

SOIL AERATION, FLOODING, AND TREE GROWTH¹

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Abstract. Roots require a supply of soil oxygen, water, and mineral nutrients. Oxygen is necessary to maintain aerobic root respiration so as to supply energy needed for mineral uptake, synthesis of protoplasm, and maintenance of cell membranes. In poorly aerated soils the anaerobic respiration of roots does not release enough energy to maintain root functions. Furthermore, many phytotoxic compounds accumulate in poorly aerated soils. Inadequate soil aeration occurs commonly as a result of soil compaction, filling in with soil over roots, impermeable layers (e.g. pavements) around roots, and flooding of soil. Root growth in compacted soils is reduced not only because of unfavorable aeration and moisture conditions, but also because of high mechanical impedance of soil to root growth. Flooding results in elimination of soil oxygen, accumulation of CO₂, transformation of nitrogen, and production of toxic compounds. Physiological responses of trees to flooding include closing of stomata, reductions in the rate of photosynthesis and uptake of essential mineral nutrients, as well as alterations in plant growth hormones. These physiological changes lead to inhibition of tree growth. Because root growth is reduced more than shoot growth by flooding, drought tolerance often is reduced after the flood waters drain away. Flood tolerance varies widely among species. Important morphological adaptations for flood tolerance include (1) initiation of adventitious roots which assist in uptake of water and mineral nutrients and (2) production of hypertrophied lenticels which assist in aerating the stem and roots and serve as openings through which toxic compounds are released.

Tree roots provide water, mineral nutrients, and hormonal growth regulators needed for their own growth as well as for growth of stem and crown tissues. To remain healthy and provide these substances at necessary rates, roots require a constant supply of soil oxygen (O₂), water, and mineral nutrients. The availability of O₂ is particularly crucial (Kramer and Kozlowski, 1979).

The gaseous composition of the atmosphere above ground varies appreciably from that of the soil atmosphere. The air above ground contains approximately 21% oxygen (O₂), 78% nitrogen, and only 0.03% carbon dioxide (CO₂). The soil contains less O₂ and more CO₂, with the latter increased as a result of respiration of roots and soil organisms. The amount of CO₂ normally increases and O₂ content decreases with increasing soil depth. The composition of soil air also

varies seasonally. The CO₂ content of soil air is highest in summer, less in autumn, still less in spring, and lowest in winter (Kramer and Kozlowski, 1979).

In well-drained soils there usually is enough exchange of gases between the soil and air to prevent depletion of soil O₂ and accumulation of CO₂, so as not to interfere with normal root respiration. Unfortunately, however, gas exchange between the soil and air around shade trees often is seriously impeded by compaction, sidewalks, a high or perched water table, pavements, dense growth of grass, or flooding of soil. Inadequate soil aeration is not limited to compacted soil or areas of heavy rainfall and floodplains, but occurs widely in heavy soils and in arid regions that are periodically irrigated. It has been estimated, for example, that a half to a third of the world's irrigated land has drainage problems (Donman and Houston, 1967). According to Reid (1977) about 24,000 ha of land in western Canada (out of 280,000 ha irrigated) are permanently waterlogged because of water seepage from irrigation channels.

The effects of irrigation on soil O₂ content may persist for some time. For example, when a citrus orchard on a sandy loam soil was flood-irrigated only a trace of dissolved O₂ was present to a 61 cm soil depth immediately after irrigation. After 12 hours O₂ had diffused to a 15 cm depth, but 7 days were needed for restoring normal oxygen to the entire soil depth (Van Gundy *et al.*, 1968).

Soil Compaction

The soil around shade trees often becomes compacted on golf courses, campsites, parks, and other recreation areas. Alterations in root functions of trees growing on compacted soil eventually lead to deterioration of tree crowns and growth reduction, although the effects on growth may not be apparent for a few years (Yingling *et al.*, 1979).

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Compaction of soil results in increased bulk density (BD) or mass per unit volume of soil. There are many examples of increase in BD of compacted soils and only a few will be given. The BD of soil on a campsite increased by 21% (Legg and Schneider, 1977). In the Washington, D.C. area compaction of several different soils resulted in an increase in BD from a range of 1.30 to 1.60 g/cm³ to a range of 1.70 to 2.20 g/cm³ (Zisa *et al.*, 1980). Most compaction occurs in the upper 15 cm of soil (Thorud and Frisell, 1976). Clay soils and those containing a high proportion of exchangeable Ca are very prone to compaction if they contain an abundance of water (Martin, 1968). Dry and coarse-textured soils are less susceptible to compaction (Hatchell *et al.*, 1970).

In developed areas one of the most common causes of O₂ deficiency is the placement of fill around tree stems. Yelenosky (1963) studied the composition of soil air under a newly paved road, an unpaved parking lot, and an adjacent, undisturbed forest in Durham, North Carolina. The poorest soil aeration was found in an area where clay fill had been placed around stems of trees. Oxygen concentrations were as low as 1% and CO₂ content was above 20% in the soil under this fill. In general oxygen concentration was lower and that of CO₂ higher as depth of fill increased. Also the O₂ content was lower and CO₂ content higher during the growing season than during the dormant season.

The next most poorly aerated soil was identified where a driveway was being constructed and paved with asphalt. The composition of the soil atmosphere changed markedly when layers of clay and gravel were laid down, rolled, and packed on the initial base level of the driveway. Within two weeks the soil O₂ content dropped from 20 to 4% while CO content increased from 0 to 16%. The O₂ content increased to 10% and CO₂ content decreased to 9.5% one day after the clay-gravel layer was disturbed by a road grader, indicating an increase in gas exchange between the soil and air. The O₂ content decreased to 6% and the CO₂ content increased to 13.5% within a day after the driveway was paved with asphalt. As winter approached the O₂ content increased and CO₂ content decreased. The following year the first measurements made at the end of March in-

dicated a soil O₂ content of 20% and a CO₂ content of 1%. One month later O₂ had decreased to 4% and CO₂ increased to 15%, indicating that increasing temperatures were stimulating respiration of roots and of soil organisms as well.

The most favorable composition of the soil atmosphere was found in an undisturbed forest that was bordered by an unpaved parking lot. The O₂ content was never lower than 18% and CO₂ content never higher than 2% in the forest soil. In soil under the adjacent parking lot O₂ was as low as 14.5% and CO₂ as high as 6%. The poor soil aeration in the parking lot was attributed to soil compaction.

Effects of soil compaction on tree growth.

Soil compaction is one of the most serious deterrents to tree growth in urban areas. Several investigators have reported a reduction in tree vigor and growth as soil compaction and BD of soil increased, as in apple trees (Slowik, 1970). Growth of *Pseudotsuga menziesii* seedlings was reduced by unfavorable soil physical conditions in areas subjected to heavy logging traffic (Youngberg, 1959). Root growth of *Pinus taeda* seedlings was negatively correlated with BD of soil over a range from 0.8 to 1.4 g/cm³ (Foil and Ralston, 1967). Both establishment and growth of *Pinus taeda* seedlings were reduced by soil compaction (Hatchell, 1970). Trampling of soil and wet-weather logging resulted in unfavorable conditions for regeneration of *Pinus ponderosa* (Pearson and Marsh, 1935). Whereas logging in wet weather on imperfectly drained silt loam soil reduced diameter growth of *Pinus taeda* trees, logging in dry weather did not (Moehring and Rawls, 1970). La Page (1962) noted that when recreational use was reduced in a previously used (*Pinus strobus*) stand the diameter growth of trees increased. Zisa *et al.* (1980) found that a BD of soil of 1.8 g/cm³ reduced establishment of *Pinus rigida*, *Pinus nigra*, and *Picea abies* trees. Root penetration was restricted at a BD of 1.4 g/cm³ on a silt loam and 1.6 g/cm³ on a sandy loam. According to Richards and Cockroft (1974), root growth was inhibited when compaction reduced soil air space to less than 15%; root growth was negligible when air space dropped to 2%. Bakker and Hidding (1970) concluded that 20% air space was needed for sufficient gas exchange between the

soil and atmosphere. Several investigators noted that when the O₂ content dropped below 10% growth of trees was severely reduced, as in *Pinus sylvestris*, *Picea abies* (Youngberg, 1970), *Pinus contorta* (Lees, 1972), and *citrus* (Patt *et al.*, 1966).

Mechanisms of Growth Inhibition of Trees

Aerobic root respiration is an essential function of a healthy growing tree. The energy released in root respiration is necessary for mineral uptake, synthesis of new protoplasm, and maintenance of cell membranes. In the absence of an adequate supply of free O₂, the anaerobic respiration of roots is very inefficient and does not release enough energy to maintain essential root functions, particularly mineral uptake. A lack of soil O₂ may also affect membranes of root cells sufficiently to cause loss of ions by leaching (Rosen and Carlson, 1984). As mineral uptake decreases, the rate of photosynthesis is reduced. Furthermore toxic products such as sulfides, methane, ferrous iron and other reduced compounds accumulate in poorly aerated soil. In particular, growing root tips have high O₂ requirements, and the small absorbing roots, which contain many living cells, often are injured when O₂ availability is low. Deficient aeration may also reduce tree growth by reducing the capacity of roots to synthesize hormonal growth regulators and organic nitrogen compounds such as amides and amino acids (Kramer and Kozlowski, 1979).

Soil compaction results in an increase in micropore space, a decrease in the number and size of macropores (pores greater than 50 μ), and a decrease in infiltration rate, total pore space, and the rate of diffusion of gases. The pores initially affected by compaction are the very large ones (150-50 μ) (Hartage, 1968). As BD increases, more of the movement of water occurs through the capillary or micropore space. With increase in soil compaction, the solid phase of soil per unit volume increases, and water available for uptake by trees is reduced. Associated with reduction in percentage of total pore space is a rapid decline in hydraulic conductivity of soil. As BD increases, maximum soil aeration decreases. A decrease in macropore space can limit diffusion of O₂ into the soil and prevent diffusion of CO₂ out of the soil. In

addition, soil compaction results in development of a soil crust which may severely reduce infiltration of water. The effects of compaction can be further complicated by a high water table, shallow bedrock, or abrupt change in soil texture (Ruark *et al.*, 1982).

The capacity of roots to penetrate soils has an important effect on their growth. Roots must force their way into a soil and can grow only in compressible soils. Individual roots can penetrate only those soil pores that have a diameter greater than that of the root. Root elongation and penetration into soils of high BD become confined to cracks rather than occurring within the soil matrix (Patterson, 1976). Prevention of root extension into compacted soil makes less water available as the water around the root tip is depleted. Capillary movement of water from moist to dry regions in soils at or below field capacity is very slow. Hence continuous root extension is necessary for absorption of enough water to meet transpiration requirements and maintain a favorable internal water balance. Reduced water uptake in compacted soils has also been attributed to effects of high CO₂ content in reducing permeability of roots (Kramer and Kozlowski, 1979).

Flooding

Temporary or continuous flooding of soil occurs commonly as a result of overflowing of rivers, storms, construction of dams, and overirrigation (Kozlowski, 1984). Like soil compaction, flooding leads to poor soil aeration, but the O₂ deficiency occurs almost immediately whereas the effects of compaction on soil aeration occur much more gradually.

Effects of flooding on tree growth. Inundation of soil for a few weeks or more during the growing season retards growth of most trees. Sometimes, however, temporary flooding with moving water may increase growth of certain flood tolerant species. An example is *Nyssa aquatica* (Klawitter, 1964). However, growth of even the most flood-tolerant species (eg. *Taxodium distichum*) is reduced if they are flooded continuously with stagnant water (Shanklin and Kozlowski, 1985). Inasmuch as inhibition of growth is traceable to altered physiological processes the reduced growth may not be obvious for some time after the

initiation of flooding.

Flooding adversely affects height growth, leaf growth, cambial growth, and reproductive growth of trees. Examples of conifers whose height growth was reduced by flooding include *Picea glauca*, *P. mariana*, and *Abies balsamea* (Ahlgren and Hansen, 1957), *Pinus-echinata*, *P. taeda*, and *P. serotina* (Hunt, 1951), *Pinus banksiana* and *P. resinosa* (Tang and Kozlowski, 1983), *Pinus halepensis* (Sena Gomes and Kozlowski, 1980d), and *Larix leptolepis* (Tsukahara and Kozlowski, 1984). Examples of reduced height growth of flooded broadleaved trees include *Alnus rugosa* and *Acer rubrum* (McDermott, 1954), *Eucalyptus* sp. (Sena Gomes and Kozlowski, 1980c), *Quercus macrocarpa* (Tang and Kozlowski, 1982a), *Platanus occidentalis* (Tang and Kozlowski, 1982b), and *Ulmus americana* (Newsome *et al.*, 1982).

Flooding not only reduces elongation of shoots, but also arrests leaf initiation and expansion, and induces leaf senescence, injury, and abscission (Kozlowski, 1982, 1984). Premature leaf shedding has been reported for both fruit trees (Rowe and Beardsell, 1973) and forest trees (Kozlowski, 1982). The number of leaves on unflooded *Betula papyrifera* seedlings doubled over a 60-day period, whereas on flooded plants it decreased by more than half (Tang and Kozlowski, 1982c), indicating extensive leaf abscission. Leaf shedding was also associated with flooding of *Liriodendron tulipifera*, *Quercus alba*, *Acer saccharinum*, *Gleditsia triacanthos*, and *Ulmus americana* (Yelenosky, 1964).

The effects of flooding on diameter growth of trees are somewhat complicated by stem swelling due to increased stem hydration. Nevertheless, in most flood-intolerant species cambial growth usually is reduced appreciably following flooding, as in *Fraxinus excelsior* (Kassas, 1951), and *Betula papyrifera* (Tang and Kozlowski, 1982c). Trees flooded for a long time often show an initial increase in cambial growth followed by reduced growth. For example, diameter growth of several species of trees that had been flooded for four years increased during the first year. By the second year *Celtis laevigata*, *Gleditsia triacanthos* and *Diospyros virginiana* trees stopped growing and died. Most *Quercus phellos*, *Q. nigra*, *Q.*

lyrata, *Q. nuttallii*, *Fraxinus pennsylvanica*, and *Liquidambar styraciflua* trees died in the third year (Broadfoot and Williston, 1973).

Flooding of soil usually leads to greatly reduced root growth and death of many of the fine absorbing roots. In poorly aerated soil, the growth of roots tends to be confined to the soil surface. Because root growth usually is decreased more than shoot growth by flooding, drought tolerance of flooded trees is reduced after the flood waters recede. This change reflects the inability of the small root systems to supply enough water to meet the transpirational requirements of the crown.

Several investigators have emphasized large reductions in root growth of flooded trees. Examples are apple (Childers and White, 1942), pear (Valoras *et al.*, 1964), citrus (Stolzy *et al.*, 1965a, 1965b), *Fraxinus pennsylvanica* (Sena Gomes and Kozlowski, 1980a), *Melaleuca quinquenervia* (Sena Gomes and Kozlowski, 1980b), *Eucalyptus* spp. (Sena Gomes and Kozlowski, 1980c), *Quercus macrocarpa* (Tang and Kozlowski, 1982a), *Platanus occidentalis* (Tang and Kozlowski, 1982b), *Betula papyrifera* (Tang and Kozlowski, 1982c), and *Ulmus americana* (Newsome *et al.*, 1982). The small root systems of flooded trees reflect the combined effect of reduction in root initiation and in growth of existing roots as well as decay of the original root system.

Oxygen concentrations higher than 10% were necessary for good root growth of apple trees. However, roots grew slowly with 3 to 5% O₂ and they survived with 0.1 to 0.3% O₂ (Boynton *et al.*, 1938). When the O₂ content dropped below 10% and CO₂ increased above 5%, very few new roots of apple trees were produced and top growth was subsequently decreased also (Boynton, 1940).

Flooding of soils causes decay of roots, largely as a result of invasion of *Phytophthora* fungi. This has been demonstrated in citrus (Fawcett, 1936; Stolzy *et al.*, 1965b) and *rhododendron* (Blaker and McDonald, 1981), among other species. Flooding of soil almost completely stopped root growth and induced root decay in *Pinus halepensis* seedlings. After 40 days of soil inundation the dry weight of the root system was lower than before flooding started, emphasizing decay of a

portion of the original root system (Sena Gomes and Kozlowski, 1980d). Very few new feeder roots were produced by citrus trees that were overirrigated. However, when the soil was allowed to dry between irrigations, new feeder roots were produced. The lack of feeder roots was associated with root rot caused by *Phytophthora parasitica* (Feld, 1982).

The decay of roots of trees in flooded soils is associated with the capacity of root-rotting fungi to tolerate low O₂ contents, weakening of the host tree, and attraction of zoospores of fungi to root exudates produced in flooded soils. Saturated soils predisposed normally resistant rhododendrons to root and crown rot caused by *Phytophthora cinnamomi* (Blaker and McDonald, 1981). The transition of soil from a drained to a saturated condition stimulates zoospore dispersal (Duniway, 1976). The zoospores are attracted to such root exudates as sugars, ethanol, and amino acids (Stolzy and Sojka, 1984).

Poor soil aeration often predisposes trees to attack by secondary fungi. For example, placing even a small amount of fill over the roots of a tree may lead to increased attack by stem canker fungi and boring insects, thereby inducing tree decline (Schoeneweiss, 1978).

Mechanisms of flooding injury. The mechanisms through which flooding of soil injures trees and reduces growth are complex. There has been vigorous debate about whether O₂ deficiency, excess CO₂, toxic compounds, or hormonal imbalances are most important in causing flooding injury. Certain early responses, such as reduced absorption of minerals, have been associated with O₂ deficiency, and some later responses, such as shedding of leaves to changes in hormonal growth regulators (Kozlowski, 1976).

Waterlogged soils produce many phytotoxic compounds including sulfides, CO₂, and soluble iron and manganese. At the same time flooded roots produce ethanol, acetaldehyde, and cyanogenic compounds. Roots of some trees such as cherries contain cyanophoric glucosides which are converted to cyanide in waterlogged soils. Flooding for even one day may kill certain trees by cyanide poisoning (Rowe and Catlin, 1977). Anaerobic microbial metabolism produces a variety of compounds including methane,

ethane, propylene, fatty acids, hydroxy and dicarboxylic acids, unsaturated acids, aldehydes, ketones, diamines, and heterocyclic compounds. Much attention has been given to the effects of ethylene which is produced by flooded roots as well as by microbial metabolism in soil (Kozlowski, 1982).

For a long time it was claimed that the adverse effects of flooding probably were traceable largely to ethyl alcohol (ethanol) accumulation. However, recent evidence shows that ethanol is readily eliminated from flooded plants. Furthermore, when ethanol was supplied to nutrient solutions at concentrations similar to those in flooded soils the plants were not injured. Nor were they appreciably injured by 100 times those concentrations (Jackson *et al.*, 1982). Hence, it appears that the adverse effects of ethanol have been exaggerated. Although toxic products such as iron, fatty acids, and ethylene decreased root growth of conifer seedlings, the inhibitory effects of oxygen deficiency were much greater (Sanderson and Armstrong, 1980a, 1980b). The prevailing view is that O₂ deficiency is the most important single cause of flooding injury and growth inhibition.

Effects of flooding on soils. Flooding induces several physical and chemical changes in soil that adversely affect growth of most trees. In a well-drained soil the composition of gas is relatively stable. Consumption of O₂, production of CO₂, and N fixation by soil organisms are counteracted by gaseous exchange between the soil and air, primarily by diffusion. When a soil is flooded the water occupies the previously gas-filled pores and gas exchange between the soil and air is limited to molecular diffusion in the soil water. Because such diffusion is slow, the supply of O₂ to soil is essentially eliminated. Furthermore, practically all of the remaining O₂ in the water and soil is consumed by microorganisms within a few hours. The O₂ concentration is high only in the few mm of the surface soil that is in contact with oxygenated water. This oxidized layer acts as a sink for various substances that diffuse upward from the mass of O₂-deficient soil. In some flooded soils the CO₂ concentration may be as high as 50% (Ponnamperuma, 1984).

The structure of soil is adversely affected by

flooding. This is characterized by breakdown of aggregates as a result of reduced cohesion, deflocculation of clay because of dilution of the soil solution, pressure of trapped air, stresses associated with uneven swelling, and destruction of cementing agents.

The surface water layer of a flooded soil contains aerobic bacteria, algae, zooplankton, and some higher plants. Below this surface layer the aerobic organisms are replaced by organisms, primarily bacteria, that can survive without free oxygen. These anaerobic bacteria are active in metabolism that causes denitrification and reduction of manganese, iron, and sulfur. They are also active in formation of methane and in N fixation.

Flooding of soil also reduces the soil redox potential, increases pH of acid soils, mainly because of change of Fe^{+++} to Fe^{++} , and decreases the pH of alkaline soils largely because of accumulation of CO_2 . Soil inundation also decreases the rate of decomposition of organic matter. In unflooded soil the decomposing leaf litter binds cations and traps mineral nutrients so as to prevent their leaching into deeper layers of soil. In an unflooded soil the organic matter is decomposed through the activities of many organisms, including bacteria, fungi, and fauna. Rapid decomposition of organic matter is associated with large amounts of energy released by respiration of aerobic organisms. By comparison, decomposition of organic matter in flooded soil is limited to the activity of anaerobic bacteria which are less diverse than aerobic microorganisms and release much less energy. The rate of decomposition of organic matter in flooded soil may be only half that in an unflooded soil. The end products of decomposition of organic matter in unflooded soils are CO_2 and humic materials. Whereas CO_2 escapes into the air the humic materials are bound to clay and hydrous oxides of aluminum and iron. The nitrogen that is released as ammonia is converted to nitrate, and S compounds are oxidized to sulfate. The major end products of decomposition of organic matter in flooded soils are CO_2 , methane, and humic materials. The anaerobic bacteria in flooded soils produce many compounds that are not found in well-drained soils. These include gases, hydrocarbons, alcohols, carbonyls, volatile fatty acids, non-volatile acids,

phenolic acids, and volatile sulfur compounds (Ponnamperuma, 1984).

Effect of Flooding on Physiological Processes of Trees

The physical and chemical changes induced in soils by flooding rapidly lead to changes in water, carbohydrate, mineral, and hormone relations of trees. These will be discussed separately.

Water relations. One of the earliest physiological responses of trees to flooding is closing of stomatal pores. We found, for example, that stomata of many tree species, including *Ulmus americana*, *Platanus occidentalis*, *Quercus macrocarpa*, *Salix nigra*, *Betula papyrifera*, *B. nigra*, *Eucalyptus camaldulensis*, and *E. globulus* began to close within a day or two after the soil was flooded. As stomata close the rate of transpirational water loss and the rate of absorption of water by roots are reduced. Flooding of soil also decreases permeability of roots to water (Kozlowski, 1982).

Food relations. Inundation of soil is rapidly followed by a reduction in the rate of photosynthesis. For example, in *Malus* sp. and *Carya illinoensis* the rate of photosynthesis was appreciably reduced within a day or two after flooding (Childers and White, 1942; Phung and Knipling, 1976). Flooding of *Populus deltoides* seedlings for 28 days reduced photosynthesis by about half (Regehr *et al.*, 1975). The rate of photosynthesis of four citrus rootstocks was reduced by 80 to 90% within 10 days after flooding (Phung and Knipling, 1976). In *Pseudotsuga menziesii* photosynthesis began to decrease within five hours after flooding (Zaerr, 1983).

The reduction in photosynthesis by flooding is traceable first to closure of stomatal pores, limiting CO_2 uptake by leaves, and subsequently to inhibition of the photosynthetic process as well as by early leaf senescence and chlorosis. Total photosynthesis for a tree is also reduced because of decreased leaf initiation and expansion and also because of shedding of leaves.

In addition to inhibiting the rate of photosynthesis, soil flooding also reduces transport of photosynthetic products from leaves to growing and storage tissues. The mechanism by which flooding of soil reduces movement of car-

bohydrates is not well understood, but there is some evidence that toxic products of anaerobic respiration are involved (Geiger and Savonick, 1975).

Hormone relations. Both the amounts and balances of plant growth regulators in shoots and roots are affected by flooding. Whereas the amounts of auxins, ethylene, and abscisic acid in shoots are increased by flooding, the levels of gibberellins and cytokinins in stems and roots are decreased. These changes may be traceable to synthesis, destruction, and translocation of these hormonal growth regulators. The production of certain growth hormones is regulated by the amounts of other growth hormones present. For example, auxins, cytokinins, gibberellins, and abscisic acid stimulate ethylene production (Reid and Bradford, 1984).

Mineral relations. Uptake of ions by roots occurs by both "passive" and "active" mechanisms. Passive uptake involves movement of ions into root cells along with uptake of water. Active uptake involves movement of ions into roots cells across cell membranes at the expense of metabolic energy. Once mineral nutrients enter root cells they may be used there or they may enter the root xylem and then move upward to the crown by mass flow in the transpiration stream. Many but not all ions that reach the crown are accumulated in leaf cells by active transport.

The restriction of O₂ diffusion into flooded soils, swelling of soil colloids, and unfavorable soil structure lower the rate of respiration and of mineral nutrient absorption by roots of flood-intolerant trees. Flooding reduces both nitrogen concentrations and total nitrogen contents of plant tissues. A contributory factor is the rapid depletion of nitrate which is highly unstable in the anaerobic zone where it is converted to nitrous oxide or nitrogen by denitrification and lost from the soil. The low nitrogen levels in flooded trees are also the result of reduced absorption of nitrate associated with effects of low O₂ availability on root metabolism. Uptake of potassium and phosphorus also is reduced in flooded soils, the result of effects of anaerobiosis on active ion uptake. In flooded soils, uptake of calcium and magnesium is also reduced but not nearly as much as is absorption of nitrogen, potassium, and

phosphorus. In contrast to reduced uptake of macronutrients, the absorption of some micronutrients such as iron and manganese increases as ferric and manganous forms are reduced and rendered more soluble by bacterial metabolites. Hence, concentrations of iron and manganese in plants are increased by flooding, but total contents often are lowered because of the greatly reduced growth of these plants in flooded soils (Kozlowski and Pallardy, 1984).

Mycorrhizal fungi that are associated with tree roots play an important role in tree physiology by increasing absorption of mineral nutrients (Kramer and Kozlowski, 1979). Because mycorrhizae are strongly aerobic, flooding of soil adversely affects mycorrhizal associations. Temporary flooding in the spring reduced the number of mycorrhizal fungi associated with tree roots and prevented formation of new populations (Filer, 1975). Submerged layers of peat and abandoned beaver flowages lacked mycorrhizal fungi (Wilde, 1954). Establishment and growth of mycorrhizal fungi were restricted to portions of conifer roots that released O₂ into the root environment (Read and Armstrong, 1972). Soil inundation reduced phosphorus uptake by mycorrhizae associated with conifers (Gadgil, 1972), further emphasizing that flooding of soil adversely affects mineral uptake by trees partly by inhibiting mycorrhizal activity.

Variations in Flood Tolerance

Responses of trees to flooding vary widely, with broadleaved trees as a group much more flood tolerant than conifers. *Taxodium distichum* is an exception and is very flood tolerant. Species such as *Nyssa aquatica*, *N. sylvatica*, *Salix* spp., *Platanus occidentalis*, and *Acer saccharinum* are more tolerant than *Cornus florida*, *Liriodendron Tulipifer* or *Liquidambar styraciflua* (Kozlowski, 1982). Rowe and Beardsell (1973) ranked fruit trees in the following order of decreasing flood tolerance: almond, peach and apricot, cherry, plum and citrus, apple, pear and quince. However, flood tolerance ratings of fruit trees are greatly influenced by rootstocks. For example, apricots, almonds, and peaches on peach rootstocks are very sensitive to flooding. Red Delicious apple scions on MM. 111 and seedling rootstocks

were more sensitive to flooding than were scions on M. 28 or MM. 106 stocks (Rom and Brown, 1979).

Flood tolerance varies not only among species, clones and cultivars but also with age of trees and other factors. Older trees usually tolerate flooding better than do seedlings or saplings. Trees are injured much more by stagnant water than by moving water. In fact growth of even the most flood-tolerant species such as *Taxodium distichum* is reduced by flooding in stagnant water (Shanklin and Kozlowski, 1985). Flooding during the dormant season is much less harmful than flooding during the growing season. The greater injury and growth reduction by flooding during the growing season are associated with high O₂ requirements of growing roots with high respiration rates. Responses of trees also vary greatly with the duration of flooding. For example, when six species of bottomland trees were flooded, only *Salix nigra* seedlings survived 32 days of flooding. When completely submerged for 16 days, however, many *Fraxinus pennsylvanica*, some *Liquidambar styraciflua*, and a few *Acer negundo* seedlings survived. By comparison, *Populus deltoides* and *Acer saccharinum* survived only when flooded for less than 16 days. The rate of recovery of surviving trees from flooding also varied, with *Salix nigra* and *Fraxinus pennsylvanica* recovering faster than the other four species (Hosner, 1958).

Adaptations to Flooding

Flood-tolerant trees survive anaerobic conditions by both physiological and morphological adaptations. The morphological adaptations make it possible for trees to maintain more normal physiological processes.

Many flood-tolerant species regenerate new roots which apparently compensate for loss of part of the original root system. Such adventitious roots may be initiated on the submerged part of the stem or on the original root system, or both. Following flooding the original roots usually die back to major secondary roots or the primary root and new roots form at these points (Hook, 1984).

There has been some disagreement about the physiological importance of flood-induced adventitious roots. However, the weight of evidence in-

dicates that they comprise an effective supplementary absorbing system while the original root system does not function effectively.

The capacity to form adventitious roots is associated with species that tolerate flooding well. For example, the more flood-tolerant trees such as species of *Salix*, *Nyssa*, and *Platanus* form abundant adventitious roots when flooded; the flood-intolerant species, *Betula papyrifera* and *Pinus halepensis* produce few or none (Kozlowski, 1982).

The order of flood tolerance: *Eucalyptus grandis*, *E. robusta*, *E. Saligna* was related to the amounts of adventitious roots formed by these species. (Clemens *et al.*, 1978). Many more adventitious roots were produced by the flood-tolerant *Eucalyptus camaldulensis* than by the less flood-tolerant *E. globulus* (Sena Gomes and Kozlowski, 1980b). Formation of adventitious roots was an important adaptation for flood tolerance of *Fraxinus pennsylvanica* seedlings as shown by the high water absorbing efficiency of these roots and by high correlation between production of adventitious roots and stomatal reopening of flooded seedlings. Water absorption was up to 90% higher in flooded plants with adventitious roots than in flooded plants without such roots. After two weeks of flood-induced stomatal closure the stomata reopened as adventitious roots formed on submerged stems (Sena Gomes and Kozlowski, 1980a). Removal of adventitious roots inhibited leaf formation in *Alnus glutinosa* (Gill, 1975).

A very important adaptation to flooding is capacity for absorption of oxygen by aerial tissues, downward transport, and diffusion out of the roots to the rhizosphere. Flooded plants live with their roots in highly reduced soils that contain many toxic compounds. Oxidation of the rhizosphere results in oxidation of reduced compounds such as ferrous and manganese ions, which are abundant in soil and are toxic to roots (Ponnamperuma, 1984). Adventitious roots of flooded *Nyssa sylvatica* seedlings oxidized the rhizosphere whereas unflooded roots did not, further emphasizing the adaptive significance of such roots (Hook, 1984).

In addition to the morphological adaptations discussed here, trees have evolved biochemical

mechanisms that permit them to survive under anaerobic soil conditions. These adaptations fall into three broad classes and include (1) maintenance of a high energy charge, (2) maintenance of a sugar supply, and adjusting carbon metabolism to avoid accumulation of toxic compounds, and (3) metabolic adjustment to maintain a low energy charge and low metabolic rate. For a good discussion of these rather complicated biochemical mechanisms the reader is referred to Davies (1980). Adaptation to survival of trees flooded with salt water is achieved by tolerating salinity or avoiding it by excluding salt passively, extruding salt actively, or diluting the entering salt. A detailed discussion of these mechanisms is beyond the scope of this paper. For further information on mechanisms of tolerance of trees to salinity, the reader is referred to Levitt (1980) and Wainwright (1984).

Conclusions

There is much the arborist can do to alleviate the effect of an unfavorable soil environment on growth of shade trees. He should first be sensitive to the need for a continuous supply of oxygen as well as good soil structure for tree growth. As Perry (1978) stated: "No oxygen — no roots; no water — no roots; rigid, impenetrable soils — no roots."

In selecting species for planting in poorly aerated soils, the arborist must not be overruled by aesthetic considerations. Rather he should give high priority to selecting species that can tolerate such soils. Bottomland species such as *Platanus occidentalis*, *Acer rubrum*, *Acer saccharinum*, *Quercus palustris*, *Populus* sp., *Quercus bicolor*, *Betula nigra*, *Salix* spp., *Acer negundo*, and *Taxodium distichum*, are examples of species that have some degree of tolerance to poor soil aeration.

Van Camp (1961) recommended several useful techniques for alleviating effects of poor soil aeration including (1) establishing aeration wells, (2) mulching soils to increase diffusion of air and infiltration of water, (3) preventing pedestrian and vehicle traffic on compacted soils, (4) lowering soil temperature by shading, (5) judiciously adding fertilizer around trees deprived of mineral nutrients, and (6) making routine examinations for

symptoms in trees that reflect an unfavorable soil environment.

Once a soil becomes severely compacted, it is difficult to improve soil aeration. Hence, prevention of poor aeration and adequate soil preparation are emphasized. Yet some things can be done to improve soil aeration. Subsoiling and installation of tile drains often are helpful. Patterson (1976) reported that several treatments reduced soil compaction on heavily used areas in the Washington, D.C. area. For example, lightweight aggregates rotary tilled into soil reduced compaction. Composts of leaves, wood chips and sewage sludge also reduced compaction, increased soil fertility, and reduced injury to soil and tree roots from heavy traffic.

Compacted soil may recover over time by natural means when protected from further compaction. Soil under a mature oak stand near St. Paul, Minnesota was artificially compacted. This treatment induced significant increases in bulk density of the 0-3, 6-9, and 9-12 inch layers of soil. During the interval between 4.5 and 8.75 years after compaction the bulk density of the 0-3 inch layer of the previously compacted soil recovered and was not different from that of the uncompacted soil. The effect of compaction persisted in the 6-9 inch layer. However, BD in this layer had been increased by compaction by only 10%, in contrast to a 27% increase in the 0-3 inch zone. In terms of ecological implications the small increase in BD at the lower depth probably was less important than the greater increase in the surface layer. The study emphasized that when soil compaction becomes a site-management problem, a rest-rotation system may restore the site if it can be taken out of use for a few years (Thorud and Frisell, 1976).

Arborists often find it necessary to change the soil level around established trees. Injury to roots from this practice can be minimized by adding the fill around trees over a period of years, thereby allowing the roots time to adjust metabolically. The coarser the fill is the better are the chances that trees will tolerate the addition (Yelenosky, 1964). The problem can also be alleviated by adding fill only around trees that can tolerate it. Such trees include *Ulmus parvifolia*, *Ailanthus altissima*, *Robinia pseudoacacia*, *Gleditsia tricanthos*, *Ulmus*

americana, and *Pinus taeda*. Species that are intermediate in fill tolerance include *Acer* spp., *Quercus* spp., and *Pinus echinata*. By comparison *Cornus florida*, *Liriodendron tulipifera*, *Betula* spp., and *Pinus resinosa* are intolerant of fill (Ruark et al., 1982).

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ABSTRACTS

DAVIES, R.J. and J.B.H. GARDINER. 1983. **Amenity planting on French motorways**. *Arboric. J.* 7: 211-216.

In France, as in Britain, much attention is given to reducing the environmental impact of motorways. Approximately 10% of the cost of a French motorway is spent on environmental improvement. This 10% includes bridges for deer and other wildlife, and rest areas for motorists, as well as tree and shrub planting. Landscaping architects design the basic planting scheme, but the scheme is not sacrosanct; where the ground is too steep for easy cultivation or the soil is shallow, no attempt is made to plant. Rarely are trees or shrubs planted on the cuts and embankments. These unplanted areas are seeded with a grass mixture. Amenity planting of trees and shrubs is therefore largely confined to flat areas of land beside the motorways, especially at junctions, tolls, and rest areas. A broad, low hedge is often planted on the central reservation. The methods used to establish trees and shrubs on motorway verges are described. Intensive soil cultivation and mulching with black polyethylene film are widely employed. Standard-sized trees are heavily pruned at planting. Unrooted cuttings are used and research is in progress to extend this technique to a wide range of species. These practices have also been used to re-establish farm hedgerows. Early growth rates are impressive.

RISHBETH, J. 1983. **The importance of honey fungus (*Armillaria*) in urban forestry**. *Arboric. J.* 7: 217-225.

Honey fungus is one of the most destructive pathogenic fungi to affect trees both in Britain and elsewhere, those growing in urban areas being no less susceptible than those in the forest or countryside. Once trees have been severely weakened by physiological stress or infection by another pathogen, a greater variety of *Armillaria* species tends to be present. Thus in broadleaved trees suppressed by competition and which subsequently died, *A. bulbosa* was to be found as well as *A. mellea*, and with pines in a similar condition any one of three species might be present, although *A. bulbosa* was not common. Broadleaved trees seriously weakened or killed by various agents, for example Dutch elm disease, beech bark disease or sooty bark disease of sycamores, had mostly been invaded by *A. bulbosa*, although *A. mellea* was occasionally present. *Armillaria* sometimes causes extensive rotting at the base of the trunk, though in conifers rot seldom extends more than 0.6 m above soil level. *A. bulbosa* was found to be characteristic of basal rots in broadleaved trees such as elm, poplar, and ash, whereas *A. ostoyae* caused rot in Norway spruce. Since all species of *Armillaria* cause root decay, wind-throw is also possible; this has been recorded after infection by *A. bulbosa* and *A. tabescens*.