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Responses of woody plants to flooding and salinity

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Summary *Flooding* affects soils by altering soil structure, depleting O_2, accumulating CO_2, inducing anaerobic decomposition of organic matter, and reducing iron and manganese. Flooding of soil with nonsaline or saline water adversely affects the distribution of many woody plants because it inhibits seed germination as well as vegetative and reproductive growth, alters plant anatomy, and induces plant mortality. In nonhalophytes, waterlogging suppresses leaf formation and expansion of leaves and internodes, causes premature leaf abscission and senescence, induces shoot dieback, and generally decreases cambial growth. However, flooding sometimes increases stem thickness because growth of bark tissues is increased more than production of xylem cells. In some plants, soil inundation induces formation of abnormal wood and increases the proportion of parenchymatous tissue in the xylem and phloem. Soil inundation inhibits root formation and branching, and growth of existing roots and mycorrhizae. Flooding also leads to decay of the root system. Root growth typically is reduced more than shoot growth. When the flood water drains away, plants may be less drought tolerant because of their low root/shoot ratios. Waterlogging of soil also inhibits initiation of flower buds, anthesis, fruit set, and fruit growth of nonhalophytes. Fruit quality is reduced by smaller fruit size, altered chemical composition, and appearance of fruits. Some fruits may crack following flooding of soil.

Soil inundation induces multiple physiological dysfunctions in plants. Photosynthesis and transport of carbohydrates are inhibited. Absorption of macronutrients is decreased in flooded plants because of root mortality, loss of mycorrhizae, and suppression of root metabolism. Soil inundation alters hormonal balances in plants, usually by increasing the proportion of ethylene.

Flood tolerance varies greatly among plant species, genotypes and rootstocks, and is influenced by plant age, time and duration of flooding, condition of the floodwater, and site characteristics. Flood-tolerant plants survive waterlogging by complex interactions of morphological, anatomical, and physiological adaptations. Important adaptations include production of hypertrophied lenticels, aerenchyma tissue, and adventitious roots.

Salinity induces injury, inhibits seed germination and vegetative and reproductive growth, alters plant morphology and anatomy, and often kills nonhalophytes. Combined flooding and salinity decreases growth and survival of plants more than

either stress alone. In angiosperms, salt injury includes leaf scorching or mottling, leaf shedding, and twig dieback. In gymnosperms, injury begins with necrosis of needle tips, spreads to the bases of the needles, and may be followed by needle shedding and shoot dieback. Injury also may include collapse of mesophyll cells, fragmentation of cuticles, and disintegration of chloroplasts and nuclei. Injury to cell membranes increases solute leakage. Salinity inhibits seed germination and adversely influences flowering, pollination, fruit development, yield and fruit quality, as well as seed production. Salinity inhibits vegetative growth of nonhalophytes, with shoot growth typically reduced more than root growth. Plant anatomy is often altered by salinity. Leaves become thicker and more succulent. The greater leaf thickness may reflect more layers of mesophyll cells, larger cells, or both. Salinity also may change the anatomy of xylem cells. In some normally diffuse-porous species, the xylem may become ring-porous. Salinity stimulates suberization of the root hypodermis and endodermis.

In nonhalophytes, salt-induced inhibition of plant growth is accompanied by metabolic dysfunctions, including decreased photosynthetic rates, and changes in protein and nucleic acid metabolism and enzymatic activity. In halophytes, physiological processes may be stimulated or not altered by salt concentrations that are inhibitory in nonhalophytes.

The precise mechanisms by which salinity inhibits growth are complex and controversial. An attractive model incorporates a two-phased response of plants. Growth is first reduced by a water stress effect (a decrease in soil water potential) followed by a specific effect (namely salt injury in old leaves which die when their vacuoles cannot sequester any more salt). The loss of these leaves decreases the availability of carbohydrates or growth hormones to meristematic regions, thereby suppressing growth.

Salt tolerance varies widely among species and genotypes. Plants adapt to salinity by tolerating or avoiding salt. In some plants salt tolerance is achieved by osmotic adjustment. This may involve absorption of ions from the soil followed by sequestering of ions in vacuoles, or it may result from synthesis of compatible solutes in the cytoplasm. Salt avoidance mechanisms include passive salt exclusion, active salt extrusion, and dilution of salt in the plant.

Keywords: flood tolerance, morphological adaptations, physiological adaptations, salt tolerance.

Introduction

Temporary or continuous flooding of soil with fresh or salt water occurs as a result of overflowing of rivers, storms, overirrigation, inadequate drainage, and impoundment of water by dams (Wainwright 1980, Kozlowski 1982, 1984*a*, 1984*b*, 1984*c*, 1985*a*, 1986, Kozlowski and Pallardy 1997*b*). Waterlogging of soil occurs not only in areas of heavy rainfall but also in arid regions where irrigation is practiced. In western Canada, more than 280,000 ha are irrigated, and approximately 24,000 ha are permanently waterlogged because of seepage from irrigation channels (Reid 1977). In some soils, waterlogging can result from sodicity-generated infiltration. For example, alteration of the physical conditions of the soil by high-exchangeable Na^+, which causes dispersion of soil colloids and results in the blocking of soil pores (hence impeding air and water movement) (Shannon et al. 1994, Ghassemi et al.1995), can lead to waterlogging.

Salinization of agricultural land is occurring throughout the world, but especially in regions where irrigation water has a high salt concentration and water evaporates rapidly from the surface soil. Salt becomes progressively concentrated in the root zone because the plant roots absorb water but very little salt. Thus, unless soil salts are removed by overirrigation, rainfall, or drainage, their concentration increases progressively. It is estimated that about a third of the world's irrigated land and half the land in semiarid and coastal regions is influenced by excess salinity, and that about 10 million ha of irrigated land are abandoned annually because of excess salinity (Epstein et al. 1980, Abrol et al. 1988, Rhoades and Loveday 1990).

There is also much concern about possible loss of wetland vegetation because of flooding and salinity resulting from natural processes and imposed hydrologic changes (Allen et al. 1996). Furthermore, the predicted global warming may cause a rise in sea levels that would flood extensive coastal areas with salt water (Daniels 1992, Wigley and Raper 1993). Although the causes of flooding and salinization of soils are known and many plant responses to flooding and salinity have been characterized, our understanding of the precise mechanisms by which flooding with saline water inhibits plant growth are poorly understood. In this review, I have focused on the effects of flooding and salinity on morphological and physiological processes in woody plants.

Flooding

Effects of flooding on soils

Soil inundation sets in motion a variety of physical, chemical and biological processes that alter the capacity of soils to support plant growth. Flooding with moving water often removes soil by scouring or adds soil by transport and silting (Brink 1954, Stone and Vasey 1965, Brinson et al. 1981). Changes in soil structure following flooding typically include breakdown of aggregates, deflocculation of clays, and destruction of cementing agents (Ponnamperuma 1972, 1984). Major chemical changes include decrease in or disappearance of O_2, accumulation of CO_2, increased solubility of mineral substances, reduction of Fe and Mn, anaerobic decomposition of organic matter, and formation of toxic compounds (Ponnamperuma 1972, 1984, Gambrell et al. 1991, Janiesch 1991).

Flooding eliminates soil O_2 because water occupies previously gas-filled pores. The O_2 concentration remains high in only the few millimeters of surface soil that are in contact with oxygenated water. Well-drained soils are characterized by redox potentials of +300 mV or greater, whereas flooded soils have redox potentials of −300 mV or lower (Pezeshki and Chambers 1985*a*, 1985*b*). The aerobic organisms typical of well-drained soils are replaced in flooded soils by anaerobes,

primarily bacteria, which cause denitrification and reduction of Mn, Fe, and S.

Many potentially toxic compounds accumulate in flooded soils. Some (e.g., sulfides, CO_2, soluble Fe and Mn) are produced in waterlogged soils (Wang et al. 1967, Hook et al. 1971, Culbert and Ford 1972). Others (e.g. ethanol, acetaldehyde, and cyanogenic compounds) are produced by roots (Fulton and Erickson 1964, Rowe and Catlin 1971, Ponnamperuma 1984). Methane, ethane, propylene, fatty acids, hydroxy- and decarboxylic acids, unsaturated acids, aldehydes, ketones, diamines, mercaptans, and heterocyclic compounds are products of anaerobic metabolism of microbes. Ethylene is produced by flooded plants (Kozlowski and Pallardy 1984) and by microbial metabolism (Lynch 1975, Lindberg et al. 1979).

Variation in flood tolerance

Flood tolerance varies greatly with plant species and genotype, rootstock, age of plants, time and duration of flooding, and condition of the floodwater (Kozlowski 1982, 1984*b*, 1984*c*, 1985*a*, 1986, Kozlowski et al. 1991, Kozlowski and Pallardy 1997*b*). Flood tolerance rankings also vary according to the criteria on which tolerance is based. For example, flood tolerances of *Parkia pendula* and *P. discolor* were similar when based on seed germination characteristics; however, flood tolerance rankings of these species differed dramatically when based on seedling survival (Scarano and Crawford 1992).

In general, woody angiosperms tolerate flooding better than most gymnosperms (Kozlowski and Pallardy 1997*b*). Examples of flood tolerance among broad-leaved trees are given by Hall et al. (1946), Hosner (1958, 1960), Dickson et al. (1965), Jawanda (1961), Rowe and Beardsell (1973), Mizutani et al. (1979), Bell and Johnson (1974), Remy and Bidabe (1962), Gill (1970), Catlin et al. (1977), Pereira and Kozlowski (1977), Baker (1977), Norby and Kozlowski (1983), and Nema and Khare (1992). Species variations in flood tolerance of gymnosperms have been reported by Ahlgren and Hansen (1957), Poutsma and Simpfendorfer (1963), Minore (1968), Zinkan et al. (1974), Boggie (1974), Krinard and Johnson (1976), Coutts and Philipson (1978*a*, 1978*b*), and Colin-Belgrand et al. (1991).

Sensitivity to flooding also varies among closely related woody plants, as shown for different species of *Eucalyptus* (Clemens et al. 1978, Sena Gomes and Kozlowski 1980*c*), *Nyssa* (Hall and Smith 1955), *Pinus* (Tang and Kozlowski 1983), and *Prunus* (Mizutani et al. 1979). *Prunus* species are relatively sensitive to flooding. For example, soil inundation for 2 to 5 days resulted in death of members of certain *Prunus* taxa, including *P. dulcis* and *P. persica*. However, Ranney and Bir (1994) found much variation in flood tolerance within this genus. For example, based on rates of survival, defoliation, and photosynthesis, *Prunus salicina* × (*P. americana* × *P. nigra*) × *P. cerisifera* 'Newport' and 'F-12/1' Mazzard cherry were flood tolerant, whereas *Prunus caroliniana*, *P. virginiana* 'Canada Red', and *P. mume* 'Peggy Clark' were sensitive to flooding. The high flood tolerance of some *Prunus* species has been attributed to low concentrations of cyanogenic glycosides in their roots (Rowe and Catlin 1971, Rowe and Beardsell 1973). Tolerance of *Vitis* cultivars to flooding also varies widely. St. George, Coudere 3309, and Riparia Gloire are among the most tolerant cultivars, whereas Kober 573B, Seyval and Cynthaniana are most susceptible (Striegler et al. 1993).

Rootstocks vary in flood tolerance (Van't Woudt and Hagan 1957, Rom and Brown 1979). Studies of two *Citrus* rootstocks showed that prolonged flooding reduced photosynthetic capacity, stomatal conductance, chlorophyll content, and ribulose bisphosphate carboxylase/oxygenase (Rubisco) more in *C. sinensis* cv. Hamlin when grafted on *C. aurantium* rootstocks than when grafted on *C. jambhiri* roots. Flooding for 30 days was essentially lethal to *C. aurantium*, with 90% of the trees killed or showing dieback, whereas *C. jambhiri* trees were affected only by continuous flooding for 60 days, with only 20% of the trees showing dieback (Vu and Yelenosky 1991).

Plant responses to flooding

Flooding during the growing season adversely affects all developmental stages of flood-intolerant plants, whereas flooding during the dormant season generally has little effect in the short term (Kozlowski 1982, 1984*b*, Kozlowski and Pallardy 1997*b*,). Plant responses to flooding during the growing season include injury, inhibition of seed germination, vegetative growth, and reproductive growth, changes in plant anatomy, and promotion of early senescence and mortality. The specific plant responses vary with many factors including plant species and genotype, age of plants, properties of the floodwater, and time and duration of flooding (Kozlowski 1984*b*). Injury and growth inhibition typically are preludes to plant mortality (Grandin and Couillard 1987, Erickson 1989, Wigley and Filer 1989, Shul'ga and Maksimov 1991). Adverse effects of flooding often lead to changes in forest distribution and composition (Hughes 1990, LaMotte 1990, Bren 1991, Frye and Grosse 1992, Oliveira-Filho et al. 1994).

Seed germination and seedling development Soil inundation has profound effects on seed germination and seedling development, and hence on species composition in riparian areas. Activation of the physiological processes necessary for seed germination requires an O_2 supply; however, soil inundation restricts O_2 availability to the embryo and thereby prevents or postpones seed germination in many species (Kozlowski and Pallardy 1997*b*). Maximum germination and respiration rates of seeds of several species are reached at O_2 partial pressures close to those of air, and decreasing the O_2 pressure leads to a gradual decrease in germination rate (Al-Ani et al. 1985).

In general, soaking seeds of upland species for several hours to a few days accelerates germination, whereas soaking for long periods inhibits germination (Toumey and Durland 1923, Kozlowski 1984*b*, Kozlowski and Pallardy 1997*b*). The capacity of seeds of wetland species to germinate under water is variable. Seeds of *Acer rubrum*, *A. saccharinum*, *Platanus occidentalis*, and *Ulmus americana* did not germinate while soaking in water, but when removed from water germination was rapid and high. By comparison, seeds of *Populus deltoides* and S*alix* spp. completed germination in water within 4 days

(Hosner 1957). Seeds of *Fraxinus pennsylvanica*, *F. caroliniana*, *Liquidambar styraciflua*, *Nyssa aquatica*, *N. sylvatica* var. *biflora*, and *Taxodium distichum* showed poor germination under water, whereas seeds of *Cephalanthus occidentalis*, *Populus deltoides*, *Salix nigra*, and *Ulmus americana* germinated readily while submerged (DeBell and Naylor 1972, Hook 1984). Seeds of some species (e.g., *Taxodium distichum* and *Nyssa aquatica*) may remain viable under water for up to two years. Regeneration of these species in deep swamps is restricted to dry periods when the surface soil is exposed (Smith and Linnartz 1980). Seeds of *Parkia pendula* and *P. discolor* germinated after submergence for seven months (Scarano and Crawford 1992).

Seeds of some closely related species show wide differences in germination responses to soil inundation. Submersion of *Quercus nuttallii* acorns did not affect their germination, whereas similar treatment of acorns of *Q. falcata* var. *pagodaefolia* lowered germination capacity. This difference accounts in part for occupation of wet flats by *Q. nuttallii* and of more drained flats by *Q. falcata* var. *pagodaefolia* (Briscoe 1961). Germination capacity of seeds of *Mora gonggrijpii* decreased from 70 to 50% after 11 days of flooding, whereas 80% of *M. excelsa* seeds were viable after 50 days of flooding (Steege 1994).

Once seeds germinate, fluctuations in the water level often determine seedling survival (Sacchi and Price 1992). Survival depends to a considerable extent on the capacity of seedlings to elongate rapidly and protrude above the water level, which, in turn, may be related to the amount of stored food in the seed. For example, in a floodplain forest, *Quercus nigra* produced heavy acorns and sturdy seedlings that showed high survival rates. Other species (*Carpinus caroliniana, Liquidambar styraciflua, Acer rubrum, Ulmus america*) produced large crops of light seeds. Seedling survival of these species was low, presumably because of low food reserves (Streng et al. 1989). Several other studies have demonstrated high resistance of heavy-seeded species to environmental stresses (Baker 1972, Harper 1977, Foster and Janson 1985).

Very young seedlings are more sensitive to flooding injury than older seedlings. For example, very young seedlings of bottomland species were killed by flooding, whereas trees at least 1-year-old survived (Kennedy and Krinard 1974). Flooding injured 1- to 4.5-year-old *Populus nigra* trees much more than trees at least 5 years old (Popescu and Necsulescu 1967). Seedlings of *Taxodium distichum* tolerated longer periods of flooding than those of *Acer saccharinum* or *Cephalanthus occidentalis*, which, in turn, withstood flooding better than those of *Celtis laevigata* or *Quercus falcata* var. *pagodaefolia* (Hosner 1958, 1960). Seedlings of *Betula nigra* withstood prolonged flooding better than seedlings of *Betula papyrifera* (Norby and Kozlowski 1983). Seedlings of *Parkia discolor* survived after 7 months of submersion but those of *P. pendula* survived only a few weeks of submersion (Scarano and Crawford 1992). Seedlings of many flood-tolerant and flood-intolerant plants are killed when they are uprooted, buried in mud, or submerged in floodwater (Brink 1954, Stone and Vasey 1965).

Many factors determine species composition and zonation along river channels. These include periodicity of flooding, duration of soil saturation, water velocity, water quality, rate of sedimentation, and meander migration (Hawk and Zobel 1974, McBride and Strahan 1984, Sharitz and Lee 1985, Bradley and Smith 1986, Blom et al. 1994, Van Splunder et al. 1995). Scouring of gravel bars by stream-flow kills many riparian tree seedlings. Nearly all the seedlings adjacent to a stream bed were removed by scouring. However, some seedlings survived when they were not subjected to the direct force of the stream-flow (McBride and Strahan 1984).

Shoot growth Flooding adversely affects shoot growth of many woody plants by suppressing leaf formation and expansion of leaves and internodes, causing premature leaf senescence and abscission, and inducing shoot dieback (Kozlowski 1984*b*, Kozlowski et al. 1991, Kozlowski and Pallardy 1997*b*).

Examples of angiosperm species showing inhibition of shoot growth by flooding include *Alnus rugosa*, *Betula nigra*, *Ulmus americana*, *U. alata*, and *Acer rubrum* (McDermott 1954), *U. americana* (Newsome et al. 1982), *Quercus macrocarpa* (Tang and Kozlowski 1982*a*), *Eucalyptus camaldulensis* and *E. globulus* (Sena Gomes and Kozlowski 1980*c*), and *Platanus occidentalis* (Tang and Kozlowski 1982*b*).

Inhibition of shoot growth in gymnosperms by flooding has been demonstrated in *Pinus echinata*, *P. taeda*, and *P. serotina* (Hunt 1951), *Picea glauca*, *P. mariana*, *Pinus banksiana*, *P. resinosa*, *P. strobus*, and *Abies balsamea* (Ahlgren and Hansen 1957), *Pinus elliottii* (McMinn and McNab 1971), *Pinus halepensis* (Sena Gomes and Kozlowski 1980*d*), *P. banksiana* and *P. resinosa* (Tang and Kozlowski 1983), and *Taxodium distichum* (Yamamoto 1992).

Although flooding for 10 days stimulated formation of secondary needles in *Pinus halepensis* seedlings, flooding for longer periods arrested their formation. After 70 days of flooding, there were only slightly more than half as many needle fascicles as there were in unflooded seedlings (Sena Gomes and Kozlowski 1980*d*). Flooding also suppressed needle formation in *Pinus banksiana* and *P. resinosa* seedlings (Tang and Kozlowski 1983). Flooding with stagnant water inhibited needle initiation in *Taxodium distichum* seedlings (Shanklin and Kozlowski 1985).

Soil inundation inhibited formation of new leaves, slowed expansion of leaves formed before flooding, and induced leaf abscission in *Betula papyrifera* seedlings. Over a 60-day period, the average number of leaves on unflooded plants approximately doubled (from 8.7 to 17.9), whereas on flooded plants it decreased by more than half (from 8.7 to 3.4) (Tang and Kozlowski 1982*c*). Flooding did not induce leaf shedding in the more flood-tolerant *Betula nigra* (Norby and Kozlowski 1983). In *Populus* spp., leaf expansion of flooded seedlings was inhibited by a decrease in cell extensibility of cell walls (Smit et al. 1989). Flooding accelerated leaf shedding of trees of the Brazil nut family (Lecythidaceae) (Mori and Becker 1991), and of peach and pecan trees (Marth and Gardner 1939, Alben 1958). Total leaf dry weight of *Larix leptolepis* plants was decreased by 45% by flooding largely as a result of extensive leaf shedding (Tsukahara and Kozlowski 1984).

Cambial growth Responses of cambial growth to flooding vary depending on species, age of plants, time and duration of flooding, condition of the floodwater (e.g., moving or stagnant), and site conditions (Kozlowski et al. 1991, Kozlowski and Pallardy 1997*b*). Some of the variation in cambial growth response to flooding may be associated with the method for measuring cambial growth, because measurements of stem diameter changes are sometimes complicated by stem swelling or hypertrophy, or both (Kozlowski 1972).

The rate of diameter growth is reduced by prolonged flooding in most flood-intolerant species including seedlings of *Betula papyrifera* (Tang and Kozlowski 1982*c*), *Acer negundo* (Yamamoto and Kozlowski 1987*d*), *Acer platanoides* (Yamamoto and Kozlowski 1987*e*), *Hevea brasiliensis* (Sena Gomes and Kozlowski 1988), *Pinus banksiana*, *P. resinosa* (Tang and Kozlowski 1983), and *Larix leptolepis* (Tsukahara and Kozlowski 1984). If the flooding occurs during the dormant season, and the flood water drains away before the growing season starts, the rate of cambial growth may be accelerated over that of previously unflooded trees (Broadfoot 1967).

In contrast to the inhibitory effects of flooding on many flood-intolerant plants, stem diameter growth of some flood-tolerant plants is increased by soil inundation. For most of the growing season, height and diameter growth rates, as well as biomass accumulation, were higher in flooded than in non-flooded *Nyssa aquatica* seedlings. The increased growth of the flooded seedlings was attributed to higher efficiency in biomass increase per unit of each nutrient absorbed (except Fe) (McKevlin et al. 1995). After 70 days, diameter increment of flooded *Fraxinus mandshurica* seedlings was much greater than that of unflooded seedlings, reflecting an increase in both the number and size of xylem cells (mostly libriform fibers). More than twice as many fibers were produced in flooded seedlings than in unflooded seedlings. Flooding had a negligible effect on bark thickness (Yamamoto et al. 1995).

Flooding often affects xylem and phloem production differently. In *Pinus halepensis*, *P. densiflora* and *Cryptomeria japonica* seedlings, waterlogged soil increased stem diameter growth more as a result of increased bark thickening and stem hypertrophy than because of xylem increment. The increase in bark thickness was associated with accelerated proliferation of phloem parenchyma cells and large amounts of intercellular space in the phloem (Yamamoto and Kozlowski 1987*a*, 1987*b*, 1987*c*). After 43 days of flooding (with the lower stems of the seedlings submerged), bark thickness of *P. halepensis* seedlings, just above and below the water level, had increased by 230%, whereas in unflooded seedlings it increased by only 130% (Yamamoto et al. 1987).

Flooding accelerated tracheid production (though less than it increased phloem production) in the upper stems of *P. halepensis* and *Thuja orientalis* seedlings (Yamamoto and Kozlowski 1986, Yamamoto et al. 1987), but not those of *Cryptomeria japonica* or *Pinus densiflora* (Yamamoto and Kozlowski 1987*b*, Yamamoto and Kozlowski 1987*c*). Tracheid diameters were increased in *Thuja orientalis* seedlings by flooding, not appreciably altered in *Pinus halepensis*, and reduced in *P. densiflora*. In *Cryptomeria japonica*, flooding consistently increased tracheid diameters, hence the tracheids were aligned in orderly radial rows (Yamamoto and Kozlowski 1987*c*). In *Thuja orientalis*, however, flooding increased diameters of some tracheids only within radial files, hence the tracheids were not arranged in orderly radial rows (Yamamoto and Kozlowski 1986).

In both *Pinus halepensis* and *P. densiflora* seedlings, flooding induced formation of short, thick-walled rounded tracheids (generally resembling those in compression wood), surrounded by intercellular spaces. The tracheids of both flooded and unflooded seedlings of both species developed three cell wall layers, including an outer S1 layer, a middle S2 layer, and an S3 layer adjacent to the cell lumen (Yamamoto et al. 1987, Yamamoto and Kozlowski 1987*a*). The S3 layer is absent in well-developed compression wood (Coté and Day 1965). In contrast to *P. halepensis* and *P. densiflora*, the tracheids of *Cryptomeria japonica* and *Thuja orientalis* that were produced after the soil was flooded had normal rectangular shapes (Yamamoto and Kozlowski 1986, Yamamoto and Kozlowski 1987*c*).

In both angiosperms and gymnosperms, flooding often increases the proportion of parenchymatous tissue in the xylem and phloem. For example, stems of flooded *Pinus halepensis* seedlings had proportionally more xylem rays, more enlarged ray cells, more resin ducts, and more phloem parenchyma cells than stems of unflooded seedlings (Yamamoto et al. 1987). In *Pinus densiflora*, flooding did not significantly influence formation of resin ducts in the xylem (Yamamoto and Kozlowski 1987*b*).

Root growth, root decay and adventitious roots Soil inundation reduces root growth of most woody plants by inhibiting root formation and branching, growth of existing roots and mycorrhizae, and by inducing root decay (DeBell et al. 1984, Kozlowski 1984*a*, 1984*b*, Kozlowski and Pallardy 1997*b*). Shallow, spreading root systems are characteristic of sites with high water tables (Lieffers and Rothwell 1986*a*, 1986*b*). Because root growth typically is reduced more than stem growth, the root/shoot ratio is decreased. When the flood water drains away, the previously flooded plants may be less drought tolerant because absorption of water by their small root systems cannot adequately replenish transpirational losses. There are many examples of reductions in root growth as a result of soil inundation (see Table 1).

Because mycorrhizal fungi are strongly aerobic, mycorrhizae are rare in flooded soils (Theodorou 1978, Lodge 1986). Flooding reduces the number of fungi around tree roots and suppresses formation of new mycorrhizal populations (Wilde 1954, Mikola 1973, Filer 1975). Roots of *Populus euramericana* trees growing along a water channel lacked mycorrhizae, whereas trees growing at some distance away from the channel had both endo- and ectomycorrhizae. However, sensitivity to flooding varied appreciably among different species of mycorrhizal fungi (Shuja et al. 1971).

Flooded soil conditions may lead to development of root rot by increasing the activity of soil fungi as well as susceptibility of the host. Decay of root systems in flooded soil occurs

Table 1. Effects of flooding of soil on root growth of various woody plant species.

Species	Source
ANGIOSPERMS	
Acer negundo	Yamamoto and Kozlowski (1987*d*)
Acer platanoides	Yamamoto and Kozlowski (1987*e*)
Betula nigra	Norby and Kozlowski (1983)
Betula papyrifera	Tang and Kozlowski (1982*c*) Norby and Kozlowski (1983) Tang and Kozlowski (1983)
Betula platyphylla var. *japonica*	Tsukahara and Kozlowski (1986)
Citrus spp.	Stolzy et al. (1965)
Eucalyptus camaldulensis	Sena Gomes and Kozlowski (1980*c*)
Eucalyptus globulus	Sena Gomes and Kozlowski (1980*c*)
Fraxinus mandshurica	Yamamoto et al. (1995)
Fraxinus pennsylvanica	Sena Gomes and Kozlowski (1980*a*)
Malus domestica	Childers and White (1942) Boynton and Compton (1943)
Persea americana	Valoras et al. (1964)
Platanus occidentalis	Tang and Kozlowski (1982*b*) Tsukahara and Kozlowski (1985)
Quercus macrocarpa	Tang and Kozlowski (1982*a*)
Ulmus americana	Newsome et al. (1982) Angeles et al. (1986)
GYMNOSPERMS	
Cryptomeria japonica	Yamamoto and Kozlowski (1987*c*)
Larix laricina	Lieffers and Rothwell (1986*a*, 1986*b*)
Larix leptolepis	Tsukahara and Kozlowski (1984)
Picea mariana	Lieffers and Rothwell (1986*a*, 1986*b*)
Picea sitchensis	Fraser and Gardiner (1967) Sanderson and Armstrong (1980*a*) Coutts (1982)
Pinus banksiana	Tang and Kozlowski (1983)
Pinus contorta	Coutts (1982)
Pinus densiflora	Yamamoto and Kozlowski (1987*b*)
Pinus halepensis	Sena Gomes and Kozlowski (1980*d*) DeBell et al. (1984) Yamamoto et al. (1987)
Pinus resinosa	Tang and Kozlowski (1983)
Pinus taeda	Lorio et al. (1972) DeBell et al. (1984)
Taxodium distichum	Shanklin and Kozlowski (1985)
Thuja orientalis	Yamamoto and Kozlowski (1986)

primarily through increased activity of *Phytophthora* fungi, which can tolerate low soil O_2 concentrations (Duniway 1979, 1983, Duniway and Gordon 1986). Disease severity is influenced by the species of host plant, species of fungus, duration of flooding, and preconditioning of the host by various environmental stresses. The expression of root rot induced by *Phytophthora* fungi may vary in different species of woody plants. For example, *P. cinnamomum* typically invaded only the fine roots of *Persea americana* but it invaded most of the root system of *Banksia* species (Zentmyer 1980). Rapid development of root decay as well as mortality of *Abies fraseri* seedlings occurred following a single flooding period of 24 or 48 h. Flooding appeared to increase infection and plant mortality by promoting production and dispersal of inoculum rather than by predisposing the host to infection (Kenerley et al. 1984).

Flooding increases disease severity by inducing both discharge and dispersal of zoospores (Duniway 1983, Wilcox and Mircetich 1985*a*). After zoospores are released from sporangia, their movement in the soil depends on high matric potentials. Disease severity in *Persea indica*, induced by *Phytophthora cinnamomum*, was a function of matric potential and not osmotic potential. The percentages of diseased roots varied from approximately 10 to 90% depending on the value of the matric potential (Sterne et al. 1977).

Phytophthora zoospores are attracted to a variety of root tip exudates, especially amino acids, sugars, alcohols and other compounds (Carlile 1986). Zoospores of five species of *Phytophthora* were attracted to vitamins, phenolic compounds, nitrogenous bases of nucleic acid, nucleotides, hormonal growth regulators, sugars, organic acids, and amino acids (Khew and Zentmyer 1973). Zoospores arriving at a root typically form cyst walls that are induced by substances emitted by the host. Germination of zoospores, which is stimulated by root exudates, rapidly follows encystment. Within an hour after zoospores of *P. cinnamomum* accumulated at *Persea* roots, germ tubes had penetrated the root surfaces (Ho and Zentmyer 1977) and disease symptoms, in the form of brown lesions, were evident within 24 h (Zentmyer 1979).

The duration of flooding affects the extent of development of root and crown rots. For two species of *Phytophthora* (*P. cryptogea* and *P. megasperma*), disease severity was mild (2–7% of the root system decayed) in non-flooded *Prunus* trees, but extreme (81–99% of the root system decayed) in trees flooded for 48 h every 2 weeks. *Phytophthora cryptogea* caused crown rot only after 48 h of flooding, whereas *P. megasperma* did not cause crown rot (Wilcox and Mircetich 1985*b*). Susceptibility of apple rootstocks to *Phytophthora* crown and root rots varied widely with duration of flooding. Crown rot incidences were 2.5, 6.3, 19, and 50% following weekly flooding periods of 0, 24, 48, and 72 h, respectively (Wilcox 1993).

Disease severity varies with the species of *Phytophthora* fungi present. When soils were artificially infected with *P. cryptogea*, *P. cambivora*, *P. megasperma*, or *P. drechslerii* at different soil water contents, *P. cambivora* caused more crown and root rot in *Prunus* and reduced growth more than other species of *Phytophthora* (Wilcox and Mircetich 1985*a*). When averaged for several rootstock and flooding treatments, mean incidences of crown rot of apple caused by *P. cryptogea*, *P. cactorum*, *P. cambivora*, and *P. megasperma* were 36, 26, 15, and 8.8%, respectively (Wilcox 1993).

Both drought and flooding may variously predispose relatively resistant plants to root and crown rots. In the absence of drought or flooding, *Rhododendron* cv. 'Purple Splendour' plants developed severe root and crown rots following inoculation with spores of *Phytophthora cinnamomum*, whereas the resistant cultivar 'Caroline' did not develop disease symptoms. However, when 'Caroline' plants were stressed by drought or flooded for 48 h before inoculation with *P. cinnamomum*, they

developed severe symptoms of root and crown rot (Blaker and McDonald 1981).

As roots of some flooded plants die, adventitious roots are produced on the original root system and on the submerged portions of stems. These flood-induced roots usually are thicker and have more intercellular space than roots growing in well-aerated soil (Hook et al. 1971). In *Ulmus americana* the primordia of flood-induced adventitious roots originate in the ray parenchyma of the secondary phloem (Angeles et al. 1986). In *Cryptomeria japonica*, they arise in the xylem parenchyma (Yamamoto and Kozlowski 1987*c*). Such adventitious roots may or may not emerge through lenticels (Angeles et al. 1986). Flood-induced adventitious roots have been reported in a wide variety of both flood-intolerant and tolerant angiosperms and gymnosperms (Table 2), but more are usually produced by flood-tolerant species (Kozlowski 1984*b*, Kozlowski and Pallardy 1997*b*).

Reproductive growth Soil inundation often inhibits flower bud initiation, anthesis, fruit set, and fruit enlargement in flood-intolerant species. It also induces early abscission of flowers and fruits. The extent of the alteration of reproductive growth varies with plant species and genotype and with the time and duration of flooding.

Flooded *Vaccinium ashei* plants had 61 to 77% fewer flower buds and 55 to 66% fewer flowers per bud than unflooded plants (Abbott and Gough 1987*a*, 1987*b*). In contrast, flowering of the tropical fruit tree, *Syzygium samaragense*, is routinely induced by flooding of orchards for 30 to 40 days in the summer (Lin and Lin 1992). Flooding slightly increased fruit set of *Averrhoa carambola* (Joyner and Schaffner 1989), whereas it reduced fruit set in *Vaccinium macrocarpa* (Bergman 1943) and *V. ashei* (Crane and Davies 1985*a*, 1985*b*, 1989). Fruit set in flooded *V. corymbosum* was decreased by 45% (Abbott and Gough 1987*a*). By comparison, *Averrhoa carambola* trees flooded for 6 to 18 weeks had better fruit set than either trees flooded for short periods or unflooded trees (Joyner and Schaffer 1989).

Substantial reductions in fruit yield following flooding have been reported for many species including *Malus domestica* (Childers et al. 1943, Childers and White 1950), *Vaccinium macrocarpon* (Bergman 1943), and *V. ashei* (Crane and Davies 1985*b*, 1989). In *V. ashei*, fruit yield was reduced up to 76% by flooding for 35 days (Crane and Davies 1985*b*). Fruit yield of *Malus* was lowered by 34% by spring flooding (April–June) but not by summer (July–August) or autumn (September–October) flooding (Olien 1987). Reductions in crop yield typically are traceable to fewer and smaller fruits. Most of the fruits of flooded *Vaccinium corymbosum* plants were shed before harvest time (Abbott and Gough 1987*a*).

Flooding often lowers fruit quality by reducing fruit size, altering the appearance of fruit and changing its chemical composition (Crane and Davies 1989). Soil inundation decreased the size of fruits of *Vaccinium macrocarpon* (Bergman 1943) and *V. corymbosum* (Abbott and Gough1987*a*). The percentage of soluble solids in *V. corymbosum* fruits was reduced by flooding (Abbott and Gough 1987*a*, 1987*b*), and the fruits of flooded *V. ashei* plants were shriveled (Crane and Davies 1985*b*).

Some fruits burst or crack following flooding, heavy rains, or irrigation, especially when long periods of drought precede soil waterlogging (Kaufmann 1972, Kozlowski 1972, Opara et al. 1997). Splitting has been documented in apples (Verner 1939, Faust and Shear 1972), citrus fruits (Kaufmann 1972) cherries (Gerhardt et al. 1949, Glenn and Poovaiah 1989, Bullock 1952, Sekse 1995), peaches and nectarines (Fogle and Faust 1976), pears (Raese 1989), and prunes (Uriu et al. 1962, Milad and Schackel 1992, Opara et al. 1997). Cracking of many fruits is caused by high internal pressures following

Table 2. Examples of species that produce adventitious roots in response to flooding.[1]

Angiosperms	Gymnosperms
Acer negundo	*Picea sitchensis*
Acer rubrum	*Pinus contorta*
Alnus glutinosa	*Pinus elliottii* var. *elliottii*
Alnus rubra	*Sequoia sempervirens*
Amorpha fruticosa	*Tamarix aphylla*
Betula nigra	*Tamarix gallica*
Cephalanthus occidentalis	*Taxodium distichum*
Cydonia oblonga	*Thuja plicata*
Eucalyptus camaldulensis	*Tsuga heterophylla*
Eucalyptus globulus	
Eucalyptus grandis	
Eucalyptus robusta	
Eucalyptus saligna	
Fraxinus americana	
Fraxinus mandshurica	
Fraxinus pennsylvanica	
Hevea brasiliensis	
Liriodendron tulipifera	
Malus domestica	
Melaleuca quinquenervia	
Nyssa aquatica	
Nyssa sylvatica	
Platanus occidentalis	
Populus deltoides	
Populus nigra	
Populus trichocarpa	
Quercus macrocarpa	
Quercus robur	
Salix alba	
Salix atrocinerea	
Salix discolor	
Salix fragilis	
Salix hookeriana	
Salix lasiandra	

[1] Sources: Andersen et al. (1984*a*), Angeles et al. (1986), Armstrong (1968), Clemens et al. (1978), DeGruchy (1956), Dreyer et al. (1991), Gill, (1972, 1975), Harrington (1987), Hook (1984), Hook and Brown (1973), Kozlowski (1984*b*), Kramer (1951), Minore (1968), Newsome et al. (1982), Norby and Kozlowski (1983), Sena Gomes and Kozlowski (1980*a*, 1980*b*, 1980*c*, 1988), Tang and Kozlowski (1982*b*), Tsukahara and Kozlowski (1985), Yamamoto and Kozlowski (1987*d*), Yamamoto et al. (1995).

osmotic absorption of water through the skin or increased absorption through the roots, or both (Opara et al. 1997). The high pressures cause mechanical failure of the dermal system and subsequently of the underlying cell wall. Because the cuticles of grapes are less extensible than the underlying epidermal and collenchymal cell walls (Considine and Brown 1981, Considine 1982), fruit cracking appears as a series of fractures in the skin, commonly forming regular and reproducible patterns that are cultivar specific (Considine and Kriedemann 1972, Fogle and Faust 1976, Considine 1982, Lavee and Nir 1986).

Physiological responses

Injury and growth inhibition of flooded plants have been attributed to multiple, often concurrent physiological dysfunctions in plants. These include altered carbohydrate, mineral, water, and hormone relations. Under anaerobic conditions, the activity of several metabolic pathways is reduced or altered (Kennedy et al. 1991). Shifts occur in carbohydrate, protein, organic acid, and lipid metabolism.

Photosynthesis Flooding of soil generally is followed by a relatively rapid decrease in the rate of photosynthesis in many angiosperm and gymnosperm species (Table 3). Several studies have shown that photosynthesis is appreciably reduced within hours to a few days after flooding is initiated (Childers and White 1942, Loustalot 1945, Regehr et al. 1975, Sena Gomes and Kozlowski 1980*a*, Bazzaz and Peterson 1984, Pezeshki and Chambers 1985*a*, Beckman et al. 1992). The rate of photosynthesis of *Pseudotsuga menziesii* seedlings was appreciably reduced within 5 h after the soil was inundated (Zaerr 1983). Flooding reduced photosynthesis of four citrus rootstocks within 24 h (Phung and Knipling 1976). Much of the early reduction in the rate of photosynthesis of flooded plants is correlated with stomatal closure, resulting in decreased CO_2 absorption by leaves (e.g., Pezeshki et al. 1996*a*).

Stomatal closure after flooding has been demonstrated in many species (e.g., Kozlowski and Pallardy 1979, Sena Gomes and Kozlowski 1980*a*, 1980*b*, 1980*c*, Newsome et al. 1982, Tang and Kozlowski 1982*a*, 1982*b*, 1982*c*, Norby and Kozlowski 1983, Pezeshki and Chambers 1985*a*, 1985*b*, Sena Gomes and Kozlowski 1986, Larson et al. 1989, Wazir et al. 1988). In amphistomatous plants, the effects of flooding on adaxial and abaxial leaf surfaces may be similar or different depending on species. Flooding induced rapid closure of stomata on the adaxial leaf surfaces of *Eucalyptus camaldulensis*, *Populus deltoides*, and *Salix nigra*. It also induced closure of stomata on the abaxial leaf surface of *Populus deltoides* but not those of *E. camaldulensis* or *S. nigra* (Pereira and Kozlowski 1977). When the flood waters drain away, the stomata reopen slowly and the rate of photosynthesis increases (e.g., Davies and Flore 1986*c*, Larson et al. 1989); however, the capacity for stomatal reopening varies with species and the duration of flooding. After 24 days of flooding, recovery of stomatal conductance to pre-flood values required 18 days for *Vaccinium corymbosum*, but more than 18 days for *V. ashei* (Davies and Flore 1986*b*). The closed stomata of *Carya illinoensis* reopened following an 8-day flooding period but the stomata did not reopen after a 15-day flooding period (Smith and Ager 1988).

Table 3. Species showing flood-induced reduction in photosynthesis.

Species	Source
ANGIOSPERMS	
Acer saccharinum	Sipp and Bell (1974)
	Bazzaz and Peterson (1984)
Averrhoa carambola	Joyner and Schaffer (1989)
Betula papyrifera	Ranney and Bir (1994)
Betula pendula	Ranney and Bir (1994)
Betula platyphylla var. *japonica*	Ranney and Bir (1994)
Carya illinoensis	Loustalot (1945)
	Smith and Ager (1988)
	Smith and Huslig (1990)
Citrus spp.	Kriedemann (1971)
	Phung and Kipling (1976)
	Crane and Davies (1989)
	Vu and Yelenosky (1991)
	Pezeshki (1993)
Fagus sylvatica	Lyr (1993)
Liquidambar styraciflua	Pezeshki and Chambers (1985*a*)
Malus domestica	Childers and White (1942)
Mangifera indica	Larson et al. (1989)
Nyssa aquatica	Pezeshki et al. (1989)
Ocotea bullata	Lübbe (1991)
Persea americana	Ploetz and Schaffer (1989)
Populus deltoides	Regehr et al. (1975)
	McGee et al. (1981)
Populus spp.	Liu and Dickmann (1993)
Prunus spp.	Ranney (1994)
Quercus falcata	Pezeshki and Chambers (1985*b*)
var. *pagodaefolia*	Pezeshki (1993)
Quercus lyrata, *Q. palustris*, *Q. petraea*, *Q. robur*, and *Q. rubra*	Dreyer et al. (1991)
	Lyr (1993)
Tilia cordata	Lyr (1993)
Vaccinium spp.	Davies and Flore (1986*a*, 1986*b*, 1986*c*)
Vitis spp.	Striegler et al. (1987)
GYMNOSPERMS	
Pseudotsuga taxifolia	Zaerr (1983)
Taxodium distichum	Kludze et al. (1994)
	Pezeshki (1994)

Some investigators suggested that stomatal closure of flooded plants is associated with a decrease in root hydraulic conductivity (Andersen et al. 1984*b*, Davies and Flore 1986*a*). Hydraulic conductivity of *Vaccinium corymbosum* plants decreased after the soil was flooded, and was followed by stomatal closure (Davies and Flore 1986*a*, 1986*b*). Syvertsen et al. (1983) reported a decrease in root hydraulic conductivity of *Citrus* together with a 47% decrease in stomatal conductance. However, several other studies have shown that stomatal closure of flooded plants is not induced by water stress in leaves resulting from reduced hydraulic conductivity. For example, the root hydraulic conductivity of *Larix laricina* seed-

lings was not affected by flooding except for a possible temporary increase on the first day after the soil was flooded (Reece and Riha 1991).

In many species, flood-induced stomatal closure is not associated with a reduction in leaf turgor or leaf water potential. Thus, although soil inundation induced stomatal closure in *Melaleuca quinquenervia* seedlings it did not create water deficits in the shoots (Sena Gomes and Kozlowski 1980*d*). Flooding was followed by rapid stomatal closure in *Populus deltoides* leaves, but the leaves remained turgid throughout 28 days of flooding (Regehr et al. 1975). In seedlings of *Eucalyptus camaldulensis*, *E. globulus*, *Ulmus americana*, *Salix nigra*, and *Quercus macrocarpa*, the stomata closed following soil waterlogging, but the leaf water potential was higher in flooded plants than in unflooded plants (Pereira and Kozlowski 1977, Tang and Kozlowski 1982*a*). The water potentials of both flooded and unflooded *Vaccinium* plants were similar over a 3- to 5-week period (Crane and Davies 1989). Xylem pressure potentials of *Quercus falcata* var. *pagodaefolia* seedlings did not change after flooding, although both stomatal conductance and the rate of photosynthesis were appreciably lowered. Thus, the evidence indicates that flooding does not cause leaf water deficits (Pezeshki and Chambers 1985*b*).

Stomatal closure of flooded plants may result from a hormonal signal transmitted from the roots to the shoots. Both ABA and cytokinins have been implicated in stomatal closure of plants growing in waterlogged soils (Davies and Kozlowski 1975*a*, 1975*b*, Reid and Bradford 1984, Zhang and Davies 1990, Else et al. 1996). Flooding of soil was shortly followed by accumulation of ABA in leaves (Shaybany and Martin 1977) and the ABA buildup was correlated with stomatal closure (Zhang et al. 1987).

The early rapid reduction in the rate of photosynthesis of many flooded plants is highly correlated with stomatal closure, whereas during prolonged flooding the rate of photosynthesis is reduced progressively more by inhibitory effects on the photosynthetic process. Nonstomatal inhibition may involve changes in carboxylation enzymes and loss of chlorophyll. For example, short periods of flooding decreased photosynthesis of *Vaccinium* spp., largely by reducing stomatal conductance (Crane and Davies 1989); however, long-term flooding decreased not only stomatal conductance but also lowered carboxylation efficiency and quantum yield (Davies and Flore 1986*b*). Similarly in *Prunus cerasus*, much of the early decrease in photosynthesis of flooded plants was attributed to stomatal inhibition, but as flooding continued, nonstomatal limitations progressively dominated (Beckman et al. 1992). Under rhizosphere hypoxia associated with flooding, both photosynthetic capacity and stomatal conductance of *Taxodium distichum* seedlings were reduced. A decrease in ribulose-1,5-bisphosphate carboxylase-oxygenase activity was among the early signals of flooding stress that contributed to loss of photosynthetic capacity (Pezeshki 1994).

Carbohydrates and carbohydrate partitioning The effects of flooding on carbohydrate and energy metabolism are particularly well known and result in lowering of the concentration of ATP, the ratio of ATP to ADP, and the energy charge as a result of blocking of oxidative phosphorylation (Vartapetian 1991). However, some components of the glycolytic pathway may be stimulated, including pyruvate decarboxylase, lactic dehydrogenase, and alcohol dehydrogenase (Kennedy et al. 1991). Soil inundation affects not only synthesis of carbohydrates but also their transport to meristematic sinks and their utilization in metabolism and production of new tissues.

Flooding often causes a change in allocation of photosynthate within plants. For example, flooding suppressed height and diameter growth of *Acer platanoides* seedlings but increased growth of bark tissues, indicating a change in carbohydrate partitioning (Yamamoto and Kozlowski 1987*e*). Similarly, the xylem increment of *Acer negundo* seedlings was decreased by flooding, whereas bark growth was increased (Yamamoto and Kozlowski 1987*d*). Soil inundation did not influence short-term height growth of *Pinus halepensis* seedlings but increased stem diameter growth, largely because of an increase in bark thickness as a result of proliferation of phloem parenchyma cells (Yamamoto et al. 1987). In some species, flooding alters the proportional use of carbohydrates for production of xylem cells and for thickening of their walls. In *Fraxinus mandshurica* seedlings, flooding increased the number of libriform fibers but inhibited thickening of their walls (Yamamoto et al. 1995).

Mineral relations and mycorrhizae Flooding typically decreases absorption of the major macronutrients (especially N, P, and K) by flood-intolerant plants. Nitrate N is rapidly depleted by denitrification under conditions of soil hypoxia. Inhibition of uptake of nitrate also is associated with effects of low O_2 tension on root metabolism (Kozlowski and Pallardy 1984). In contrast, uptake of Fe and Mn is often increased by flooding because ferric and manganic forms are converted to soluble ferrous and manganous forms (e.g., Jones and Etherington 1970). Nevertheless, the total amount of Fe and Mn in plants usually declines because of the slower growth of flooded-plants compared with unflooded plants (Ponnamperuma 1972). The abundant ferrous and manganous ions in flooded soils may be toxic to some plants (Crawford 1989).

There are many examples of reduced uptake of macronutrients (especially nitrogen, phosphorus, and potassium) by flooded woody plants as a result of a reduction in O_2 supply to the roots (e.g., Labanauskas et al. 1966, 1968, 1972, Reyes et al. 1977, Slowik et al. 1979, Lee et al. 1982, Rosen and Carlson 1984, Olien 1989, Osundina and Osonubi 1989, Smith and Bourne 1989, Larson et al. 1992). Decreasing the O_2 concentration around *Pinus elliottii* roots inhibited absorption of P, Ca, and Mg (Shoulders and Ralston 1975). Active absorption of K by roots required O_2 transport from stems exposed to air. Absorption of K stopped when N_2 replaced air around the lower stem and roots (Fisher and Stone 1990). In flooded soil, the leaf nutrient contents of *Quercus* species decreased markedly, especially for N and to a lesser extent for S and K (Dreyer et al. 1991).

The reduced uptake of macronutrients and decreased leaf nutrient contents of flood-intolerant plants have been attributed to root mortality, loss of mycorrhizae, and reductions in

root metabolism, transpiration, and hydraulic conductivity. These impediments often operate concurrently. Mineral concentrations of plants growing in flooded soils are reduced not only by lower mineral absorption but also by leakage of ions from roots to the rhizosphere. For example, efflux of K from roots of *Prunus domestica* generally increased as the O_2 concentration of the rhizosphere decreased. When the O_2 concentration of the soil solution was < 1%, K leaked from the roots. However, when the roots were reaerated after 18 h of anaerobiosis, uptake of K from the soil solution occurred within 24 h (Rosen and Carlson 1984).

Flood-tolerant species often absorb more mineral nutrients in response to soil inundation than unflooded, well-watered plants. Such responses have been shown for *Acer rubrum*, *A. saccharinum*, *Fraxinus pennsylvanica*, *Nyssa aquatica*, *Platanus occidentalis*, *Populus deltoides*, and *Taxodium distichum* (Hosner and Leaf 1962, Dickson et al. 1972). The high nutrient-uptake efficiency of flood-tolerant plants has been attributed to several adaptations, such as production of hypertrophied lenticels, aerenchyma tissue, and adventitious roots which play a role in oxygen transport in trees and oxidation of the rhizosphere.

In well-aerated soils, mycorrhizae increase mineral uptake, largely because of their extensive absorbing surface (Kozlowski and Pallardy 1997*a*). Fungal hyphae typically permeate the soil volume that is not penetrated by roots. The high respiration rates of mycorrhizal roots, which may be twice as high as those of nonmycorrhizal roots (Rygiewicz and Andersen 1994), accentuate mineral uptake. The high absorbing capacity of mycorrhizal roots is also associated with reductions in air gaps between the roots and soil particles, low resistance of the fungus to ion transport, increased rate of root growth, and more rapid hydrolysis of certain soil nutrients (Reid 1984, Kozlowski and Pallardy 1997*a*).

Hormone relations: shoot growth, cambial growth and root regeneration Both vegetative and reproductive growth are regulated by complex interactions among naturally occurring growth hormones and regulatory compounds (Kozlowski and Pallardy 1997*a*, 1997*b*), including phenolic compounds (Siqueira 1991), polyamines (Galston 1983, Smith 1985, Slocum and Flores 1991, Faust and Wang 1992), brassinosteroids (Mandava 1988, Iwahari et al. 1990, Roddick and Guan 1991, Sakurai and Fujioka 1993), and jasmonates (Sembdner and Parthier 1993).

Both initiation and acceleration of leaf abscission are regulated by hormonal interactions. Ethylene and ABA accelerate abscission, whereas auxins, cytokinins, and gibberellins delay it. When auxin flow from the leaf blade to the abscission zone is substantial, abscission is postponed. Once the abscission processes are initiated, ethylene accelerates abscission by inducing degradation of IAA, blocking IAA transport, and increasing production of ABA (Addicott 1991). Several investigators have shown high correlations between leaf abscission in flooded plants and ethylene production (Smith and Restall 1971, Drew et al. 1979, Kawase 1981). Applied auxins, gibberellins, and cytokinins retard senescence of green leaves (Brian et al. 1959, Osborne and Hallaway 1960). In contrast, applied ethylene can accelerate abscission of both leaves and fruits (Addicott 1991).

The abnormal anatomies of cambial derivatives in xylem and phloem tissues of flooded plants have been attributed to dysfunctions in normal hormone relations. Some investigators suggested that ethylene has an important role in inducing formation of reaction wood (compression wood in gymnosperms and tension wood in angiosperms) in flooded plants (Brown and Leopold 1973, Barker 1979); however, this suggestion is not supported by the more recent evidence. Thus, the abnormally rounded and thick tracheids of flooded *Pinus halepensis* seedlings have S3 wall layers (Yamamoto et al. 1987) that are not present in tracheids of well-developed compression wood. The slightly abnormal tracheids of *Pinus halepensis* that were induced by ethrel applications had some but not all of the features of well-developed compression wood (Yamamoto and Kozlowski 1987*a*). Furthermore, compression wood in *Pinus densiflora* seedlings was induced by tilting of stems but not by applying ethrel to upright plants. Also, the formation of compression wood in tilted seedlings was inhibited by exogenously applied ethrel (Yamamoto and Kozlowski 1987*b*).

The observed correlation between the amount of ethylene produced in many flooded plants and formation of adventitious roots has tended to obscure the complexity of the mechanism of induction and growth of such roots. In addition to ethylene, the formation of adventitious roots requires a balanced supply of other growth hormones, carbohydrates, nitrogenous compounds, enzymes, and rooting cofactors that act synergistically with auxin (Haissig 1974, 1982, 1983, 1986, 1990). In some flooded plants, adventitious rooting is not related quantitatively to the amount of induced ethylene. For example, more ethylene is produced by flooded *Eucalyptus globulus* seedlings than by *E. camaldulensis* seedlings, yet the latter species produces more adventitious roots (Tang and Kozlowski 1984). Although flooding greatly stimulated ethylene production in young *Betula papyrifera* seedlings, it did not induce formation of adventitious roots (Tang and Kozlowski 1982*c*). Auxins translocated to roots from the shoots appear to be more important than ethylene in regulating formation of adventitious roots in *Acer negundo* seedlings. Blockage of basipetal auxin transport by application of 1-*N*-naphthylphthalamic acid (NPA) to stems reduced formation of adventitious roots. However, application of naphthaleneacetic acid (NAA) to stems below the point of NPA application restimulated production of adventitious roots, indicating that auxins have a dominant role in the hormonal complex that regulates development of adventitious roots (Yamamoto and Kozlowski 1987*e*).

Phytotoxic compounds A variety of toxic compounds in flooded soils and plants variously contribute to injury, growth reduction, and mortality of woody plants. Injury to flooded plants has been attributed to products of anaerobic plant metabolism such as aldehydes, organic acids, and ethanol. Although ethanol is abundantly produced in leaves, stems, and roots of flooded plants (Crawford and Zochowski 1984, Andreev and Vartapetian 1992, Marschner 1995, Kelsey 1996), and removal of ethanol from roots of *Pinus contorta* stimulated growth

(Crawford and Finegan 1989), nevertheless, the weight of evidence indicates that ethanol is not very phytotoxic because plants readily eliminate ethanol and transport it from poorly-aerated to well-aerated regions where it is metabolized (Kennedy et al. 1992). Furthermore, when ethanol was supplied to nutrient solutions at concentrations up to 100 times those found in flooded plants, the plants were not injured (Jackson et al. 1982). Ethanol occurs in the cambial region of unflooded tree stems but does not induce injury (Kimmerer and Stringer 1988). Perata and Alpi (1991) concluded that the harmful effects ascribed to ethanol probably were caused by acetaldehyde.

Some compounds such as methane and sulfides, and reduced iron and manganese may accumulate in flooded soils and contribute to root injury (Glinski and Stepniewski 1985, Crawford 1989). Reduction of organic matter may be associated with production of phytotoxic organic acids (Lynch 1977). In hot climates, toxic hydrogen sulfide is produced in flooded soils that are rich in organic matter (Crawford 1989). A special case of phytotoxicity involves certain flood-intolerant *Prunus armeniaca*, *P. domestica*, and *P. persica* plants that are killed within a day of being subjected to flooding (Rowe and Beardsell 1973) because anaerobiosis induces hydrolysis of cyanogenic glycosides in roots to produce highly toxic cyanide. Toxic products of flooding, including reduced iron, fatty acids, and ethylene slowed root growth of gymnosperms, but the inhibitory effects of O_2 deficiency were considered to be greater (Sanderson and Armstrong 1980*a*, 1980*b*).

Adaptations to flooding

The mechanisms by which flood-tolerant plants survive waterlogging are complex and involve interactions of morphological, anatomical, and physiological adaptations (Hook 1984, Kozlowski et al. 1991, Crawford 1993, Kozlowski and Pallardy 1997*b*).

Oxygen transport and rhizospheric oxidation A primary adaptation of plants to flooding is the capacity for absorption of O_2 by aerial tissues, basipetal O_2 transport through stems, and diffusion of O_2 out of roots to oxidize the rhizosphere. By this mechanism, absorption of minerals by roots is increased and toxic compounds of flooded soils are oxidized to nontoxic compounds (Kozlowski and Pallardy 1984, 1997*b*). Rhizospheric oxidation may occur enzymatically by microbes associated with roots and directly by molecular O_2 (Armstrong 1975). Increased O_2 uptake by aerial tissues and its efficient transport in plants are favored by production of hypertrophied lenticels, aerenchyma tissues, and adventitious roots. More than one of these adaptations may be present in the same plant (Hook 1984).

Hypertrophied lenticels In herbaceous plants, O_2 enters plants largely through the leaves (Leyton and Rousseau 1958, Chirkova 1968). It is unlikely, however, that roots of trees that are beyond the seedling stage are supplied by O_2 entering the leaves because of resistance to gas movement and consumption of O_2 by respiration during its movement down the stem. Lenticels at the stem base appear to be more important points of O_2 entry (Coutts and Armstrong 1976). Blocking of lenticels at the bases of *Salix* spp. cuttings severely inhibited O_2 diffusion from the roots to an anaerobic medium, hence preventing oxidation of the rhizosphere (Hook et al. 1971, Hook 1984).

Hypertrophied lenticels form on submerged parts of stems and on roots of a wide variety of woody angiosperms and gymnosperms (Table 4). Formation of hypertrophied lenticels involves both increased phellogen activity and elongation of cork cells (Angeles et al. 1986). The large hypertrophied lenticels with breaks in the closing layers facilitate exchange of dissolved gases in the flood water (Hook et al. 1970, Hook 1984). Furthermore, potentially toxic compounds associated with anaerobiosis (including acetaldehyde, ethanol, and ethyl-

Table 4. Examples of species that form hypertrophied lenticels on submerged roots and stems.

Species	Source
ANGIOSPERMS	
Betula nigra	Norby and Kozlowski (1983)
Cydonia oblonga	Andersen et al. (1984*a*)
Eucalyptus camaldulensis	Sena Gomes and Kozlowski (1980*c*)
Eucalyptus globulus	Sena Gomes and Kozlowski (1980*c*)
Fraxinus pennsylvanica	Sena Gomes and Kozlowski (1980*a*)
Hevea brasiliensis	Sena Gomes and Kozlowski (1988)
Platanus occidentalis	Tang and Kozlowski (1982*b*)
	Tsukahara and Kozlowski (1985)
Populus deltoides	Pereira and Kozlowski (1977)
Pyrus communis	Andersen et al. (1984*a*)
Pyrus betulaefolia	Andersen et al. (1984*a*)
Pyrus calleryana	Andersen et al. (1984*a*)
Pyrus persica	Andersen et al. (1984*a*)
Quercus macrocarpa	Tang and Kozlowski (1982*a*)
Salix nigra	Pereira and Kozlowski (1977)
Ulmus americana	Newsome et al. (1982)
GYMNOSPERMS	
Abies balsamea	Hahn et al. (1920)
Araucaria bidwellii	Hahn et al. (1920)
Larix laricina	Hahn et al. (1920)
Picea canadensis	Hahn et al. (1920)
Picea mariana	Hahn et al. (1920)
Picea pungens	Hahn et al. (1920)
Picea rubens	Hahn et al. (1920)
Pinus banksiana	Hahn et al. (1920)
Pinus caribaea	Hahn et al. (1920)
Pinus clausa	Topa and McLeod (1986*a*, 1986*b*)
Pinus coulteri	Hahn et al. (1920)
Pinus monticola	Hahn et al. (1920)
Pinus ponderosa	Hahn et al. (1920)
Pinus resinosa	Hahn et al. (1920)
Pinus rigida	Hahn et al. (1920)
Pinus serotina	Topa and McLeod (1986*a*, 1986*b*)
Pinus strobus	Hahn et al. (1920)
Pinus sylvestris	Hahn et al. (1920)
Pinus taeda	Topa and McLeod (1986*a*, 1986*b*)
Pinus virginiana	Hahn et al. (1920)
Taxus brevifolia	Hahn et al. (1920)
Taxus cuspidata	Hahn et al. (1920)

ene) are released from plants through these lenticels (Chirkova and Gutman 1972).

Aerenchyma Both root and stem tissues of some flooded plants become permeated with tissues with large intercellular spaces. Such aerenchyma tissues may form by separation or disintegration of cells, followed by further enlargement through cell collapse (Esau 1965). Species that do not readily respond to soil anaerobiosis by enlarging their internal air spaces typically undergo anoxia in their roots (Coutts and Armstrong 1976).

Aerenchyma tissues were better developed in roots of *Pinus serotina* and *P. taeda* than in roots of the less flood-tolerant *P. clausa*. Hence, the capacity for rhizospheric oxidation by *P. clausa* was lower. Only 15 days of flooding were needed to increase the porosity of roots of *P. serotina* and *P. taeda* (Topa and McLeod 1986*b*). Aerenchyma tissues were present in the stele of *Pinus contorta* roots but not in roots of *Picea sitchensis*. The greater flood tolerance of *Pinus contorta* was attributed to more efficient transport of O_2 (Philipson and Coutts 1980). Aerenchyma tissues also occur in mangroves (Gill and Tomlinson 1975), and the flood-tolerant tropical fruit tree, *Syzygium samarangense*, develops extensive aerenchyma in the root cortex. The aerenchyma allows for effective O_2 transport within the roots. The supply of O_2 is adequate for conversion of 1-aminocyclopropane-1-carboxylic acid to ethylene.

The periderm of unflooded *Ludwigea octovalis* plants is comprised of compact, brick-shaped, thick-walled phellem cells without intercellular spaces, whereas the periderm of flooded plants is loose, with elongated, thin-walled phellem cells and abundant intercellular spaces (Angeles 1992). An additional adaptation for internal stem aeration is the greater permeability of the cambium to air in some flood-tolerant species. For example, cambial permeability was greater in *Nyssa aquatica* and *Fraxinus pennsylvanica* seedlings than in the less flood-tolerant *Platanus occidentalis, Liriodendron tulipifera*, and *Liquidambar styraciflua* seedlings. The differences were attributed to greater intercellular spaces among the cambial ray initials of the flood-tolerant species (Hook and Brown 1973). Radial and tangential sections of anaerobically grown loblolly pine roots showed a pathway for radial diffusion of O_2 through intercellular spaces between ray parenchyma cells in maturing secondary xylem. Such spaces were absent in the xylem of aerobically grown roots (Topa and McLeod 1986*b*).

Root regeneration Many flooded plants produce adventitious roots on the original roots or on the submerged portion of the stem, or both (Table 2). Four lines of evidence indicate that adventitious roots compensate physiologically for loss by decay of portions of the original root system following flooding. First, flood tolerance and production of adventitious roots are often correlated (Clemens et al. 1978, Sena Gomes and Kozlowski 1980*b*, 1980*c*). Second, flood-induced adventitious roots increase water absorption by roots (Hook and Scholtens 1978, Jackson and Drew 1984, Tsukahara and Kozlowski 1985). Third, flood-induced adventitious roots oxidize the rhizosphere and transform some soil-borne toxins to less harmful compounds (Hook et al. 1970, Hook and Brown 1973). Fourth, flood-induced adventitious roots increase the supply of root-synthesized gibberellins and cytokinins to the leaves (Reid and Bradford 1984).

Metabolic adaptations Metabolic adaptations to flooding have been reviewed by Davies (1980), Crawford (1989), Drew (1990), Jackson et al. (1991), Crawford (1993), Armstrong et al. (1994), and Marschner (1995). Armstrong et al. (1994) concluded that survival of flooding by woody plants depends on more than one of the following adaptations: (1) control of energy metabolism, (2) availability of abundant energy resources, (3) provision of essential gene products and synthesis of macromolecules (e.g., RNA, proteins, and membrane lipids), and (4) protection against post-anoxic injury. Crawford (1989) outlined two basic biochemical adjustments to flooding: (1) adaptation to hypoxia or short periods of anoxia that involve accumulation of malate as the primary product of anaerobic respiration and control of glycolysis and ethanol production, and (2) adaptations to flooding for long periods that involve stimulation of glycolysis, production of ethanol, and synthesis of ATP. Ethanol is lost through roots and accumulation of malate is prevented. The flood-tolerant *Nyssa sylvatica* var. *biflora* adapts metabolically to flooding by exhibiting normal glycolytic activity to maintain intermediary metabolism and produce ATP, increasing alcohol dehydrogenase activity for recycling NAD^+, and increasing its starch reserves for use in sink growth and respiration (Angelov et al. 1996).

Salinity

Salinization transforms fertile and productive land to barren land, and often leads to loss of habitat and reduction of biodiversity (Ghassemi et al. 1995). Salinity limits vegetative and reproductive growth of plants by inducing severe physiological dysfunctions and causing widespread direct and indirect harmful effects, even at low salt concentrations (Shannon et al. 1994). In addition to the salts in irrigation water, salts enter the soil from tidal flooding (Perry and Williams 1996) and from salt spray along seacoasts (Moss 1940). Salts used in deicing roads also enter the soil (Howard and Haynes 1993). As much as a ton of salt is applied to a mile of highway (Smith 1972). In 1969, about 6 million tons of salt (consisting of 95% NaCl and 5% $CaCl_2$) were applied to roads in northern states of the United States (Westing 1969). Susceptibility to salt injury varies with both species and the source of contamination (Kutscha et al. 1977, Braun et al. 1978, Stevens et al. 1996, Romero-Aranda and Syvertsen 1996).

Variation in salt tolerance

Salt tolerance of plants is difficult to quantify because it varies appreciably with many environmental factors (e.g., soil fertility, soil physical conditions, distribution of salt in the soil profile, irrigation methods, and climate) and plant factors (e.g., stage of growth, variety, and rootstock) (Perez and Moraes 1994, Ghassemi et al. 1995, Kozlowski and Pallardy 1997*b*). Woody plants usually are relatively salt tolerant during seed germination, much more sensitive during the emergence and young seedling stages, and become progressively more toler-

ant with increasing age through the reproductive stage (with the exception of anthesis) (Shannon et al. 1994).

There are many examples of variations in salt tolerance of species and genotypes of woody plants (Holmes 1961, Monk and Peterson 1962, Braun et al. 1978, Dirr 1978, Francois and Clark 1978, Tal 1986). Salt tolerance of closely related species often varies widely, as among species of *Acacia* (Craig et al. 1990), *Casuarina* (Clemens et al. 1983), *Melaleuca* (Van der Moezel and Bell 1987), *Sonneratia* (Ball and Pidsley 1995), *Pinus* (Townsend and Kwolek 1987), and *Eucalyptus* (Sharma et al. 1991, Fernando 1992, Sun and Dickinson 1993, Dunn et al. 1994). Variations in salt tolerance have also been demonstrated among provenances of *Pinus pinaster* (Saur et al. 1993, 1995), *Eucalyptus microtheca* (Prat and Fathi-Ettai 1990, Morabito et al. 1994, Farrell et al. 1996), and *Taxodium distichum* (Allen et al. 1994*b*).

Most fruit trees are sensitive to salinity including *Malus domestica*, *Prunus armeniaca*, *Pyrus* spp., *Prunus domestica*, *Prunus persica*, and *Citrus* spp. *Olea europaea* and *Ficus* spp. are moderately tolerant but *Phoenix dactylifera* is very tolerant (McKersie and Leshem 1994, Gucci et al. 1997). There are wide variations in tolerance of rootstocks to salinity (Walker and Douglas 1982, Behboudian et al. 1986). For example, salt tolerance of six citrus rootstocks varied appreciably. Salinity inhibited growth most in *Citrus jambhiri* hybrid or variant and *Poncirus trifoliata*. Growth was reduced least in *Citrus aurantium* and *C. reshni*. *Citrus jambhiri* and *C. paradisi* × *P. trifoliata*, and *C. sinensis* × *P. trifoliata* exhibited intermediate tolerance (Zekri and Parsons 1992). Salt-sensitive species sometimes accumulate toxic amounts of salts over a long period of time, even from soils considered to be nonsaline (Bernstein 1980).

Plant responses to salinity

Injury Salinity adversely affects nonhalophytes by inducing injury, inhibiting growth, altering plant morphology and anatomy, often as a prelude to tree mortality (Moss 1940, Ehlig and Bernstein 1958, Holmes 1961, Holmes and Baker 1966, Hofstra and Hall 1971, Waisel 1972, Dirr 1976, Sucoff et al. 1976, Downton 1977*b*, Ogden 1980, Strzyszcz 1981, Shaw et al. 1982, Fraser 1983, Kozlowski 1986, Blood et al. 1991, Pedersen 1993, Kozlowski and Pallardy 1997*b*, pp 271-277). Injury is more severe when salts absorbed from the soil are augmented by salts deposited on leaves.

Injury is induced not only by the osmotic effects of salts but also by specific toxic effects resulting from the accumulation of Cl^- and Na^+. Levitt (1980) summarized evidence for nonosmotic effects of salinity on injury to plants as follows: (1) organic solutes do not injure plants at osmolalities higher than the critical concentrations for salt injury, (2) individual salts have different critical concentrations for inducing injury, (3) certain organic solutes increase the critical salt concentration for injury, and (4) injurious effects of salts are antagonized by Ca^{2+}.

Both Cl^- and Na^+ may cause injury, but symptoms of Cl^- injury usually appear first. Chloride injury develops as marginal chlorosis of leaves of broad-leaved trees, followed by extensive scorching of leaf blades (Harding et al. 1958, Pandey and Divate 1976, Klincsek 1994). Sodium accumulation in leaves is typified by leaf mottling and necrotic patches (Schaffer et al. 1994) or by tipburn (McKersie and Leshem 1994), or both. Salt injury to leaves often is followed by leaf shedding and twig dieback (Lumis et al. 1973, Sucoff et al. 1976).

In *Citrus*, the exclusion of Na^+ and Cl^- ions occurs continuously and progenies separate widely on the basis of their capacity to restrict foliar accumulation of these ions (Sykes 1992). Townsend (1980, 1983) reported wide variations in salt injury to 2-year-old woody plants grown in solution culture. *Cornus florida* and *Platanus occidentalis* sustained most foliar injury, followed in order by *Quercus palustris*, *Gleditsia triacanthos*, *Pinus strobus*, and *Sophora japonica*. Injury appeared first as yellowing of leaf tips followed by yellowing and browning in several species. *Cornus florida* leaves also developed a purplish color. Further injury was characterized by interveinal chlorosis and necrosis. Symptoms of salt injury in *Casuarina inophloia* were visible at a leaf chloride concentration of 17.8 mg g^{-1} and a sodium concentration of 12.9 mg g^{-1}; leaf necrosis on *Eucalyptus* species growing in saline soil occurred at an average chloride concentration of 10.6 mg g^{-1} dry weight (Rogers 1985). *Kandelia cordel* seedlings grew at salinities up to 260 mM (best growth was at 85 mM), but growth was inhibited by salinities > 340 mM. As salinity was increased, Na replaced K to a large extent in all tissues. Chloride was the major balancing anion in all tissues (Hwang and Chen 1995*a*, 1995*b*).

Salinity injures cell membranes and increases solute leakage (Hautala et al. 1992). The effects of NaCl on membrane leakage are counteracted by Ca^{2+} (Leopold and Willing 1984, Cromer et al. 1985). Collapse of mesophyll cells is a feature of NaCl toxicity in pines (Stewart et al. 1973). Application of NaCl to foliage of *Thuja occidentalis* and *Picea glauca* induced fragmented cuticles, disrupted stomata, collapsed cell walls, coarsely granulated cytoplasm, disintegrated chloroplasts and nuclei, and disorganized phloem.

Seed germination In both nonhalophytes and halophytes, salinity reduces the total number of seeds germinating and postpones initiation of germination processes; however, within each group the responses are variable and species specific (Ungar 1982, 1991). Salinity influences seed germination primarily by lowering the osmotic potential of the soil solution sufficiently to retard water absorption by seeds (Khan and Ungar 1984), but also by toxicity to the embryo (Zekri 1993). Differences in germination of *Eucalyptus camaldulensis* seeds from three sites in Australia were attributed to variations in tissue tolerances to Na^+ or Cl^-, or both (Sands 1981). Seeds of many halophytes accumulate less than 10% of the ionic content present in shoots, indicating that they possess a mechanism for preventing excess ion accumulation in the embryo (Ungar 1991).

Seed germination of many nonhalophytes may be inhibited by 0.5% salt, whereas some halophytes can grow in soils containing 20% salt, although most halophytes grow in soils with 2 to 6% salt (Strogonov 1964). Seeds of many halophytes not only retain viability for a long time when exposed to strong

salt solutions, but also germinate readily after the salt stress is relieved (Woodell 1985). Seeds of several species of *Tamarix* germinate in the presence of high concentrations of salt (Waisel 1960).

There are many examples of inhibition of seed germination by salinity (Bangash 1977, Ladiges et al. 1981, Clemens et al. 1983, Agami 1986, Totey et al. 1987, Arce et al. 1990, Hooda and Yamadigni 1991, Zekri 1993, Perez and Moraes 1994). Salt-induced inhibition of germination can sometimes be partially alleviated by exogenous kinetin (10 and 20 ppm) and gibberellin (17 ppm). However, the growth regulators have no effect on germination at high salt concentrations (> 400 mM NaCl).

Vegetative growth Salinity reduces vegetative and reproductive growth of nonhalophytes (Table 5). Combined flooding and salinity typically decrease growth and survival more than does either stress alone (Van der Moezel et al. 1988, 1991, Marcar et al. 1993, Noble and Rogers 1994). In contrast to the effect of flooding with fresh water, flooding with saline water typically inhibits shoot growth more than root growth (e.g., Jarrell and Virginia 1990). An exception is *Atriplex* spp. in which root growth is reduced more than shoot growth by flooding with salt water (Osmond et al. 1980). Unlike nonhalophytes, some halophytes grow well even when their roots are exposed to high salinity. Dry weight increases of *Avicennia marina*, *Rhizophora stylosa*, and *Aegiceros* were greatest in 25% seawater (Clough 1984, Burchett et al. 1989).

Salinity reduces shoot growth by suppressing leaf initiation and expansion as well as internode growth and by accelerating leaf abscission (e.g., Ziska et al. 1990, Zekri 1991). The decrease in growth is related to the chloride content of the leaves (Shortle et al. 1972). Salinity induces early leaf shedding in both angiosperms (Dragstad 1973) and gymnosperms (e.g., Ehlig and Bernstein 1959, Dragstad 1973).

Growth of salt-tolerant *Olea europaea* plants flooded with saline water for 4 weeks recovered readily when salinization was relieved. The rate of recovery depended on the salt concentration to which the plants had been exposed (0, 50, 100, or 200 mM NaCl). Growth was inhibited by all salt solutions but growth rates of plants treated with 50 or 100 mM NaCl returned to the rates of control plants within 4 weeks of relief from flooding. Plants exposed to 200 mM NaCl recovered to only 60% of the growth rate of control plants after 4 weeks (Tattini et al. 1995).

Reproductive growth Salinity adversely influences several aspects of reproductive growth, including flowering, pollination, fruit development, yield and quality, and seed production (Lumis et al. 1973, Waisel 1991, Shannon et al. 1994). Reproductive growth of *Citrus* is particularly sensitive to saline flooding (Bernstein 1969, Heller et al. 1973, Hoffman et al. 1984).

High salinity in irrigation water reduced flowering intensity, fruit set, number of fruits, and fruit growth of *Citrus sinensis* (Cole and McLeod 1985, Howie and Lloyd 1989). Fruit yield was correlated with canopy leaf area for both salinity treatments. Because the inhibitory effect of salinity on fruit growth was not apparent during the late stages of fruit development,

Table 5. Species showing growth reduction following exposure to salinity.

Species	Source
ANGIOSPERMS	
Acacia spp.	Craig et al. (1990)
Acacia nilotica	Nabil and Coudret (1995)
Acacia saligna	Shaybany and Kashirad (1978)
Acer rubrum	Dochinger and Townsend (1979)
Acer saccharum	Shortle et al. (1972)
Amorpha fruticosa	Ling (1981)
Citrus spp.	Bernstein (1969)
	Zekri (1991, 1993)
Cornus florida	Townsend (1980)
Eucalyptus spp.	Aoki et al. (1973), Sheikh (1974)
	Blake (1981), Sands (1981)
	Prat and Fathi-Ettai (1990)
	Van der Moezel et al. (1991)
	Fernando (1992)
	Marcar et al. (1993)
	Dunn et al. (1994)
	Morabito et al. (1994)
Fragaria spp.	Ehlig and Bernstein (1958)
Kandelia candel	Hwang and Chen (1995*a*)
Kochia prostrata	Francois (1976)
Leucaena leucocephala	Ali et al. (1987)
	Gorham et al. (1988)
Melaleuca ericifolia	Ladiges et al. (1981)
Melaleuca spp.	Van der Moezel et al. (1991)
Olea europaea	Tattini et al. (1995)
Platanus occidentalis	Townsend (1980)
Populus euphratica	Liphschitz and Waisel (1970*b*)
	Sheikh (1974)
Prosopis glandulosa	Jarrell and Virginia (1990)
Psidium quajava	Walker et al. (1979)
Sonneratia alba	Ball and Pidsley (1995)
Ulmus pumila	Smirnov (1981)
Vitis species	Groot Obink and Alexander (1973)
	Pandey and Divate (1976)
	Downton (1977*a*, *b*)
	West and Taylor (1984)
GYMNOSPERMS	
Cryptomeria japonica	Aoki et al. (1973)
Picea abies	Pedersen (1993)
Pinus aristata	Townsend and Kwolek (1987)
Pinus banksiana	Townsend and Kwolek (1987)
Pinus cembra	Townsend and Kwolek (1987)
Pinus densiflora	Yoshida (1972)
	Townsend and Kwolek (1987)
Pinus nigra	Townsend and Kwolek (1987)
Pinus parviflora	Townsend and Kwolek (1987)
Pinus peuce	Townsend and Kwolek (1987)
Pinus pinaster	Saur et al. (1993, 1995)
Pinus ponderosa	Townsend and Kwolek (1987)
Pinus resinosa	Townsend and Kwolek (1987)
Pinus strobiformis	Townsend and Kwolek (1987)
Pinus strobus	Townsend and Kwolek (1987)
	Townsend (1983)
Pinus thunbergii	Yoshida (1972)
	Townsend and Kwolek (1987)
Taxodium distichum	Allen et al. (1994*a*, 1994*b*, 1996)

fruits on trees irrigated with 20 mol m^{-3} NaCl eventually grew to the same size as fruits on trees irrigated with 5 mol m^{-3} NaCl but they reached this size later (Howie and Lloyd 1989). Yield of *Citrus paradisi* fruits was linearly related to the chloride concentration in the soil solution above a threshold value of 4.5 meq l^{-1} (Bielorai et al. 1978).

Growth of *Psidium guajava* fruits on salt-treated plants lagged behind controls during early fruit enlargement; however, in the later stages, salinity advanced fruit ripening by 1 to 3 weeks but fruit weights were reduced (Walker et al. 1979). Salinity also decreased the size of *Fragaria* fruits (Ehlig and Bernstein 1958). Salinity reduced flowering intensity, fruit retention, number of fruits at harvest, and fruit size of *Prunus salicina* (Hoffman et al. 1989). Salinity reduced the number of fruiting forms initiated in *Gossypium hirsutum*, number of bolls maturing, weight of seeds and lint per boll, and fiber length (Longenecker 1973, 1974).

Salinity in irrigation water often negates the positive effects of regulated deficit irrigation (RDI) on reproductive growth. Regulated deficit irrigation involves withholding irrigation during the period of rapid shoot elongation to prevent excessive vegetative growth that could inhibit reproductive growth (Kozlowski and Pallardy 1997*b*, pp 410–411). Under nonsaline conditions, RDI usually reduces vegetative growth of fruit trees while maintaining or even increasing fruit size and yield (Chalmers et al. 1981, Mitchell et al. 1986, 1989). However, under saline conditions, restricted irrigation of *Prunus persica* resulted in reduced vegetative growth, small fruits and lowered yield as well as increased uptake of sodium and chloride ions (Boland et al. 1993, 1996).

Morphological and anatomical changes Salinity often alters the morphology and anatomy of woody plants. Chloride ions from sea salt altered the growth form and injured leaves of *Quercus lobata* and *Q. agrifolia* up to 60 km inland (Ogden 1980). Leaves of plants that grow on saline soils often are thicker and more succulent than those of trees growing on salt-free soils (Boyce 1954, Gates 1972, Waisel 1991, Shannon et al. 1994). The epidermal cell walls and cuticles of leaves of salinized plants also are thicker. By increasing the internal surface area per unit of leaf surface, leaf succulence may increase CO_2 absorption per unit of leaf area (Shannon et al. 1994).

Increase in leaf thickness in response to salinity has been attributed to an increase in number of mesophyll cell layers or cell size, or both. In salinized *Gossypium hirsutum* plants, the leaves were thicker because the number of cell layers increased and the mesophyll cells were larger, whereas in *Citrus*, increase in the size of spongy mesophyll cells, rather than an increase in cell layers, accounted for thicker leaves (Zekri and Parsons 1990). The large cells of leaves of salinized plants result from increased cell wall extensibility together with higher turgor pressures (Strogonov 1964, Jennings 1976, Munns and Termaat 1986).

Salinity not only inhibits the rate of cambial growth but also influences the anatomy of cambial derivatives. For example, the xylem of salt-treated *Populus euphratica* trees was ring-porous rather than typically diffuse-porous (Liphschitz and Waisel 1970*b*). The xylem vessels of halophytic trees are more numerous and narrower than those in mesophytic trees (Strogonov 1964). Following exposure of *Aesculus hippocastanum* trees to salinity, the number of xylem vessels increases and their size decreases. Salinity also increases production of fibers and calcium oxalate crystals in the bark (Eckstein et al. 1976). After exposure to salinity, the xylem increments in salt-tolerant *Salix* clones are wider with fewer vessels and more fibers and rays per unit area than in salt-sensitive clones (Eckstein et al. 1978).

Salinity often promotes suberization of the hypodermis and endodermis in roots, with formation of a well-developed Casparian strip closer to the root apex than is found in nonsalinized roots (Walker et al. 1984). The walls of root cells of salinized plants often are unevenly thickened and convoluted (Shannon et al. 1994).

Physiological responses

Salt-induced slowing of plant growth is accompanied by a variety of metabolic dysfunctions in nonhalophytes, including inhibition of enzymatic activity (Levitt 1980, Kaiser et al. 1988), photosynthesis (Downton 1977*a*, Ziska et al. 1990), absorption of minerals (Dutt et al. 1991), protein and nucleic metabolism (Bar-Nun and Poljakoff-Mayber 1977), and respiration (Boyer 1965, Kleinkopf and Wallace 1974, Kalir and Poljakoff-Mayber 1976). Addition of NaCl to mitochondria isolated from leaves of a nonhalophyte (*Pisum sativum*) and a halophyte (*Suaeda maritima*) appreciably reduced the rate of O_2 uptake by both species (Flowers 1974). Salinity affects synthesis of carbohydrates as well as transport of photosynthetic products and their utilization in production of new tissues. In many halophytes, important physiological processes are stimulated or not appreciably altered by salt concentrations that inhibit these processes in nonhalophytes (Levitt 1980).

Enzymatic activity Salinity inhibits the *in vitro* activity of many enzymes (Greenway and Munns 1980, Blum 1988). Most enzymes of halophytes (except membrane-bound ATPase) are as sensitive to salinity as the enzymes of nonhalophytes (Larcher 1995). Isolated enzymes from many halophytes lose approximately half of their activity at salt concentrations approximating those in leaf cells (Osmond and Greenway 1972, Flowers et al. 1977, Billard and Boucard 1982).

Gas exchange Salinity reduces the rate of photosynthesis of both nonhalophytes and halophytes (e.g., Downton 1977*a*, Bedunah and Trlica 1979, Walker et al. 1979, Cornelius 1980, Walker et al. 1981, 1982, Ball and Farquhar 1984, Pezeshki and Chambers 1986, Pezeshki et al. 1987, 1988, 1989, Ziska et al. 1990, Lin and Sternberg 1992, Golombek and Lüdders 1993, Tattini et al. 1995, Mickelbart and Marler 1996). Although both stomatal and nonstomatal factors have been implicated in the reduction of photosynthesis following flooding with saline water, most of the reduction in photosynthetic rates is the result of nonstomatal effects. In the long term, total photosynthesis is reduced as a result of inhibition of leaf formation and expansion as well as early leaf abscission (Kozlowski and Pallardy 1997*b*).

Following irrigation of *Fraxinus pennsylvanica* seedlings with low concentrations of salt solution, the leaves progressively dehydrated, causing partial stomatal closure and decreased CO_2 absorption. However, after plants were flooded with high concentrations of salt solution, photosynthetic inhibition was attributed to ion toxicity, membrane disruption, and complete stomatal closure (Pezeshki and Chambers 1986). For the first few days after flooding of *Ficus carica* plants with salt solution, stomatal conductance was reduced but the rate of photosynthesis was not appreciably altered; however, longer-term salinity treatment greatly inhibited the rate of photosynthesis by nonstomatal effects (Golombek and Lüdders 1993). Despite parallel reductions in stomatal conductance and photosynthesis in flooded *Taxodium distichum* seedlings, the leaf internal CO_2 concentrations were relatively stable over a range of salt concentrations in the floodwater. The salinity of floodwater caused excessive accumulation of several ions (Na, K, Ca, and Mg) in the leaves and this increase in leaf ionic content was considered to be the primary cause of the saline-induced reduction in photosynthetic rates (Pezeshki et al. 1987). A decline in photosynthetic rate of *Prunus salicina* flooded with saline water was associated with increases in leaf chloride content and declines in 1,5-bisphosphate carboxylase activity and the pool sizes of triosephosphate, ribulose 1,5-bisphosphate and phosphoglycerate (Ziska et al. 1990). In many plants, salinity lowers the efficiency of the electron transport chain and injures the light harvesting complex (Banuls et al. 1990, Banuls and Primo-Millo 1992, Brugnoli and Björkman 1992).

Protein metabolism Salinity decreases protein synthesis and increases its hydrolysis in some plants, resulting in production of amino acids. Salts have antagonistic effects on proteins: (1) breaking of electrostatic bonds and (2) increasing hydrophobic interactions (Melander and Horvath 1977). Strogonov (1964) reported that amino acids that accumulate in response to salinity are toxic in the following order: serine and valine > tyrosine > isoleucine > leucine > threonine > lysine > and proline.

Mineral nutrition Salinity often upsets the nutritional balance of plants by one or more mechanisms including osmotic effects of salts, competitive interactions among ions in the substrate, and effects on membrane selectivity. As root elongation slows, the amount of ions reaching the roots by diffusion decreases (Kuiper 1984). High concentrations of Cl^- reduce NO_3^- uptake by plants (Guggenheim and Waisel 1977), and high concentrations of NO_3^- inhibit phosphate uptake (Lamaze et al. 1987). Salinity decreases uptake of K, Ca, and Mg in phylloclades of *Casuarina equisetifolia* (Dutt et al. 1991).

Hormones Salinity promotes senescence of plant tissues by increasing the production of ABA and ethylene (Kefu et al. 1991, Zhao et al. 1992). Salt decreases the cytokinin concentration in roots and shoots of salt-resistant plants but not of salt-sensitive plants (Kuiper et al. 1990). However, the effects of NaCl on salt-sensitive plants do not appear to be mediated by cytokinins because growth reduction precedes the change in cytokinins.

Mechanisms of growth inhibition

The mechanisms by which salinity inhibits plant growth have eluded precise characterization, although there has been considerable success in describing their physiological manifestations (Cheeseman 1988). Over the years emphasis has been placed on three aspects of the physiological effects of salinity on plant growth: (1) turgor regulates stomatal conductance and cell expansion, thereby affecting growth of plants in soils of low water potential, (2) plant growth is limited by a lowered rate of photosynthesis, and (3) excessive uptake of salts affects production of a specific metabolite that directly inhibits growth. The mechanisms of short- and long-term inhibition of shoot growth by salinity may vary. Munns and Termaat (1986) suggested that early growth inhibition was traceable to water stress rather than a specific toxic effect of salt. Hence the water status of roots might regulate shoot growth through a hormonal system, especially one involving ABA. Support for this view comes from the observation that inhibition of leaf expansion by salt occurred after 1 min (Yeo et al. 1991). An opposing view is that nutrition of the shoot apical meristem may be disturbed and the shoot meristem may provide the inhibitory signal to expanding leaves (Lazof and Läuchli 1991). Inhibition of shoot growth after weeks to months of salinization has been attributed to excessive salt accumulation in leaves, resulting in a water deficit in the symplast, and to toxic ionic effects (Rengel 1992).

Munns (1993) concluded that the absorbed salts do not directly control growth by influencing turgor, photosynthesis, or activity of a specific enzyme. While emphasizing the complexity of salinity effects, she developed a model that incorporates a two-phased plant growth response to salinity: growth is first reduced by a decrease in soil water potential (a water stress effect), and later a specific effect appears as salt injury in the old leaves, which die because of a rapid increase of salt in cell walls or cytoplasm when vacuoles can no longer sequester incoming salts. Munns (1993) proposed that accumulation of salt in the old leaves accelerated their death, and loss of these leaves decreased the supply of carbohydrates or growth hormones to meristematic regions, thereby inhibiting growth.

Adaptations to salinity

Woody plants may adapt to salinity by variously tolerating or avoiding salt, or both. Most highly salt-tolerant halophytes withstand high tissue salt concentrations (Gorham 1996) largely through osmotic adjustment (Bernstein 1961, Epstein 1980, Wyn-Jones 1984, Waisel 1991, McKersie and Leshem 1994, Gucci et al. 1997). The absorbed salts typically are sequestered in vacuoles, hence reducing the salt concentration to which the cytoplasm and chloroplasts are exposed (Shannon et al. 1994, Larcher 1995). In some plants, osmotic adjustment results from synthesis in the cytoplasm of compatible organic solutes (including proline, glycine, betaine, and other amino acids in addition to sugars). The cytoplasm often contains high concentrations of organic compounds that counterbalance the high salt concentrations in the vacuoles but do not inhibit the functioning of enzymes and membranes (Hanson and Hitz

1982). Gucci et al. (1997) did not find major differences in capacity of *Olea europaea* cultivars Frantiol (salt tolerant) and Leccino (salt sensitive) to accumulate mannitol or soluble carbohydrates in response to salinity stress. Osmotic adjustment in both cultivars occurred primarily because of accumulation of inorganic ions. Differences in water relations of these cultivars were attributed to variations in their exclusion capacities for Na^+ and Cl^- ions. Because osmotic adjustment involves physiological maintenance costs associated with synthesis of solutes, ion transport, and repair of cell structures (Yeo 1983, Stavarek and Rains 1985), there is an associated decrease in plant growth (Van Volkenburgh and Boyer 1985).

Although most salt-tolerant halophytes and nonhalophytes respond to saline stress by osmotic adjustment, there are exceptions including some halophytes (e.g., *Suaeda maritima*) that grow faster as salinity increases (Clipson et al. 1985) and some plants that can adapt to salinity if exposed to low concentrations of salinity. For example, unadapted *Atriplex nummularia* cell cultures show a dose-dependent inhibition of dry weight increase in the presence of 50–350 mM NaCl. Cells adapted to 342 or 428 mM NaCl are capable of sustained growth in the presence of salt. Turgor of NaCl-adapted cells is similar to that of cells of unadapted plants, indicating that the cells do not respond to salt by osmotic adjustment (Casas et al. 1991).

Salt avoidance mechanisms may involve passive salt exclusion, active salt extrusion, or dilution of salt as it enters a plant (Kozlowski and Pallardy 1997*b*). Application of the growth inhibitor paclobutrazol promoted avoidance of salt stress in *Prunus persica* by reducing uptake and accumulation of Na^+ and Cl^- in plant tissues (Abou El-Khashab et al. 1997). Most halophytes appear to tolerate salinity primarily by excluding Na^+, Cl^-, and other ions from leaf tissues (Greenway and Munns 1980, Allen et al. 1994*a*, Ashraf 1994). Certain plants release excess salt through salt glands. Such glands are well known in *Tamarix* and in mangrove species, including species of *Aegialitis*, *Aegiceras*, *Avicennia*, and *Laguncularia*. Salts are either eliminated into the vacuoles of glands or secreted to the outside of the secretory cells. Although glands excrete mostly NaCl, other ions (e.g., potassium, calcium, magnesium, sulfate, phosphate, and various organic solutes) have been found in the excreted solutions (Waisel 1972). The release of salt through glands is influenced by the salt concentration of the growth medium, light, temperature, oxygen pressure, and inhibitors of metabolism (Fahn 1979, Liphschitz and Waisel 1982, Fahn 1988).

Because differences in resistance of fruit trees to salinity are often associated with variable salt exclusion by roots, scions are grafted on salt-excluding rootstocks (Blum 1988). For example, avocado scions grafted on Mexican rootstocks were less salt-tolerant than scions on Guatemalan stocks because of differences in Cl^- exclusion. The less tolerant trees contained high concentrations of chloride in their leaves (Downton 1978). Variations among citrus rootstocks in resistance to salinity are well known (Walker and Douglas 1982, Behboudian et al. 1986) and traceable to variations in salt exclusion (Blum 1988). Rootstocks of *Vitis* spp. vary greatly in their capacity for reducing the chloride concentration in scions (Downton 1977*b*). Use of salt-resistant rootstocks has contributed greatly to commercial production of grapes (Downton 1984).

As the leaves of some plants (e.g., *Rhizophora mucronata*) grow, they maintain a rather constant salt concentration by dilution, achieved by absorption of enough water to prevent an increase in salt concentration (Levitt 1980). Another dilution mechanism occurs in *Atriplex* species. The leaf cells enlarge sufficiently, because of an increase in water content, to prevent an excessively high concentration of salt in the cell sap (Repp 1958). *Atriplex* also possesses leaf bladders that accumulate salt and later collapse to release salt solution or they are shed (Osmond et al. 1969, Waisel 1991). Bladders of *Atriplex confertifolia* contain up to 18% of their dry weight as Na^+ (Breckle 1974).

Some halophytes possess mechanisms for both salt tolerance and avoidance. For example, Waisel et al. (1986) concluded that *Avicennia marina* has three mechanisms of salt resistance: (1) salt exclusion by low permeability of roots to salts, (2) salt tolerance, and (3) release of salt through glands. Many plants adapt to salinity by more than one mechanism, and these tolerance mechanisms interact. Thus, adaptation to salinity is determined by the integrated effects of several mechanisms (Gorham 1996).

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