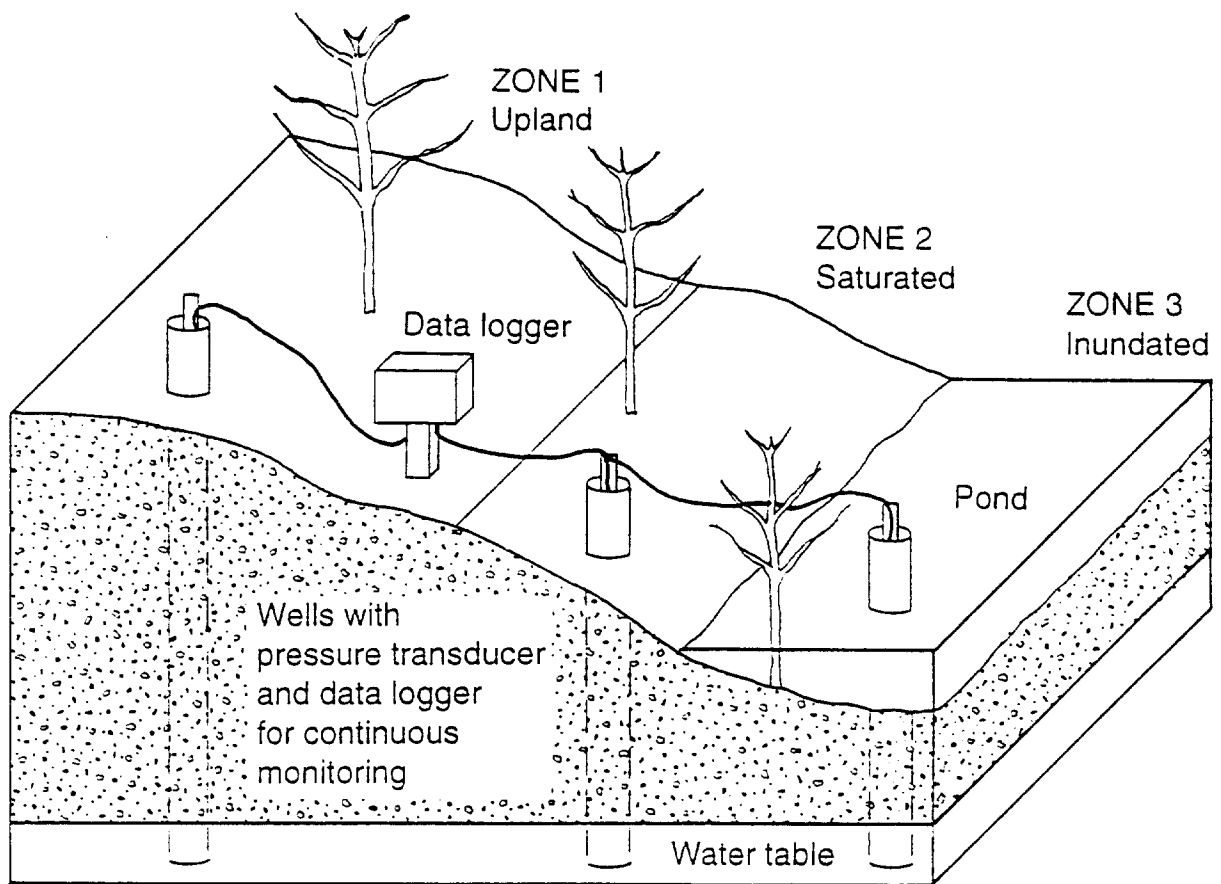


Figure 3. Schematic of *Acer rubrum* seedling field experiment. 100 seedlings per zone.

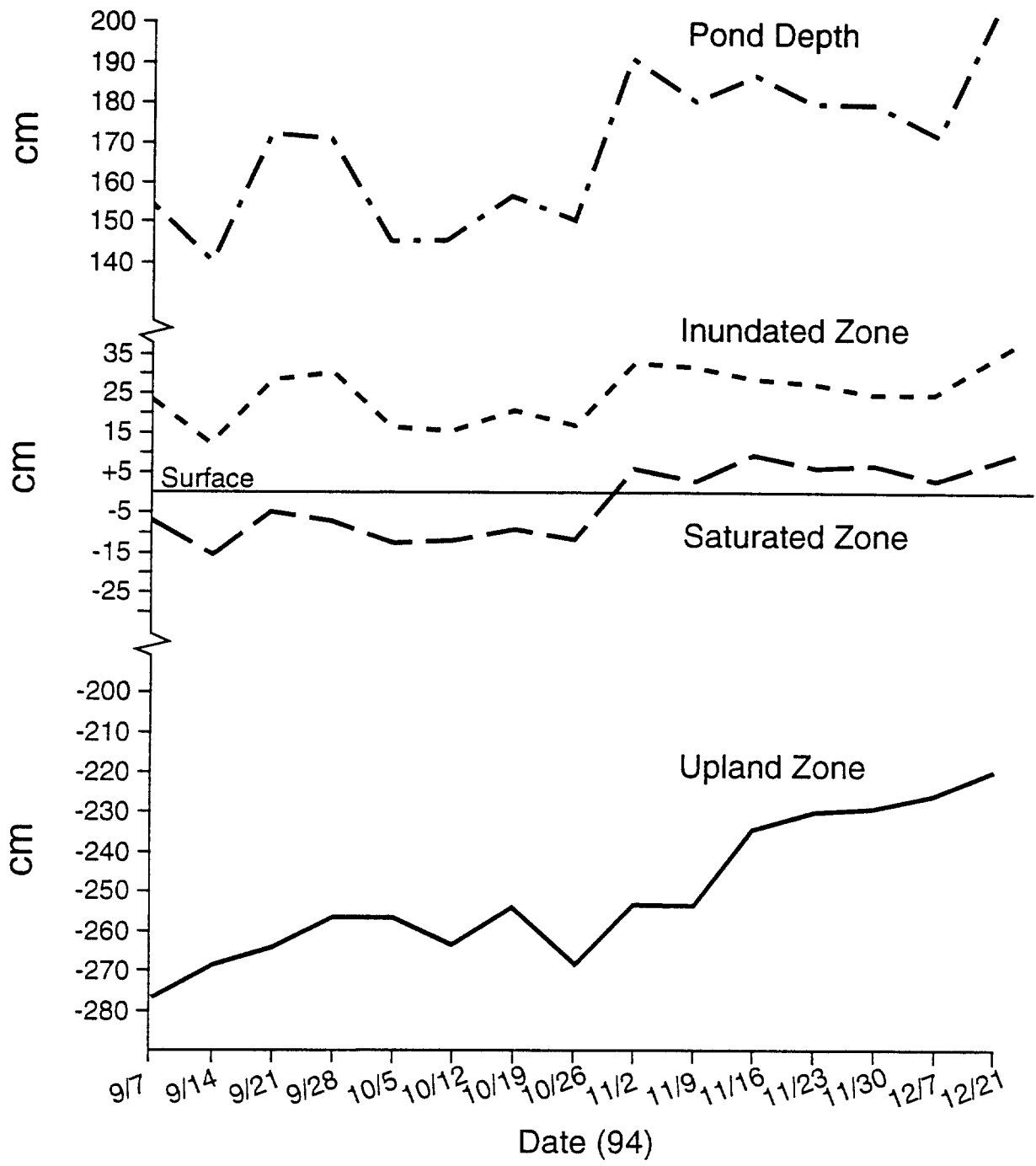


Figure 4. Water table depths along the transitional gradient over time.



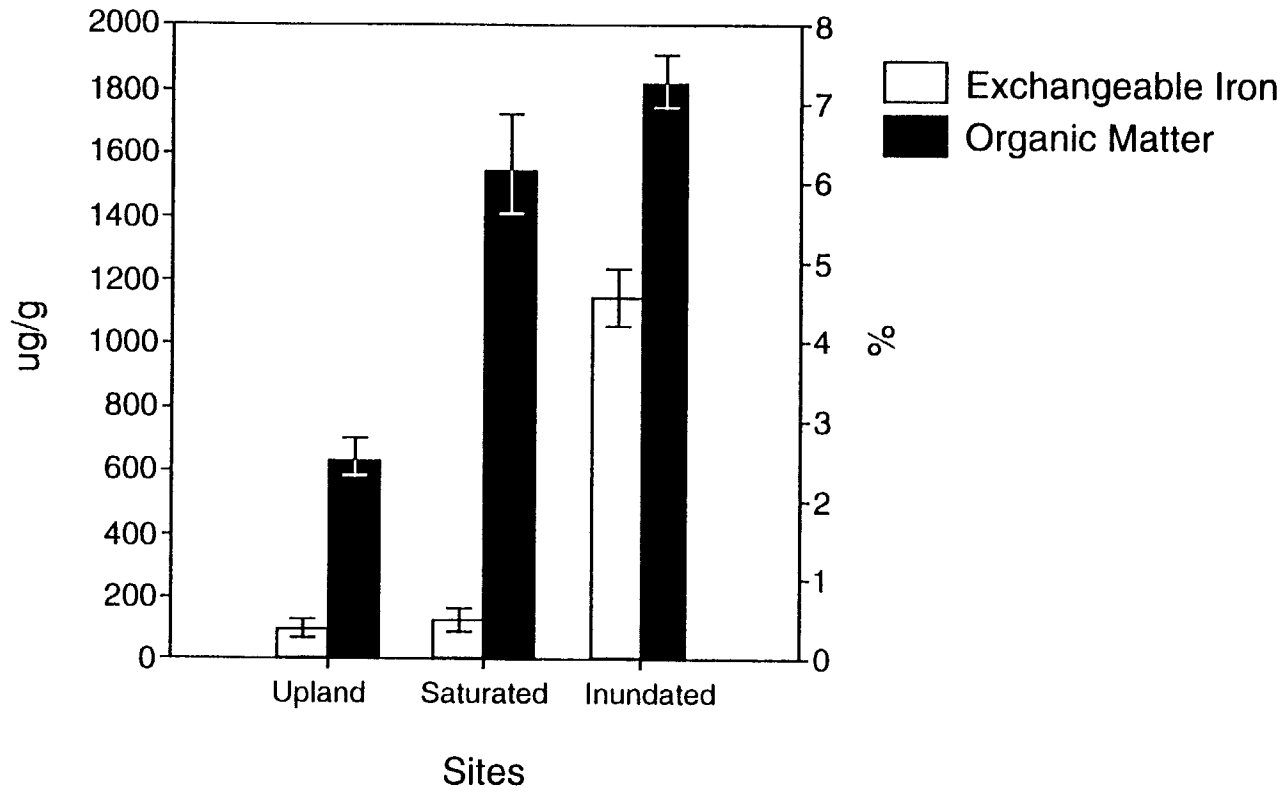


Figure 5. Exchangeable iron and organic matter in upland, saturated, and inundated sites. (Sample taken October 5, 1993 at 15cm depth)

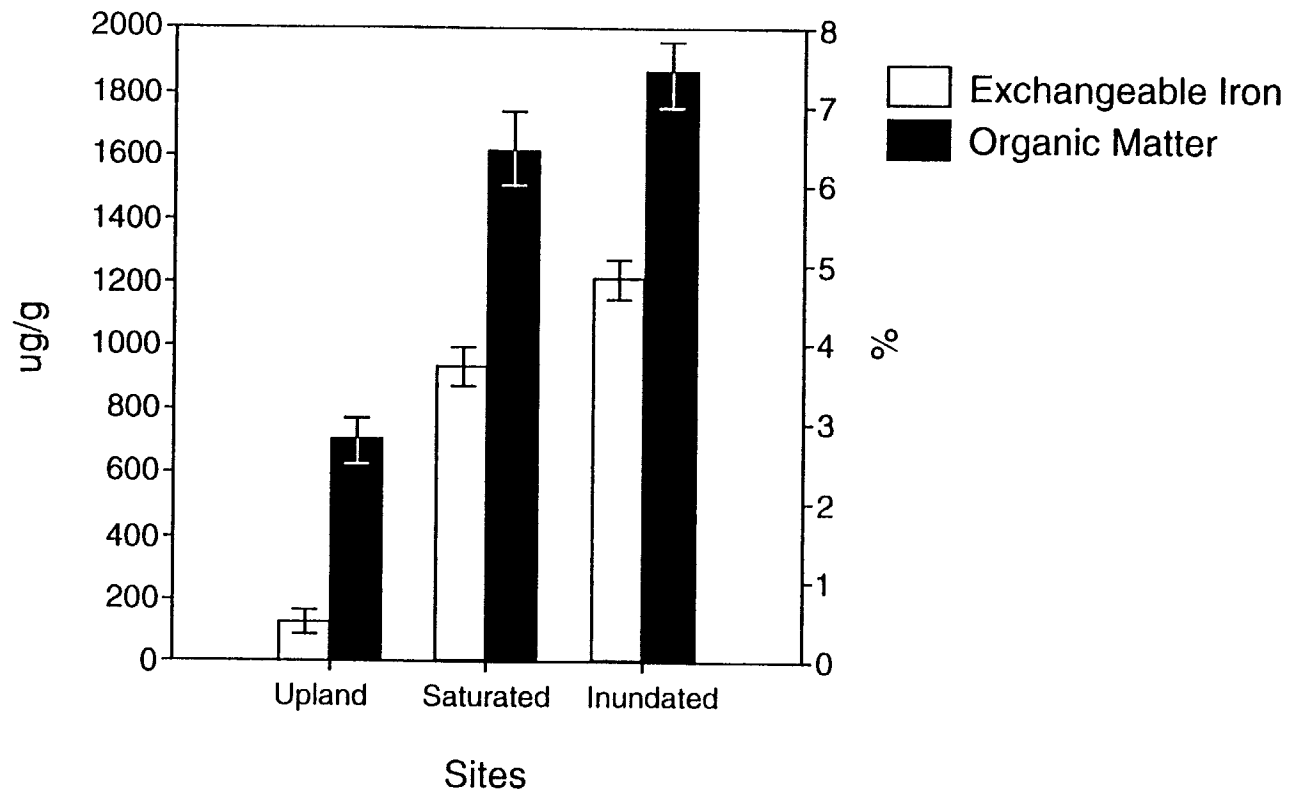
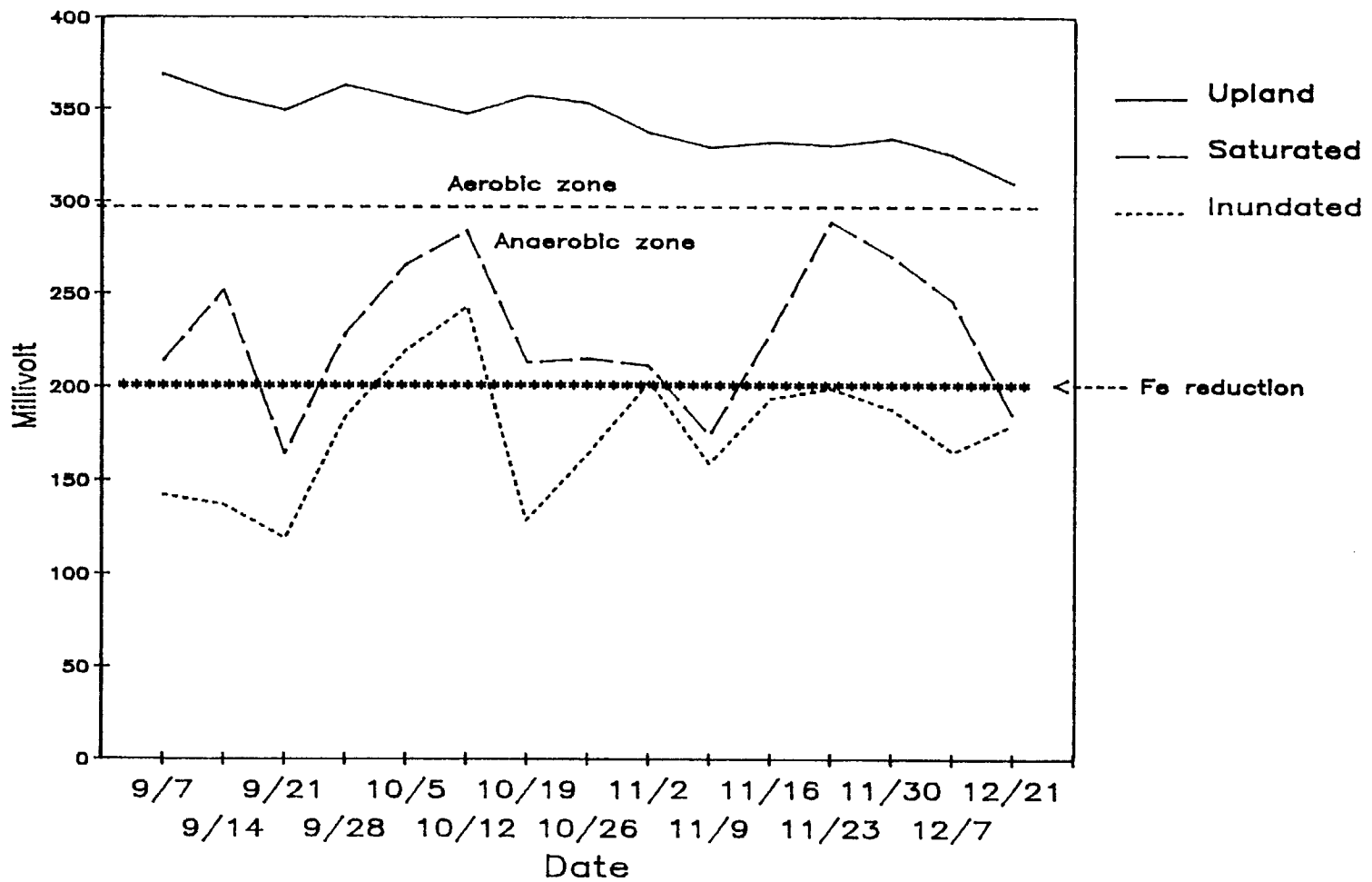
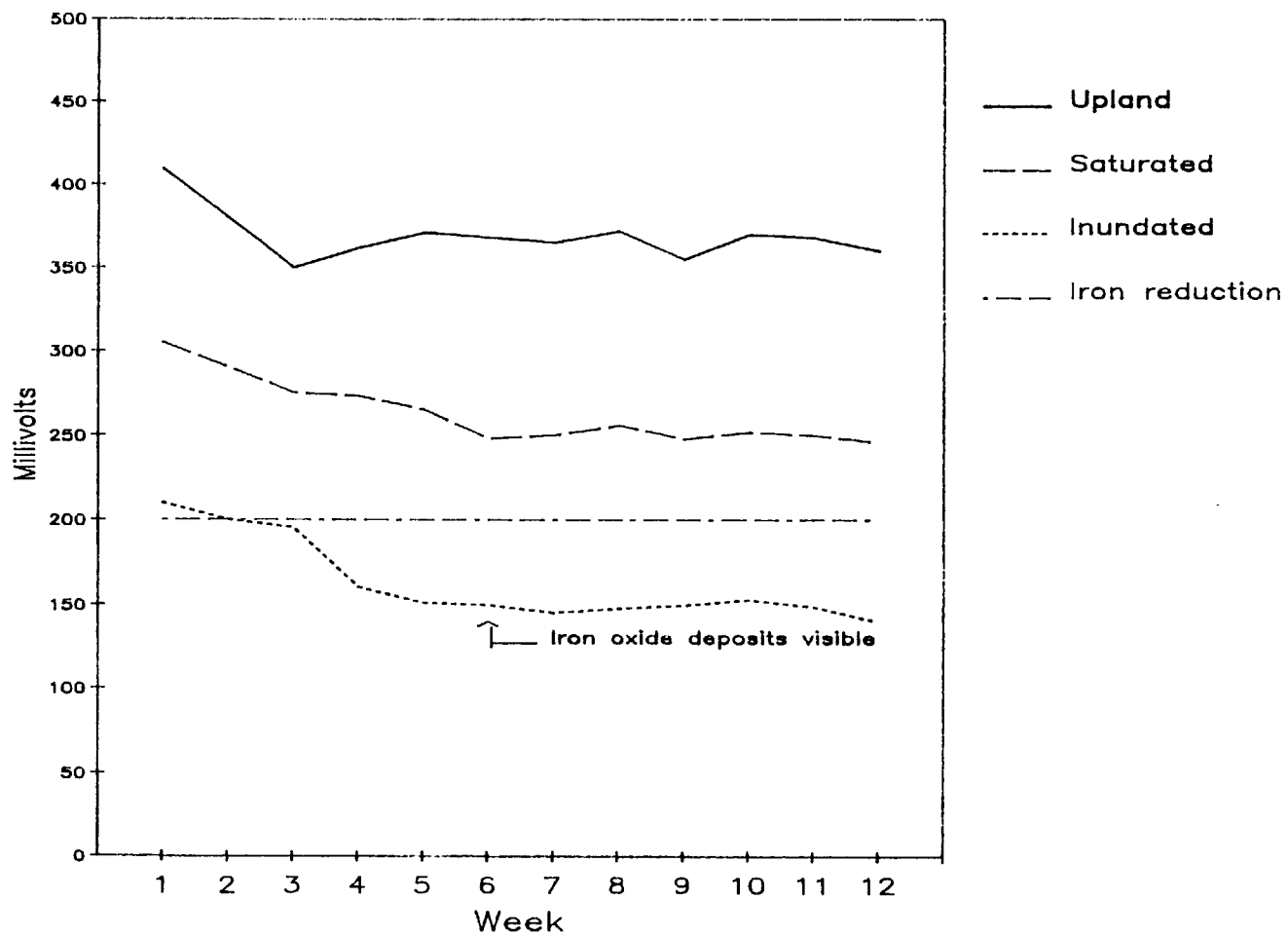


Figure 6. Exchangeable iron and organic matter in upland, saturated, and inundated sites. (Sample taken November 16, 1993 at 15cm depth)



pH between 6 and 7

Figure 7. Average field redox measurements within upland, saturated, and inundated sites over time.



pH between 6 and 7

Figure 8. Average redox measurements in the laboratory experiment over time.

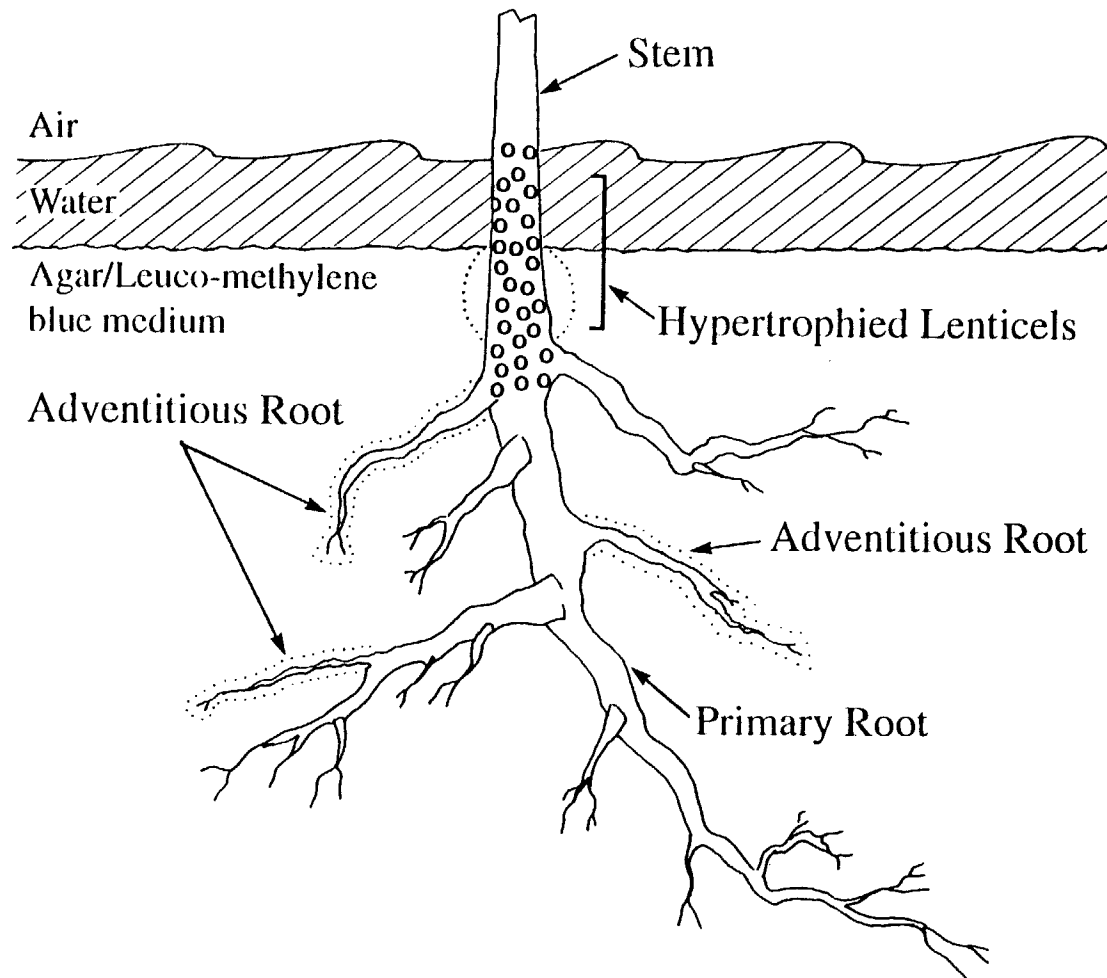


Figure 9. Oxidation pattern of *Acer rubrum* seedlings grown under inundated conditions. Dashed lines indicate areas of oxidized methylene blue.

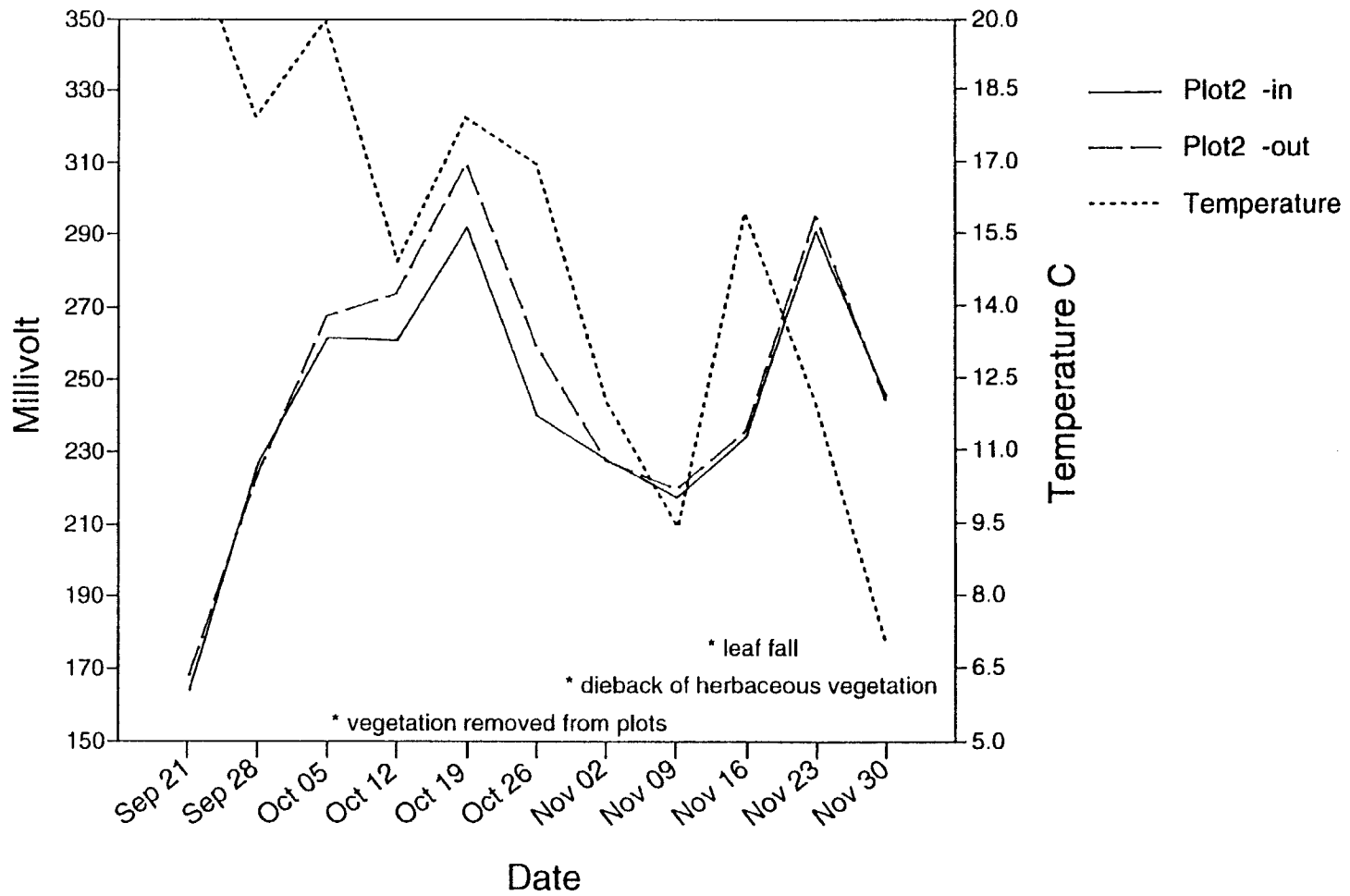


Figure 10. Average redox potential within denuded plots and immediately adjacent to denuded plots in the saturated wetland zone. (Herbaceous area)

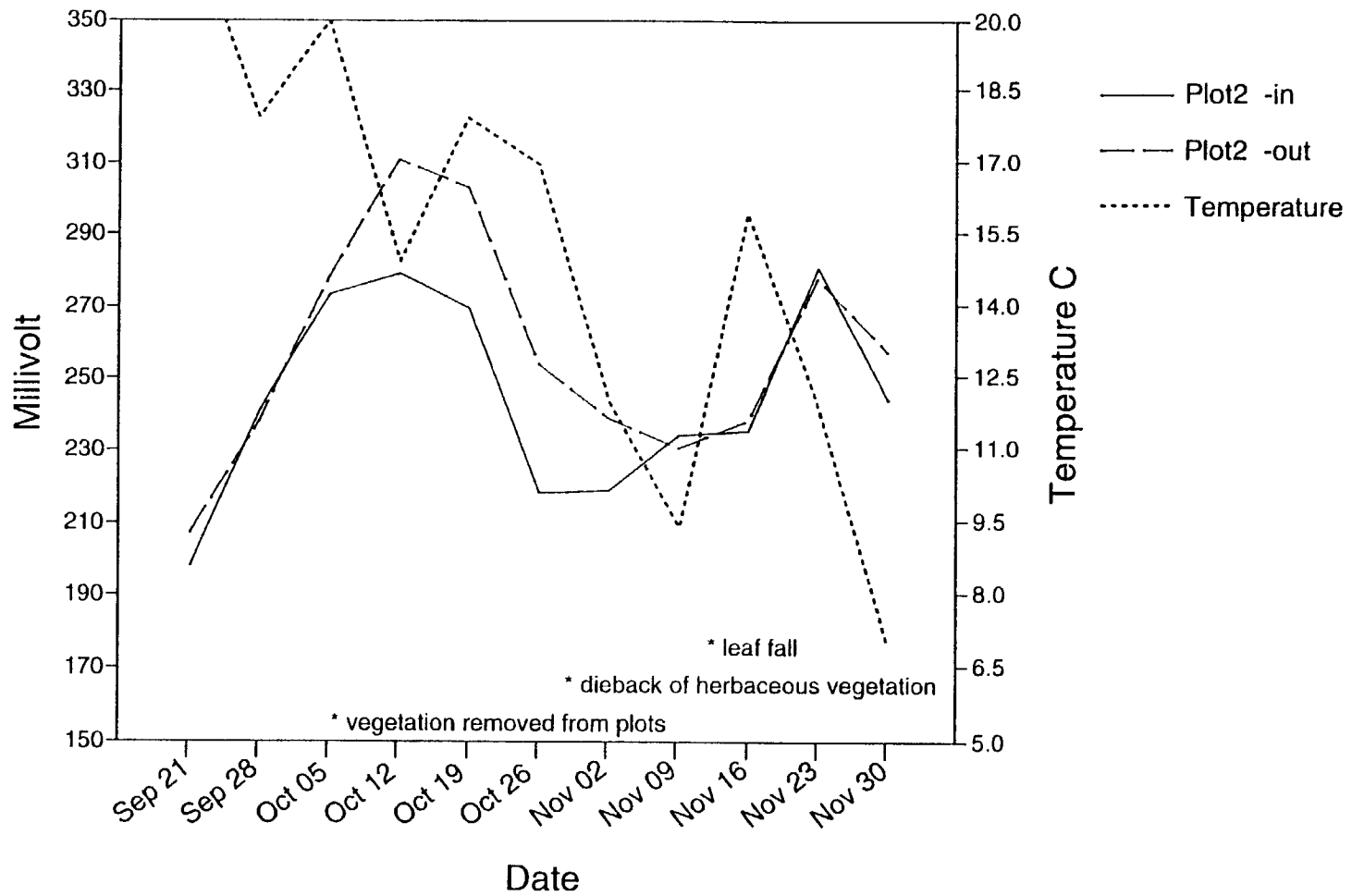
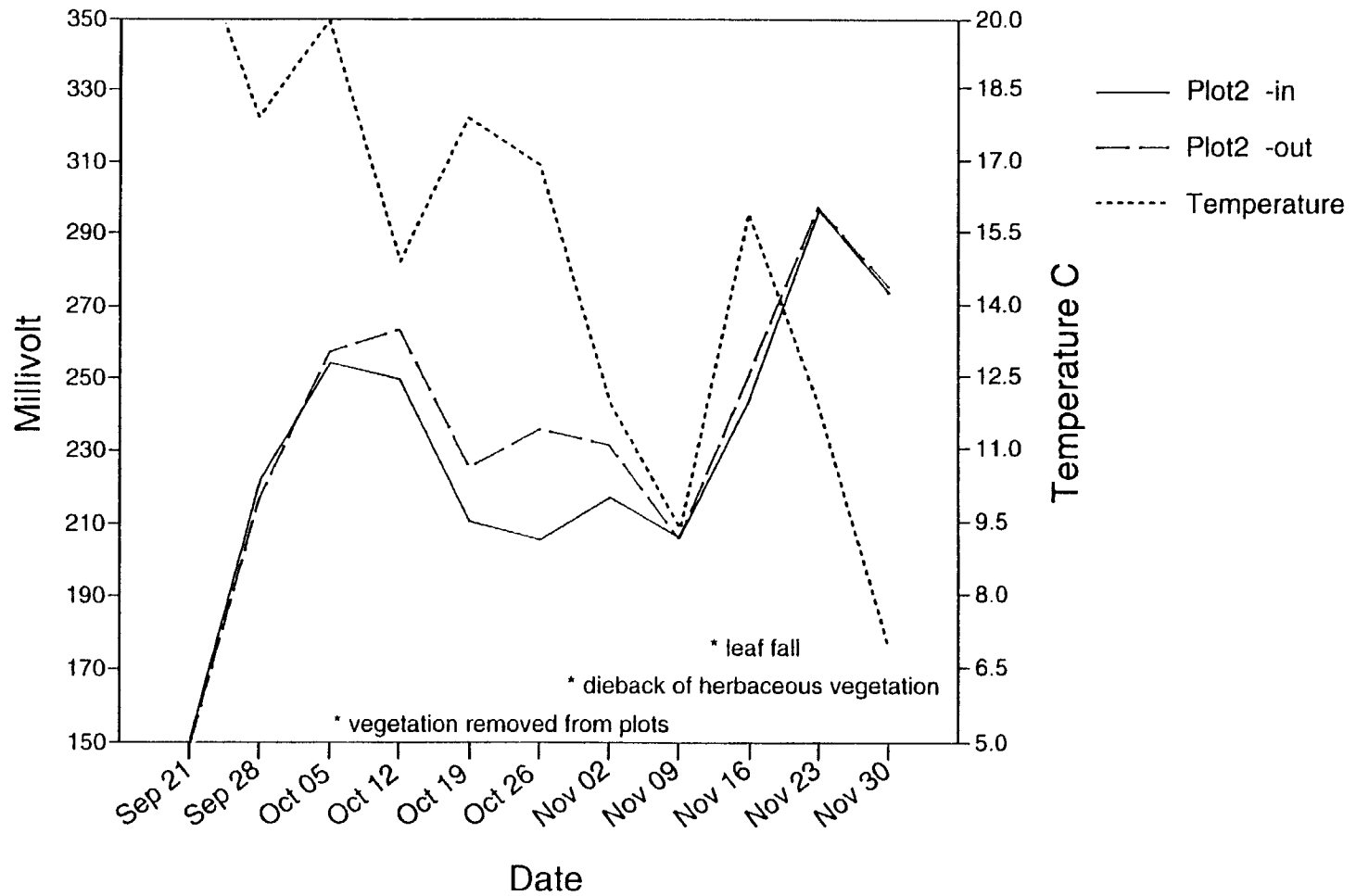


Figure 11. Average redox potential within denuded plots and immediately adjacent to denuded plots in the saturated wetland zone. (Tree area)



**Figure 12. Average redox potential within denuded plots and immediately adjacent to denuded plots in the saturated wetland zone. (Shrub area)**



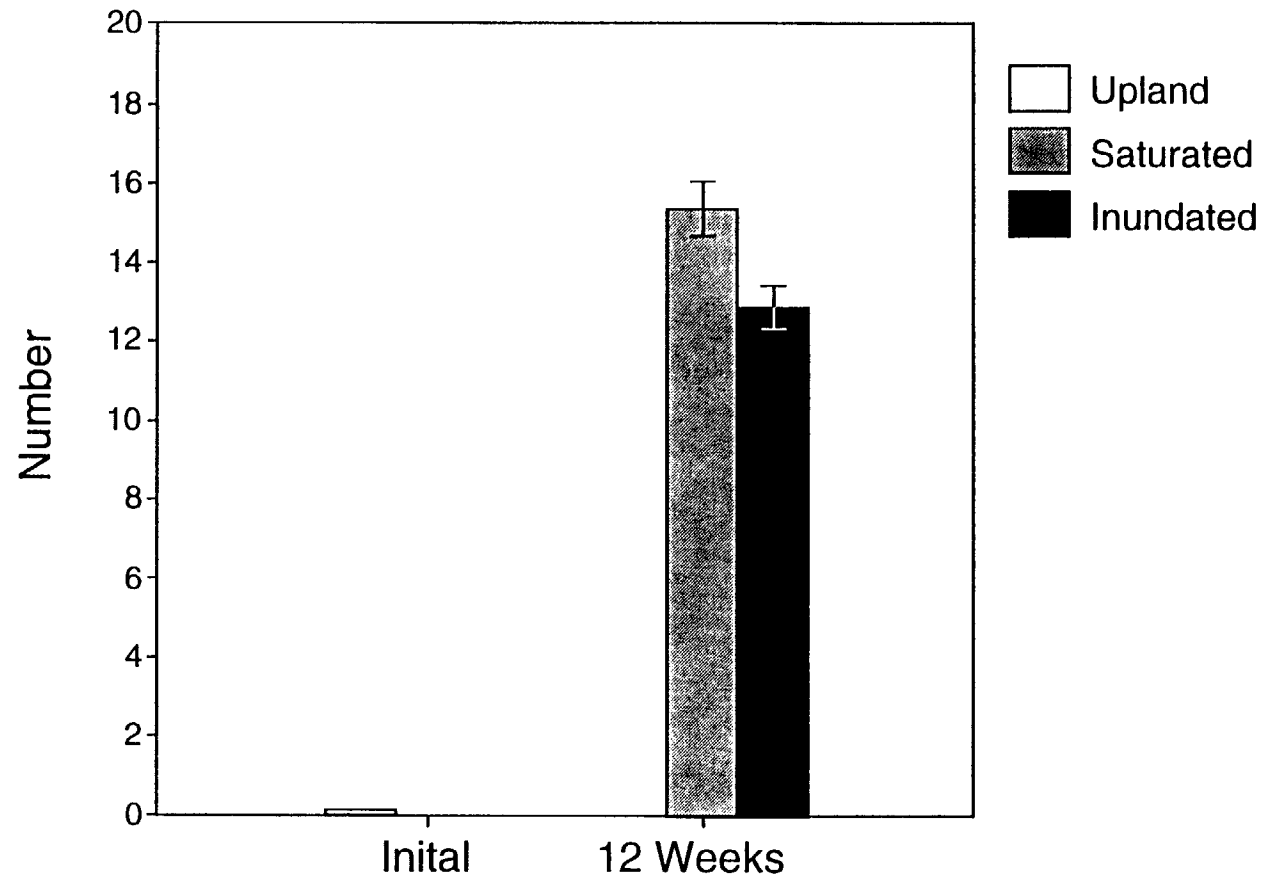


Figure 13. Average number of hypertrophied lenticels in laboratory grown *Acer rubrum* seedlings over time.

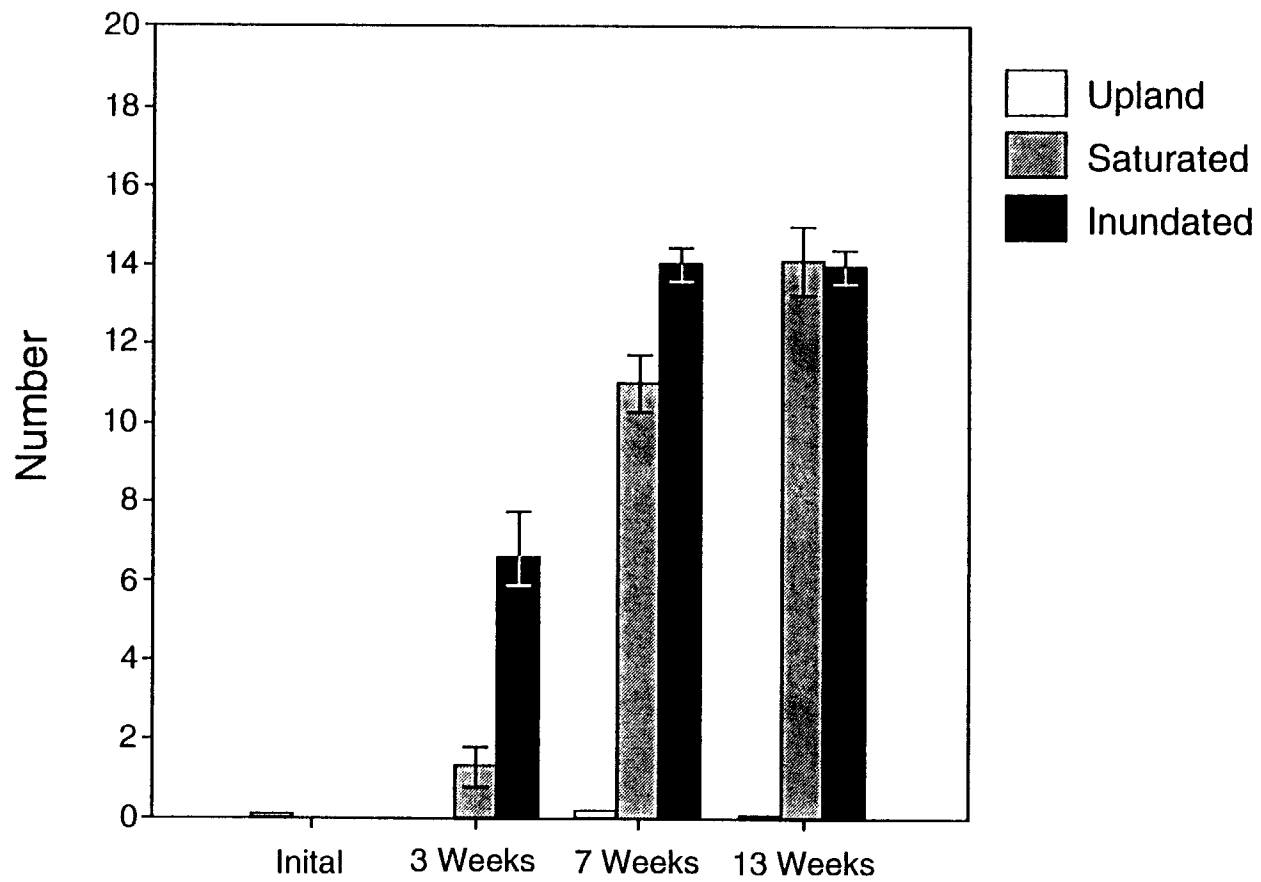


Figure 14. Average number of hypertrophied lenticels of field grown *Acer rubrum* seedlings over time.

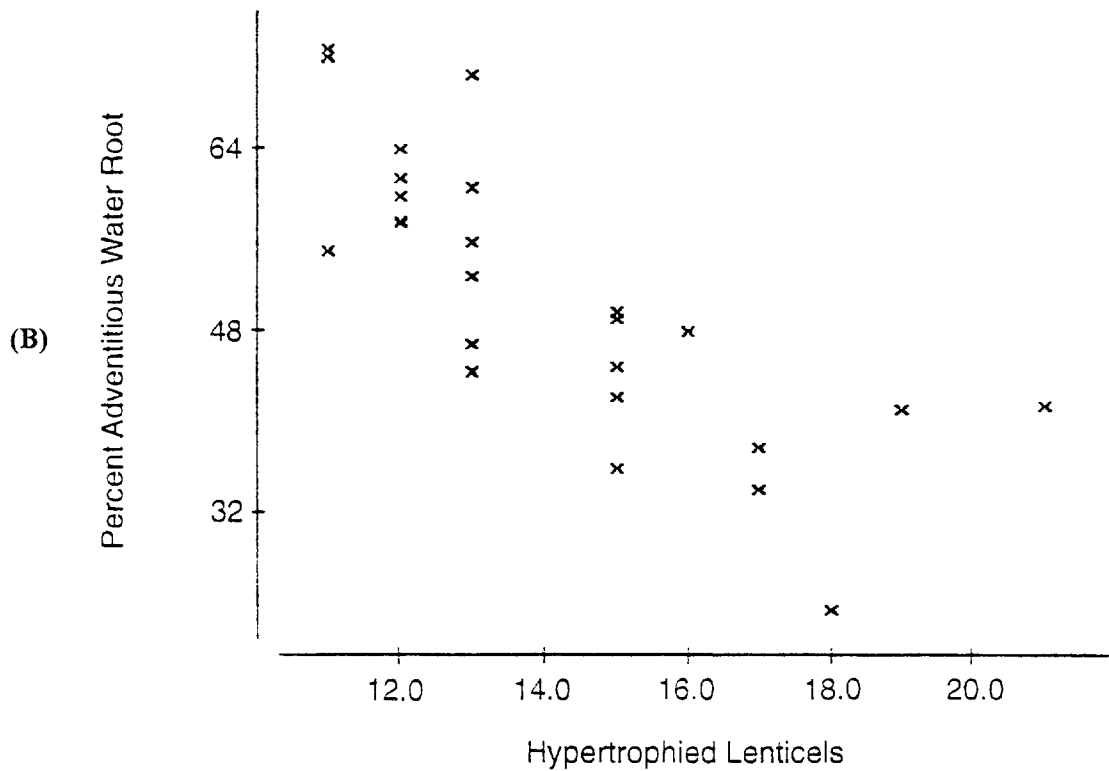
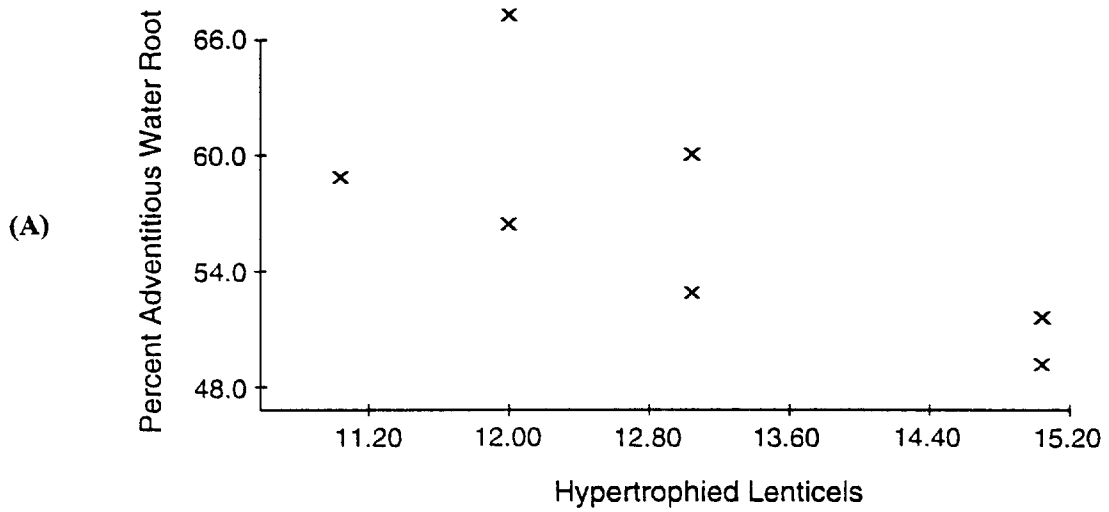
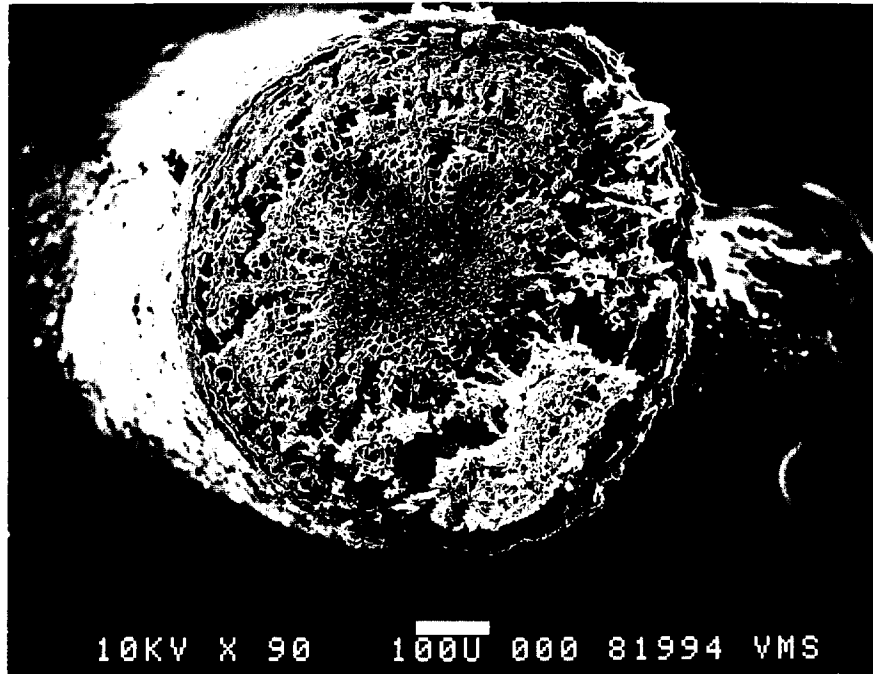


Figure 15. Negative correlation between percent adventitious water root and number of hypertrophied lenticels of *Acer rubrum* seedlings after 12 weeks of inundation in the laboratory (A) and 13 weeks of inundation in the field (B). (Laboratory: Spearman correlation,  $r_{sp} = -0.843$ ,  $N = 7$ ; Field:  $r_{sp} = -0.716$ ,  $N = 25$ )



Figure 16. Photograph of hypertrophied lenticels (white arrows) and adventitious root (black arrow) of *Acer rubrum* seedlings.

(A)



(B)

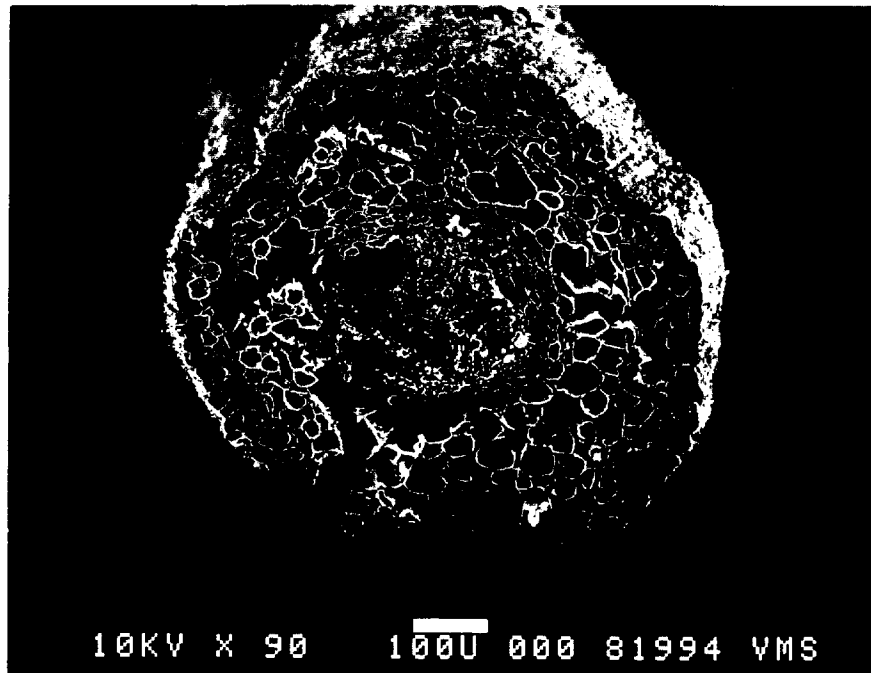


Figure 17. Scanning electron micrograph of the root of *Acer rubrum* seedlings. A) parenchyma tissue of seedling from upland site; B) aerenchyma tissue of adventitious root from inundated site.

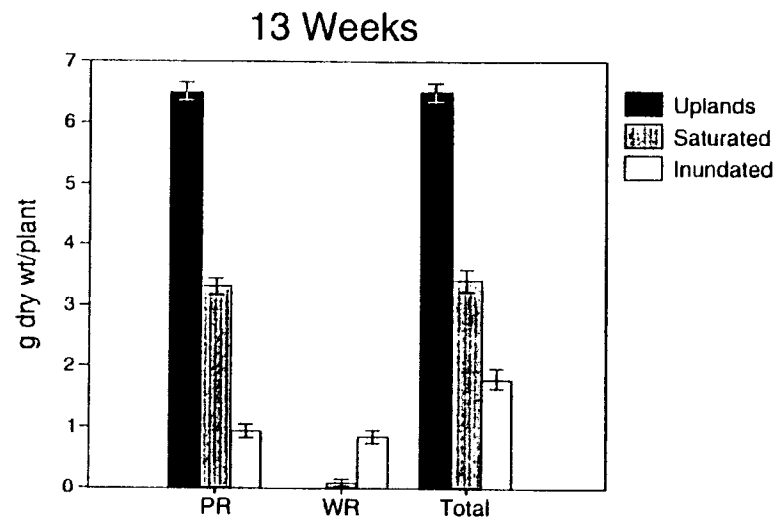
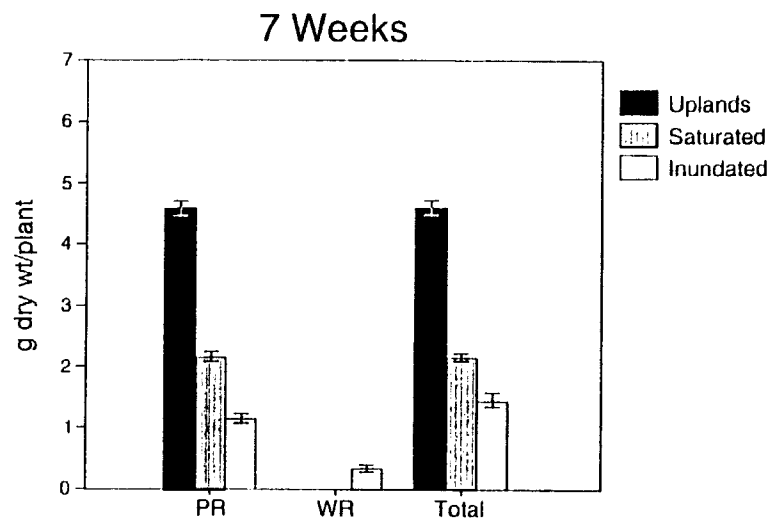
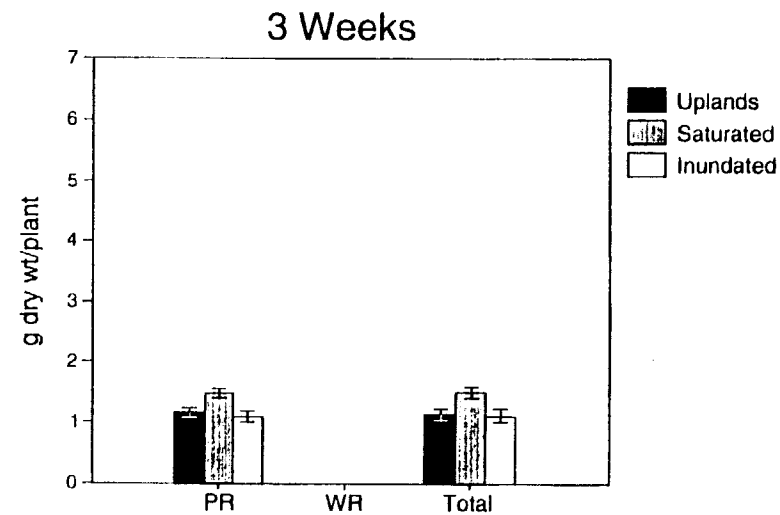
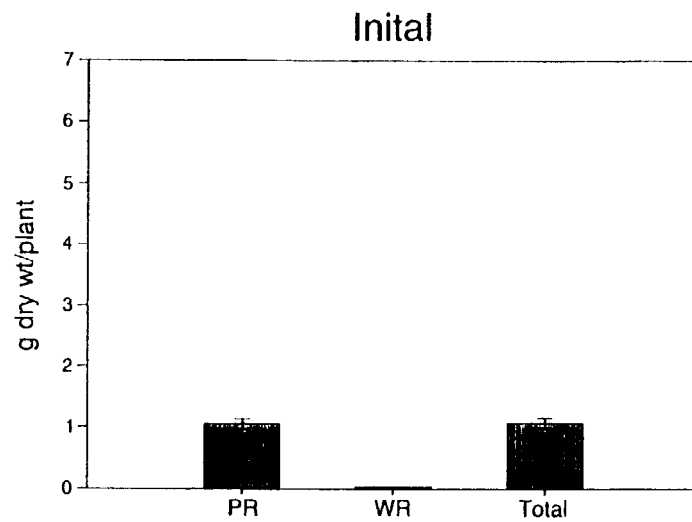


Figure 18. Average root dry weight in grams of field grown *Acer rubrum* seedlings over time (PR=primary root, WR=adventitious water root)

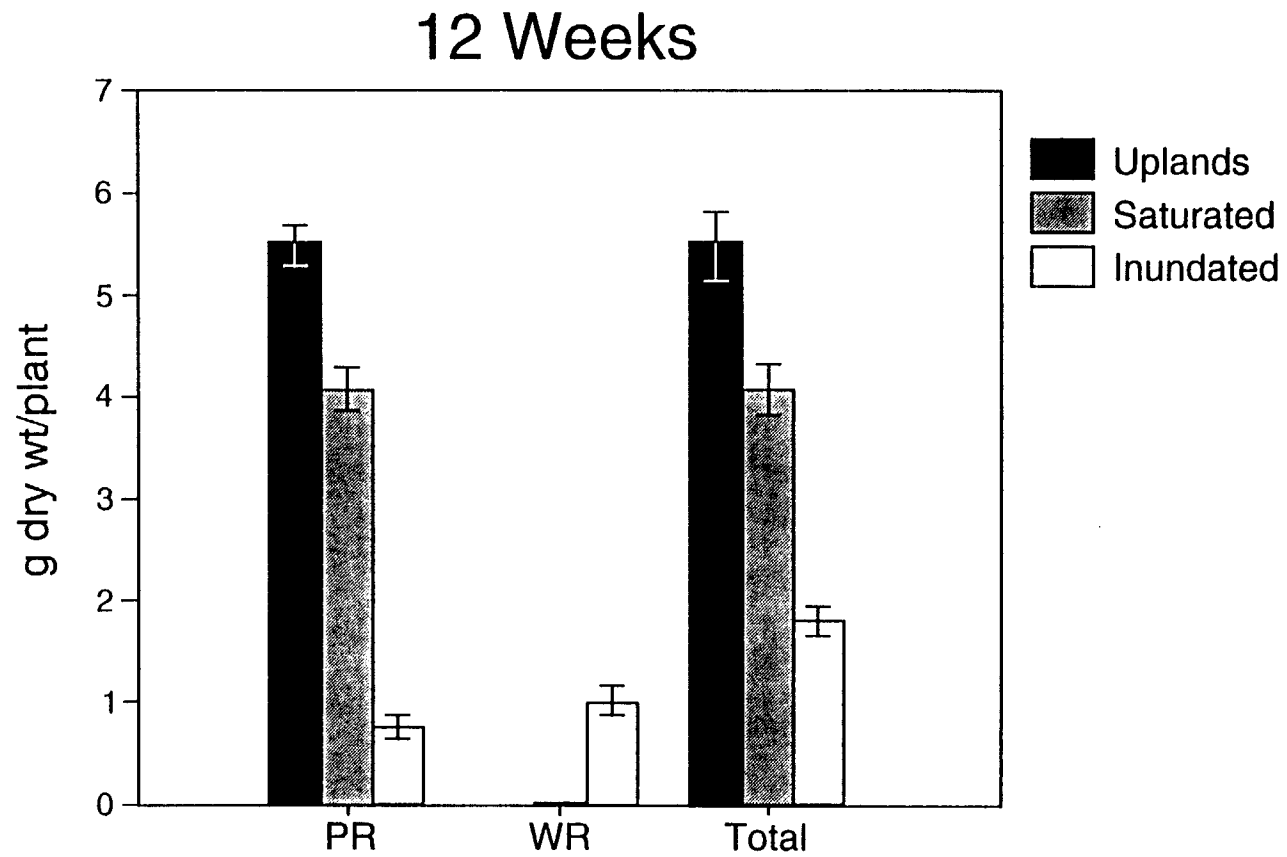


Figure 19. Average root dry weight in grams of laboratory grown *Acer rubrum* seedlings after 12 weeks. (PR=primary root, WR=adventitious water root)

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