



Roots and Root Systems

INTRODUCTION

The size of root systems has been studied extensively and described by Weaver (1920, 1926), Weaver and Bruner (1927), and others in the United States and by Kutschera (1960) in Europe. However, the physiology of roots received less attention until recently, at least partly because they are usually underground and more difficult to study. Nevertheless, even casual consideration of their functions indicates that physiologically vigorous root systems are as essential as vigorous shoots for successful plant growth because root and shoot growth are so interdependent that one cannot succeed without the other. We will discuss briefly the functions of roots, root growth and structure, and development of root systems in relation to water and mineral absorption in this chapter. Knowledge of root structure is important because it affects the pathway and resistance to water and solute movement, while the extent of root systems affects the volume of soil available as a source of water and mineral nutrients. Much research on factors affecting root growth and root functioning is summarized in books edited by McMichael and Persson (1991) and Waisel *et al.* (1991), in papers by Epstein (in Hashimoto *et al.*, 1990), Feldman (1984), and Zimmermann *et al.* (1992), and in a review by Aesbacher *et al.* (1994), and some of the more important and interesting topics are discussed in this chapter.

FUNCTIONS OF ROOTS

The functions of roots include anchorage, the absorption of water and mineral nutrients, synthesis of various essential compounds such as growth regula-

tors, and the storage of food in root crops such as sugar beet and cassava (*Manihot*, spp.).

Anchorage

The role of roots in anchorage often is taken for granted, but it actually is very important because the success of most land plants depends on their ability to stand upright. For example, part of the success of the Green Revolution resulted from development of cereal crops with short, stiff stems that resist blowing over by wind and rain (lodging), but stiff stems are useless unless they are firmly anchored in the soil by vigorous root systems. The mechanical strength of roots also is important in preventing overthrow of trees by wind and winter injury to crops such as winter wheat by frost heaving. Resistance to uprooting by grazing animals may also be important for small herbaceous pasture plants. Roots also increase the stability of soil on slopes (Hellmers *et al.*, 1955). Coutts (1983) discussed the relationship between tree stability and their root systems, and Ennos *et al.* (1993) and Crook and Ennos (1993) studied the mechanics of root anchorage and pointed out that resistance to lodging in maize and wheat is improved by increased spread and bending strength of roots.

Roots as Absorbing Organs

The importance of deep, wide spreading root systems for absorption of water and minerals cannot be overemphasized and is discussed later in this chapter and in Chapter 6.

Synthetic Functions

Root cells possess many of the synthetic functions of shoot cells and some aerial roots even produce functional chloroplasts. Flores *et al.* (1993) cited examples of photosynthesis in aerial roots of orchids and mangroves and reported that roots of several genera of *Asteraceae* and *Orchidaceae* can become adapted to photoautotrophy in solution culture by exposure to light and high concentrations of CO₂. According to Johnson *et al.* (1994), phosphorus deficiency stimulates dark fixation of CO₂ in proteoid roots of lupine and increases production of citrate and its secretion into the rhizosphere where it increases the availability of phosphorus. Bialzyk and Lechowski (1992) observed significant absorption of CO₂ from the root medium and transport of carbon compounds from roots to shoots in tomato.

Most roots are dependent on shoots for thiamin and sometimes for niacin and pyridoxine, and receive auxin from the shoots. The nitrogen-fixing role of *Rhizobium* bacteria in root nodules is important and the activities of microorganisms in the rhizosphere may also be important (Box and Hammond, 1990; Curl and Truelove, 1986; Wild, 1988, pp. 526–530). The role of fungi

causing mycorrhizal infection and the effects of pathogenic fungi are discussed later.

Nicotine is synthesized in the roots of tobacco and is translocated to the shoots, and tobacco shoots grafted on tomato root systems contain no nicotine (Dawson, 1942). Ammonia also is converted to organic compounds in roots, but in most species much of the nitrate is translocated to the shoots and reduced. According to a review by Oaks (1992), nitrate reduction in roots differs in legumes and cereals because legume roots export asparagine to their shoots, but cereals do not. Biles and Abeles (1991) found peroxidases and other proteins synthesized in the roots in the xylem sap of several species of plants. According to Rao (1990), flavonoids produced in roots protect them against pests such as fungi and nematodes and have allelopathic effects.

It was suggested long ago that roots probably synthesize hormones essential for shoots (e.g., Went, 1943). Among these are cytokinins (Kende, 1965; Skene in Torrey and Clarkson, 1975), gibberellins (Skene, 1967), and abscisic acid (Davies and Zhang, 1991). It has been suggested that reduced shoot growth of plants whose roots have been subjected to stress such as deficient soil water, deficient aeration, high salinity, or low temperature is caused at least in part by a change in the amount and kind of growth regulators supplied from the roots (Blum *et al.*, 1991; Davies and Zhang, 1991; Itai and Vaadia, 1965; O'Leary and Prisco, 1970; Skene in Torrey and Clarkson, (1975). However, Jackson *et al.* (1988) claimed that stressed pea roots are not a source of excess abscisic acid (ABA) and Munns (1990) argued against ABA as a chemical signal. In contrast, Khalil and Grace (1993) reported that when one-half of a split root system of sycamore maple was water stressed there was a large increase in ABA in the drying roots and the xylem sap, and a decrease in stomatal conductance in the shoots. Of course these stresses are likely to also reduce the supply of water and minerals, which likewise reduces shoot growth. The relative importance under field conditions of decreased absorption of water and minerals versus changes in root metabolism and in the supply of hormones to the shoots deserves further study (McIntyre, 1987). Gowing *et al.* (1993) discuss the current state of knowledge concerning the production and response to ABA.

Roots as Sensors of Water Stress

In recent years considerable attention has been given to the possibility that roots of plants in drying soil function as primary sensors of water stress. According to this view, as the soil dries changes in root metabolism such as a decrease in cytokinin production, an increase in ABA production, and a disturbance of nitrogen metabolism send biochemical signals to the shoots that produce physiological changes such as a decrease in growth, stomatal conductance, and rate of photosynthesis, regardless of the water status of the leaves. The root sensor effect has been demonstrated in pot experiments with split root

systems (Khalil and Grace, 1993), with roots in pressure chambers (Davies *et al.*, 1986; Passioura, 1988a; Schulze, 1986a; Turner, 1986 and others), and with maize under field conditions (Tardieu *et al.*, 1991). Tardieu *et al.* (1991) reported that in the field the entire root system of maize must be in dry soil before the ABA concentration in the xylem sap increases.

Under field conditions in areas with adequate rainfall and many sunny days shoots of plants often are subjected to water stress even though the roots are in moist soil. Examples are the curling of leaves of corn plants in moist soil and the midday water stress in flooded rice reported by Tazaki *et al.* (in Turner and Kramer, 1980). It therefore seems doubtful if roots usually are primary sensors of water stress under those conditions (Kramer, 1988), although opposing arguments are presented by Zhang and Davies (1990), Davies *et al.* (1990), and Tardieu *et al.* (1991). Davies and Zhang (1991) and Davies *et al.* (1994) have good reviews of the role of roots as sensors.

Experiments of Kitano and Eguchi (1992a,b) seem to demonstrate that a change in shoot water status can directly affect stomatal conductance. Cramer and Bowman (1991) approached this problem by comparing leaf elongation of intact maize plants and shoots from which the roots have been removed, when placed in a saline solution. The short-term response of leaves on shoots without roots was similar to that on shoots with roots. This led them to conclude that signals from roots are not necessary for the occurrence of short-term reduction of leaf elongation by high salinity in maize. Day *et al.* (1991) reported that chilling one-half of a split root system of *Pinus taeda* did not decrease photosynthesis, suggesting that no nonhydraulic signal originated in the chilled roots.

Of course as the soil dries both roots and shoots dehydrate, altering the biochemistry in both and changing the biochemical and hydraulic communications between them. This makes it difficult to determine the relative importance of chemical and hydraulic messages. This topic is discussed again in Chapters 6 and 9.

ROOT GROWTH

Root growth results from cell division and the pressure developed by enlargement of newly formed cells. Cell enlargement is discussed in Chapter 11 and root growth at the cellular level is discussed by Barlow in Gregory *et al.* (1987). Bret-Harte and Silk (1994) question how sufficient carbon for growth reaches root meristems, which are several millimeters beyond the termination of the phloem. The older portions of roots are anchored in the soil and the tips are pushed forward through the soil by cell enlargement at rates of a few millimeters to a few centimeters daily, often following a tortuous path of least resistance through crevices and around pebbles and other obstructions. Generally, root tips tend to return to their original direction of growth after passing around

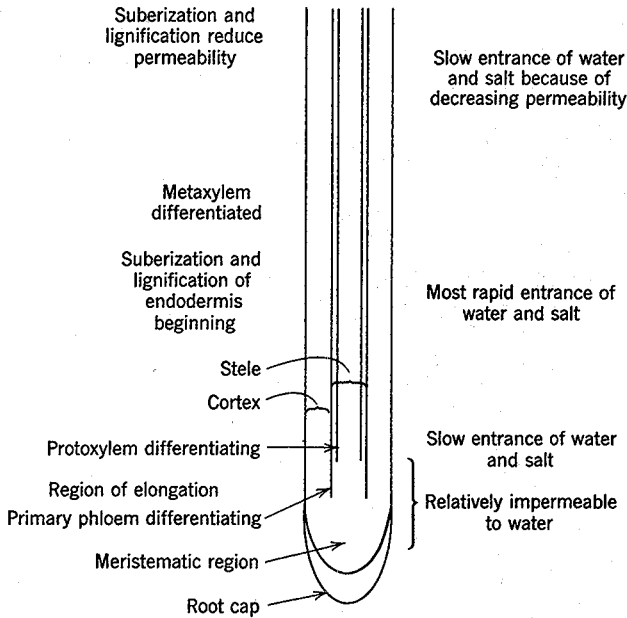


Figure 5.1 The location of primary tissues in an elongating root and relative amounts of absorption at various distances behind the apex. The distance from the apex at which various stages of maturation occurs depends on the species and the rate of root elongation. According to McCully and Canny (1988) the metaxylem of maize and soybean roots becomes capable of significant water conduction 15 to 30 cm behind the root apex. From Kramer (1983).

obstacles, a characteristic observed in the 19th century by Darwin and others, which is known as exotropy (Wilson, 1967). Despite numerous temporary deflections, branch roots of many plants tend to grow outward for a time before turning downward (Wild, 1988, p. 121 and Fig. 5.11). The cause of this change in sensitivity of roots to gravity deserves more study.

During growth and maturation roots undergo changes in anatomy at various distances behind the apex that affect the permeability to water and solutes. The approximate order of maturation of tissues is indicated in Fig. 5.1, but the length of the various zones varies widely, depending chiefly on the species and the rate of growth. In slowly growing roots, differentiation of new tissues occurs much closer to the root tips than in rapidly growing roots (Peterson and Perumalla, 1984). A diagram of a cross section through a fully differentiated dicot root is shown in Fig. 5.2, and a scanning electron micrograph of a cross section of a young barley root is shown in Fig. 5.3.

Enlarging roots often develop pressures sufficient to lift sidewalks and crack masonry walls, as many readers must have noted. Clark (1875) discussed a

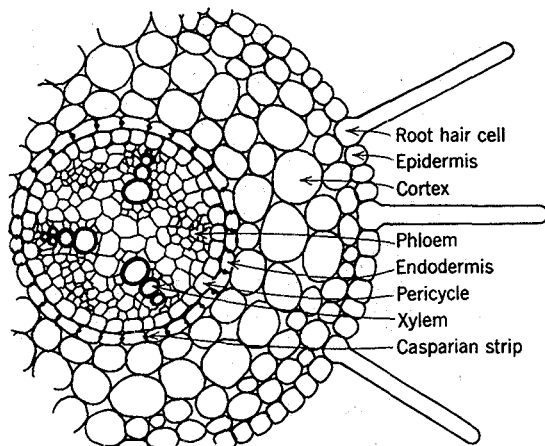


Figure 5.2 Cross section through a squash root in the region where salt and water absorption occur most rapidly. The endodermal cell walls usually become much thickened, except for passage cells opposite the xylem which often remain unthickened. The pericycle usually gives rise to branch roots and the cork cambium found in older roots. From Kramer (1983), after Crafts and Broyer (1938).

number of examples of the pressure developed by growing roots and described an experiment in which a growing squash fruit supported 5000 lb. Gill and Bolt (1955) also presented some data on the pressures developed by growing roots. Dr. Richter (Private communication) found that enlargement of tap roots and large branch roots of pine compresses the soil in their immediate vicinity sufficiently to increase its bulk density. This might decrease infiltration of water around the base of tree trunks. It seems possible that the large number of roots produced beneath grasses (Dittmer, 1937; Pavlychenko, 1937) might temporarily reduce the pore space, but their death and decay would soon increase it. The effect of root growth on soil bulk density deserves further investigation.

Epidermis and Root Hairs

The epidermis and associated root hairs have received considerable attention because they make direct contact with the soil and are the surfaces through which most of the water and minerals usually enter roots. The epidermis is composed of relatively thin-walled, elongated cells, which produce protrusions from the epidermal cells, or from cells of the hypodermis lying beneath it, termed root hairs. The development of root hairs is discussed by Hofer in Waisel *et al.* (1991, Chapter 7) and by Schiefelbein and Somerville (1990).

Root hairs greatly increase the root surface in contact with the soil and decrease the distance that ions and water must travel to reach root surfaces. This presumably facilitates absorption of water and minerals, at least in some situa-

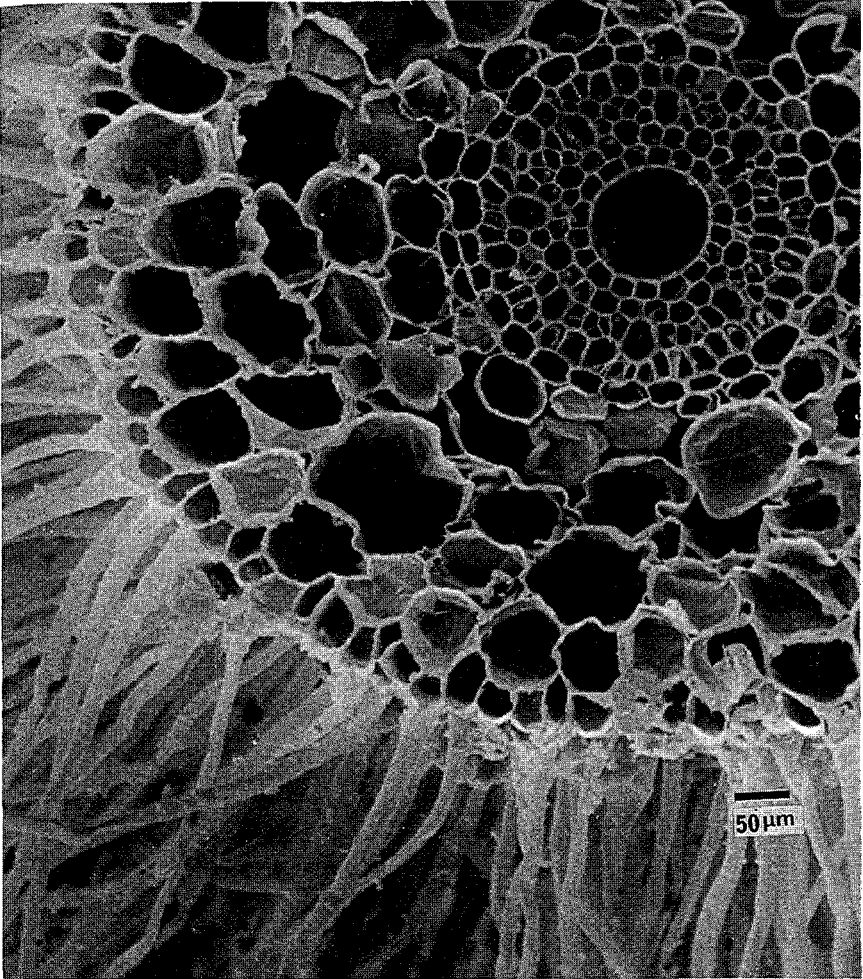


Figure 5.3 Scanning electron micrograph of a young barley root showing numerous root hairs, a large central xylem vessel, and a few small vessels. The endodermal cell walls are not yet thickened. From Kramer (1983), courtesy of Prof. A. W. Robards and A. Wilson, Department of Biology, University of York, England.

tions (Itoh and Barber, 1983). Because of their small diameter they can penetrate soil pores too small to be penetrated easily by roots. On growing roots the root hair zone moves forward as the roots elongate and the older root hairs usually are destroyed by suberization of epidermal cells. However, they persist for months on some herbaceous plants (Dittmer, 1937; Scott, 1963; Weaver, 1925) and indefinitely on some woody plants (Hayward and Long, 1942). The

number of root hairs varies widely among species and with soil conditions, generally being most abundant in moist, well-drained, well-aerated, loamy soils (Itoh and Barber, 1983; Kramer, 1983, pp. 125–127; Meisner and Karnok, 1991). Their formation usually is inhibited by oxygen deficiency and by the presence of ectotrophic mycorrhizae. The number of root hairs reported varies from 20 to 500 per cm^2 of root surface on roots of trees to 2500 on roots of winter rye (Kramer, 1983, p. 126). The large number of root hairs on roots of a cereal is shown in Fig. 5.3. However, observations of McCully and Canny (1988) and Kevekordes *et al.* (1988) question whether extensive absorption of water occurs in the root hair zone of maize and other grasses and some dicots because in their observations the late metaxylem elements were alive and incapable of significant longitudinal water conduction in the apical 15 to 30 cm of maize and soybean roots. This deserves more attention.

The importance of root hairs in the absorption of water and minerals seems to vary among species and cultivars, and perhaps with the growth stage of the plant. For example, Bole (1973), using cultivars of wheat known to differ in root hair frequency, found that the amount of root hair development did not significantly affect phosphorus uptake from a clay loam soil with either a low or high phosphorus content. He also found that rape and flax roots, which bear few or no root hairs, absorbed more phosphorus per unit of length than wheat roots with numerous root hairs. In contrast, Itoh and Barber (1983) reported that root hairs clearly contribute to the phosphorus uptake of Russian thistle and tomato and to a lesser extent lettuce, but not of wheat. Perhaps some of the discrepancies in the literature result from differences in plant demand for minerals at the time of the experiment, which depends on rapidity of growth (Raper *et al.*, 1977; Vessey *et al.*, 1990). Also, if root density is high roots may compete with one another for water and minerals, even if no root hairs are present. It seems that the contribution of root hairs to water and mineral absorption is variable and deserves more study.

The epidermal cells and root hairs are covered by thin films of cutin wherever they are exposed to air (Scott, 1963, 1964), and the root cap and adjacent epidermal cells are covered by a layer of mucigel consisting of polysaccharides secreted by root cells and perhaps partly by associated microorganisms. The mucigel acts as a lubricant to elongating roots and improves contact with the soil (Foster, 1981; Jenny and Grossenbacher, 1963; Oades, 1978). It may also protect roots from aluminum toxicity (Hecht-Buchholz and Foy, 1981; Horst *et al.*, 1982), but Delhaize *et al.* (1993) attribute aluminum tolerance of wheat to the excretion of malic acid. Roots release large amounts of organic matter (Barber and Martin, 1976) which stimulate microorganisms and result in formation of a unique layer high in organic matter in the soil around them, called the rhizosphere (Box and Hammond, 1990; Curl and Truelove, 1986; Wild, 1988, pp. 526–530). Root exudates may use 2 to 20% of the carbon fixed by photo-

synthesis (Clarkson, 1985, p. 102), and Lambers in Gregory *et al.* (1987, Table 9) gives an average of 5%.

Endodermis

A conspicuous part of the primary structure of many roots is the endodermis (see Fig. 5.2), the innermost layer of the cortex, the walls of which often become conspicuously thickened, plus strips of suberized tissue on the radial walls, the Casparian strips. This is shown in Fig. 5.4. A similarly thickened layer of cells, the exodermis, sometimes develops beneath the epidermis of roots (Esau, 1965; Peterson, 1988). This decreases their permeability and presents a barrier to inward apoplastic movement of water and solutes in the cell walls. However, there is considerable evidence that some water and minerals enter roots even where the endodermis is suberized (Fig. 5.5). Thickening of the endodermis often is quite uneven, with pits and plasmodesmata in the walls which permit symplastic movement of materials from cell to cell (Clarkson and Robards in Torrey and Clarkson, 1975), and the endodermis often is pierced by branch roots that may provide openings for apoplastic radial water movement (Dumbroff and Peirson, 1971; McCully in Gregory *et al.*, 1987; McCully and Canny, 1988; Peterson and Perumalla, 1984; Peterson *et al.*, 1981; Queen, 1967). The development and functioning of the endodermis are discussed in Torrey and Clarkson (1975) and in Clarkson (1993), and there is much interesting information on tissue development during root growth in books on plant anatomy. Benfey and Schiefelbein (1994) stated that a number of mutants have been identified in roots of

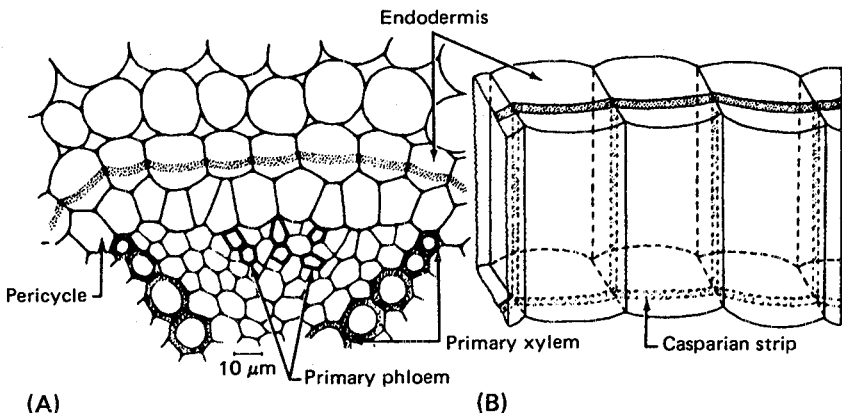


Figure 5.4 Structure of endodermis. (A) Cross section of part of a morning glory root (*Convolvulus arvensis*) showing location of endodermis. (B) Diagram of endodermal cells, showing Casparian strips on radial walls of endodermal cells. From Kramer (1983). Adapted from Esau (1965) by permission of John Wiley and Sons, New York.

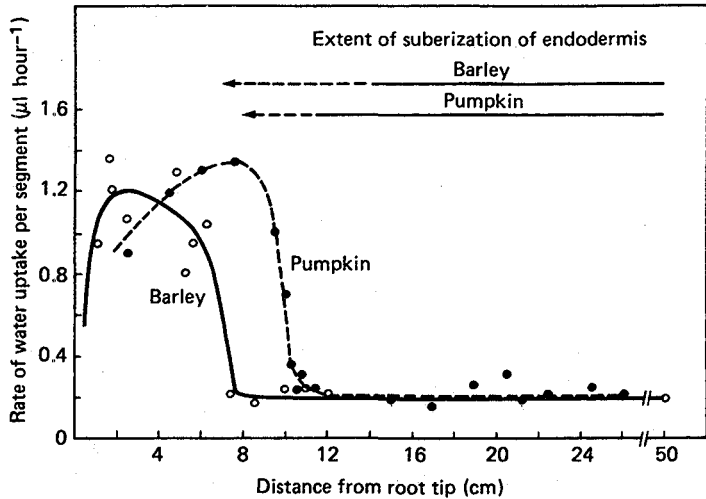


Figure 5.5 Rate of water uptake at various distances behind the apex of barley and pumpkin (*Cucurbita pepo*) roots with varying degrees of suberization of the endodermis. Note that there is measurable uptake even where suberization is complete. From Kramer (1983), after Agricultural Research Council Letcombe Laboratory Annual Report (1973, p. 10).

Arabidopsis that affect growth and reaction to environmental stimuli. The pathway of radial movement of water in roots is discussed in Chapter 6.

Secondary Growth

Secondary growth of roots, resulting from cambial activity, increases root diameter, but causes loss of primary tissues such as the epidermis and cortex, including the hypodermis and endodermis, and development of a suberized outer layer of bark which must significantly modify the pathway of and increase resistance to water and solute entrance. According to Addoms (1946), the entrance of water into suberized roots occurs through lenticels, gaps around branches, and wounds in the bark. The variation in root structure with age and stage of development means that there are large variations in permeability and uptake of water and ions along roots (Fig. 5.5), making it difficult to estimate average uptake per unit of root length.

Root Contraction

A seldom mentioned aspect of root growth that has been observed in many species is their contraction (Esau, 1965, pp. 519–521). It is said to occur in over 450 species, including alfalfa, sugar beet, carrot, and various bulbous mon-

ocots. In at least some instances it is brought about by longitudinal contraction and radial expansion of parenchyma cells, resulting in distortion of the vascular tissue. Its importance is uncertain, although Esau speculated that it might pull the shoot apex into the soil surface where the environment is more favorable for growth and the development of adventitious roots.

Rate and Periodicity of Root Growth

The rate of root elongation varies widely among species, with the season, with variation in such soil conditions as water content, aeration, and temperature, and with variations in the shoot environment that affect the supply of carbohydrates. The principal roots of maize were observed to grow 5 or 6 cm per day for 3 or 4 weeks (Weaver, 1925) and the expansion of a maize root system over time is shown in Fig. 5.6. A rate of 10 or 12 mm per day is said to be common in grasses, but rates of 3 to 5 mm seem to be more common in tree roots (Barney, 1951; Reed, 1939; Wilcox, 1962). A few studies indicate that roots sometimes elongate more rapidly at night than during the day (Lyr and Hoffman, 1967; Reed, 1939). Such behavior is most likely to occur when high rates of transpiration produce daytime water stress.

Reich *et al.* (1980) reported that in a constant environment flushes of oak root growth occurred between flushes of shoot growth. There also are seasonal cycles in root growth of perennial plants at least partly related to soil temperature (Lyr and Hoffman, 1967; Romberger, 1963). Turner (1936) and Reed (1939) observed root growth every month of the year in loblolly and shortleaf pine, with the most growth occurring in the spring and summer and the least in the winter. Periods of slow root growth in the summer coincided with periods of low soil moisture (Fig. 5.7). According to Teskey and Hinckley (1981), physiologically optimum soil temperatures and water potentials never occurred simultaneously in the Missouri oak-hickory forest that they studied.

Root extension into previously unoccupied soil is important because it makes additional water and minerals available. Thus the ability of roots to resume growth promptly after transplanting, known as the root growth potential (RGP), is very important to the success of transplants. Conditions in the nursery such as water supply, fertilization, density of seedlings, and time of lifting affect the capacity of seedlings to generate new roots when outplanted. Evidence that roots can grow on water mobilized from stem tissue after transplanting exists and this may aid in establishment (Matyssek *et al.*, 1991a,b). Occasionally, warm winter weather reduces the root growth potential of seedlings of some cooler climate species (Stone and Norberg, 1979). The factors involved in root growth potential of forest tree seedlings are discussed in detail by Kramer and Rose (1986).

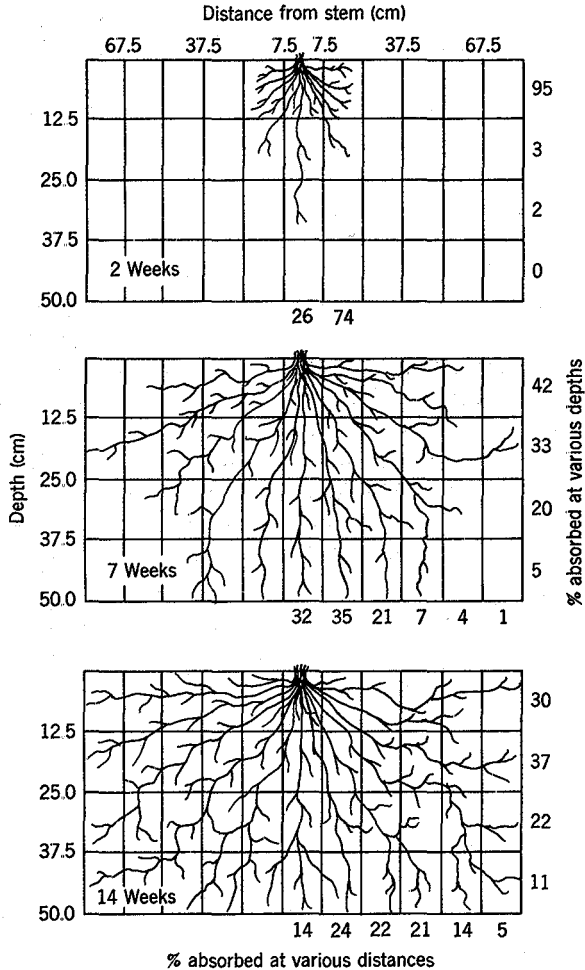


Figure 5.6 Expansion of a maize root system growing in a clay loam soil, based on the uptake of radioactive phosphorus placed in the soil at various depths and distances horizontally from the seedlings. Numbers at right are percentages of total ^{32}P absorbed from various depths, those across the bottom are percentages absorbed at various distances horizontally from the seedlings. From Kramer (1983), after Hall *et al.* (1953).

Depth and Spread of Roots

In deep, well-aerated soil, roots penetrate to great depths and spread widely. Peanut roots reached a depth of 120 cm in 40 to 45 days, but after attaining a certain density showed no further increase (Ketrings and Reid, 1993). In prairie soils, corn and sorghum roots regularly penetrate to 2 m, alfalfa roots have been

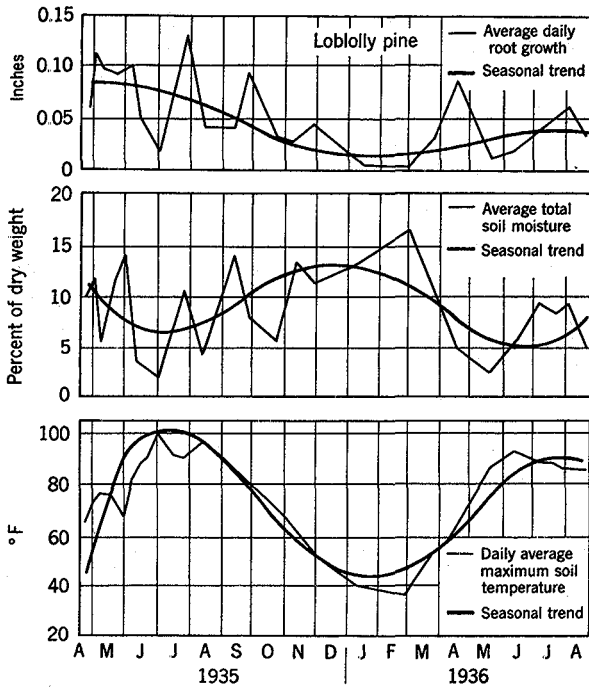


Figure 5.7 Effects of soil temperature and water content on growth of roots of shortleaf pine (*Pinus echinata*) in a forest at Durham, North Carolina. From Kramer (1983), after Reed (1939).

found at depths of 10 m, and Wiggins (1936) found that roots of 18-year-old apple trees penetrated to a depth of at least 10 m and fully occupied the soil between the rows, which were about 10 m apart. Jaafar *et al.* (1993) describe a study of sunflower root development in relation to shoot growth and flowering in a well-watered deep silt loam. The roots penetrated to a depth of 1.8 m at the beginning of disk flowering and 2.0 m by the end of flowering. Roots of several kinds of fruit trees growing in a deep loam soil in California penetrated at least 5 m and the greatest number of roots occurred between 0.6 and 1.5 m (Proebsting, 1943). Hough *et al.* (1965) placed ¹³¹I in a forest soil and found that it was absorbed in detectable amounts from as far away as 16 to 17 m by longleaf pine and turkey oak. Hall *et al.* (1953) used uptake of ³²P to measure root extension of crop plants, and a study of corn root extension is shown in Fig. 5.6.

The situation is very different in heavy, poorly aerated soils. For example, Coile (1937) found that over 90% of roots less than 2.5 mm in diameter occurred in the top 12.5 cm of soil under pin and oak stands in the heavy clay soil of the North Carolina Piedmont. Pears growing in an adobe soil in Oregon had about 90% of their roots in the upper meter (Aldrich *et al.*, 1935). Even in

sandy soils trees often form root mats near the surface because the surface soil contains more mineral nutrients released by decomposition of leaf litter and is wetted by summer showers (Woods, 1957).

The branching and rebranching of root systems often produce phenomenal numbers of roots. Pavlychenko (1937) estimated that a 2-year-old crested wheat grass plant possessed over 500,000 m of roots occupying about 2.5 m³ of soil. Nutman (1934) estimated that a 3-year-old coffee tree growing in the open bore about 28,000 m of roots, 80% of which occurred in a cylinder 1.5 m deep and 2.1 m in diameter. Kalela (1954) estimated that a 100-year-old pine bore about 50,000 m of roots with 5,000,000 root tips. Considerable further information on the extent of root systems has been summarized by Miller (1938, pp. 137–148) and by Weaver (1926). Much information on conifer root systems has been summarized by Sutton (1969).

Longevity of Roots

Although the larger roots of perennial plants are perennial and some are approximately as old as the plants, mortality is heavy among the smaller roots. The short mycorrhizal roots of pine often die over winter and some of the small roots on apple and other fruit trees live only a week or two (Kinman, 1932; Rogers, 1929). Grier *et al.* (1981) reported a high turnover of roots in a mature forest of *Abies amabilis* in the Washington Cascades, and Caldwell (in Lange *et al.*, 1976) found high rates of root replacement in mixed deciduous forests and cool desert shrub communities. According to Reid *et al.* (1993), most of the fine roots on *Actinidia deliciosa*, a woody vine, survive less than 60 days.

A considerable variation in longevity also exists among the roots of herbaceous plants. It often is stated that the primary roots of grasses live only a few weeks and are succeeded by adventitious secondary roots, but this is not always true. The primary roots of barley, rye, wheat, and various wild grasses are the only roots present and maintain the plants for an entire season. Weaver and Zink (1946) found that the seminal roots of several species of prairie grasses survived two seasons and that some were alive after three seasons.

THE ABSORBING ZONE OF ROOTS

Consideration of root anatomy suggests that entrance of water and minerals into young roots probably occurs chiefly in a region a few centimeters behind root tips, approximately where root hairs are most abundant. However, this is questioned by observations that the xylem is not yet fully functional in the root hair zone of maize and soybean (McCully and Canny, 1988). This situation deserves study in roots of other kinds of plants. Little water enters through the meristematic regions (Frensch and Steudle, 1989), probably because of a lack of functional xylem to carry it away. Farther back the xylem becomes functional, but suberization and lignification of the hypodermis and endodermis usually

reduce the permeability in older regions. Figure 5.1 shows diagrammatically the location of the absorbing zone in relation to root tissues, and Fig. 5.5 shows the uptake of water in relation to suberization of the endodermis in barley and pumpkin roots.

It formerly was believed that mineral absorption occurred chiefly near the root apex. However, this was based on mineral accumulation studies, and experiments in which radioactive tracers were supplied to roots of transpiring plants at various distances behind the tips indicate that absorption and translocation often occur far behind the apex (Clarkson *et al.*, 1975; Richter and Marschner, 1973; Wiebe and Kramer, 1954). The difference between the zone of mineral accumulation in root cells and mineral absorption through roots is shown in Fig. 5.8. Research by Lazof *et al.* (1992), using secondary ion mass spectrometry, indicates slow influx of NO_3^- into root tips and emphasizes the importance of finely branched lateral roots in absorption.

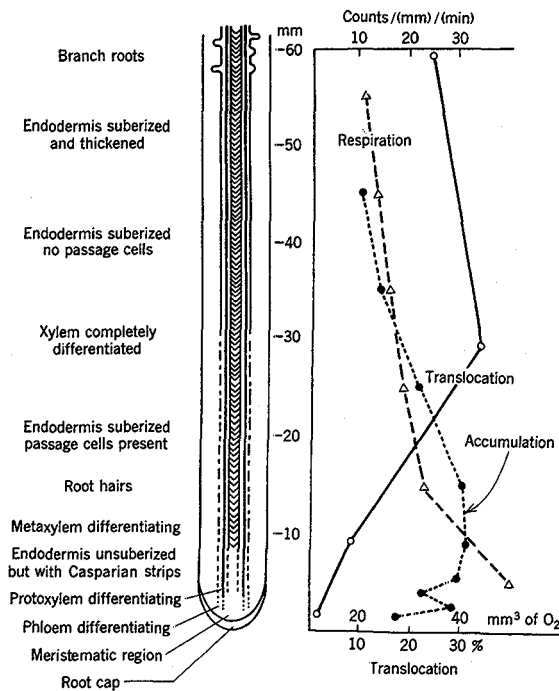


Figure 5.8 Diagram of the apical region of a barley root showing the relationship between the regions where salt is accumulated and where it is absorbed and translocated to the shoot. The curve for respiration is based on data of Machlis (1944), that for translocation on data of Wiebe and Kramer (1954), and that for accumulation on data of Steward and Sutcliffe (1959). The relative positions of those regions probably are similar in most or all growing roots, but the actual distances behind the root tip will vary with the species and the rate of growth. From Kramer (1983).

Absorption through Suberized Roots

Most discussions of absorption deal with young roots and leave the impression that absorption through older, suberized roots is unimportant. Haussling *et al.* (1988), for example, quite properly stressed the importance of growing roots for water and ion uptake of conifers, but absorption through suberized roots must be important in perennial plants where unsuberized roots are often scarce or absent, especially in cold or drying soil. For example, on sunny winter days evergreens such as conifer and citrus trees lose large amounts of water that must be replaced by absorption through suberized roots because few or no unsuberized roots are present (Reed, 1939; Reed and MacDougal, 1937; Roberts, 1948). Kramer and Bullock (1966) found that less than 1% of the root surface in the upper 10 cm of soil under pin and yellow poplar stands in North Carolina was unsuberized in midsummer. Chung and Kramer (1975), Kramer and Bullock (1966), and Queen (1967) all observed a significant uptake of water and phosphorus through suberized roots growing in solution cultures. It seems that the unsuberized root surfaces are too limited in extent, too short lived, and occupy too small a volume of soil to supply all of the water and minerals required by many perennial plants (Chung and Kramer, 1975) and that older, suberized roots must play an important role in absorption, despite their lower permeability. Passioura (1988b) objected to conclusions based on uptake from solution cultures, but MacFall *et al.* (1990, 1991a), using NMR imaging, observed depletion of soil moisture around suberized pine roots growing in fine sand (see Fig. 5.9). This occurs because water sometimes is absorbed more rapidly than it moves toward roots. This is discussed briefly in Chapter 6 in the section on availability of soil water.

Mycorrhizae

The roots of many plants are invaded by fungi that form symbiotic associations called mycorrhizae. These are of two types: endotrophic (VAM, for vesicular arbuscular mycorrhizae) in which the fungus penetrates the root cells, but has little effect on external appearance, and ectotrophic in which the fungus covers the external surface and causes marked hypertrophy and extensive branching of roots, as shown in Fig. 5.10. Mycorrhizae seem to increase the rate of mineralization and solubilization, increasing the supply of minerals, especially phosphorus, available to roots (MacFall, 1994). The presence of mycorrhizal roots also appears to increase the absorption of water and increase drought tolerance, at least in some circumstances (Dixon *et al.*, 1983; Dudridge *et al.*, 1980; Huang *et al.*, 1985; Lamhamedi *et al.*, 1992; MacFall, 1994; Sylvia *et al.*, 1993). Fungal hyphae extend out into the soil and increase the absorbing surface. However, Graham *et al.* (1987) reported that the inoculation of citrus trees with a VAM fungus did not improve their water status, and Hammond *et al.* (1987) found no increase in tolerance of flooding or salinity. Daniels

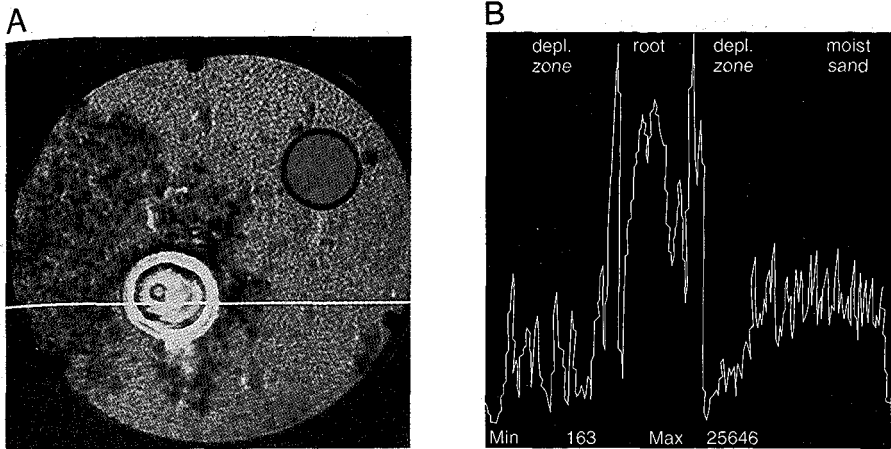


Figure 5.9 (A) A magnetic resonance image showing water depletion (the dark region) around the taproot of a *Pinus taeda* seedling in sand initially at field capacity, after 4.5 hr of transpiration. The circular object at the upper right is a reference tube containing a solution of CuSO_4 and H_2O which has a density similar to sand containing 25% water. On the right (B) is a plot of the relative water content along the white line shown in (A). The diameter of the taproot was about 5 mm. From MacFall *et al.* (1991a).

et al. (1987) found that although inoculation with a mycorrhizal-forming fungus improved the growth of well-watered corn, sudan grass, and big bluestem, only the growth of big bluestem was improved by mycorrhizae under water stress.

Endotrophic or VA Mycorrhizae. The role of VA (vesicular–arbuscular) or endotrophic mycorrhizae is discussed by Safir (1987), in McMichael and Persson (1991), and in Waisel *et al.* (1991, Chapters 33 and 34). Some factors controlling VAM symbiosis are discussed by Koide and Schreiner (1992) and Volpin *et al.* (1994), and McArthur and Knowles (1992) suggest that phosphorus deficiency makes plants more susceptible to VAM fungi. Johansen *et al.* (1993) reported that colonization of subterranean clover with VAM fungi increased the uptake of ^{32}P and ^{15}N . According to Syvertsen and Graham (1990), VAM colonization of roots of citrus seedlings did not affect gas exchange, stomatal conductance, or water-use efficiency. They cited work indicating that VAM infection increased the hydraulic conductance of roots of citrus and green ash seedlings only if the plants were deficient in phosphorus (also see Safir *et al.*, 1971, 1972). According to Anderson *et al.* (1988), the colonization of roots of green ash seedlings with VAM fungi did not increase root hydraulic conductance. Of course beyond a certain root density, a further increase in absorbing surface does not increase overall absorption because the new root surface merely competes with the existing surface. Although endotrophic mycorrhizae

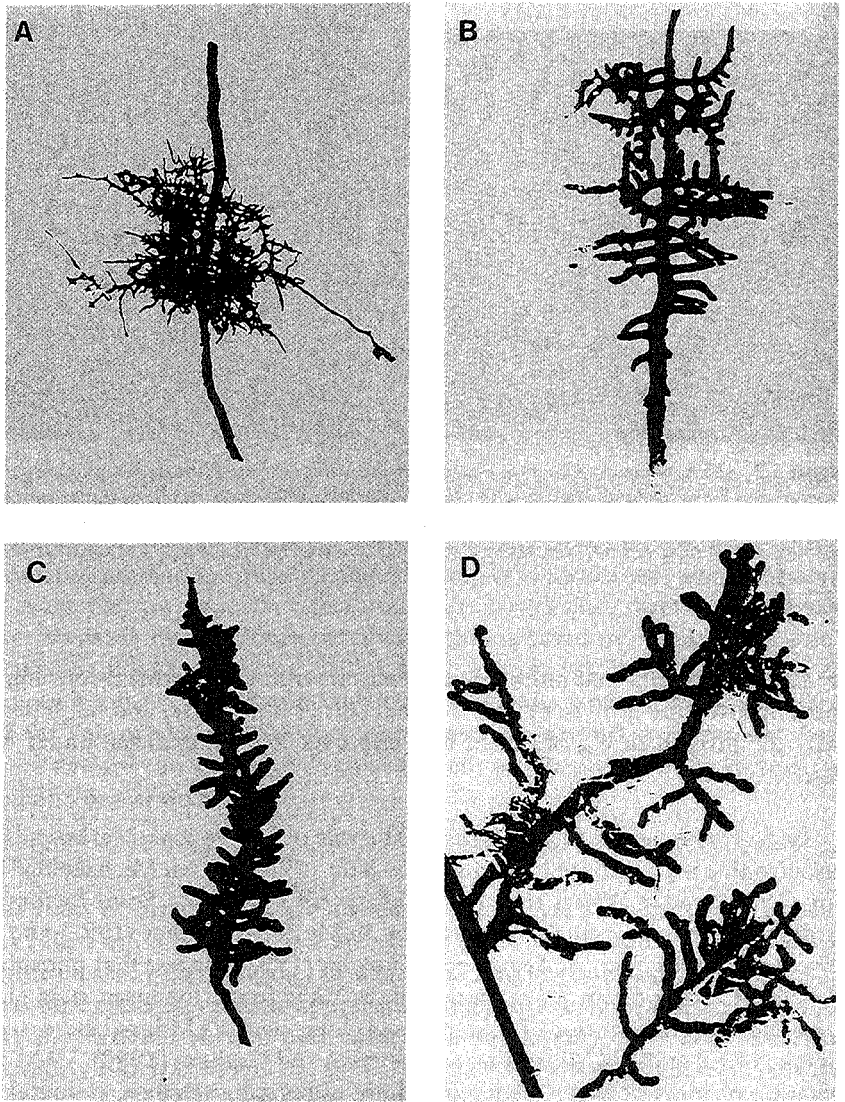


Figure 5.10 Mycorrhizal root development on Douglas fir. (A) Typical cluster, (B) pinnately branched cluster, (C) orange mycorrhiza, and (D) yellow mycorrhiza with rhizomorphs extending into the soil. From Kozlowski *et al.* (1991).

are more common on herbaceous plants, Janos (1980) reported that they also are important on many species of tropical lowland trees. Occasionally, both types of mycorrhizae occur on the same plant.

Ectotrophic Mycorrhizae. According to Bowen (1984, p. 170) and others, ectotrophic mycorrhizae increase the competitive capacity of trees (and presumably some other plants) and compensate for unfavorable soil conditions such as high pH, excess salt, toxic elements such as aluminum, and deficient aeration. For example, inoculation with mycorrhizal-forming fungi improves tree seedling growth on mine dumps (Marx, 1980; Walker *et al.*, 1989) and increases tolerance of aluminum (Cumming and Weinstein, 1990; Kasuga *et al.*, 1990). Mycorrhizal roots are said to be less susceptible to disease and live longer than the average nonmycorrhizal short root. The beneficial effects of inoculating tree seedlings with mycorrhizal-forming fungi, especially *Pisolithus tinctorius*, are discussed by Marx *et al.* (1984, 1985). MacFall *et al.* (1991b) reported that the growth of red pine seedlings was greatly increased in phosphorus-deficient soil by inoculation with the mycorrhizal-forming fungus *Hebeloma arenosa*, but that the effect on growth decreased as the phosphorus concentration of the soil was increased. Iron was accumulated and copper, calcium, cobalt, boron, and sodium were excluded in mycorrhizal roots in low phosphorus soil as compared with nonmycorrhizal seedlings. Apparently the fungus increases the supply of phosphorus to tree seedlings in phosphorus-deficient soil and regulates compartmentalization of poly phosphorus in mycorrhizal roots (MacFall *et al.*, 1992). Augé and Duan (1991) reported that the presence of mycorrhizae on rose roots hastened stomatal closure when the mycorrhizal-infected half of a split root system was water stressed. They suggested that mycorrhizal roots supply a nonhydraulic signal that affects stomatal aperture.

Although most attention has been given to mycorrhizae in connection with trees and other woody plants (Perry *et al.*, 1987), they may be important in improving water and mineral absorption of herbaceous plants, including cultivated crops, especially on infertile soil (Gerdemann in Torrey and Clarkson, 1975; Safir, 1987; Safir *et al.*, 1972). For example, Bethlenfalvay *et al.* (1987) concluded that mycorrhizal infection increased legume nodule activity and decreased water stress in soybean. However, mycorrhizae require considerable carbohydrate, estimated at 7–10% of that translocated to the roots, and that might reduce yield (Gregory *et al.*, 1987, pp. 140–141, 161–162). Björkman (1942) and Wenger (1955) found that girdling and shading decrease the development of mycorrhizal roots, presumably by reducing the supply of carbohydrate. Mycorrhizae are discussed in more detail in Harley and Smith (1983), by Marks and Kozlowski (1973), and by Mukerji *et al.* in McMichael and Persson (1991). The latter state that there is evidence that the presence of mycorrhizae increases nodulation and nitrogen-fixation by legumes. In contrast, Johnson *et al.* (1992) suggest that the yield decrease accompanying continuous cropping of corn and soybean may be caused by an increase in detrimental VAM fungi. MacFall (1994) has an interesting review of ideas concerning the role of mycorrhizae in forestry and agriculture. She suggests that they play a role in acceler-

ated mineralization and soil biogeochemistry as well as in nutrient uptake through increased absorbing surface. Norris *et al.* (1994) provide a summary of methods for research on mycorrhizae.

DEVELOPMENT OF ROOT SYSTEMS

The amount of water and mineral nutrients available to plants depends on the volume of soil occupied by their roots, and it is well established that plants with deep root systems are more tolerant of drought than shallow-rooted plants. Coile (1940) concluded that the inability of loblolly pine seedlings to compete with hardwood seedlings under closed canopies results from their reduced photosynthesis in the shade (Kramer and Decker, 1944), resulting in failure to produce the deep taproots characteristic of oak and hickory seedlings. Thus pine seedlings are more dependent than hardwood seedlings on water in the surface soil, which is quickly depleted during summer droughts. Fayle (1978) observed that poor growth of red pine plantations was associated with poor vertical root development, and Meyer and Alston (1978) stated that wheat yield in semiarid regions depends on the geometry of the root system in relation to the distribution of soil water at various depths. The development of a maize root system over time is shown in Fig. 5.6. Boyer *et al.* (1980) concluded that newer soybean cultivars yield better than older cultivars because they have a higher root density and therefore are less subject to afternoon shoot water deficits than older cultivars. Frederick *et al.* (1990) questioned this but used only leaves stored for various times to measure water potentials, which may have obscured the differences.

There are some limitations to the concept that very high root density is always favorable. For example, Andrews and Newman (1968) removed 60% of the roots from densely rooted wheat plants without reducing transpiration, even in drying soil, and Eavis and Taylor (1979) reported that treatments increasing the ratio of root length to leaf area did not significantly increase transpiration or leaf water potential. Also, Newman and Andrews (1973) found that although uptake of phosphorus by wheat was well correlated with root growth, uptake of the more mobile potassium was not. Raper and Barber (1970) observed an increased uptake of potassium per unit of root surface in a soybean genotype with lower root density than in one with higher root density. Presumably, as root density increases, competition between roots of the same plant for water and minerals also increases as well as competition between roots of adjacent plants, decreasing the uptake per unit of root surface and the benefits from further increase in root length density.

The depth and lateral spread of root systems depend on both heredity and environment. Figure 5.11 shows the variety of root systems produced by various species of plants growing in the same deep, well-aerated prairie soil and Fig. 5.12 shows the hereditary and environmental limitations on root growth of

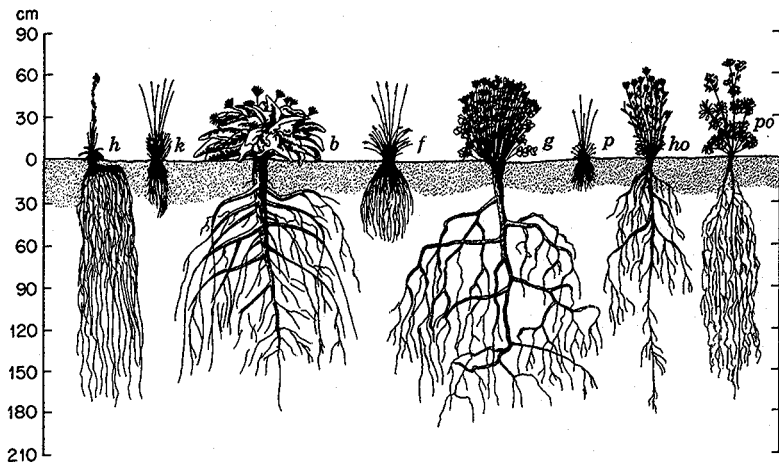


Figure 5.11 Differences in depth and spread of root systems of several species of prairie plants growing in a dry, well-aerated prairie soil: *h*, *Hieracium scouleri*; *k*, *Koeleria cristata*; *b*, *Balsamina sagittata*; *f*, *Festuca ovina ingrata*; *g*, *Geranium viscosissimum*; *p*, *Poa sandbergii*; *ho*, *Hoorebekia racemosa*; *po*, *Potentilla blaschkeana*. (From Kramer (1983), after Weaver (1919).

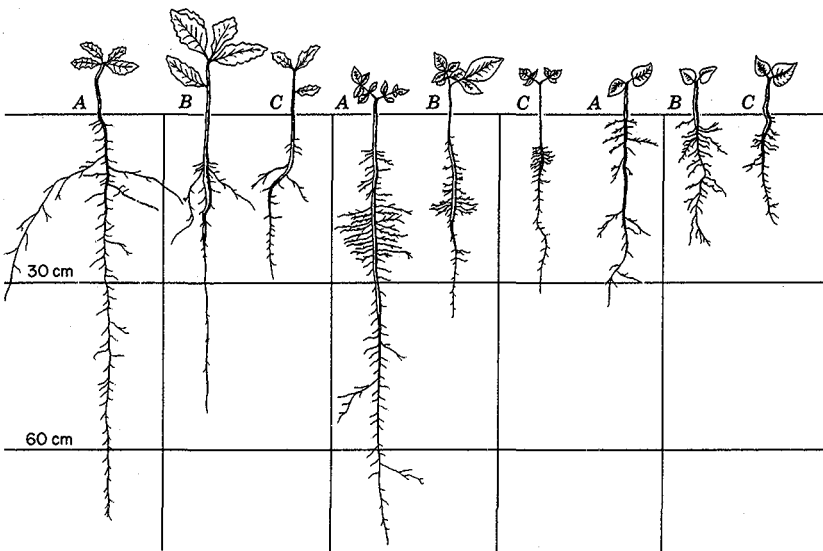


Figure 5.12 Interaction of heredity and environment on amount of root growth produced by three tree species growing in three environments. Left, *Quercus rubra*; center, *Hicoria ovata*; right, *Tilia americana*. Seedlings A were growing in open prairie, B in an oak forest, and C in the deep shade of a moist linden forest. It was necessary to water the linden seedlings in the prairie to prevent death from desiccation. Oak developed the deepest and linden the shallowest root systems in all three habitats. From Kramer (1983), after Holch (1931).

seedlings of three tree species growing in three different environments. Taylor and Terrell (1982) give extensive data describing the spread, depth, and density of root systems in various plant species.

Root-Shoot Interrelationships

The optimum growth of plants depends on maintenance of an efficient balance of functions between roots and shoots, such that neither suffers serious deficiencies in supplies of essential substances contributed by the other. Borchert (1973) suggested that rhythmic shoot growth in a uniform environment may result from cyclic feedback between root and shoot growth, tending to maintain a constant root-shoot ratio. However, it is doubtful if a constant root-shoot ratio is generally maintained in most growing plants. Roberts and Struckmeyer (1946) concluded that the composition and reserve conditions in the shoot were a large and perhaps controlling factor in the production of roots. Sachs *et al.* (1993) proposed that a plant can be regarded as a colony of shoots and roots competing for vascular connections with the remainder of the plant, and their success in this is important for their development.

Effects of Shoots on Roots. Roots are dependent on shoots for carbohydrates, growth regulators, and some other organic compounds, and severe reduction in leaf area by pruning, insect defoliation, grazing, or diversion of food into fruit and seed production is likely to reduce root growth.

The development of fruits and seeds sometimes reduces root growth significantly, and Fig. 5.13 shows the effect of seed filling on root growth of maize. There was steady increase in root density at all depths until pollination, after which roots began to die more rapidly than they were produced, resulting in a decrease in root density, especially of the older roots in the surface soil, and a decrease in total root weight (Mengel and Barber, 1974). In another experiment, Loomis (1935) found that if the ears were removed corn root growth continued until frost. Figure 5.14 shows that as apple shoot growth increased, root growth decreased and vice versa and that pruning stimulated shoot growth, but reduced root growth (Head, 1967). Buwalda (in McMichael and Persson, 1991), pp. 431-441) found that most of the root growth of kiwi vines (*Actinidia deliciosa*) occurs after shoot and fruit growth is nearly completed. Also, partial defoliation reduces root growth more than fruit growth, suggesting that, as might be expected, kiwi fruits are stronger sinks for photosynthate than roots.

A heavy crop of coffee is said to sometimes reduce the carbohydrate supply to the roots so severely that some die, resulting in injury to the trees (Nutman, 1933), and fruiting of a tropical palm also is said to reduce root growth (Piñero *et al.*, 1982). Root growth of tomato is reduced during fruiting (Hudson, 1960, and others), and Eaton (1931) reported that both root dry weight and root-shoot ratio of cotton were nearly tripled by preventing boll and branch forma-

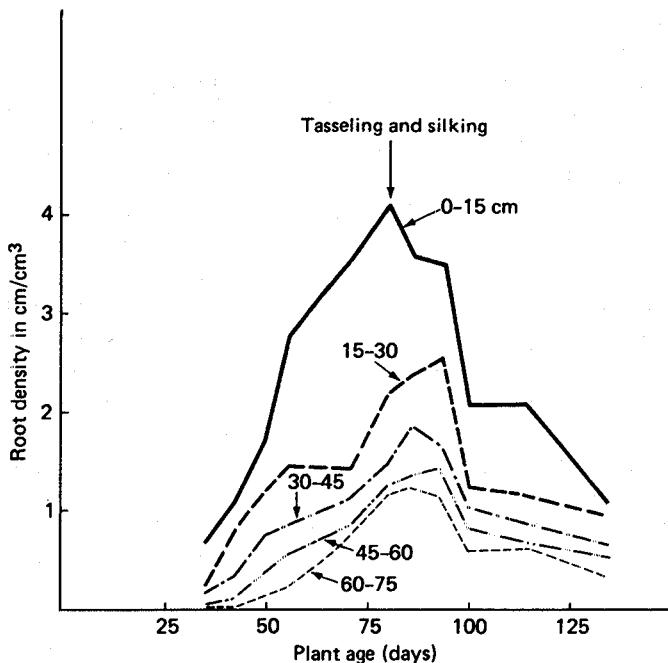


Figure 5.13 Effects of seed development and filling on root growth of maize. Note that root density began to decrease at all depths in the soil after tasseling and silking because old roots died more rapidly than new roots were formed. From Kramer (1983), after Mengel and Barber (1974).

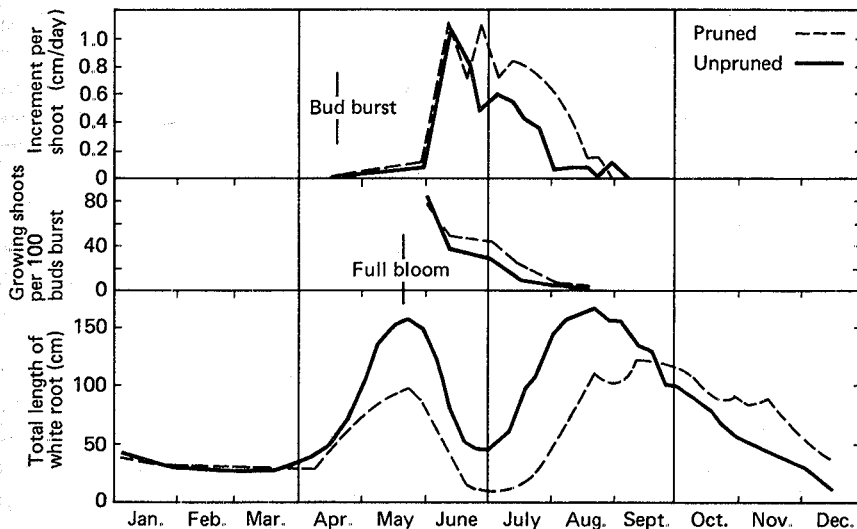


Figure 5.14 Relationship between root and shoot growth of apple. As shoot growth (upper curves) increased, root production (lower curve) decreased. Pruning stimulated shoot growth and reduced midsummer root growth. From Kramer (1983), after Head (1967).

tion. These effects on root growth usually are explained in terms of diversion of carbohydrates from roots to shoot growth or to fruit and seed development. For example, Tripp *et al.* (1991) reported that the increased yield of tomato fruit on plants supplied with a high concentration of CO₂ results from the diversion of photosynthate from roots to fruits because high CO₂ increases seed number in tomato fruits and makes them stronger sinks. However, Van der Post (1968) reported that the appearance of flowers on cucumbers stopped root growth before the fruits were large enough to be important sinks for carbohydrates, suggesting hormonal controls. Wilson (1988) reviewed the extensive literature on root–shoot ratios and concluded that Thornley's (1972) model explains reactions of the root–shoot ratio to environmental factors such as water deficits, light, CO₂, and mineral supply, also to defoliation and root pruning. This model was simplified by Johnson and Thornley (1987) who put more emphasis on the carbon and nitrogen status of plants in the vegetative stage than on hormones. However, as Bingham and Stevenson (1993) state, the carbohydrate supply is only one component of the complex of factors controlling root growth.

Effects of Roots on Shoots. It is not surprising to learn that damage to root systems severe enough to reduce water and mineral absorption inhibits shoot growth. In addition, shoots are dependent on roots for growth regulators such as abscisic acid, cytokinins, and gibberellins. However, it is somewhat surprising to find that the mineral content of the leaves and the quality of citrus fruit are affected by the kind of rootstock on which the trees are growing, yet those effects have been observed worldwide (Haas, 1948; Sinclair and Bartholomew, 1944). For example, more soluble sugar and total acids are found in fruits from orange trees grown on citrange and trifoliolate orange roots than in fruits from trees grown on rough lemon roots. Also, the juice from the Washington navel orange is less bitter in fruit grown on trifoliolate orange roots than in fruit grown on other rootstocks such as sour orange, sweet orange, or its own roots. Gregoriou and Economides (1993) found that rootstocks affected fruit size and composition of ortanique tangor, but the differences were too small to be of practical importance. The reasons for these differences are not fully understood.

Horticulturists know that rootstocks differ in disease resistance and tolerance of flooding, salinity, and low temperature, which affect the success of the shoots growing on them. For example, trifoliolate orange rootstocks tend to exclude sodium from the shoots grafted on them (Walker, 1986), and Lloyd *et al.* (1987) state that the uptake of sodium and chloride by Valencia oranges varies with the rootstocks on which they are grown. Apparently trifoliolate orange rootstocks sequester sodium at the root–shoot transition zone. Maas (1993) surveyed the recent literature on the effects of salinity on citrus. Reciprocal root and shoot grafts between bean genotypes differing in drought tolerance indi-

cated that the differences in tolerance were in the roots (White and Castillo, 1989). In contrast, Delves *et al.* (1987) concluded from reciprocal grafts that the shoot controls supernodulation in soybeans.

It has been known for centuries that the kind of rootstock affects the size and vigor of trees grafted on it. Pears are dwarfed by grafting them on quince roots, and apples are not only dwarfed to one-third of their normal size, but begin to fruit at a younger age when grafted on a dwarfing root system such as M9. Also, on the M9 rootstock about 70% of the photosynthate goes into fruits compared to 40 or 50% in normal trees. However, in California, apple trees on M9 root systems grow too small and M7a and M106 are better for early bearing (Micke *et al.*, 1992). (Numbers with the prefix M indicate that the root systems originated at the horticultural research station at East Malling, England.) The physiology of these root-shoot interactions are not well understood, but some information has been provided in reviews by Lockard and Schneider (1981) and Tubbs (1973). The role of roots as sensors of water stress was mentioned earlier in this chapter and will come up again in later chapters. The importance of chemical signals from roots in controlling shoot processes was reviewed by Davies and Zhang (1991), Gowing *et al.* (1993), and others.

There seems to be renewed interest in electrical potentials as coordinating signals in plants. They received considerable attention a few decades ago, and their role in relation to leaf movement in plants sensitive to touch is well known. Lund (1931) and Rosene (1935) discussed their possible role in coordinating plant growth, and some more recent work is discussed by Fromm and Spanwick (1993). Fromm and Eschrich (1993) claim that electrical signals from roots affect photosynthesis and transpiration in the shoots of willow trees. Hamada *et al.* (1992) reported that there is a decrease in electrical potential on the surface of roots at the point where branch roots will emerge, about 10 hr before emergence. While the role of electrical potentials over distances of a few centimeters seems well established (see references in Fromm and Spanwick), their effectiveness over long distances is more speculative. Perhaps the use of modern technology will result in clarification of their importance. Malone (1993) regards hydraulic signals as important.

The increase in wood production of trees accompanying fertilization usually is attributed to an increase in leaf area and photosynthesis. However, Axelsson and Axelsson (1986) state that there is increasing evidence that the decreased allocation of photosynthate to fine root production by well-fertilized trees is an important factor contributing to increased shoot growth. King (1993) supported the view that increasing the supply of nitrogen decreases root production relative to shoot growth.

Root-Shoot Ratios. The preceding discussion of the interdependence of roots and shoots suggests that there might be some optimum ratio of roots to

Table 5.1 Amount of Dry Matter in Metric Tons per Hectare Incorporated Annually into Roots and Shoots of Various Plant Species^a

Species	Roots	Shoots	Root-shoot ratio
<i>Zizania aquatica</i> (wild rice)	0.6	4.0	0.15
<i>Hordeum</i>	3.0	12.0	0.25
<i>Andropogon scoparium</i> (first year)	3.5	14.2	0.25
<i>Triticum</i> (average)	2.0	6.8	0.29
<i>Medicago sativa</i> (average)	3.2	7.4	0.43
<i>Zea mays</i> (average)	4.5	8.7	0.52
<i>Solanum tuberosum</i> (average)	4.0	2.6	1.54
<i>Beta</i> (average)	9.5	3.1	3.06
<i>Pinus sylvestris</i> (average)	1.6	8.9	0.17
<i>Picea abies</i> (average)	2.1	11.9	0.18
<i>Fagus sylvatica</i> (average)	1.6	8.2	0.19
Ghana rain forest	2.6	21.7	0.12

^aFrom Bray (1963).

shoots. However, root-shoot ratios vary widely among species, with age, and with environmental conditions. Table 5.1 summarizes some data from Bray (1963) giving ratios varying from 0.15 to 0.20 for various trees, 0.5 for maize, and 3.0 for the storage roots of beets. Such data are not very accurate because of differences in methods and amounts of roots recovered, but they indicate the wide range of root-shoot ratios found among plants in the field. This variation results in part from the wide variations in water supply and other environmental factors to which plants often are subjected during a growing season, as well as to genetic variations among plants such as grasses and root crops.

Perhaps the root-shoot ratio should be considered in terms of root and leaf surface but it is difficult to measure root surface. Fiscus (1981) found that there was a linear relationship between root and leaf surface in growing bean plants. A correlation exists between the sapwood area and leaf area in trees (Chapter 7), and Kaufmann and Fiscus (1985, p. 83) state that the amounts of conducting tissue in roots, stems, and leaves are strongly correlated. Various aspects of root-shoot relations have been reviewed by Klepper (in Waisel *et al.*, 1991).

Root Grafting

The extent of the root system of plants, especially trees, sometimes is increased by natural grafting to the roots of adjacent trees. Bormann and Graham (1959) found so many root grafts in stands of white pine that they regarded the entire stand as a physiological unit, and Kozlowski and Cooly (1961) found a similar situation in stands of angiosperm and gymnosperm trees. Other examples of extensive root grafting include Monterey pine in New Zealand (Will, 1966), slash pine in Florida (Schultz, 1972), red pine in New England (Stone

and Stone, 1975b), and quaking aspen in the western United States (Grant, 1993).

Root grafting also is common in tropical trees (LaRue, 1952) and probably will be found wherever a search is made for it. Root grafts provide pathways for transfer of water, solutes, and even fungal spores from one root system to another (Epstein, 1978; Kuntz and Riker, 1955). Bormann and Graham (1960) found that 43% of the untreated trees in a 30-year-old white pine stand were killed by "backflash" to untreated trees through root grafts from treated trees when the plantation was thinned by injecting ammonium sulfate into the trunks of trees to be removed.

Stumps and their attached roots sometimes survive on carbohydrates supplied from intact trees to which they are connected by root grafts. An example of root grafting involving stumps is shown in Fig. 5.15. Apparently root grafting occurs rarely in herbaceous plants, probably because their roots are too short lived for grafts to develop. However, Bormann (1957) found that if roots of tomato plants became firmly intertwined, water moved from one plant to the other even though no grafts occurred. It appears that materials can be transferred between roots by grafting, through fungal hyphae, or between adjoining roots by diffusion through the soil. Woods and Brock (1970) found that radioactive calcium and phosphorus supplied to stumps of red maple were found in the foliage of 19 other species occurring up to 8 m from the donor stumps. They suggested that the root mass of an ecosystem should be regarded as a functional unit rather than a group of separate root systems, a view also held by Bormann

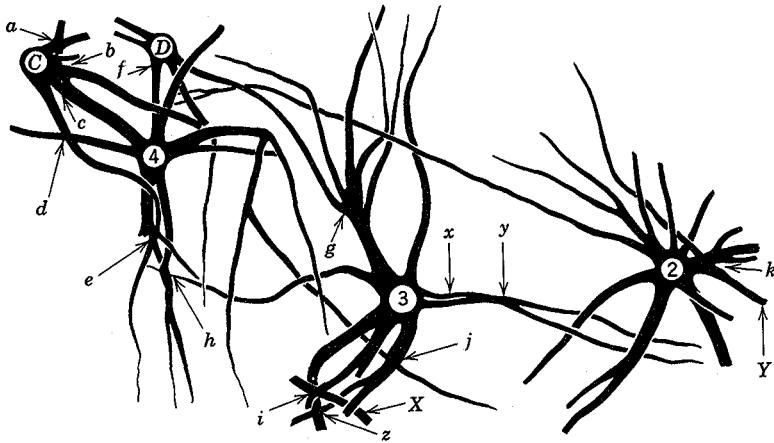


Figure 5.15 Root grafting among roots of three 18-year-old trees of *Pinus radiata* and roots from living stumps of two trees removed 9 years previously. Grafts *a* through *g* were between trees 3 and 4 and roots of stumps C and D. Grafts *b* through *k* were between roots of trees 3 and 4 or between trees 3 and 4 and roots X and Y of trees removed during root excavation. Grafts *x*, *y*, and *z* are between two roots of the same tree. From Kramer (1983), after Will (1966).

and Graham (1959). Another example is the large stands of quaking aspen trees formed by vegetative reproduction (Grant, 1993). One stand consists of 47,000 trees covering 106 acres and can be regarded as a single organism because the tree roots are interconnected and the trees are genetically identical.

Metabolic Cost of Root Systems

A large amount of photosynthate goes into root growth. Some is used in the production of new tissue, some in the respiration supplying energy for the metabolic processes involved in growth, and some in the maintenance respiration of existing tissue (Amthor, 1989; Lambers in Gregory *et al.*, 1987). Caldwell (in Lange *et al.*, 1976) reported that 50% of the annual net primary dry matter production of a deciduous forest and a fescue meadow and 75% of the annual production of short grass prairie and shrub steppe communities goes into the production of new roots. Woods (1980) concluded that the turnover in root biomass of a New England deciduous forest exceeds that of leaves, and Harris *et al.* (1977) reported that root dry matter production is 2.8 times that of above-ground wood production in pine and hardwood forests of the southeastern United States. The economics of root systems are discussed in detail in Givnish (1986).

There has been considerable discussion of why plants often produce more roots than seems necessary and Caldwell (in Lange *et al.*, 1976) was unable to find a satisfactory explanation. It has been argued that death and replacement of roots are efficient because they reduce root respiration at times when they are not needed, but this is doubtful. Part of the problem is the difficulty in determining what constitutes an adequate root system. For example, Teskey *et al.* (1985) reported that they could remove one-fourth of the roots from forest trees in the Pacific Northwest without increasing tree water stress, but Carlson *et al.* (1988) found that removal of any roots from 5-year-old loblolly pine seedlings in Oklahoma increased tree water stress. The benefits of large root systems seem to depend on soil water storage capacity in the root zone and on rainfall patterns, and may vary from year to year.

The role of root density and the extent of root systems in the success of plants have been discussed by Kummerow and by Taylor in Turner and Kramer (1980), by Barley (1970), by Fitter (1987), and also in Waisel *et al.* (1991, Chapter 1). Passioura (1972) discussed the configuration, i.e., branching patterns and depth of rooting, in relation to water and mineral absorption and plant success in competition. The data of Newman and Andrews (1973) indicate that at high densities wheat roots compete with each other for potassium; they probably also compete for water. In their experiments the distance between roots ranged from 4 to 1.5 mm at root length densities of 4 to 16 cm/cm³ of soil.

Natural selection probably favored survival of plants with large root systems

because they are most likely to survive occasional severe droughts. They also are more likely to encounter the nutrients that are distributed irregularly in many soils. This probably resulted in evolution of root systems that are larger than necessary for most cultivated crop plants in humid regions. It therefore seems probable that plant breeders should consider the possibility that selection for smaller root systems would be practical for crops grown in fertile soil in regions with dependable rainfall or with irrigation. According to O'Toole and Bland (1987) the extensive genotypic variation in root systems of various crop plants provides opportunities for selecting root systems with characteristics suitable for special situations.

ENVIRONMENTAL FACTORS AFFECTING ROOT GROWTH

Root growth is greatly affected by environmental factors such as soil texture and structure; aeration; moisture; temperature; pH; salinity; the presence of toxic elements such as aluminum, lead, and copper; competition with other plants; and the presence of bacteria, fungi, and soil-inhabiting animals such as nematodes. A few of these factors are discussed briefly and more extensive discussions can be found in Waisel *et al.* (1991), in Wild (1988), and in a review by Feldman (1984).

Soil Texture and Structure

The physical properties of soil affect root growth directly by restricting root penetration and indirectly by effects on aeration and water content. For example, hardpan layers of natural occurrence (fragipans) and those resulting from tillage operations (tillage pans) often seriously restrict root system development, as shown in Fig. 5.16. Plant growth in such soils often benefits from deep tillage. Figure 5.17 shows the inhibitory effect of various degrees of soil compaction on root penetration and growth of maize in a clay soil, and compaction by heavy machinery reduces the yield of wheat (Oussible *et al.*, 1992). Tardieu (1988) reported that wheel compaction of soil reduced maize root density and water extraction. Sarquis *et al.* (1992) reported that high atmospheric pressure applied to corn plants had little effect on root growth, but a mechanical pressure of 100 kPa on the soil increased ethylene production four-fold and root diameter seven-fold, but decreased root elongation 75%. Further information on the effect of changes in soil structure can be found in Emerson *et al.* (1978) and in Glinski and Lipiec (1990, pp. 75–96); both have references dealing with the effects of soil bulk density on root growth. The term “impedance,” borrowed from physics, often is used to refer to the physical resistance of the soil to root extension, but this is undesirable because impedance originally referred to the apparent resistance in an alternating current circuit rather than the physical resistance of the soil.



Figure 5.16 Effect of a compacted layer of soil on root penetration by 11-week-old oat plants. (Left) Undisturbed soil with dense mass of roots above the compacted layer, but few below it. (Right) Uniform penetration of roots into soil loosened by tillage to a depth of 50 cm. The restriction of root penetration was caused by mechanical resistance, as aeration was not limiting below the compacted layer. From Kramer (1983). Courtesy of H. D. DeRoo, Connecticut Agricultural Experiment Station.

In addition to the physical restriction on root penetration caused by various kinds of hardpan layers, there also are chemical barriers. Most important is the effect of a pH below 5.0 which increases the concentration of soluble aluminum

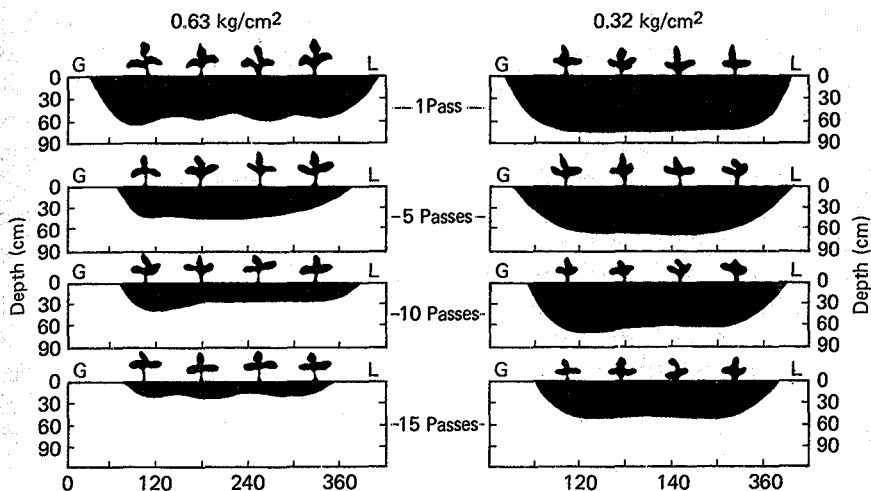


Figure 5.17 Effect on root penetration of soil compaction at 0.63 and 0.32 kg cm^{-2} for 1, 5, 10, and 15 passes over a clay soil prior to seeding. From Kramer (1983), after Cassel in Raper and Kramer (1983).

to a toxic level. This condition is common in the acid soils to the southeastern United States and in various tropical soils. The importance of physical and chemical soil barriers to root extension has been discussed by Cassel in Raper and Kramer (1983) and the effects of soil pressure on roots have been discussed by Dexter (1987).

Soil Moisture

Either a deficiency or an excess of soil water limits root growth. Water itself is not directly injurious to roots, as shown by their vigorous growth in well-aerated nutrient solutions, but an excess of water in the soil displaces air from the noncapillary pore space and produces oxygen deficiency that may reduce growth and functioning and cause death of roots. This is discussed further in the section on flooding.

A severe deficiency of soil water usually brings about a reduction in or cessation of root growth, and little or no root growth occurs in soil dried to the permanent wilting percentage. This inhibits water and mineral absorption. The effect of seasonal variation in soil water content on root growth of shortleaf pine in the field is shown in Fig. 5.7. Kaufmann (1968) reported that the root growth of loblolly and scotch pine seedlings in slowly drying soil was reduced to about 25% of the rate at field capacity at a soil water potential of -0.6 or -0.7 MPa , and shoot growth was reduced much more than root growth in drying soil. Teskey and Hinckley (1981) reported that root elongation in a Missouri oak-hickory forest was greatest at a soil water potential of -0.1 MPa , but the num-

ber of growing root tips was greater in somewhat drier soil. Vartanian (1981) reported that drying soil reduced root elongation but increased the number of new lateral roots in *Sinapis alba*. Above a soil temperature of 17°C, soil water potential was the dominant limiting factor for root growth in the experiments of Teskey and Hinckley but below 17°C, temperature was most often limiting. During their study, physiologically optimum soil temperature and soil water potential never occurred simultaneously, with one or the other always being limiting. Waring and Schlesinger (1985) cited several experiments suggesting that tree roots do not grow much at a soil water potential below -0.7 MPa, but Logsdon *et al.* (1987) reported growth of maize roots at a soil matric potential of -1.09 MPa. Newman (1966) found that flax root growth was reduced at a soil water potential of -0.7 MPa, but some growth occurred in soil drier than -2.0 MPa. Caution must be used in field experiments to make certain that roots in dry soil are not being supplied with water from other parts of the root systems growing in moist soil (Portas and Taylor, 1976) or by roots of other plants with deeper root systems (Dawson, 1993).

Soil water deficits often reduce shoot growth before root growth is reduced, resulting in increased root-shoot ratios in moderately water-stressed plants. Mild plant water stress also may reduce leaf growth before photosynthesis is reduced (Boyer, 1970), resulting in a surplus of carbohydrates which are available for root growth. Osmotic adjustment also occurs in root tips (Sharp *et al.*, 1990), prolonging root cell expansion, and the combined result is that the absolute size of root systems of mildly stressed plants sometimes exceeds that of well-watered plants (Jupp and Newman, 1987; Sharp and Davies, 1979). However, Westgate and Boyer (1985b) found similar osmotic adjustment in leaves and roots of maize, yet roots grew more than leaves during a period of water stress. The difference in growth of the two organs was attributed to internal factors other than water stress, since the difference remained when the water potential was the same in roots and leaves. Steinberg *et al.* (1990b) reported a 50% greater increase in root biomass than in shoot biomass in young peach trees subjected to water stress.

If root elongation is stopped by soil water stress, roots tend to become suberized to their tips. This is sometimes regarded as a protective adaptation, especially in desert plants, because it decreases water loss from roots to drying soil, but it also reduces their capacity to absorb water when the soil is rewetted. Svenningsson and Liljenberg (1986) found that roots exposed to repeated dehydration contained much less membrane lipid than controls and that the lipid composition was different (Svenningsson and Liljenberg, 1986; Norberg and Liljenberg, 1991). Perhaps as a result plants subjected to severe water stress usually do not regain their full capacity to absorb until several days after the soil is rewetted (Brix, 1962; Kramer, 1950; Leshem, 1965; Loustalot, 1945).

Cruz *et al.* (1992) discussed some of the effects of water stress on the hydraulic conductance of sorghum roots.

Hydrotropism. It has been claimed, at least since the time of Darwin (1880), that roots can detect water at a distance and grow toward moist soil. This seems to be based largely on observations of the large masses of roots developed around leaky drains, under leaking water taps, and wherever roots encounter moist soil (Oppenheimer, 1941), but this is not necessarily evidence for hydrotropism. Roots extend in all directions and if a randomly growing root encounters an area high in moisture or minerals it is likely to branch profusely and grow. Greacen and Oh (1972) found that wet soil had less resistance to root growth than the same soil at a lower water content and that root growth was more rapid in the wetter soil.

Hydrotropism is difficult to separate from geotropism (gravitropism), and Wareing and Phillips (1981, p. 179) concluded that it is unlikely that true hydrotropism exists. However, research with mutant plants having roots insensitive to gravity indicates that at least some roots show a hydrotropic response (Takahashi and Scott, 1991).

Soil Aeration.

Soil aeration is important physiologically and therefore has effects both on natural vegetation, such as in marshes and swamps, and on cultivated crops. The difference in tolerance of poor aeration between rice and tobacco or cypress and dogwood is striking. Insufficient oxygen often limits root growth in soils which lack sufficient noncapillary pore space for good gas exchange. Poor penetration of nitrogen and oxygen can limit nitrogen fixation by roots of legumes (see Chapter 10). On wet sites roots often tend to be concentrated on hummocks where aeration is best (Lieffers and Rothwell, 1987). Aeration is seldom a problem in sandy soils, but is often a serious limitation in fine-textured soils if less than 10% of the volume consists of noncapillary pore space. Examples are the Shelby loam shown in Fig. 4.2 and the deeper horizon of the old field soil shown in Fig. 4.3. Oxygen diffuses nearly 10,000 times as rapidly in air as in water, and since the concentration of oxygen at 15°C is 30 times greater in air than in water, the actual transport of oxygen to roots is about 300,000 times greater through air-filled pore spaces than when they are filled with water. Even in unflooded soil the presence of water films on the roots reduces the oxygen supply, and flooding of the capillary pore space of soil is likely to result in roots suffering severe oxygen deficiency. Thus two aspects of the aeration problem exist: chronic inadequate aeration in soils deficient in noncapillary pore space and acute episodic deficiency in aeration caused by flooding the soil.

Table 5.2 Oxygen Consumption and Carbon Dioxide Production from a Bare Soil and under Kale in Summer and Winter at Rothamsted, England (Rates are in $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)

Soil temperature at 10 cm	July (17°C)		January (3°C)	
	Cropped	Bare	Cropped	Bare
Oxygen used	24	12	2.0	0.7
Carbon dioxide produced	35	16	3.0	1.2

*From Wild (1988, p. 300).

Roots and soil organisms use large amounts of oxygen and produce large quantities of carbon dioxide during the growing season, as indicated in Table 5.2. Unless there is a rapid exchange of gas between the soil and the air the oxygen supply soon becomes limiting for plant growth, as indicated by the data in Fig. 5.18. According to Wild (1988, p. 300), the rate of respiration observed in soil might exhaust the entire oxygen supply to a depth of 25 cm in 2 days in a soil containing 20% of air space, unless it is replenished. The rate of exchange between soil and aboveground air decreases with decreasing soil porosity and increasing water content, and the effects can be easily observed in legumes that require oxygen and nitrogen for nitrogen fixation by the roots.

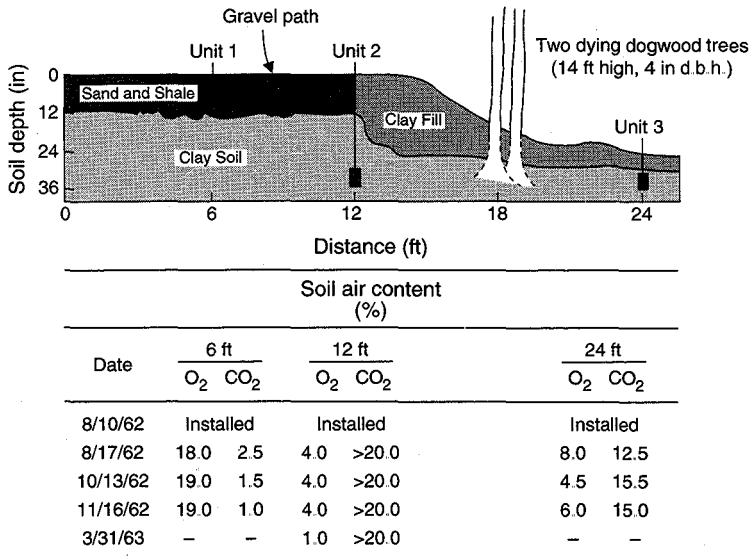


Figure 5.18 Changes in oxygen and carbon dioxide concentration of soil beneath sand and clay fills. From Kozlowski *et al.* (1991), after Yelenosky (1964).

Figure 10.1 shows that the activity for nitrogen fixation can increase initially as water is removed from soil, although severe water deficiency causes lower activity for metabolic reasons. Aeration often becomes seriously limiting in soils compacted by traffic or saturated with water. Raising the soil level by filling or sealing the surface with pavement often creates aeration problems for tree roots (see Fig. 5.18), and trampling by pedestrian traffic around picnic sites and on golf greens also creates aeration problems for trees and grass. Urban trees often are short lived because of the unfavorable environment to which their roots are subjected (Kramer, 1987).

It seems likely that the growth of both cultivated crops and native vegetation is often reduced by undetected deficiencies in root aeration. McComb and Loomis (1944) suggested that root respiration and decomposition of organic matter produce sufficiently anaerobic conditions in prairie soils to hinder tree root growth and exclude trees from grasslands. Howard (1925) stated that in India several species of trees were killed whenever a dense stand of grass developed over their roots, producing anaerobic conditions, and Richardson (1953) reported that grass cover reduced root and shoot growth of *Acer pseudo-platanus*. Karsten (1939) demonstrated in pot experiments that the addition of starch to soil high in nitrogen resulted in anaerobic conditions severe enough to kill wheat seedlings.

There is some uncertainty concerning the relative importance of low oxygen versus high carbon dioxide in inhibiting root growth and function in poorly aerated media, but it seems probable that under field conditions the inhibitory effects of low oxygen are more important than the effects of high carbon dioxide. It appears that bulk air oxygen concentrations above 10% are adequate for roots of most plants. However, it is difficult to determine the actual oxygen concentration at root surfaces from measurements of the oxygen concentration of the bulk air. Methods of measuring soil aeration are discussed by Stolzy *et al.* (1981) and in Glinski and Stepniewski (1985, Chapter 6). The oxygen diffusion rate to root surfaces is the critical factor in soil aeration and this is often measured with platinum electrodes simulating roots. In general it appears that oxygen diffusion rates of $0.4 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ measured with a platinum electrode are adequate and that rates of 0.2 mg are limiting, while the adequacy of intermediate rates depend on the temperature and the plant species. Berry (1949) found oxygen deficiency in the meristematic region of onion roots, and according to Fiscus and Kramer (1970) the interiors of roots usually are subjected to a low concentration of oxygen, as measured with platinum electrodes inserted into them. These observations suggest that root tissues are better adapted than stem tissues to function with low oxygen concentrations. Although Bowling (1973) doubted if the deficiency normally occurring in roots is large enough to affect ion transport significantly, Thomson and Greenway (1991) reported that in a low oxygen concentration the stele of maize roots becomes anoxic. How-

ever, the cortex remains aerobic because oxygen is supplied to it from the shoots through the aerenchyma. Ion transport is significantly reduced in poorly aerated roots.

Flooding Injury. The most severe examples of deficient aeration result from flooding the soil with water because this displaces the soil air, and the low solubility and relatively slow diffusion rate of oxygen in water drastically reduces the supply to roots. Cannell *et al.* (1984) reported that winter flooding of wheat and barley in England caused more injury than summer drought, and Orchard and Jessop (1984) found that the stage of growth at which flooding of sorghum and sunflower occurred affected the amount of injury.

There seem to be multiple causes of injury to shoots of plants growing in flooded soil. The first symptom of flooding injury often is wilting (see Fig. 6.10), and an extreme example is the "flopping" of tobacco when the soil in low areas of a field is saturated by rain, followed by bright sun. This is caused by increased resistance to water flow through roots (Kramer, 1940a, 1951; Smit and Stachowiak, 1988). Similar effects can be produced by saturating the soil with CO₂ or more slowly by displacing the soil air with nitrogen (Kramer, 1940a). Prolonged flooding reduces growth and causes epinasty, leaf chlorosis and death, and development of adventitious roots near the water line. Root elongation ceases and mineral absorption is reduced (Huck, 1970). Some of these effects are incompatible with water stress (Kramer, 1951) and usually water stress is soon eliminated by stomatal closure, probably related to increase in ABA in the shoots (Jackson, 1991). The yellowing and death of leaves have been attributed to a decrease in the supply of cytokinins from roots (Burrows and Carr, 1969). Drew *et al.* (1979a) claimed that the disturbance of nitrogen metabolism is a major cause of poor growth of flooded plants and that the addition of nitrate reduces injury from flooding. There usually is a reduction in the amount of gibberellins in the shoots of flooded plants (Reid and Crozier, 1971) and an increase in ABA. The ABA usually is assumed to come from the roots (Zhang and Davies, 1990), but this is questioned by Jackson *et al.* (1988).

Stem hypertrophy often occurs near the water line on flooded plants and adventitious roots develop on some kinds of plants (Kramer, 1940a). This may result from an accumulation of auxin near the water line (Phillips, 1964), but Drew *et al.* (1979b) attributed the formation of adventitious roots to ethylene. A precursor of ethylene is formed in the roots of flooded plants and moves upward in the xylem (Bradford and Yang, 1980). The new adventitious roots, which usually contain more air space (aerenchyma) than existing roots, seem to take over the functions of the dying roots; plants that develop adventitious roots usually survive flooding better than those that do not (Jackson, 1955; Tsukahara and Kozlowski, 1985; Yu *et al.*, 1969). Roots formed in a poorly aerated environment often contain large air spaces in the cortical parenchyma, called aerenchyma, produced by the breakdown of cells (Fig. 5.19). Formation of

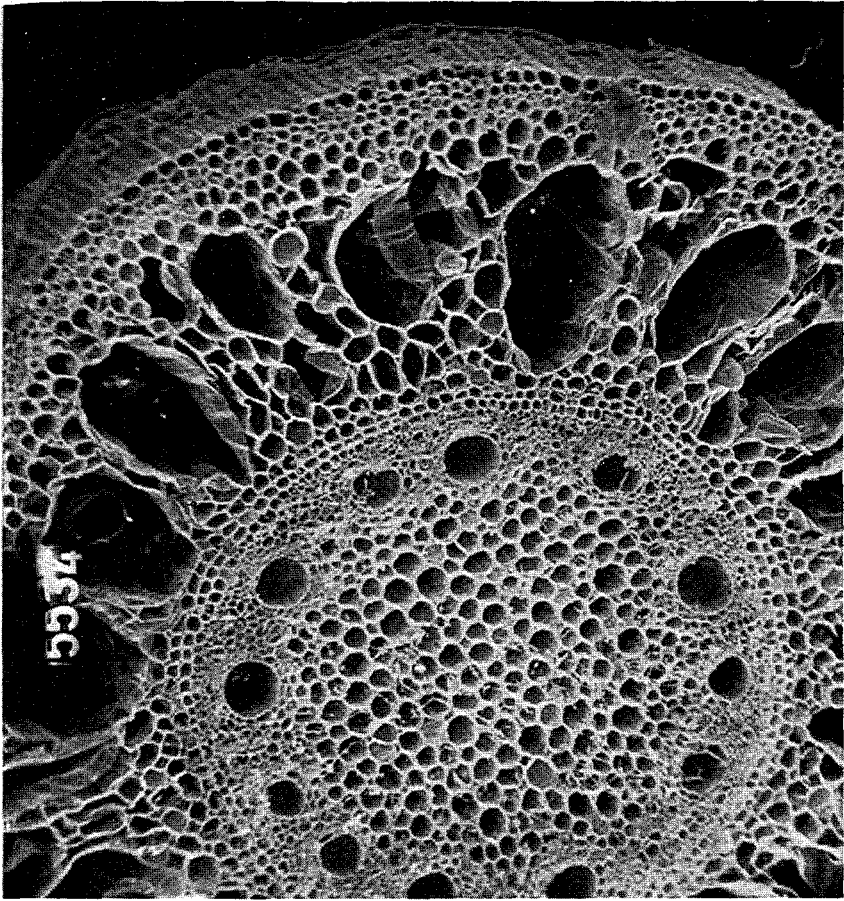


Figure 5.19 Scanning electron micrograph of an adventitious root of corn grown in an unaerated nutrient solution. The section was made 8 to 10 cm behind the root tip. The air spaces in the cortex are formed lysigenously by the breakdown of cells. From Kramer (1983), from Agricultural Research Council Letcombe Laboratory Annual Report (1978, p. 42); courtesy of M. C. Drew.

aerenchyma may result from the high concentration of ethylene stimulating cellulase activity, digestion of the middle lamella, and separation of cells (Kawase, 1979), but this problem deserves more study. Drew *et al.* (1980) reported that the strands of living tissue between air spaces in aerenchyma seem healthy and function effectively in the transport of water and ions to the xylem. It is not clear why some cells of the cortex die while strips of adjacent cells remain uninjured. As aerenchyma seldom occurs nearer than 2 or 3 cm behind the root tip, the apical region does not benefit from it. Crawford (1976) suggested that deep roots often suffer from oxygen deficiency, and Van Noordwijk and Brou-

wer (1988) thought that the depth of root penetration depends partly on the amount of oxygen supplied through internal air spaces from above ground.

It often is assumed that injury to roots in flooded soil results from accumulation of products of anaerobic respiration such as aldehydes, organic acids, and alcohol (Glinski and Stepniewski, 1985, pp. 141–144). However, Jackson *et al.* (1982) concluded that the concentration of ethanol occurring in roots of flooded plants is not toxic and probably seldom causes injury. Barta (1984) also questioned whether ethanol toxicity is an important factor in root injury. Furthermore, ethanol is found in the cambial region of tree trunks, but causes no injury (Kimmerer and Stringer, 1988). Roberts *et al.* (1985) found by use of nuclear magnetic resonance spectroscopy that flooding injury in root tip cells is correlated with a decrease in pH of the cytoplasm. If acidosis was delayed by treatment with $\text{Ca}(\text{NO}_3)_2$, root tips survived much longer. Acidosis results from leakage of H^+ from the vacuole into the cytoplasm through the tonoplast, suggesting that properties of the tonoplast may be a factor in the difference between some flooding tolerant and intolerant species. They concluded that acidification of the cytoplasm is an important cause of injury under anaerobic conditions.

Compounds such as methane, sulfides, and reduced iron sometimes accumulate in flooded soil and cause injury to roots. Mendelssohn *et al.* (1981) reported metabolic adaptation to anoxia in *Spartina*, which grows in soil frequently inundated with salt water. The interesting problems of flooded soil were discussed by Ponnampertuma in Kozlowski (1984) and in Chapter 26 of Wild (1988). The book "Flooding and Plant Growth" edited by Kozlowski (1984), contains useful information on effects of flooding, including a chapter on its relation to plant diseases.

Differences in Flooding Tolerance. It is obvious that there are significant differences among species in tolerance of flooding. Cattails, rushes, rice, mangroves, bald cypress, and tupelo gum thrive in saturated soil, whereas tobacco, tomato, dogwood, longleaf pine, and plants of many other species are killed by flooding the soil. Among shade trees, American elm and honey locust are more tolerant than most other species (Yelenosky, 1964). According to Lin and Lin (1992), orchards of waxapple (*Syzygium samarangense*) survive the 30 or 40 days of flooding, used to induce flowering, without injury.

There are two principal reasons for differences in flooding tolerance: morphological differences resulting in differences in the transport of oxygen to roots and biochemical differences in response to anaerobic conditions such as an increase in alcohol dehydrogenase activity. In some plants, swamp tupelo (*Nyssa sylvatica*, *V. biflora*), waxapple, and *Spartina*, for example, both mechanisms seem to operate (Hook *et al.*, 1971; Huang and Morris, 1991; Lin and Lin, 1992). According to Laan *et al.* (1990) there was little difference in respiratory pathways between flooding tolerant and intolerant species of *Rumex*, but roots

of tolerant species were more permeable to gas. Laan and Blom (1990) stress the importance of photosynthesis in submerged leaves and reserve carbohydrates in increasing flood tolerance of *Rumex*. There is so much literature on flooding tolerance that only a few papers can be cited and readers are referred to books edited by Glinski and Lipiec (1990), Glinski and Stepniewski, (1985), and Kozłowski (1984) for additional information. There are a number of papers in Volume 39 of *Aquatic Botany* (1991) on aeration problems, and they also are discussed in the book edited by Jackson *et al.* (1991).

Andrews *et al.* (1993, 1994) reviewed some work on effects of deficient aeration at the molecular level. Induction of alcohol dehydrogenase (ADH) formation in corn root tips was small and transient in anoxic conditions (zero O₂) compared to induction by hypoxic conditions (4% O₂ by vol.), and root tips died sooner than older portions of roots. According to Mujer *et al.* (1993), rice and several species of *Echinochloa*, which are tolerant of anaerobic conditions, produce stress proteins which intolerant species of *Echinochloa* do not produce. They cite other relevant research, and more work at the molecular level is likely in the future.

The development of shallow root systems in surface soil and an increase in the amount of internal air space (aerenchyma) are important for survival of plants in waterlogged soil (Armstrong *et al.*, 1991). It is well known that trees and other plants growing in poorly drained soil often develop shallow root systems concentrated in the better aerated surface soil, and seedlings in swamps often start life on hummocks. The adventitious roots formed on flooded plants usually contain considerable aerenchyma in their cortex which facilitates movement of oxygen to the roots and increases flooding tolerance (Tsukahara and Kozłowski, 1985; Jackson, 1955). Glinski and Lipiec (1990, pp. 119–122) and Luxmoore *et al.* (1970) concluded that at least part of the oxygen requirement of maize roots is supplied by transport from the shoots, but Greenwood (1967) found internal aeration of roots of several herbaceous plants to be effective only to about 5 cm below the soil surface. Yu *et al.* (1969) also reported limited gas penetration of existing roots in several species under anaerobic conditions, although porosity of new roots was increased. Van Noordwijk and Brouwer (1988) concluded that the depth of root penetration into soil depends partly on their porosity to gas movement from shoots and described methods of measuring root porosity. The role of root porosity and internal aeration in flooding tolerance seems to deserve more study.

The mechanism by which oxygen moves from shoots to roots has received considerable attention. Some movement occurs by diffusion along concentration gradients caused by the release of oxygen during photosynthesis and its use in root respiration (Laing, 1940; Raskin and Kende, 1985; Waters *et al.*, 1989). However, Armstrong (1968) found that in some instances oxygen entered stems from the air through lenticels a few centimeters above the soil surface and none came from the leaves, but this may have been an unusual situation. D. Barber

et al. (1962) observed that $^{15}\text{O}_2$ diffused from shoots to roots of flooded barley and rice plants. Rice allowed much faster diffusion than barley. Evidence has been found of pressure-induced flow of air from shoots to submerged roots and rhizomes. According to Grosse *et al.* (1991), this was observed by Pfeffer in 1897 (see Pfeffer, 1900), but the early observations were neglected. Grosse *et al.* (1992) regard gas pressure caused by warming of the stem as important for supplying air to the roots and rhizosphere of several tree species, but not for others. Schroeder (1989) invoked thermo-osmotic transport to explain gas transport to roots of European alder. Dacey (1981, 1987) reported that in the water lily, *Nuphar*, and in *Nelumbo*, which have floating or emergent leaves, warming of the leaves by the sun causes a downward flow of gas. Raskin and Kende (1985) stated that pressure flow in rice results from the use of oxygen in respiration and the solution of CO_2 produced in respiration, whereas Huang and Morris (1991) concluded that pressurization in *Spartina* is caused by water vapor accumulation in intercellular spaces. Sorrell (1991) pointed out that there can be no true flow of air through the air spaces unless there are openings to the exterior for its escape. Enough oxygen sometimes leaks out of roots and rhizomes to oxidize substances in the rhizosphere (Armstrong, 1968; Mendelssohn and Postek, 1982), and this oxidation of the rhizosphere is considered to be important by some investigators, for example, Hook in Kozlowski (1984). Armstrong and Armstrong (1991) and Armstrong *et al.* (1992) reported convective or mass flow of gas to the roots in *Phragmites*, caused by the venturi effect of wind blowing over hollow, broken culms.

Constable *et al.* (1992) found that the concentration of CO_2 in the air spaces of cattail stems was high at dawn, but that it decreased to a near atmospheric concentration by midday, then rose again in the late afternoon. These changes were attributed to the use of CO_2 in photosynthesis, which might contribute to the high productivity of some wetland plants. Brix (1990) suggested that CO_2 from the sediment in which many aquatic plants grow might move to the shoots and be used in photosynthesis. Such movement must be by diffusion along concentration gradients in the intercellular space or in solution in the transpiration stream. Early work on the uptake of CO_2 through roots was reviewed by Livingston and Beall (1934) who thought it reached the leaves chiefly in the transpiration stream, although some might escape into the air from the soil. Their experiments in which the CO_2 concentration of the soil was enriched showed variable results. Billings and Godfrey (1967) concluded that photosynthesis in some plants of wet alpine meadows uses CO_2 from their hollow stems before their leaves are fully expanded. Farmer and Adams (in Waisel *et al.*, 1991) reviewed the recent literature and regarded the uptake of CO_2 from sediments through roots as important for some aquatic plants. Bialzyk and Lechowski (1992) reported that CO_2 is fixed in tomato roots and carbon compounds are transported from roots to shoots.

The metabolic effects of deficient aeration were mentioned in the section on causes of injury, but will be discussed briefly here. Injury often has been ascribed to the accumulation in roots of incompletely oxidized compounds, especially ethanol. In fact, tolerance of flooding often has been attributed to the ability to control ethanol accumulation by increased alcohol dehydrogenase activity, but the importance of this is uncertain. However, Hole *et al.* (1992) and Andrews *et al.* (1993) reported that when maize roots were grown with low oxygen, production of a number of enzymes involved in glycolysis and fermentation was induced and tolerance of anoxia was increased. Kimmerer and MacDonald (1987) reported that there is high alcohol dehydrogenase activity in leaves of many woody plants, but it is not related to flooding tolerance. As mentioned previously, Jackson *et al.* (1982) and others concluded that the concentration of ethanol rarely reaches a toxic level in roots, and Roberts *et al.* (1985) found that acidification of the cytoplasm is an important cause of injury. Thus there is considerable uncertainty concerning the relative importance of various metabolic effects of inadequate aeration. Waters *et al.* (1991) point out that it is difficult to generalize concerning reasons for differences in tolerance among species because of variations in prior treatment and in criteria used by different investigators that may obscure real differences. It therefore seems impossible to generalize concerning the relative importance of structural and metabolic factors in respect to flooding tolerance.

Formation of Intercellular Spaces and Aerenchyma. There has been frequent mention of the importance of aerenchyma and intercellular spaces in roots. Cells are closely packed in meristematic regions, but as they enlarge they often tend to separate, leaving intercellular spaces. These were termed schizogenous in origin because they were supposed to develop by splitting of the middle lamella. Another and usually larger type of intercellular space (lysigenous) develops by disintegration of entire cells (see Fig. 5.19). The large intercellular spaces formed in poorly aerated roots and in water plants are termed aerenchyma. According to Kawase (1979) the high concentration of ethylene in poorly aerated tissue stimulates cellulase activity and separation of cells, but this needs more study. Some intercellular spaces function as secretory ducts, such as resin and latex ducts. Further discussion of intercellular spaces can be found in plant anatomy texts such as Esau (1965, pp. 62–63).

Under ordinary conditions intercellular spaces in roots are filled with gas, but Canny and Huang (1993) reported that they are sometimes filled with fluid which usually is similar in composition to the vacuolar sap of adjacent cells. According to Burström (1959) the internal atmosphere usually is 79% nitrogen, 2 to 15% CO₂, and the remainder is oxygen. However, according to Burström (1959), intercellular spaces near root tips sometimes are filled with CO₂ which dissolves and they then become filled with water, resulting in dwarf roots.

Zimmermann *et al.* (1992) reported the presence of air-filled, radial, intercellular spaces in NMR images of cross sections of roots. Ethylene often accumulates in the intercellular spaces of submerged tissue because it is relatively insoluble in water (Voesenek *et al.*, 1993).

Root and Earthworm Channels. Death and decay of old roots often provide channels through which new roots grow downward and they also improve soil aeration. This is very noticeable in forest soils where root channels also increase the infiltration of water (Gaiser, 1952). Research by Hasegawa and Sato (1987) indicated that water absorption from the subsoil by roots growing downward in deep soil cracks is important for crop plants in soils that develop cracks. The role of earthworm activity in loosening soil and improving plant growth was noted by Gilbert White in 1777 and was publicized by Charles Darwin (1881). Earthworm channels not only provide pathways for root growth, but also improve aeration and increase the infiltration of water. Bouma *et al.* (1982) and Hartenstein (1986) discuss earthworm activity, and Wild (1988) also discussed the numerous insects and other animals occurring in soil. Wang *et al.* (1986) discussed the importance of channels formed by decaying roots and soil-inhabiting organisms on root growth and soil aeration. Passioura (1988b, p. 247) pointed out that the tendency of roots to clump in earthworm and old root channels often invalidates the assumption that roots are uniformly distributed in undisturbed soil. The importance of the feeding activity of soil-inhabiting animals on roots is seldom mentioned but probably deserves more study than it has received (Brown and Gange, 1991). For example, nematodes often cause serious injury to roots.

Aeration and Root Diseases. Important interactions exist between soil aeration and root diseases. For example, the root systems of citrus trees growing in soil frequently saturated by irrigation are prone to attack by *Phytophthora* and pine trees growing in poorly aerated clay soil in the southeastern United States suffer a slow decline (little leaf) because fungal attacks on their root systems cause nitrogen deficiency (Campbell and Copeland, 1954). "Damping off" or death of seedlings caused by attack of the lower stem by fungi sometimes is a serious problem in wet soil. Soil saturation is favorable for the release, spread, and germination of the spores of some pathogenic fungi. It also is favorable for at least some kinds of nematodes. This topic deserves more attention than can be given to it in this book and interested readers are referred to Kozlowski (1984, Chapter 7) and Ayres and Boddy (1986) for more detailed discussion.

Oxygen Toxicity. Although oxygen is essential for aerobic organisms, an excess can be toxic. Loehwing (1934) reported that a continuous aeration of root systems with normal air containing 20% oxygen can inhibit growth. More

recent research indicates that metabolic processes such as photosynthesis give rise to such reactive toxic compounds as superoxide ($O_2^{\cdot-}$), H_2O_2 , and OH^- . These compounds injure some enzyme systems and react with unsaturated fatty acids of membrane lipids, causing damage to membranes and the cells and organelles that they enclose. Environmental stresses such as bright light, water and temperature stress, and some herbicides cause excessive production of superoxide, resulting in damage by photoinhibition and photooxidation. Aerobic organisms possess several protective mechanisms, including catalase and superoxide dismutase. Some of the literature on oxygen toxicity has been reviewed by Scandalios (1993).

Soil Temperature

Root growth often is limited by low soil temperatures, and occasionally exposed surface soil becomes hot enough to limit root growth. Overheating of the surface soil can be reduced by mulching, but a thick mulch slows rewarming of the soil in the spring, which often is undesirable (Wild, 1988, Chapter 8). An example of the effect of temperature on root growth is shown in Fig. 5.20, and the effect of seasonal change in temperature on pine root growth is shown in Fig. 5.7. There are wide differences in the optimum temperature for root growth of different species, and this has important ecological and economic effects. For example, roots of bluegrass are injured at the high midsummer temperatures favorable for Bermuda grass (Brown, 1939) and a low soil temperature often limits growth of cotton roots early in the season (Arndt, 1945). Roots of plants growing in containers sometimes are injured by low temperatures, and unusually cold weather that freezes the surface soil sometimes injures shallow roots such as those of nursery seedlings.

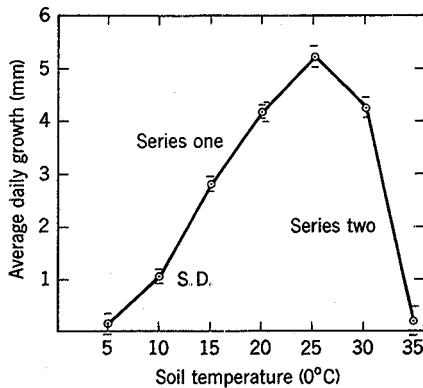


Figure 5.20 Relationship between soil temperature and root elongation of *Pinus taeda* seedlings under controlled conditions. From Kramer (1983), after Barney (1951).

The effects of low soil temperature on water absorption are discussed in Chapter 6. In addition to a decrease in water and mineral supply, a decrease in synthetic activity reduces the supply of hormones to the shoots and results in decreased shoot growth (Duke *et al.*, 1979). The use of cold water for irrigation is said to be a limiting factor for rice yields in such varied locations as northern Italy, Korea, on the island of Hokkaido, and in the Sacramento Valley of California. Occasionally, the use of cold water in the winter on greenhouse crops such as cucumbers has proven injurious (Schroeder, 1939). However, chilling root systems of young soybean plants to 10°C for a week had only temporary effects and did not reduce yield (Musser *et al.*, 1983). Effects of soil temperature are discussed in more detail in Glinski and Lipiec (1990, pp. 152–161) and in Wild (1988, Chapter 8).

Root Competition

The size of root systems usually is reduced when they are grown in competition with other plants. For example, Pavlychenko (1937) reported that root systems of barley and wheat were nearly 100 times larger when grown without competition than when grown in rows 15 cm apart. Although roots often seem to be intertwined in the soil, there is evidence of a mechanism that prevents roots of some kinds of plants from growing very close to one another. This was reported for roots of trees by Lyford and Wilson (1964) and for soybean by Raper and Barber (1970a), as shown in Fig. 5.21, but seems not to occur in tomato (Bormann, 1957). Considerable information on root competition has been summarized by Caldwell in Gregory *et al.* (1987). The detrimental effects of one plant or crop on another can be attributed to the (1) depletion of water

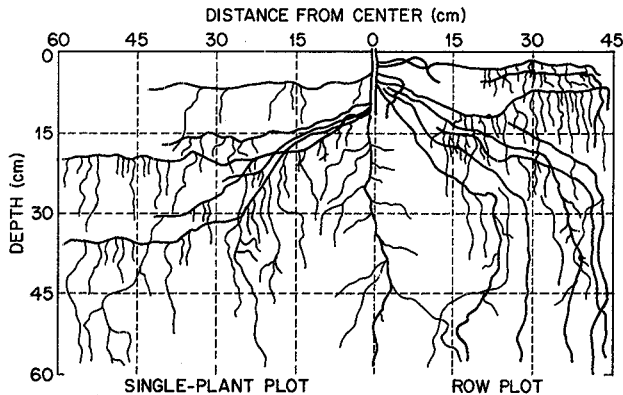


Figure 5.21 Difference in lateral root extension of an isolated soybean root system (left side) and that of a plant growing in a row. From Kramer (1983), after Raper and Barber (1970a).

or nutrients, especially nitrogen; (2) release of toxic substances from roots or leaves; or (3) production of toxic substances during decomposition of plant remains.

Early in this century there was considerable interest in the effects of decomposition of the residue of one crop on the growth of subsequent crops (see Miller, 1938, pp. 164–174), and examples of more recent research were summarized by Putnam and Duke (1978). Although in certain experiments some sequences of crops seemed better than others the results were often contradictory and were so frustrating that research was largely abandoned.

Allelopathy

It has been known for more than 2000 years that some plants seem to inhibit the growth of other plants growing in their vicinity, a phenomenon known as allelopathy. Pliny (died AD 79) reported that walnut trees are injurious to some other plants and the injury is now attributed to a compound called juglone, excreted from their roots (Gries, 1943). Colton and Einhellig (1980) found that extracts from the leaves of velvetleaf (*Abutilon theophrasti*) are injurious to soybean, and Booker *et al.* (1992) found that ferulic acid, an allelochem occurring in soil, decreases ion and water uptake of cucumber seedlings. Putnam (1983) describes chemicals involved in allelopathy. Einhellig *et al.* in Thompson (1985) found that treatment of sorghum root systems with coumaric and ferulic acid or extracts from certain allelopathic weeds reduced water absorption and suggested that one factor in allelopathic reactions is increased plant water stress.

Alfalfa is said to be both allelopathic to other plants such as sorghum and autotoxic, with its residue inhibiting alfalfa seed germination and seedling growth (Hegde and Miller, 1990, 1992). According to Tesar (1993), delaying reseeding alfalfa at least 2 weeks after plowing it under reduces autotoxic effects. Keever (1950), Muller (1969), Webb *et al.* (1967), and others attempted to explain success or failure of plants in natural succession to toxic effects of substances released by competing vegetation, but this is difficult to prove or disprove. In contrast to the examples of inhibition just mentioned, black locust is said to stimulate the growth of neighboring trees because nitrogen fixation in its roots increases the nitrogen supply for neighboring plants (Chapman, 1935). Other possible interactions are discussed in Kozlowski *et al.* (1991, pp. 102–104). There seems to be increasing interest in allelopathy in forestry, chiefly as a factor in seedling establishment, and the increasing interest in agroforestry also has stimulated interest in root interactions (Huck, 1983; Sureshi and Rai, 1988). Possible interactions between shade trees and various kinds of ornamental plant ground cover deserve more attention (Shoup and Whitcomb, 1981). Rice (1984) and Harborne (1988) reviewed the literature on allelopathy, and allelopathy in woody plants was reviewed by Norby and Kozlowski (1980).

Thompson (1985) edited a collection of papers on allelopathy, Putman and Duke (1978) discussed allelopathy in agriculture, and Putnam and Tang (1986) edited a book on allelopathy.

The Replant Problem

When old orchards and vineyards are replanted the new plants sometimes grow poorly or even die. Although this has been attributed to injurious products of root decay (Israel *et al.*, 1973; Proebsting and Gilmore, 1941), there seem to be other possible causes. These include an increase in nematodes and various fungi, poor drainage, and inadequate aeration. Survival of replants often is improved by deep plowing and soil fumigation. The success of soil fumigation suggests that nematodes and fungi are more important than allelopathic compounds. Unfortunately, fumigation also often kills beneficial organisms as well as harmful ones, necessitating reinoculation of the soil with beneficial organisms to restore full productivity. Catska *et al.* (1982) reported that changes in soil microflora have contributed to the decline of apple trees in Czechoslovakia. Yadava and Doud (1980) reviewed the replant problem in horticulture. Although it has not yet been recognized widely in forestry, the increasing use of short rotations is likely to result in its appearance.

Crop rotation is a related problem. For many years rotation was regarded as essential in improving the control of weeds, diseases, and insects; decreasing injury from toxic products of root decay; and increasing the nitrogen supply by including a legume in the rotation. However, an increased use of fertilizers and pesticides and an increased disease resistance of newer cultivars of crop plants has resulted in a decreased dependence on crop rotation. Nevertheless, the long-term effects of rotation on soil, root growth, and crop yield need further study. An extensive review of the numerous effects and benefits of crop rotation has been done by Sumner (1982).

Biochemistry of Competition and Infection

It seems that root competition, allelopathy and autotoxicity, symbiotic relationships such as those with mycorrhizal fungi and nitrogen-fixing bacteria and fungi, and attacks by parasitic organisms involve complex biochemical interactions involving host recognition and defense mechanisms. Research at the cellular and molecular level is beginning to contribute to a better understanding of these interactions. An example is the change in root metabolism associated with the development of mycorrhizal roots on Eucalyptus (Hilbert *et al.*, 1991), although this is questioned by Guttenberger and Hampp (1992). Kapolnik *et al.* (in Schultz and Raskin, 1994) discuss signals between roots and fungi in the formation of VA mycorrhizae. Another example is germination of the seed of witchweed (*Striga*) in response to phenolic compounds synthesized in roots of

potential hosts (Lynn and Chang, 1990; Lynn and Boone in Schultz and Raskin, 1994). Lynn and Chang (1990) also discussed the role of specific phenolic compounds believed to be involved in root infection by *Rhizobium* and the general nature of the signals promoting host recognition and infection. There probably will be much more research in this area in the near future.

Atmospheric Conditions

Attention has thus far been on the soil atmosphere, but the atmospheric conditions to which the tops are exposed obviously can have important indirect effects on root growth. For example, low light intensity usually limits root growth and reduces the root–shoot ratio because it reduces the supply of carbohydrates available to the roots. An increase in atmospheric CO₂ often is accompanied by an increase in the ratio of roots to shoots in herbaceous plants. Rogers *et al.* (1992) reported that high atmospheric CO₂ more than doubled the root weight of soybeans, but the effects on roots of woody plants are variable (Sionit and Kramer, 1986). The variable results might have resulted from root restriction in some experiments (Thomas and Strain, 1991). According to Norby (1987), an increase in atmospheric CO₂ increases the nitrogen fixation of some woody species and it also increases mycorrhizal development (O'Neill *et al.*, 1987). Bottomley *et al.* (1993) claimed that high atmospheric CO₂ caused increased water content of the upper roots and lower stems of water-stressed beans. Some effects of CO₂ were reviewed by Bowes (1993), but he gives no data on root growth.

Miscellaneous Effects

Other interesting and sometimes puzzling results of environmental effects on root growth have been reported. For example, Carmi *et al.* (1983) found that restricting the root systems of beans in very small pots kept well watered and fertilized depressed shoot growth, but not the rate of photosynthesis per unit of leaf area. In another study (Carmi, 1993), root restriction reduced the accumulation of nitrogen compounds in the leaves, but this was not regarded as the major cause of reduced growth. The inhibitory effect of small container size and reduced soil volume on growth of well-watered and fertilized ornamental plants also may be important (Krizek and Dubik, 1987). One can speculate that reduced growth might be related to the smaller number of growing root tips and the reduced synthesis of growth regulators. A reduction in sink size may also reduce photosynthesis by feedback inhibition. Thomas and Strain (1991) found that the reduction of root size by growing cotton in small containers eliminated the increase in plant biomass observed in plants grown in larger containers when both were exposed to high atmospheric CO₂. According to Fuleky and Nooman in McMichael and Persson (1991), growing maize in small pots in-

creased root density and uptake of phosphorus per unit of root. Masle and Pasioura (1987) reported that an increased bulk density of soil reduced leaf area and root and shoot dry weight of wheat, possibly by changes in hormones exported to the shoots from the roots. However, Tardieu *et al.* (1991) questioned if mechanical restraint on roots caused by soil compaction sends signals to the shoots in maize. Much remains to be learned about root–shoot interactions and the effects of environmental factors on root growth and indirectly on shoot growth.

METHODS OF STUDYING ROOT SYSTEMS

Observation of the development of root systems seems to have begun with work of Duhamel du Monceau about 1764–1765 on root systems of trees and reached a peak in the first half of this century with the observations of Weaver (1925) in the United States and Kutschera (1960) in Europe. The early work was summarized by Böhm (1979) and some later work by Glinski and Lipiec (1990) and Caldwell and Virginia (in Pearcy *et al.*, 1989), along with Vogt and Persson (in Lassoie and Hinckley, 1991), to whose bibliographies the reader is referred. Epstein (in Hashimoto *et al.*, 1990) has a good review of methods useful for studying roots and root systems, with special reference to the mineral nutrition of plants.

The oldest method of studying root systems was to excavate them, a method that requires much time, energy, and a disregard for getting dirty. One form of excavation requires cutting a trench and then removing soil by hand or by a stream of water or air, while mapping the roots on the face of the trench. This was used effectively on fruit trees by Oskamp and Batjer (1932) and on forest trees by Coile (1937) and many others (see Böhm, 1979). Occasionally soil is removed in the horizontal plane to expose the spread of tree root systems. Another approach, the monolith method, is to remove large blocks of soil and wash out the roots. Sometimes these blocks are enclosed in steel boxes driven into the soil to hold the soil mass together while removing it. Boards covered with spikes, called pinboards, are sometimes driven into the soil mass to preserve the root arrangement while the soil is washed away. Root frequency sometimes is sampled in cores of soil removed with various kinds of soil augers, which frequently are driven into the soil and removed by tractor power (Jaafar *et al.*, 1993). W. S. Clark (1875), who made the first measurements of root growth in the United States, known to the authors, grew plants in greenhouse benches and washed out the roots.

Another method, apparently introduced by Sachs in 1873, is to install glass plates in the soil and observe root growth against them. From this has developed the elaborate rhizotrons at East Malling, Auburn, Alabama, Ames, Iowa, and elsewhere which have large underground observation tunnels and observation

windows large enough to follow the development of tree root systems. Minirhizotrons also have come into use, consisting of plastic tubes about 5 cm in diameter and 2 or 3 m long which are driven into the ground, usually at an angle. A camera and a fiber optic illumination system can be lowered down the tube to record root growth over time. An example is described by Upchurch and Ritchie (1988) and another by Box and Ramseur (1993). Buckland *et al.* (1993) discussed the problems involved in converting minirhizotron observations into root length density data. The advantages and disadvantages of various methods are discussed by Böhm (1979, pp. 75–76) and by Glinski and Lipiec, (1990, Chapter 7). Heeramon and Juma (1993) concluded that destructive sampling is still the best method to study root growth.

Couchat *et al.* (1980) used neutron radiography to study root growth in sand, and nuclear magnetic resonance imaging shows promise for some purposes (Brown *et al.*, 1986, 1991; Omasa *et al.*, 1985b; Rogers and Bottomley, 1987). MacFall *et al.* (1990, 1991a) showed development of a water depletion zone around suberized pine roots by NMR imaging (Fig. 5.9) and Omasa *et al.* (1985b) used it to show changes in root and soil water content. The use of nuclear magnetic resonance technology for research on plants has been discussed by Kramer *et al.* (in Hashimoto *et al.*, 1990) and for plants and soil by MacFall and Johnson (1994). An example of its use is described in a paper by Zimmermann *et al.* (1992). Hegde and Miller (1992) reported that scanning electron microscopy is useful for studying root anatomy and morphology. However, these methods cannot provide images of large root systems.

Several indirect methods have been used to estimate root density and the rate of root extension in the soil. One method is to measure the decrease in soil water content, assuming that a decrease is closely related to root density. This is most useful if rainfall is infrequent or if rain shelters are available. Root extension also has been followed by injecting small quantities of a radioactive isotope of phosphorus, sulfur, or rubidium into the soil at various depths below and distances from seedlings and noting when it appears in the plant. An example is shown in Fig. 5.6. Sometimes the tracer is injected into the plant and is recovered from root samples in soil cores (Fusseder, 1983). Some success has been attained in using ^{14}C as a tracer of carbon transport to the roots and to distinguish between living and dead roots. These methods are discussed in Chapter 8 of Böhm (1979).

Measurement of the ratio of deuterium to hydrogen (D/H ratio) in xylem sap has proven useful in studying plant–soil water relations (White in Rundel *et al.*, 1988). For example, White *et al.* (1985) found that bald cypress growing in a swamp showed no isotopic change in response to rain because most of its roots were below the surface of the water table, whereas trees on a dry site used rainfall water exclusively for several days after a rain. Trees on intermediate sites used both at first, but a few days after a rain they were using groundwater ex-

clusively. In another study, Flanagan *et al.* (1992) used the difference in the D/H ratio between rain water and soil water to determine the relative uptake of rain and groundwater by woody plants in a pinyon-juniper woodland.

SUMMARY

The principal functions of roots are anchorage, absorption of water and minerals, and synthesis of nitrogen compounds and growth regulators such as abscisic acid, cytokinins, and gibberellins which have essential roles in shoot growth and functioning. Roots may also play a role as sensors of water stress which causes them to send biochemical signals to shoots that reduce leaf growth and stomatal conductance even before there is any significant reduction in leaf turgor.

Growing roots typically show several well-defined regions, including the root tip and root cap, a light colored zone covered with root hairs, and a darker colored region where suberization of epidermal cells occurs. Root hairs increase root contact with the soil and presumably increase the absorbing surface for water and minerals, although the importance of this seems to vary among species and with various ions. The effective absorbing surface also is increased by the presence of mycorrhizal fungi. Secondary growth causes loss of epidermis and cortex and the development of bark which decreases root permeability to water. Nevertheless, considerable absorption of water and minerals occurs through suberized roots, especially when root elongation is slowed by cold or dry soil.

Root elongation varies from a few millimeters to a few centimeters per day, and it sometimes results in root systems hundreds of kilometers in length and occupying large volumes of soil. The depth and the spread of root systems are controlled by heredity and environment, varying widely among species and with water content, temperature, and aeration of the soil. Flooding soil injures the roots of most plants, but is tolerated by a few such as rice, cattails, and cypress trees. Tolerance of flooding depends on the presence of aerenchyma which facilitates movement of oxygen from shoots to roots, on physiological adaptations that permit metabolism at low oxygen concentrations, or on a combination of the two.

Successful plant growth depends on maintenance of a balance between root and shoot growth, but there are wide differences among species with respect to successful root-shoot ratios. Severe defoliation usually drastically reduces root growth, chiefly because it reduces the supply of carbohydrates. The development of fruits and seeds also reduces root growth, but hormonal controls may be involved in addition to competition for carbohydrates. Flushes of root and shoot growth often alternate, probably because of competition for food. There is a strong interdependence between roots and shoots and anything that inhibits one is likely to affect the other.

Roots of trees often form so many root grafts that the trees of a stand are interconnected and form essentially one organism. In general, plants tend to produce more roots than are necessary for survival, except during very severe droughts. However, root growth often is inhibited by soil resistant to root penetration; by deficient aeration, low pH, or an excess of toxic elements such as aluminum; and by competition with other roots. Roots of a few species of plants produce substances toxic to other plants (allelopathy), and growth sometimes is retarded when orchards and vineyards are replanted to the same species. Small containers that restrict root growth often inhibit shoot growth, even when well watered and fertilized.

In conclusion, conditions favorable for root growth are just as important to the success of plants as conditions favorable for shoot growth.

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