

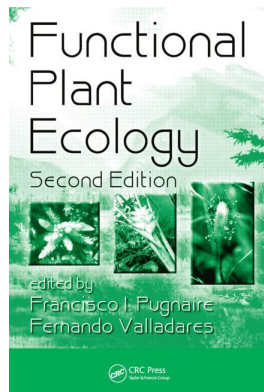
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## **Functiona Plant Ecology**

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### **Structure and Function of Root Systems**

Publication details

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch5>

Robert B. Jackson, William T. Pockman, William A. Hoffmann, Timothy M. Bleby, Cristina Armas

**Published online on: 20 Jun 2007**

**How to cite :-** Robert B. Jackson, William T. Pockman, William A. Hoffmann, Timothy M. Bleby, Cristina Armas. 20 Jun 2007, *Structure and Function of Root Systems from: Functiona Plant Ecology* CRC Press

Accessed on: 05 Dec 2023

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch5>

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# 5 Structure and Function of Root Systems

*Robert B. Jackson, William T. Pockman,  
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and Cristina Armas*

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## INTRODUCTION

The study of root structure and functioning is centuries old (Hales 1727, reprinted 1961). While great progress has been made (e.g., Brouwer et al. 1981), our knowledge is limited by the difficulties in studying roots *in situ*. These limitations color our perception of plants. A typical layperson knows that forests can grow 50–100 m in height, but rarely recognizes that root systems can grow to similar depths (Canadell et al. 1996). The individual may also never consider the functional consequences of roots that typically spread well beyond the canopy line of most plants (e.g., Lyford and Wilson 1964). Just as there is a quiet bias in maps of the world that consistently present the northern hemisphere “on top,” our perception of plants would change if they were drawn “upside-down”—roots on top and

shoots underneath. A small shrub such as *Prosopis glandulosa* would suddenly appear as majestic as a tree, and many trees would suddenly seem shrubby. The bias of human perception shadows our view of the plant world.

Root and shoot functioning are often studied separately, in part because the techniques and equipment needed can differ substantially. In reality, roots and shoots are functionally integrated. This integration is evident in patterns of standing biomass and allocation. With the exception of forests, most natural systems have root:shoot ratios (the ratio of root to shoot biomass) between 1 and 7, including tundra, deserts, and grasslands (Jackson et al. 1996, 1997). Most forest systems typically have root:shoot ratios of approximately 0.2, with the majority of biomass stored as woody biomass in the boles of trees. Even for forests, half or more of annual primary production is usually allocated belowground (e.g., 60% for a *Liriodendron tulipifera* forest, Reichle et al. 1973). This is not to imply that roots are more important to the functioning of plants than are shoots, but just to demonstrate that they are no less important.

The purpose of this chapter is to provide an introduction to the structure and functioning of root systems. We begin by outlining the basics of root morphology and development. We next examine four broad categories of root functioning: anchoring, resource uptake, storage, and sensing the environment. Information on more specialized root functions such as reproduction and aeration is available elsewhere (e.g., Drew 1997). We discuss two important root symbioses, mycorrhizal associations, and symbiotic nitrogen fixation. We end by examining global patterns of root distributions for biomes and plant functional types. Interested readers will find references in each section that provide comprehensive detail on each topic.

## ROOT MORPHOLOGY AND DEVELOPMENT

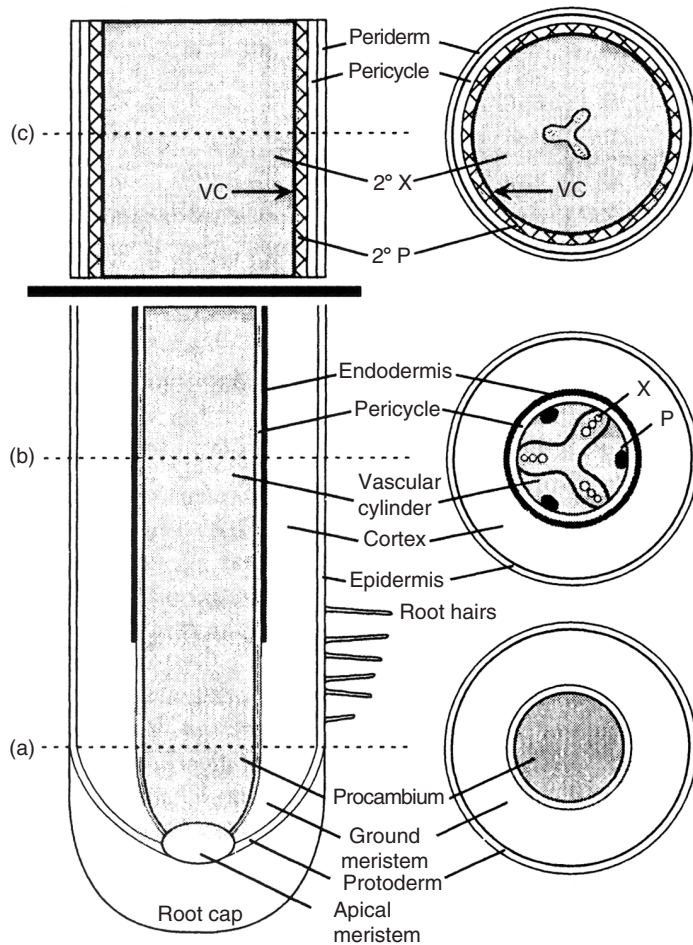
We begin by reviewing the generalized structure of primary roots, including the main tissue types within roots and changes that occur with secondary growth and tertiary root morphology. A more detailed discussion of these and other structural features can be found in complete botanical and anatomical texts (e.g., Esau 1977, Mauseth 1988).

### PRIMARY ROOT ANATOMY

As in other plant organs, cell division during primary root growth occurs in the apical meristem, giving rise to the undifferentiated cells of the protoderm, ground meristem, and procambium (Figure 5.1a). Root length increases as these newly produced cells elongate and differentiate in the region immediately behind the root tip. As a result, root anatomy and functioning change with distance from the tip and all developmental stages may be present in a single root.

### Epidermis

The epidermis is derived from the protoderm and generally consists of a single layer of cells forming the outermost root tissue (Figure 5.1b). A key feature of the epidermis is root hairs, elongated cells projecting into the surrounding soil (Hofer 1991). Root hair density is typically greatest in the most distal region of the primary root behind the root tip. This so-called root hair zone has been widely regarded as the location of most water and nutrient uptake (but see Section “Vascular Cylinder”). Although root hairs persist in some species, their distribution is generally restricted to the distal portion of the root because the oldest root hairs are lost and new ones are produced only near the root tip. Root hair density ranges from 20 to 2500 per  $\text{cm}^2$  (Dittmer 1937, Kramer 1983) and can more than double the root surface area in contact with the soil, resulting in a greater accessible soil volume (Kramer 1969). In many but not all species, nutrient absorption increases in proportion to root hair density (Bole 1973, Itoh and Barber 1983).



**FIGURE 5.1** Longitudinal and cross-sectional schematics of generalized root anatomy. Cross sections are indicated by broken lines through the longitudinal section on the left. Drawing is not to scale to allow illustration of the key features of the root. (a) Undifferentiated cells of the protoderm, ground meristem, and procambium produced by divisions of the root apical meristem located immediately behind the root cap. (b) Differentiated primary tissues: epidermis (from protoderm), cortex and endodermis (from ground meristem) xylem (X), phloem (P), and pericycle (from procambium). (c) Root anatomy after substantial secondary growth. Differentiation of cells between xylem and phloem bundles (b) has produced the vascular cambium (VC). Divisions of the cambial initials give rise to secondary xylem ( $2^{\circ}$  X) and phloem ( $2^{\circ}$  P). The cortex, and with it the endodermis, has ruptured and sloughed off with growth of the vascular cylinder and is not visible at this stage. The suberized lignified periderm, ultimately derived from the pericycle, has developed and assumed the function of sealing the root from the surrounding soil. The primary xylem is visible at the center of the secondary xylem. (Adapted from Raven, P., Evert, R., and Eichhorn, S., *Biology of Plants*, 4th edition, Worth, New York, 1986. With permission.)

## Cortex

The cortex is derived from the ground meristem, composed largely of parenchyma cells. It lies between the epidermis to the outside and the vascular cylinder at the center of the root (Figure 5.1b). The cortex may develop large air canals that increase oxygen availability to root cells, and it can be an important site for carbohydrate storage (Mauseth 1988). Perhaps the most

studied feature of the cortex is the endodermis, a single cell layer defining the interior edge of the cortex. The central feature of the endodermis is the casparian band formed by the deposition of suberin in the primary cell wall and middle lamella of each adjoining endodermal cell. The result is a continuous suberized barrier preventing passage of soil solutes from the cortex into the vascular cylinder without crossing a cell membrane (Weatherley 1982, Clarkson 1993). Recent studies suggest that a more complex model of water and solute uptake may be appropriate but support the importance of the casparian band in providing control over solute flow into roots (Steudle 1994, Steudle and Meshcheryakov 1996). Many taxa also form an exodermis, an anatomically similar cell layer located at the outer edge of the cortex (Perumalla et al. 1990, Peterson and Perumalla 1990).

### **Vascular Cylinder**

The vascular cylinder develops from the procambium in the center of the root and is delimited by a single layer of parenchyma cells called the pericycle (Figure 5.1b). In cross section, the primary xylem is arranged in finger-like projections from the center of the root toward the pericycle. Phloem bundles occur between these xylem projections. The smallest xylem conduits, the protoxylem, occur at the tips of these projections whereas the larger conduits of the metaxylem are located more centrally and mature later. Root uptake of water and nutrients requires axial transport through functional xylem conduits, which are dead at maturity. Although the root hair zone is often cited as the site of maximum uptake, studies of maize and soybean suggest that water absorption in the root hair zone may be restricted because the largest metaxylem conduits are still alive and nonconducting (McCully and Canny 1988). Future work addressing the relative timing of maturity of the xylem, endodermis, and root hairs across taxa will improve our understanding of the contribution of different developmental stages of the root to resource uptake (McCully 1995).

### **Lateral and Adventitious Roots**

The production of lateral roots is an important feature determining the tertiary (three dimensional) structure of the root system and the distribution of surface area for resource uptake. Lateral roots occur in gymnosperms and dicots and arise from root primordia in the pericycle and, less commonly, the endodermis (Peterson and Peterson 1986). As a root primordium elongates, it passes through the cortex and epidermis. Vascular tissues differentiate within the developing root and are connected with the plant's vascular system at the base of the primordium. Many cortical cells are crushed during lateral root emergence, though anticlinal divisions of the endodermis (in which the cell plate forms perpendicular to the nearest tissue surface) minimize disruption of the casparian band around the emerging lateral root. Nevertheless, lateral root growth may provide a pathway for the flow of water in or out of the vascular cylinder that is not controlled by the casparian band (Kramer and Boyer 1995, Caldwell et al. 1998).

Adventitious roots originate from aerial or underground plant stems. They occur in most plant taxa and are particularly important in the monocotyledons, comprising most of the root system (for review see Davis and Haissig 1994). Adventitious roots develop from root primordia, which can arise in most tissues of plant stems. As in lateral roots, these primordia differentiate into cell types typical of a root, and vascular connections are formed with existing xylem and phloem at the root origin.

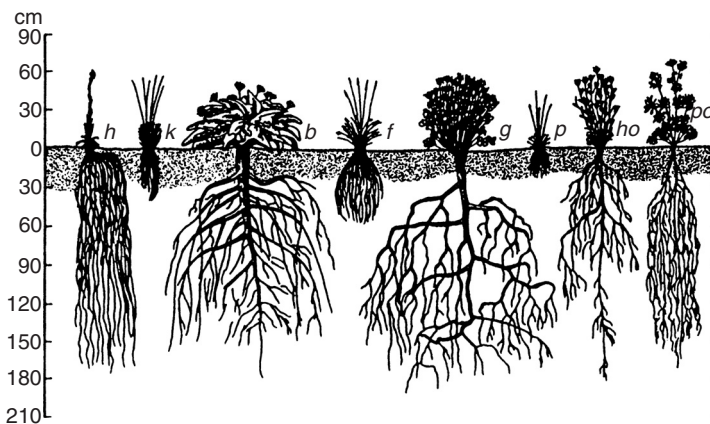
### **SECONDARY GROWTH**

Secondary growth in roots is clearly important for the ability of plants to become "woody" and perennial. It occurs commonly among gymnosperms, to varying degrees among dicotyledonous plants, and is absent among the monocots (Mauseth 1988). The initiation of

secondary growth is preceded by the formation of a vascular cambium derived from undifferentiated procambium and parts of the pericycle (Figure 5.1c). The vascular cambium forms a ring of meristematic cells between the phloem and xylem. These cambial initials give rise to xylem and phloem cells by periclinal divisions (the cell plate forms parallel to the nearest tissue surface) and accommodate increases in root diameter by occasional anticlinal divisions, which maintain the continuity of the cambium. Likewise, the pericycle undergoes both periclinal and anticlinal divisions giving rise to the phellogen, a meristematic tissue that produces the periderm. These changes are not accompanied by further divisions of the cortex, which becomes fractured and lost as the root increases in diameter. The periderm, which includes the suberized cells of the cork, becomes the outer surface of the root and assumes the protective function formerly provided by the epidermis and endodermis.

### TERTIARY ROOT MORPHOLOGY

Root development among seed plants begins with the elongation of the taproot. For gymnosperms and dicots, the three-dimensional structure of the taproot and its branched lateral roots define the morphology of the root system (Figure 5.2). In contrast, the early demise of the taproot and the subsequent growth of adventitious roots in monocots result in a fibrous root system emanating from the base of the stem (limiting the rooting depth of monocots). This difference, combined with the lack of secondary growth in roots of monocots, defines an important functional difference between taxa that possess these very different root systems (Caldwell and Richards 1986). Although the absence of secondary growth limits the rooting depth of monocots, they often have very high root length densities in the soil volume they explore (Glinski and Lipiec 1990). In contrast, the taproot system of dicots and gymnosperms is often capable of exploring soil volume that extends both laterally and vertically beyond the reach of many monocots. Despite their different structural characteristics, both fibrous and taproot systems are capable of differential root proliferation in response to resource patches in the soil (e.g., Drew 1975, Bilbrough and Caldwell 1995). The exploitation of such resources is addressed later in this chapter.



**FIGURE 5.2** Differences in rooting system morphology among prairie grasses (family Gramineae) and herbs: *h*, *Hieracium scouleri* (Compositae); *k*, *Koeleria cristata* (Gramineae); *b*, *Balsamina sagittata* (Balsaminaceae); *f*, *Festuca ovina ingrata* (Gramineae); *g*, *Geranium viscosissimum* (Geraniaceae); *p*, *Poa sandbergii* (Gramineae); *ho*, *Hoorebekia racemosa*; *po*, *Potentilla blaschkeana* (Rosaceae). (From Kramer, P. and Boyer, J., *Water Relations of Plants and Soils*, Academic Press, San Diego, CA, 1995; after Weaver, J.E., *The Ecological Relations of Roots*, Publication 286, Carnegie Institution of Washington, Washington D.C., 1919. With permission.)

## ROOT FUNCTIONS

Root systems have at least five broad functions: anchoring plants, capturing resources, storing resources, and sensing and modifying the environment. Such distinctions are arbitrary, but provide a useful framework for examining root functioning.

### ANCHORING

Probably the most fundamental root function is to hold plants in place. This need is most obvious in protecting trees from windthrow, but shrubs and herbaceous vegetation are also exposed to the vagaries of wind, trampling, and herbivores. Resistance to toppling has economic importance for crop species, too, whose root systems tend to be fairly shallow (Brady 1934).

In general, there are three kinds of mechanical failure in plants—uprooting, stem failure, and root failure. The biomechanics of root anchoring can be studied by uprooting plants mechanically and recording the resistance with a strain gauge (e.g., Somerville 1979, Mattheck 1991). Results from these and other experiments show that resistance to windthrow has two primary components: the resistance of leeward laterals to bending and the resistance of windward sinkers and taproots to uprooting. Bending tests on the leeward laterals of a deep-rooted larch species showed that they provided approximately 25% of tree anchorage support (Crook and Ennos 1996). Consequently, about three quarters of the stability in that system came from taproots and windward sinkers. Where there is a prevailing wind direction, there is often an asymmetrical development of structural roots—for example, greater root development on the leeward side than on the windward side of a tree (Nicoll and Ray 1996). The cross-sectional structure of individual roots can also differ depending on the location of the roots. Secondary growth above the center of a root can lead to a classic T-beam structure (swollen on top and thinner on the bottom). This type of thickening is more common in roots relatively close to the trunk (<1 m away), particularly on the leeward side of trees. Roots with an I-beam structure can be more prevalent at greater distances, especially on the windward side. Such roots resist vertical flexing (Nicoll and Ray 1996). Stokes et al. (1996) developed a theoretical model of anchoring, resistance to uprooting, and root branching patterns. Not surprisingly, deep roots were especially important.

### RESOURCE UPTAKE

Leaves and roots play analogous roles in plants. Leaves are the structures primarily responsible for carbon and energy uptake and fine roots take up most of the water and nutrients acquired by plants. This dichotomy of structure and function is useful conceptually because above- and belowground resources are generally separated. In practice, however, it is difficult to disentangle aboveground and belowground processes (e.g., Donald 1958, Jackson and Caldwell 1992). Light availability powers the enzymes responsible for phosphate transport; adequate root surface area depends on the amount of CO<sub>2</sub> taken up by shoots. In turn, carbon and energy uptake requires soil water for the maintenance of turgor and stomatal conductance and nitrogen to build photosynthetic proteins such as RuBP Carboxylase. This interdependence has led to many perspectives on the “balance” of root and shoot processes (e.g., Brouwer 1963). In the following discussion of resource uptake by roots, we focus on the uptake of water, nitrogen, and phosphorus. A more detailed discussion can be found in Nye and Tinker (1977), Marschner (1995), and Casper and Jackson (1997), on which much of the following section is based. Additional perspectives can be found in Chapter 8, which describes the acquisition, use, and loss of nutrients.

Soil resources typically reach the surface of roots by three processes: root interception, mass flow of water and nutrients, and diffusion (Marschner 1995). Root interception occurs

as a root grows through the soil, physically displacing soil particles and clay surfaces and acquiring water and nutrients. This process typically accounts for >10% of the resources taken up by roots. Mass flow, which is driven by plant transpiration, depends on the rate of H<sub>2</sub>O movement to the root and the concentration of dissolved nutrients in the soil solution. Nutrient diffusion toward the root occurs when nutrient uptake by the root exceeds the supply by mass flow and a depletion zone around the root is created. The supply of nutrients by diffusion is especially important for those with large fractions bound to the soil matrix, such as K<sup>+</sup> and H<sub>2</sub>PO<sub>4</sub><sup>-</sup>. In nature, mass flow and diffusion work in concert to supply N, P, and K and are difficult to separate in the field (Nye and Tinker 1977).

Water moves into and out of roots passively based on the water potential gradient in the soil–plant system. In contrast, nutrient uptake is generally an enzymatic process that follows apparent Michaelis–Menten kinetics:

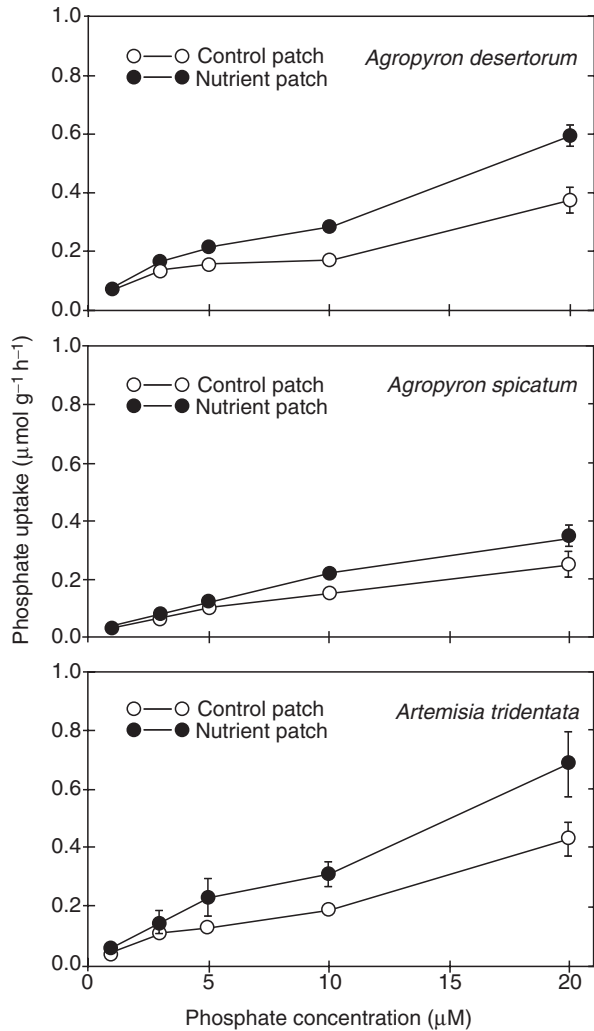
$$V = V_{\max} C_1 / (C_1 + K_m),$$

where  $V$  is the flux of ion into the root per unit time,  $V_{\max}$  is the maximum influx rate,  $C_1$  is the soil solution concentration at the root surface, and  $K_m$  is the soil solution concentration where influx is 50% of  $V_{\max}$  (Nye and Tinker 1977). The equation sometimes includes a  $C_{\min}$  term, the soil solution concentration at which net influx into the root is zero (Barber 1984). Because nutrient uptake is generally enzymatic, it is sensitive to reductions in photosynthesis by shoots (e.g., Jackson and Caldwell 1992).

The belowground competitive ability of plants is often directly proportional to the size of their root systems. This is in contrast to shoot systems, where a relatively small portion of leaves can overtop a canopy and acquire most of the available light. There are many examples where root systems with the highest densities and occupying the most space are the strongest competitors (Aerts et al. 1991, Casper and Jackson 1997). Consequently, a plant may grow higher root densities or extend the volume of soil explored to acquire more water and nutrients. Plants can also increase resource uptake by selective foraging. Plants frequently respond to enriched patches of soil water and nutrients by proliferating roots, selectively growing roots in the zone of enrichment (e.g., Duncan and Ohlrogge 1958, Berendse et al. 1999, chapter 8). Proliferated roots tend to be smaller in diameter and greater in density than those found in the background soil. A second, related factor that may increase resource uptake is a change in fine-root demography. In a Michigan hardwood forest, not only did roots proliferate in response to water and nitrogen patches, but the new roots lived significantly longer than new roots in control patches (Pregitzer and Hendrick 1993). Architectural adjustment (changes in root topology, length, or branching angles) is another type of morphological plasticity that can increase nutrient uptake. Fitter (1994) examined the architectural attributes of 11 herbaceous species and showed that roots in relatively high-nutrient patches typically had a more herringbone branching pattern than roots in low-nutrient patches, concentrating higher-order lateral roots in the patches and increasing the efficiency of nutrient uptake.

Physiological plasticity can selectively increase nutrient uptake by altering enzyme attributes or other physiological traits. A species with more enzymes per root surface area (greater  $V_{\max}$ ), a higher ion affinity of enzymes (smaller  $K_m$ ), or a greater ability to draw nutrients down to a low level (smaller  $C_{\min}$ ) will be at a competitive advantage (ignoring other factors). Plants in the laboratory and in the field have been shown to increase  $V_{\max}$  and decrease  $K_m$  in response to localized nutrients (e.g., Drew and Saker 1975, Jackson et al. 1990). For example, Jackson et al. (1990) showed that grass and shrub species in the field were able to selectively increase physiological rates of phosphate uptake in portions of their root system in fertilized soil patches (Figure 5.3). For water uptake, osmoregulation can lower cell water potential and maintain net uptake in the face of drying soils (Kramer and Boyer 1995). It is the suite of





**FIGURE 5.3** The rate of phosphate uptake for roots from enriched and control soil patches as a function of solution phosphate concentration (mean  $\pm$  SEM;  $n = 6-8$ ). Soil patches on opposite sides of plants in monoculture field plots were treated with 750 ml of nutrient solution or distilled water and samples of the soil patches were cored 1 week after treatment. Roots from each core were subsampled and immersed in  $^{32}\text{P}$  solutions. Results were similar for 3-day experiments as for the week-long experiments shown here. (From Jackson, R.B., Manwaring, J., and Caldwell, M., *Nature*, 344, 58, 1990. With permission.)

morphological and physiological attributes that determine resource uptake by plants. While their genetic make-up plays a fundamental role in the type of root system plants possess, there is often great flexibility in how those genes are expressed based on environmental cues.

Extensive overviews of morphological and physiological plasticity and resource capture can be found in Hutchings and de Kroon (1994) and Robinson (1994). See also Chapter 8 in this volume.

## STORAGE

Plants must cope with variable environments where the timing of resource availability and uptake may not coincide with demand by the plant. The storage of carbohydrates, nutrients,

and, to a lesser extent, water when resources are abundant provides insurance for future periods of high demand. Although many plant organs are involved in storage, roots are the most important storage site for many species. Roots play a particularly important role in cases where complete regeneration of aerial biomass is necessary. Perennial and biennial herbaceous species enduring seasonal environments or intense herbivory must rely heavily on belowground reserves. Woody plants in fire-prone environments such as Mediterranean-type ecosystems and savannas also depend heavily on roots for nutrient and carbohydrate storage (Miyanishi and Kellman 1986, Bowen and Pate 1993, Bell et al. 1996). Even in environments not typically subjected to fire, woody roots are an important site for storage, with carbohydrate concentrations often exceeding those in stems (Loescher et al. 1990).

In many species, belowground storage occurs in modified stems such as rhizomes, bulbs, corms, stem tubers, lignotubers, and burls (de Kroon and Bobbink 1997). These organs are functionally similar to roots with respect to storage and are included in our discussion. Among true roots, storage can occur in all size classes of roots, but specialized, large-diameter roots such as root tubers and taproots often play the most important role.

Most of the mineral nutrients required by plants are stored in roots (Pate and Dixon 1982), but the majority of studies have focused on carbon, nitrogen, and phosphorus. Consequently, most of our discussion is devoted to these elements. A large number of chemical compounds are involved in their storage. In roots, starch is the most important form of carbon storage, though other polysaccharides can be important (Lewis 1984). In particular, fructan, a polymer of fructose, is common in many monocots and a few dicot families (Pollock 1986). Sucrose, monosaccharides, sugar alcohols, and lipids can also be prevalent (Glerum and Balatinecz 1980, Lewis 1984, Dickson 1991). Nitrogen is stored as specialized storage proteins, amino acids, amides, or nitrate (Tromp 1983, Staswick 1994). Phosphorus is stored primarily as phosphate, phytic acid, and polyphosphate (Bieleski 1973).

Within the cell, the vacuole is the most important site for the storage of sugars, phosphate, and nitrogen (Bieleski 1973, Willenbrink 1992), whereas starch storage occurs in plastids (Jenner 1992). In roots, storage occurs primarily in parenchyma cells (Bieleski 1973, Jenner 1992, Bell et al. 1996).

Plant storage of materials can be classified as accumulation or reserve storage (Chapin et al. 1990). Accumulation occurs when the uptake of a resource is greater than the plant's immediate capacity to use the resource. The plant would not be able to use the resource for other functions, so its storage does not compete with growth and maintenance. In contrast, reserve formation occurs at a time when the resource could otherwise be used for growth. Because reserve formation competes directly with growth and maintenance, there is a substantial cost in forming reserves.

Both accumulation and reserve formation are strongly influenced by resource availability. Shading reduces root carbohydrate concentrations (Jackson and Caldwell 1992, Bowen and Pate 1993), whereas elevated CO<sub>2</sub> can increase carbohydrate storage (Chomba et al. 1993). Nitrogen and phosphorus accumulation is typical under high nutrient availability (Chapin 1980), a response typically referred to as luxury consumption.

Low availability of one resource often increases the storage of other resources. For example, root carbohydrate storage has been found to be greater under water stress because tissue growth was more inhibited than photosynthesis (Busso et al. 1990). Low nutrient availability can also increase root carbohydrates (Jackson and Caldwell 1992) as has been shown for leaves (Waring et al. 1985, McDonald et al. 1991), presumably because low nutrient availability results in lower tissue production, reducing demand for photosynthate. These cases represent accumulation rather than reserve formation, because the storage results from low demand for the resource within the plant.

Demand for resources within the plant also largely determines the timing of storage. In herbaceous perennials and deciduous woody plants, root reserves are retranslocated at the

beginning of the growing season to supply developing leaves, stems, and flowers. As a result, lowest reserve concentrations occur around the end of leaf flush (Woods et al. 1959, Daer and Willard 1981, Chapin et al. 1986, Keller and Loescher 1989, Wan and Sosebee 1990). After leaf maturation, the root undergoes a transition from carbohydrate source to carbohydrate sink, and replenishment of carbohydrate reserves begins. Root carbohydrate concentration reaches a peak around the time of leaf-fall (Woods et al. 1959, Daer and Willard 1981, Chapin et al. 1986, Keller and Loescher 1989, Wan and Sosebee 1990). In contrast to deciduous species, evergreen plants show lower seasonal fluctuations in the concentration of stored carbohydrates (Chapin et al. 1986, Dickson 1991).

Similar trends are observed in woody plants subjected to fire, but replenishment of the reserves often takes longer (Miyanishi and Kellman 1986, Bowen and Pate 1993). This slower replenishment may result from the greater amount of aerial biomass that must be replaced or may represent an adaptation to a less frequent form of disturbance. On the other hand, grasses tolerant to frequent grazing exhibit rapid recovery of carbohydrate reserves after grazing occurs (Owensby et al. 1970, Oesterheld and McNaughton 1988, Ordo and Trlica 1990).

If disturbance recurs before adequate replenishment is complete, further recovery will be compromised (Miyanishi and Kellman 1986, Kays and Canham 1991). Overall, the cost associated with rapid replenishment of reserves can be quite large if replenishment competes with plant growth (Chapin et al. 1990).

## PRODUCING HORMONES AND SENSING THE ENVIRONMENT

In addition to anchoring the plant and taking up and storing resources, roots sense their environment (Mahall and Callaway 1991) and convey information on the balance between root and shoot functioning in the form of hormones. Plants produce a variety of hormones, including auxin, cytokinins, gibberellins, ethylene, and abscisic acid (ABA). Depending on how broad the definition of a hormone is, other compounds such as jasmonates and polyamines may also be considered. Plant responses to hormones depend on changes in their concentration and in the sensitivity of tissues responding to the hormone (Trewavas 1981).

There are two groups of hormones where roots are the dominant sites of synthesis: cytokinins and ABA. Cytokinins, named for their role in stimulating cytokinesis, are produced primarily in roots and are then transported in the xylem to leaves where they retard senescence and maintain metabolic activity (Torrey 1976). Cytokinins affect numerous plant processes, including cell division and morphogenesis. They affect protein synthesis and stimulate chlorophyll development. Cytokinin production also helps to coordinate root and shoot activity in plants. Roots become active in the spring and produce cytokinins that are transported to the shoot and activate dormant buds (Mauseth 1995). Cytokinins help to balance total leaf area relative to the root system by affecting rates of leaf expansion. Roots that produce cytokinins delay the senescence of shoot tissue. Cytokinins also provide a link from N uptake and the N status of roots to the synthesis of proteins. There are many other examples of how cytokinins help integrate the functioning of roots and shoots.

Unlike most plant hormones, ABA is primarily a growth inhibitor. ABA and gibberellins are both synthesized from mevalonic acid, the pathway that produces carotenoids and the general class of compounds known as terpenes. First characterized in 1963, ABA was proposed to play a role in the abscission of cotton bolls (Ohkuma et al. 1963). Subsequent evidence suggested that ethylene rather than ABA is a more important controller of abscission. Instead ABA affects such plant processes as dormancy, senescence, stress responses (including water, freezing, and salt stress), water uptake, and stomatal regulation.

The role of roots in ABA synthesis is particularly important for stomatal closure and water stress. Changes in leaf cell turgor were originally thought to be the sole cause of

stomatal closure in response to soil dehydration. However, when leaf cell turgor was maintained by pressurizing the root system, stomatal closure still occurred when part of the root system was in dry soil (Gollan et al. 1986). These data suggested that a chemical signal was produced in response to decreasing soil water status. Subsequent studies have identified ABA as the most important such signal (Davies and Zhang 1991). In leaves, ABA causes stomata to close at low concentrations ( $< \mu\text{M}$ ) by inhibiting  $\text{K}^+$  influx to guard cells and activating  $\text{K}^+$  efflux; its concentration can increase 50-fold in leaves experiencing water stress (Salisbury and Ross 1985, Walton and Li 1995). Experimental evidence suggests that ABA production in the roots is stimulated by reduced cell turgor and ABA moves to the shoots in the xylem stream (Tardieu et al. 1992). Further evidence for the importance of ABA in regulating plant water status is that mutants unable to produce ABA wilt permanently (Taiz and Zeiger 1991).

The relative contributions of water potential and ABA signals in determining leaf responses to water stress are a matter of continuing research. Reports that stomata often begin to close before any damage or detectable change in leaf water status occurs (Davies and Zhang 1991) have been interpreted as evidence that ABA signals from the roots provide a feed-forward mechanism for avoiding water stress. Tardieu et al. (1991, 1992) showed that there was a strong correlation between [ABA] in the xylem and leaf stomatal conductance ( $g_s$ ) in maize plants, but little relationship between  $g_s$  and leaf turgor or water potential. The time lag between ABA production in the root and its arrival at the leaf suggests that root signals may not be well suited for stomatal regulation over short timescales (Kramer 1988). Seasonal studies showed that ABA signals were correlated with maximum stomatal conductance during progressive drying over many days but not on a diurnal basis (Wartinger et al. 1990). Such data suggest that water potential and ABA root signals combine to affect stomatal responses to soil water status (Tardieu and Davies 1993).

A rich literature on the synthesis and effects of ABA and cytokinins is available for the interested reader (e.g., Addicott 1983, Davies and Jones 1991, Davies 1995). In addition, Davies (1995) provides an excellent physiological overview of the production and function of plant hormones.

## RELEASING EXUDATES AND MODIFYING THE ENVIRONMENT

Roots not only sense their environment, they have the capacity to modify it by secreting organic molecules and water. The secretion of organic molecules is an active process requiring metabolic energy, whereas the secretion of water is a passive process driven by natural gradients in water pressure, which exist between roots and soil. These secretions have a strong influence on the biochemical and physical properties of the rhizosphere and surrounding soil, and they play an important role in the establishment and maintenance of terrestrial plant communities (Walker et al. 2003).

Organic compounds secreted by roots are broadly referred to as root exudates. Root exudates are diverse in their composition, ranging from low-molecular mass carbon compounds (numbering upward of 100,000 compounds) to complex molecules such as polysaccharides and bioactive proteins, many of which are species-specific (Flores et al. 1999, Inderjit and Weston 2003). Overall, from 5% to 21% of all photosynthetically fixed carbon is transferred to the rhizosphere (Marschner 1995). In purely physical terms, root exudates play an important role in promoting healthy root growth by maintaining good root–soil contact, lubricating the root tip, protecting roots from desiccation, stabilizing soil micro-aggregates, and allowing selective adsorption and storage of ions (Griffin et al. 1976, Bengough and McKenzie 1997, Rougier 1981, Hawes et al. 2000). In biological terms, root exudates play an active role in rhizosphere processes, allowing individuals to regulate below-ground interactions with neighboring plants and soil organisms, including bacteria, fungi, and insects (Bais et al. 2004).

The production of root exudates can lead to either positive or negative ecological interactions among plants and soil organisms. On the positive side, root exudates can be used to encourage beneficial symbioses. For example, the roots of some leguminous species secrete isoflavonoids and flavonoids, which promote the activation of *Rhizobium* genes responsible for the nodulation process, and which may also play a role in colonization by vesicular-arbuscular mycorrhiza (Peters et al. 1986, Trieu et al. 1997). On the negative side, parasitic plant species often use compounds secreted from host roots as chemical messengers to initiate the development of invasive organs (haustoria) required for heterotrophic growth (Estabrook and Yoder 1998, Keyes et al. 2000).

Many root exudates are designed to expose other organisms to allelopathic chemicals, which are used by a plant to prevent other organisms from growing too close to it. Exudates can possess antimicrobial or antifungal properties, providing the plant with defensive advantages, a means to limit herbivory, or phytoinhibitory properties to prevent the growth of competing plants (Inderjit and Weston 2003, Bais et al. 2004). For example, an invasive forb species in the western United States, the spotted knapweed (*Centaurea maculosa*), actively displaces native plant species by exuding a phytotoxin called catechin. This compound is secreted in two forms (actually mirror images of the same molecule): (–)-catechin, which has an allelochemical activity on native plant species; and (+)-catechin, which has antimicrobial properties. The secretion of these molecules accounts in part for the extremely invasive behavior of *C. maculosa* (Callaway and Aschehoug 2000, Bais et al. 2002, 2003). Interestingly, there is also evidence to suggest that allelopathic compounds may in fact help plants to direct root growth, by segregating roots from each other and serving as a root navigation tool to detect and circumvent physical obstacles (Falik et al. 2005).

The secretion of exudates is a remarkable metabolic feature of plant roots, but an equally remarkable physical feature is their ability to move water. Plants release water into the soil through a phenomenon known as hydraulic redistribution (Burgess et al. 1998), a passive mechanism whereby water moves from regions of wet soil to those of dry soil via roots. Quite simply, roots act as conduits for the movement of water across gradients in pressure, from regions of high water potential (wet soil) to regions of low water potential (dry soil). Water can be hydraulically “lifted” from deep, wet soil layers to shallow, dry soil layers (Dawson 1993), and in the same way, water can also be redistributed downward (e.g., Burgess et al. 2001) or laterally (e.g., Smart et al. 2005).

For redistribution to occur, however, conditions must be just right. Roots belonging to the same root system must simultaneously span regions of wet soil and dry soil, and contact between roots and soil must be close. Importantly, the water potential gradient between wet and dry soil must be strong enough to drive water movement toward dry soil rather than toward the atmosphere, which has a much lower water potential. For this reason, redistribution mostly occurs at night when stomata are closed and transpiration has ceased. Interestingly, this mechanism predicts that redistribution can occur in plants that are fully senesced (Leffler et al. 2005) or winter-dormant (Hultine et al. 2004) and that CAM plants can redistribute water during the day when their stomata are closed (Yoder and Nowak 1999).

Hydraulic redistribution is widespread. It has been documented in over 60 species covering a range of plant types, from grasses to trees, and in a range of environments, from deserts to rainforests, and we are beginning to understand that it has important ecological consequences (see reviews by Caldwell et al. 1998, Ryel 2004). By itself, hydraulic redistribution is a significant physical process affecting soil water dynamics because it allows water to move through the soil matrix in a manner that is not otherwise possible due to gravity, preferential flow, or “normal” infiltration.

Plants may use hydraulic redistribution to enhance survival and growth through benefits associated with increased soil moisture, particularly improved water status. During drought, for example, plants with dimorphic root systems (i.e., shallow lateral and deep taproots) can

hydraulically lift water at night and then reabsorb it during the day. This can limit cavitation in fine roots and partially offset reductions in transpiration caused by a lack of soil moisture near the surface (Domec et al. 2004). The actual volume of water redistributed is often small, but for some tree species it can be relatively large, representing a substantial portion of the total amount of water transpired during the day, upward of 20% (Brooks et al. 2002). Redistributed water may also be useful for maintaining viable fine roots (Espeleta et al. 2004) and promoting root growth in soil layers that would otherwise be too dry to explore (Ryel et al. 2003), and redistribution may also benefit plants by increasing nutrient availability and microbial activity in dry soil (McCulley et al. 2004). Hydraulic redistribution can affect competition for water among neighboring plants, playing either a positive role, by increasing the amount of water available to be shared among competitors (Zou et al. 2005), or a negative role, by transferring water away from competitors (Hultine et al. 2003). Finally, at larger scales, there is growing evidence to suggest that hydraulic redistribution may play an important role in water, carbon, and nutrient cycling at the ecosystem scale (Jackson et al. 2000), and it may even affect the climate of densely vegetated ecosystems, such as the Amazon rainforests (Lee et al. 2005).

## ROOT SYMBIOSES

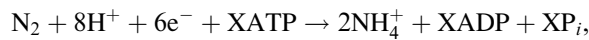
There are numerous symbioses in nature. Arguably two of the most important for higher plants are mycorrhizae and symbiotic nitrogen fixation. Mycorrhizae (literally “fungus-root”) are mutualistic associations between plant roots and soil fungi. In general, the fungus acts as a fine root matrix, exploring the soil and transporting nutrients and water back to the plant. In return, the plant typically supplies the fungus with a dependable carbon source. Fossil evidence indicates that mycorrhizae are as old as vascular land plants; they have been hypothesized as necessary for plant colonization of land in “soils” that would have been extremely nutrient poor (Pirozynski and Mallock 1975). Excellent introductory texts for the functioning and importance of mycorrhizae are Harley and Smith (1983) and Allen (1991).

Mycorrhizae are critical components of the rhizosphere (in all terrestrial biomes, and >90% of forest and grassland species are typically mycorrhizal [Brundrett 1991]). The direct and indirect benefits of mycorrhizae to plants include increased phosphorus status and, to a lesser extent, improved nitrogen and water uptake (e.g., Fitter 1989). Mycorrhizae have been shown to supply 80% of the P taken up by plants and 25% of the N (e.g., Marschner and Dell 1984). Increased resource uptake occurs primarily through the greater efficiency with which fungi explore the soil than plant roots, but there is also evidence that the fungi mobilize resources otherwise unavailable to the plant (see below). Such potential benefits come with pronounced carbon costs, estimated as 15% of net primary productivity for ectomycorrhizae (Vogt et al. 1982, for a Pacific fir forest) and 7%–17% of the energy translocated to roots for arbuscular mycorrhizae (e.g., Harris and Paul 1987).

There are four broad classes of mycorrhizae: arbuscular mycorrhizae (AM), ectomycorrhizae (ECM), ericoid mycorrhizae, and orchid mycorrhizae. Arbuscular mycorrhizae are a type of endomycorrhizae, with hyphae, arbuscules (exchange organs), and often storage vesicles produced within the cortex of root cells. Fungi in AM are limited to Zygomycetes. Only 150 or so fungal species have been shown to participate with vascular plants in AM, so there is little specificity between fungi and host plant (though this apparent lack of specificity may also reflect present limitations in fungal taxonomy). Ectomycorrhizae are characteristic of certain woody plants, particularly those in the pine, willow, and beech families. They are characterized by a mantle or hyphal sheath around highly branched roots and by a hyphal network called the Hartig net that grows between cortical root cells. In contrast to AM, ECM do not generally penetrate living root cells. There are thousands of fungal species that form ECM, usually Basidiomycetes, and there is much greater host-fungus specificity than for AM.

By far the majority of the world's mycorrhizal associations are AM or ECM. The absence of mycorrhizae is apparently limited primarily to early successional annuals of such relatively "advanced" families as the Brassicaceae, Chenopodiaceae, Amaranthaceae, and Zygophyllaceae (Allen 1991). Two other less prevalent but important forms of mycorrhizae are those of plants in the Ericaceae and Orchidaceae. Ericaceous mycorrhizae are intermediate between AM and ECM. They sometimes form a sheath around the root but they also penetrate the outer root cortical cells with hyphal coils. Ericaceous plants often grow in acidic, nutrient-poor soils such as heathlands. The fungus can constitute 80% of their extensive mycorrhizal association by mass (Raven et al. 1986). These specialized, expensive mycorrhizae seem to be particularly beneficial for mobilizing and taking up organic nitrogen that would otherwise be unavailable to the plant (Read 1983). Orchids also have a unique mycorrhizal relationship. Their seeds will not germinate in nature in the absence of the mycorrhizal fungus, typically a Basidiomycete in such genera as *Rhizoctonia*. Orchids also have an early nonphotosynthetic stage of growth where carbon is obtained solely from the mycorrhizal fungus. Mature orchids receive more typical resources such as nutrients and water from mycorrhizae.

A second important root symbiosis is the fixation of nitrogen by plants and bacteria. Biological nitrogen fixation adds approximately  $150 \times 10^{12}$  g N to terrestrial ecosystems each year, roughly  $1 \text{ g m}^{-2}$  on average for all of the earth's land (e.g., Burns and Hardy 1975, Vitousek et al. 1997). Functionally the reciprocal benefits of symbiotic N fixation are similar to those for mycorrhizae; the plant supplies carbon and energy to the symbiont and the symbiont supplies a resource to the plant. The two symbioses differ in that biological fixation supplies only nitrogen and the symbiont is a bacterium rather than a fungus. In addition to sugars, the plant also supplies an environment conducive to N fixation in which bacterial enzymes are protected from atmospheric oxygen and light. A two-protein, enzyme complex called nitrogenase catalyzes the fixation of N through the following chemical reaction:



where the value for the number of ATPs, ADPs, and  $\text{P}_i$ s is approximately 15. The ammonium is converted to amino acids or ureides before it is transported to the plant.

The most important N-fixing bacteria are those in the genus *Rhizobium*, which colonize the roots of legumes. The bacterium enters the root through root hairs that curl in response to a chemical secreted by the bacterium. A bacterial infection thread then penetrates the root cortex and induces formation of the nodule where N fixation occurs. A second important group of symbionts are actinomycete bacteria; they fix N as in roots of such plant genera as *Alnus*, *Myrica*, and *Ceanothus*.

In addition to the symbioses of *Rhizobium*, actinomycetes, and higher plants, there are also rhizosphere bacteria such as *Azospirillum*, which fix nitrogen on the surface of roots of many plant species. It is debatable whether these relationships constitute a true symbiosis. There is clearly not the tight coupling that is seen with *Rhizobium* and legumes, and the quantities of N fixed are much smaller. Nevertheless, this source of N is important for a number of grasses and crop species.

## GLOBAL PATTERNS OF ROOT DISTRIBUTIONS

Despite tremendous natural variation in the soil around plants and in the plasticity individual plants show to such variation (Snaydon 1962, Jackson and Caldwell 1993), there are broad patterns in the distributions of roots observed for biomes and plant functional types. Jackson et al. (1996, 1997) constructed a global database of climate, soil, and root attributes from

more than 250 literature studies. The data were separated by terrestrial biomes and plant functional types and fitted to an asymptotic model of vertical root distribution:

$$Y = 1 - \beta^d,$$

where  $Y$  is the cumulative root fraction (a proportion between 0 and 1) from the soil surface to depth  $d$  (in cm) and  $\beta$  is the fitted extinction coefficient (Gale and Grigal 1987).  $\beta$  provides a simple numerical index of rooting distributions. Low  $\beta$  values (e.g., 0.90) correspond to proportionally more roots near the surface than do high  $\beta$  values (e.g., 0.98).

Examining the data for plant functional types, typical  $\beta$  values were 0.957 for grasses and 0.972 and 0.980 for trees and shrubs, respectively (Jackson et al. 1996). Cumulative root biomass in the top 30 cm of soil varied from 75% for a typical grass to 45% for an average shrub. Shrubs had 87% of their root biomass in the top meter of soil while grasses had almost 99%. These estimates for total root biomass are slightly deeper than those in Jackson et al. (1996) because only profiles to approximately 2 m soil depth or greater were used in this revised analysis. Terrestrial biomes also showed clear patterns for root distributions. Deserts, temperate coniferous forests, and savannas had some of the deepest distributions ( $0.970 \leq \beta \leq 0.980$ ), while tundra, boreal forests, and temperate grasslands the shallowest profiles ( $\beta = 0.913, 0.943, \text{ and } 0.943$ , respectively). Tundra typically had 60% of roots in the upper 10 cm of soil while deserts had approximately 20% of roots in the same depth increment.

The database was also used to examine global patterns of root biomass and annual belowground net primary production (NPP) (Jackson et al. 1996, 1997). Average root biomass ranged from  $<1 \text{ kg m}^{-2}$  for deserts and croplands to  $4\text{--}5 \text{ kg m}^{-2}$  for most forest systems. When root biomass estimates were combined with the extent of each biome, global root biomass was estimated to be approximately  $290 \times 10^{15} \text{ g}$  (or  $140 \times 10^{15} \text{ g C}$ , equivalent to approximately 20% of atmospheric C). The standing biomass of live and dead fine roots ( $<2 \text{ mm}$  diameter) was approximately  $80 \times 10^{15} \text{ g}$ . Assuming conservatively that fine roots turn over once per year on average, they represent one-third of global NPP for plants, approximately  $20 \times 10^{15} \text{ g C year}^{-1}$  (Jackson et al. 1997). The average C:N:P ratio was 450:11:1 for fine roots and 850:11:1 for more coarse roots ( $2 \leq x \leq 5 \text{ mm}$ ).

The upper meter of soil contains the majority of root biomass in most systems. Nevertheless, what constitutes the functional rooting depth of an ecosystem is an important and more difficult question. For woody plants much of surface root biomass is in large-diameter roots that play a strong role in anchoring and transport but not in resource uptake. Furthermore, even where fine root biomass distributions are known with depth, root functioning is often not proportional to root biomass. As an example, Gregory et al. (1978) showed that winter wheat had only 3% of its root system by mass below 1 m soil depth; this small fraction of roots supplied almost 20% of the water transpired by the wheat canopy during mid-summer. The importance of relatively deep roots may frequently be underestimated because few studies examine root abundance and functioning below 1 m soil depth (Jackson et al. 1996). Some of the root distributions estimated above are undoubtedly too shallow. There are a number of other uncertainties in this type of analysis, particularly seasonal and spatial dynamics that are masked by pooling data across space and time.

Although 2 or 3 m is “deep” for the typical ecological study, roots clearly grow much deeper. Of the 255 species examined for maximum rooting depth by Canadell et al. (1996), almost 10% grew roots below 10 m depth. At least eight woody species have been shown to grow roots below 40 m (Table 5.1). The functional significance of such roots can be profound. In the Brazilian cerrado and in Amazonian rainforests, roots have been found at least 18 m deep in the soil (Rawitscher 1948, Nepstad et al. 1994). More than 75% of transpired water in



**TABLE 5.1**  
**The Ten Deepest Records for Rooting Depth**

Species	System	Maximum Rooting Depth (m)	Reference
<i>Boscia albitrunca</i>	Kalahari desert	68	Jennings (1974)
<i>Juniperus monosperma</i>	Colorado plateau	61	Cannon (1960)
<i>Eucalyptus</i> sp.	Australian forest	61	Jennings (1971)
<i>Acacia erioloba</i>	Kalahari desert	60	Jennings (1974)
<i>Prosopis juliflora</i>	Arizona desert	54	Phillips (1963)
<i>Eucalyptus calophylla</i>	Australian forest	45	Campion (1926)
<i>Medicago sativa</i>	Agricultural field	40	Meinzer (1927)
<i>Eucalyptus marginata</i>	Jarrah forest	40	Dell et al. (1983)
<i>Acacia raddiana</i>	Niger desert	35	Anonymous (1974)
<i>Quercus douglassii</i>	California woodland	24	Lewis and Burgy (1964)

Sources: Generated in part from Stone, E., Kalisz, P., *Forest Ecol. Manage.*, 46, 59, 1991. With permission; From Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.-D., *Oecologia*, 108, 583, 1996. With permission.

these systems can come from below 2 m soil depth, particularly during the dry season (Nepstad et al. 1994). Where resources, particularly water, are available at depth in the soil, deep roots can be disproportionately important for resource uptake. The depth to which roots grow and their distribution in the soil are also likely to be quite important for the maintenance of leaf area in evergreen systems and in determining the boundaries between evergreen and deciduous vegetation.

## CONCLUDING REMARKS

Roots function in anchoring the plant, capturing soil resources, sensing and modifying the environment, and storing reserves. The physical difficulties in studying roots and the soil represent both a frustrating barrier and a tremendous opportunity for the creative scientist. There are numerous unanswered questions on root functioning in need of a novel approach (Jackson 1998). What is the relationship of root biomass to root functioning? In what systems are the phenologies of roots and shoots tightly coupled? Is the distribution of microbes and soil fauna in the soil coupled to plant rooting depth? How prevalent are deep roots and are they important only for water uptake? Do general patterns exist for such questions globally?

Fortunately, such tools as minirhizotrons and stable isotopes are improving our understanding of the turnover and functioning of root systems. Future progress will also likely be made by combining new approaches in ecological studies with the mechanistic insights of molecular biology. For example, Zhang and Forde (1998) recently showed that a nitrate-inducible gene in *Arabidopsis* (ANR1) is a key determinant of developmental plasticity in roots. Perhaps most of all, it is important to remember that the functioning of roots is intimately linked to that of shoots. This integration occurs through the mutual exchange of resources and plant signals. Attempts to understand root or shoot functioning must eventually take this integration into account.

## ACKNOWLEDGMENTS

This chapter is reproduced unchanged from the first edition except for the addition of a new Section “Releasing exudates and modifying the environment.”

We wish to thank the National Science Foundation, the Andrew W. Mellon Foundation, and the Department of Energy's National Institute for Climate Change Research for support of this work. C. Armas is supported by a Fulbright fellowship from the Spanish Government (FU2005-0282). L. Anderson, C. Bilbrough, H. de Kroon, and E. Jabbagy provided helpful comments on the manuscript.

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