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Beyond the Roots of Young Seedlings: The Influence of Age and Order on Fine Root Physiology

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Introduction

The increasingly widespread use of minirhizotrons, below-ground video cameras, and root image analysis software has generated information on fine root (<1 mm in diameter) dynamics in many species and ecosystems (Johnson and others 2001; Eissenstat and Yanai 2002). These techniques have also revealed the daunting complexity of the fine root system. Within the fine root system of a single field-grown plant are roots of numerous branching orders, lengths, diameters, ages, colors, and degrees of mycorrhizal colonization (Afek and others 1990; Pregitzer and others 1997; Wells and Eissenstat 2001; Anderson and others 2002; Mihail and others 2002; Waisel and Eshel 2002). Fine roots continually emerge, age, and die throughout the favorable growing season at rates that differ among subsets of the root population and change in response to seasonal and environmental factors (Hendrick and Pregitzer 1993; Pregitzer and others 1993; Reid and others 1993; Forbes and others 1997; Ruess and others 1998; Majdi and others 2001; Wells and Eissenstat 2001; Wells and others 2002a). The demographic characteristics of the fine root population are constantly shifting, and the consequences of these shifts for whole-plant physiology and growth are very poorly understood.

The heterogeneity of the fine root system should not be surprising. Above ground, individual leaves exhibit well-characterized differences in anatomy and physiology with age and position in the crown (Esau 1965; Nobel 1975; Coleman 1986). An appreciation of these differences is implicit in most aboveground sampling strategies and is incorporated into models of whole-canopy function. Until recently, however, physiological differences among individual roots less than 1 mm in diameter were not frequently acknowledged. Most water and nutrient uptake models use total fine root length as a model parameter and assume constant rates of uptake along this length (Chen and Barbar 1990; Smethurst and Commerford 1993; Teo and others 1995; but Gao and others 1998). However, a number of studies indicate that roots of different ages and positions are anatomically and physiologically dissimilar (Atkinson and Wilson 1979; Palta and Nobel 1988; Lopez and Nobel 1991; McKenzie and Peterson 1995; Pregitzer and others 1997; Bouma and others 2001; Kosola and others 2002).

At present, the majority of our information on fine root physiology derives from studies of the young, white seminal roots of crop seedlings grown in solution culture (Clarkson 1985; McCully 1999). Such studies have been extremely valuable in elucidating the details of root anatomy, development,

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ion uptake, and metabolism. However, physiological data from young crop roots grown in artificial media may have limited relevance to the complex fine root systems of field-grown, perennial plants. In contrast to the primary roots of crop seedlings, the fine roots of perennial plants often lived months and even years (Hendrick and Pregitzer 1992; Majdi and Nylund 1996; Eissenstat and Yanai 1997; Eissenstat and others 2000). Many fine roots, especially in woody species, are short (rarely more than several cm), determinate in length, and highly branched (McCully 1999; Draye 2002; Persson 2002; Pregitzer and others 2002). Although fine roots are white when first produced, many become brown with age and remain in this state, without visible secondary thickening, for the majority of their life span (Richards and Considine 1981; Hendrick and Pregitzer 1992; McKenzie and Peterson 1995).

The assumption of uniform physiological activity among all roots within the fine root system is almost certainly inaccurate. However, little information exists with which to formulate a more accurate description of functional heterogeneity within the root system. Obtaining reasonable quantities of fine root tissue of known age and branching order is a technical challenge (Pregitzer and others 1997; Kosola 1999; Bouma and others 2001), and relatively few studies have examined the physiological changes that accompany root aging or the functional differences among roots of different branching orders. An understanding of the basic physiological differences among categories of fine roots is necessary if we are to better predict changes in root system function from observations of root system demography.

In the present review, we will highlight what is known about the morphology, physiology, and life history of fine roots in relation to their age and position in the branched hierarchy of the root system. We will focus particularly on the fine root systems of woody plants and on the ways in which they differ from the young root systems of annual crop plants.

Root Longevity and the Age Distribution of Fine Root Populations

The age distribution of annual root systems is relatively simple. Root and leaf production tend to occur synchronously during the early growing season and then slow or cease at the onset of reproductive growth (Beyrouty and others 1987; Snapp and Shennan 1992). Frequently, little root mortality occurs until the latest stages of reproductive development (Fisher and others 2002). This pattern of root production during the growing season has several consequences for the age distribution of the root population. First, all fine roots in annual crop species are less than one year in age and differ in age by, at most, several months. Second, the root population is enriched in young, white roots early in the season and dominated by aging roots as the season progresses. This pattern of root growth supports a strategy of high nutrient uptake early in the growing season, followed by retranslocation of nutrients from roots and leaves to reproductive structures later in the season (Cheng and others 1990; Box and Ramseur 1993; Liedgens and others 2000; Liedgens and Richner 2001).

Production schedules for the fine roots of woody plants are more complex. The ability of perennial plants to draw upon stored nutrient reserves reduces the need for high nutrient uptake rates to occur simultaneously with new leaf production. In fact, root and leaf production are frequently asynchronous. In fruit trees, nutrients required for spring leaf and flower production are supplied from stored reserves, and significant new fine root growth may not occur until well after the initiation of leaves and flowers (Rogers 1939; Tromp and Ova 1973; Millard and Thomson 1989; Wells and Eissenstat 2001; Grassi and others 2002). In many trees, the production of fine roots occurs at some level throughout the growing season and is punctuated by one or more seasonal ''flushes'' of very high production (Rogers 1939; Head 1966; Lyr and Hoffman 1967; Head 1969; Atkinson 1980; Glenn and Welker 1993; Reid and Bowden 1995). In apple and peach, an initial flush of new root production often occurs during, or following, bloom. A second flush may occur in the late summer or early fall (Rogers 1939; Head 1966, 1967; Rogers and Head 1969).

The fine roots of perennial plants can be extremely long-lived. Median life spans of 250 to 350 d have been observed for Norway spruce (Majdi and Kangas 1997). Sugar maple fine roots were reported to have median life spans of over 400 d in a 60-y-old central Pennsylvania planting and 125 to 340 d in a Michigan hardwood forest (Hendrick and Pregitzer 1992; Hendrick and Pregitzer 1993; Eissenstat and others 2000). In a survey of eleven hardwood and coniferous tree species in West-central Poland, a number of species exhibited median life spans greater than 930 d (J. Withington unpublished data). In these minirhizotron studies, the fine roots did not increase appreciably in diameter with age, nor did they appear to become ''woody.'' Consid-

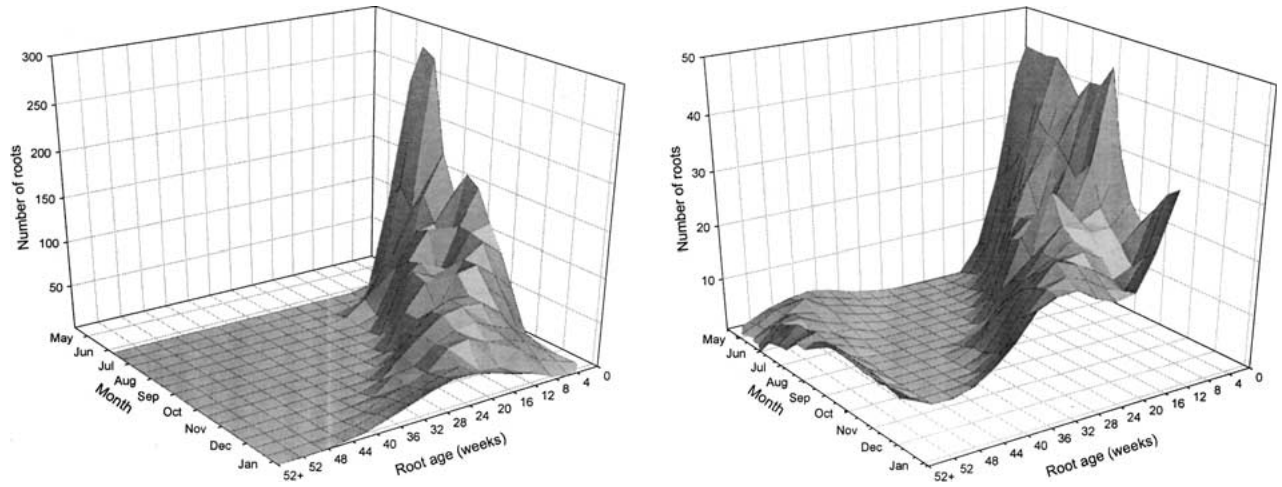

Figure 1. Age distributions through time of fine roots (<1 mm diameter) visible on minirhizotrons in a West Virginia peach orchard during the 1996 (left panel) and 1997 (right panel) growing seasons (data from Wells and others 2002a). Six butyrate minirhizotron tubes were installed beneath each of six 15-y-old Loring peach trees on Halford rootstock planted in a Hagerstown silt loam soil in April of 1996. Tubes were 70 cm in length, 6 cm in outer diameter, and were scribed with a single vertical transect of thirty 1.8 × 1.2 cm windows. Data from two minirhizotrons per tree are shown (12 tubes total). Raw data were smoothed using the Loess function in Sigmaplot (SPSS, Inc. Chicago, IL) with a bandwidth of 0.50.

erably shorter root life spans have been reported in other woody species, including apple (36-144 d; Wells and Eissenstat 2001), kiwifruit (28 d; Reid and others 1993), and pin cherry (42 d; Pregitzer and others 1993). Nonetheless, it is clear that the fine roots of woody plants may persist for many months without undergoing visible radial thickening.

Long life spans of the fine roots of woody plants, coupled with production schedules that feature multiple yearly flushes, result in root populations that have a complex and constantly-shifting age distribution. Whereas the fine roots of annual plants are all relatively similar in age, the root systems of perennial plants exhibit a broad range of root ages. In addition, the median age of the perennial fine root system can shift from older to younger and back again in response to repeated flushes of new root production during the growing season.

Demographic Characteristics of a Peach Root System Observed with Minirhizotrons

Observational data collected in a West Virginia peach orchard during two growing seasons after minirhizotron installation illustrate key aspects of woody plant fine root demography: (1) broad root age distribution, (2) enrichment in older roots and (3) shifts in root median age during the growing season (for experimental details see Wells and others 2002a). New fine roots were ontinually produced throughout the spring and summer in this orchard (Figure 1). A fall flush was also observed in both years of the study: in September of 1996 and in late October of 1997. The initial flush of root production in the summer of 1996 was particularly high and may have represented wound-induced root proliferation in response to minirhizotron installation (Joslin and Wolfe 1999).

The age distribution of the root system broadened throughout the course of the study. One month after minirhizotron installation, all roots fell into the 0–4 week age class. By the time of the fall flush in 1996, fine root ages ranged from less than 1 week to 20 weeks, and by the summer of 1997, fine root ages ranged from less than 1 week to greater than 1 year (Figure 1). This range of root ages probably underestimated that of the undisturbed bulk soil.

Although new fine roots were continually produced during the growing season, the majority of the fine root system was older than 1 month at all but the earliest spring sampling dates each year (Figure 1). On all but three sampling dates, 40–70% of the fine roots were brown, indicating that their epidermal and cortical tissues were senescent or absent (Figure 2). Similar results have been reported in a northern hardwood forest, where the majority of a June fine root cohort (<30 cm depth) was brown within 20 days of its production, but the cohort exhibited a median life span greater than 300 days (Hendrick and Pregitzer 1992). Rogers (1939)

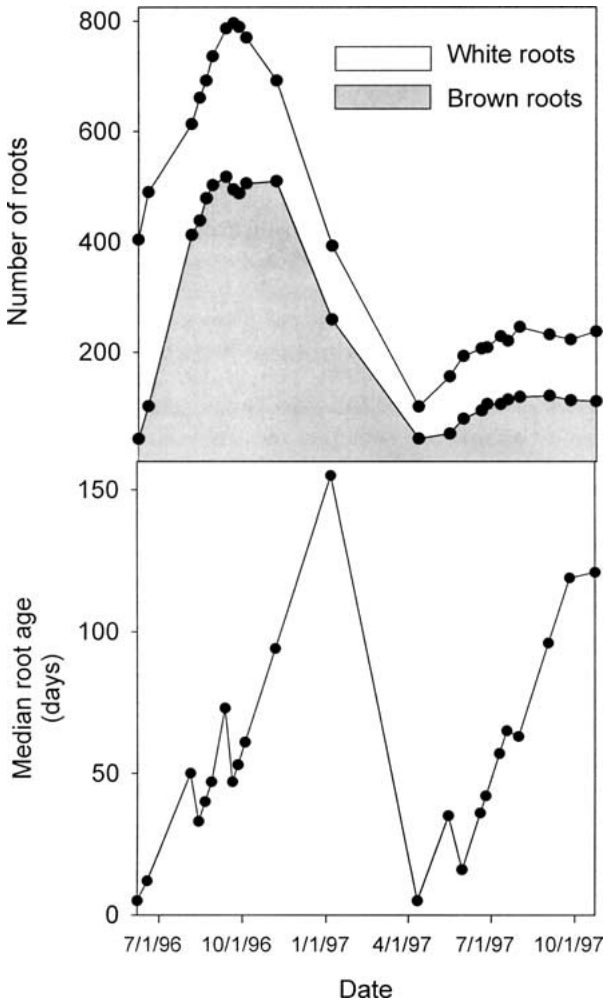

Figure 2. Number of white and brown fine roots visible on 12 minirhizotrons in a West Virginia peach orchard from June 1996 through October 1997 (top panel) (data from Wells and others 2002a). Median root age of all fine roots visible on the minirhizotrons over the same interval (bottom panel).

reported that portions of apple root systems viewed through rhizotrons consisted entirely of brown roots in several instances during the growing season. Kramer and Bullock (1966) found that actively growing root tips accounted for less than 1% of the total root surface area in loblolly pine and yellow poplar stands.

The median age of the peach root population was always youngest in the early spring and oldest in the late fall and winter. During the summer, the median root age increased and decreased in response to changing root production and mortality rates (Figure 2). In some instances, marked shifts in median root age occurred independently of any significant change in root numbers or root distribution among color classes. Given that root physiology can change markedly with age, these shifts in root system median age may have caused significant changes in the tree's capacity for below-ground resource capture over the course of the growing season.

Changes in Fine Root Function with Age

Among fine absorptive roots of low order (see below), there is typically a rapid decline in nutrient uptake capacity with age. The time course and extent of this decline depend on the plant species and the nutrient being measured. Numerous experiments in cereals, annual crops, and woody plants confirm that young, apical regions of the root exhibit the greatest rates of nutrient uptake from solution, although in many cases there is measurable uptake by all portions of the root system (Kramer and Bullock 1966; Russell and Sanderson 1967; Clarkson and others 1968; Grasmanis and Barley 1969; Eshel and Waisel 1972; Atkinson and Wilson 1979; Van Rees and Comerford 1990; Clarkson 1991; Comas and others 2000; Bouma and others 2001). It is important to note that the proportion of absorbed ions that are translocated out of the root may increase with age, as has been shown for ^{86}Rb in cherry (Atkinson 1980).

The time course of the decline in nutrient uptake with age differs among woody species with contrasting root life spans and morphologies. Consider a comparison between the coarse, dense roots of citrus and the thinner roots of apple (Eissenstat and others 2000; Bouma and others 2001). Fine roots of citrus typically have median life spans five times longer than those of apple (ca. 300 days vs. 60 days). Maximum uptake capacity (I_{max}) of young citrus roots is also considerably lower than that of apple (ca. 400 pmol P g^{-1} s^{-1} vs. 2000 pmol P g^{-1} s^{-1}). The decline in phosphate uptake with root age differs in apple and citrus roots. Bouma and others (2001) reported that citrus root uptake capacity for phosphate peaked at 4 days of age, dropped to about 35% of maximum within 1 week, and remained at that level for the oldest roots examined (Figure 3). In contrast, apple roots maintained a relatively high uptake capacity for phosphate during the first 25 days of life, after which their uptake capacity exhibited a gradual but continuous decline with age. These results suggest that longer-lived roots may exhibit lower maximum rates of uptake, but that their age-related declines in uptake are less pronounced. Such hypotheses will require further testing. In grape, whose roots are similar in structure and longevity to apple (median lifespan ca. 50–

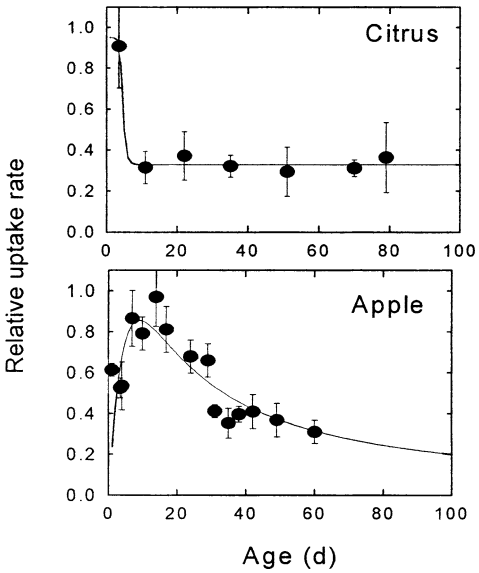

Figure 3. Relative uptake rate of phosphorus as a function of root age in apple ('Red chief Delicious' on M26 rootstock) and citrus (Red grapefruit on sour orange rootstock) roots growing in the field (±SE) (Bouma and others 2001). Relative P uptake was determined by measuring ^{32}P uptake from 1-cm excised root segments from mature trees at concentrations ranging from1 to 1000 μM P. ©New Phytologist Trust

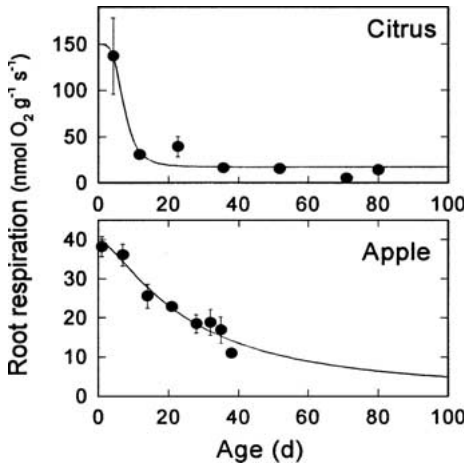

Figure 4. Respiration of 1st and 2nd order roots of apple (''Red chief Delicious'' on M26 rootstock) and citrus (Red grapefruit on sour orange rootstock) roots growing in the field (±SE). Roots of known age were collected from root boxes and O_2 consumption of the excised roots determined with an oxygen electrode. Figures redrawn from Bouma and others (2001). ©New Phytologist Trust.

70 days), nitrate uptake capacity declined to 30% of maximum within 10 days (3309C rootstock; A. Volder unpublished data). There was little subsequent decline in uptake capacity between 10 and 23 days.

Respiration also declined with individual root age in citrus and apple (Figure 4). Citrus exhibited very high respiration in 4-day old roots, perhaps related to the growth of thick, lignified, tangential exodermal walls (Eissenstat and Achor 1999). Within 1 week, respiration had declined precipitously and remained essentially constant at 20 nmol O_2 g^{-1} s^{-1} for roots between 20 and 80 days old. Apple roots, on the other hand, exhibited a more gradual, linear decline with age and showed no evidence of stabilizing at a constant rate. In the oldest roots examined (ca. 40 days), respiration had reached levels of 11 nmol O_2 g^{-1} s^{-1}. In a separate study, Concord grape root respiration declined linearly with age to minimum rates of only 12 nmol O_2 g^{-1} s^{-1} in roots over 50 days old (Comas and others 2000). Similar declines in individual root respiration with age have been noted in roots of the cactus species *Ferocactus acanthodes* and *Opuntia ficus-indica* (Palta and Nobel 1989).

Hydraulic conductivity of individual roots may also change with age, a phenomenon that has implications for both water and nutrient uptake (Kramer 1983). In *Ferocactus acanthodes* and *Opuntia ficus-indica*, hydraulic conductivity at 20°C increased with root age up to 11–17 weeks and decreased with age thereafter. Similar results have also been reported for a number of other species (Oosterhuis 1983; Drew 1987). The initial increase in hydraulic conductivity with age has been attributed to maturation of xylem vessels and secondary xylem development, while the eventual decrease may reflect suberin deposition and/or cork periderm formation. Not all species exhibit this pattern of change in hydraulic conductivity with age. In *Agave desertii*, for example, maximum hydraulic conductivity occurs very early in the life of an individual root (Nobel and others 1990).

Age-related changes in the hydraulic properties of fine roots in woody species have received less attention. A number of early studies suggest that older, suberized roots are somewhat less permeable to water but may nonetheless be important in water uptake (Nightingale 1935; Chapman and Parker 1942; Hayward and others 1942; Kramer 1946; Kramer and Bullock 1966). For example, Kramer and Bullock found that the rate of water movement into individual young, white root segments ranged from 4.2 to 97 mm^3 cm^{-3} h^{-1}, while the rate for older, ''suberized'' segments ranged from 4.36 to 32 mm^3 cm^{-3} h^{-1} (roots 1–2 mm in diameter). Based on the relative abundance of ''suberized'' and unsuberized roots at their field site, the authors concluded that 75% of water uptake by the pine root

system occurred through ''suberized'' roots. Potential routes of water entry into older roots include lenticels, breaks in the cork periderm, and passage cells in the root endodermis.

Changes in Root Anatomy with Age

Reduced rates of water and nutrient uptake by fine roots may result from a number of processes including (1) development of apoplastic barriers to water and solute movement, (2) loss of epidermal and cortical tissues, and (3) qualitative and quantitative changes in membrane proteins involved in nutrient and water uptake. The first two mechanisms have been studied in some detail but much less is known about age-related changes in the expression of ion channels, carriers, pumps, and aquaporins in root cell membranes. Changes in membrane physiology with root age deserve further study, and this effort will be greatly assisted by the ongoing identification of genes encoding various membrane transport proteins from roots (for example, see Crawford and Glass 1998).

Pioneering work on the relationship between root age and uptake focused on the potential for age-related root anatomical changes to alter root function (Clarkson 1996). Apoplastic barriers formed by Casparian bands and suberin lamellae in the endo- and exodermis have received particular attention, but there are still misconceptions regarding the importance of the Casparian band in restricting nutrient uptake. Although the Casparian band in the endodermis restricts apoplastic movement of solutes into the stele, band formation occurs within the first few millimeters of the root tip in rapidly extending roots and closer to the tip in short laterals. Rapid zones of nutrient uptake and translocation usually occur somewhat more distal from the root tip where the xylem has matured. Thus, zones of the root that are most active in nutrient uptake also possess Casparian bands in the endoermis (Clarkson and others 1968).

Although the endodermal Casparian band may not represent an impediment to nutrient uptake, secondary deposition of suberin lamellae in the walls of maturing endodermal cells may result in major reductions in water and ion uptake (Clarkson and others 1968; Clarkson 1996). Furthermore, many species also develop an exodermis, a cortical layer just below the epidermis, which serves as an apoplastic barrier to water and solute uptake (Perumalla and Peterson 1986; Peterson and others 1993). Like the endodermis, the exodermis often forms close to the root tip and has Casparian bands and suberin lamellae when mature. Typically, the exodermis matures more slowly than the endodermis and may take several months to fully develop its secondary walls and suberin lamellae (Perumalla and Peterson 1986; Eissenstat and Huang 2000). As with the endodermis, stressful conditions may accelerate suberin deposition and cause the exodermis to form closer to the root tip. Both the endodermis and the exodermis may contain passage cells that permit limited uptake of water and nutrients.

Root Browning

Another mechanism by which water and nutrient uptake may be curtailed in older roots is the senescence of the root cortex, a phenomenon we refer to as ''browning.'' Minirhizotron images indicate that new fine roots are white in color and become brown (but not necessarily woody) several weeks to months after their production (Wang and others 1995; Comas and others 2000; Wells and Eissenstat 2001). Some brown roots eventually take on a blackened or shriveled appearance before disappearing, whereas others are retained and function in more than one growing season. Brown roots are frequently referred to in the older literature as ''suberized,'' implying that they have undergone deposition of endo- and/or exodermal suberin lamellae. However, neither suberization nor the development of secondary xylem are directly linked to root browning (McCrady and Comerford 1998).

In *Eucalyptus pilularis* and *Pinus banksiana,* browning is associated with condensed tannin accumulation in cortical cell walls and death of the epidermis and cortex, leaving a dead, tannin-filled sheath surrounding an intact and living stele (McKenzie and Peterson 1995). Cortical cell death and persistence of a functioning stele have also been reported in grape (Comas and others 2000), apple (Rogers 1968), loblolly pine (McCrady and Comerford 1998), wheat and barley (Liljeroth 1995), soybean (Kossiak and others 1997) and chickpea (Spaeth and Cortes 1995). It is unknown whether the details of the browning process are identical in all species, but the general phenomenon of cortical pigmentation followed by cortical cell death appears to be common across taxa.

Although root browning itself is a normal developmental process that occurs under axenic conditions (Liljeroth 1995), a number of external factors can trigger the initiation of browning and increase browning rate. Interactions with nematodes and fungal pathogens trigger browning in a number of plant species (Dunn 1979; Allen and others 1989;

Liljeroth 1995). In wheat, cultivars that exhibit a rapid rate of browning are also more resistant to root rot fungus, suggesting that root browning may play a role in root defense (Liljeroth 1995). In peach, a decreased browning rate was observed when roots were protected from below-ground insect herbivory by the application of broad spectrum soil insecticide (Wells and others 2002b). In grape, roots surrounded by many neighbors browned more quickly than roots that were solitary (Anderson and others 2002). Evidence also suggests that low soil water content and high soil temperature can also increase the root browning rate (Rogers 1939; Bartsch 1987).

Loss of cortical and epidermal tissues reduces the membrane surface area available for nutrient uptake. Cortical cells are also the sites of mycorrhizal carbon and nutrient exchange, and roots that have shed their cortex are therefore incapable of obtaining nutrients through mycorrhizal symbioses. Not surprisingly, most studies that have compared brown roots with white roots of the same species have found them to exhibit reduced rates of nutrient uptake (Chapman and Parker 1942; Kramer 1946; Atkinson and Wilson 1979; Van Rees and Comerford 1990). Reductions in the respiration rate of brown roots have also been noted (Comas and others 2000).

Root Order and the Branched Hierarchy of the Root System

Fine root anatomy and function differ not only by age, but also by position in the branched hierarchy of the root system. The above-ground growth of plants is often described as modular, meaning that growth occurs through the repetition of a small number of discrete, self-replicating structural units, or modules (Maillette 1992). One year's leafy twig or one leaf with its axillary bud are two examples of above-ground growth modules (Watkinson and White 1986; Thomas 2001). Root growth may also be considered modular (Pregitzer and others 2002), with one root apical meristem and the primary tissues immediately arising from it comprising a single below-ground growth module. New modules may arise at many points from the pericycle of an existing root module, giving rise to a complex, branched hierarchy of individual roots that differ in both age and position (Pages 2002).

The position of an individual root within the branched hierarchy of the root system is often termed its ''root order.'' Here we will refer to roots with no dependent laterals as 1st-order, roots with a single set of dependent laterals as 2nd-order, and so on. In this scheme, the higher a root's order, the more hierarchical levels of lateral roots are dependent upon it. 1st-order roots are the most distal roots in the branched hierarchy and correspond to ''external links'' in the topological analysis scheme proposed by Fitter (1987). Just as the fine root population exhibits an age distribution, it also exhibits a distribution of roots among various root orders.

Whether most plant species exhibit a characteristic, fixed number of root orders at maturity is a question that has received surprisingly little attention. In many annual crop species, the number of root orders and the morphology of the roots within each order appear to be relatively fixed. In the nodal root system of maize, for example, individual nodal roots bear one order of short (mode $\leq$ 3 cm) lateral branch roots. Thirty percent of these branch roots bear an additional order of laterals that are shorter still (McCully 1999). Therefore, at maturity, the maize nodal root system consists of three hierarchical orders: very short 1st-order laterals, short 2nd-order, and relatively long nodal framework roots. The branching architecture of other cereals is similar.

Much less information exists on the number of root orders exhibited by herbaceous and woody dicots. Pregitzer and others (1997) carefully excavated complete root systems from four plant species common to the forest seedling ground-cover layer in a Michigan hardwood forest. Two perennial herbaceous species bore a maximum of five total root orders, while ash bore six and sugar maple bore seven. Seven root orders may be the maximum observed for any tree species (Lyford 1975). In a subsequent study of root architecture in nine North American trees, Pregitzer and others (2002) noted that fine root branches emerging from woody perennial roots rarely bore more than 3 to 4 hierarchical root orders. In the same study, 1st- and 2nd-order roots made up the majority of fine root numbers and accounted for over 75% of fine root length.

Differences in Development and Function Among Root Orders

Roots of different orders exhibit differences in morphology, anatomy, physiology, and life history. These differences are most pronounced in woody perennials whose highest root orders consist of long-lived woody roots that function primarily in anchorage, storage, and transport. However, differ-

ences among root orders also exist within the fine, absorptive root system (<1–2 mm in diameter) in both woody and non-woody plants. Higher-order roots are always older than the lower-order roots that arise from them, and many of the physiological differences among root orders reflect this fact. There are also differences among root orders that are independent of root age: roots that are destined to give rise to one or more hierarchical levels of lateral roots are often developmentally distinct from roots that will remain 1st-order roots throughout their life span.

Although all fine roots begin their life as 1st-order, absorptive roots, it appears that only a subset of the fine root population undergoes the transition from 1st-order to higher-order root. Evidence suggests that individual roots are predetermined to become higher-order, semi-permanent components of the root system from the time of their initiation (Pages 2002; Persson 2002). These roots are sometimes referred to as ''framework,'' ''long,'' or ''pioneer'' roots, in contrast to ''fibrous'' or ''short'' 1st- or 2nd-order roots. It is usually possible to identify a pioneer root at the time of emergence. Pioneer roots often have prominent root tips, are of larger diameter, and extend more rapidly and indeterminately into the soil than roots destined to remain 1st- or 2nd-order (Pages 2002). In bearing citrus trees, 1st- and 2nd-order pioneer roots develop secondary xylem and cork periderm, while 1st- and 2nd-order fibrous roots do not (Eissenstat and Achor 1999). In citrus seedlings, however, 2nd-order fibrous roots do exhibit secondary development. Seedlings in the process of developing the framework for their mature root system apparently produce more fine roots with the potential for secondary growth, affording the plant an advantage if a major portion of the root system is damaged or fails to develop. Pioneer roots must persist to become the eventual progenitor of lower order roots, and allocation of energy to their defense should therefore be high. Anecdotal data in citrus indicate that young ''pioneer'' roots are much less susceptible to the root rot fungus *Phytophthora nicotianae* (J.H. Graham, personal commun.) and the citrus nematode *Tylenchulus semipenetrans* (L.W. Duncan, personal commun.) than corresponding young ''fibrous'' roots.

As young ''pioneer'' or ''framework'' roots develop secondary xylem and a periderm from their vascular and cork cambiums, respectively, there is subsequent senescence of the cortex and epidermis and loss of a symbiotic relationship with mycorrhizal fungi. The cork periderm, which forms interior to the endodermis, also leads to mortality of the endodermal passage cells (Peterson and others 1999). Hence, secondary development represents a major transition in which the pioneer root's function changes from water and nutrient absorption to transport, anchorage, and production of lower order absorptive roots. The cork periderm is notable as a barrier to water and nutrient absorption not only because of its heavily suberized cork cells, but also because of its lack of passage cells (Peterson and others 1999; Taylor and Peterson 2000). These anatomical features undoubtedly also help framework roots defend against pathogens and root herbivores.

Root orders also differ markedly in life span. In peach, 1st-order roots had median life spans of 95–105 days while 2nd and 3rd-order roots had median fine life spans of 226–259 days (Wells and others 2002a). Significantly longer life spans for higher order roots have also been demonstrated in kiwifruit (Reid and others 1993). Longer life spans of higher order roots are not surprising: loss of a single higher order root entails the loss of all the lateral roots that depend upon it.

Summary: Beyond Young, White Fine Roots

Early in their lives, fine absorptive roots exhibit high capacities for water and nutrient uptake and benefit from symbiotic associations with mycorrhizal fungi. As they age, most fine absorptive roots eventually undergo pigmentation, cortical cell death, loss of mycorrhizal associations, and substantial reductions in the capacity for water and nutrient absorption. Some of these changes in root function occur very rapidly in relation to the life span of the root. Decreasing physiological activity with root age has led to a general perception that only young, white roots or root tips are important in resource acquisition. However, fine root demographic studies suggest that young, white roots make up only a small fraction of total fine root length in woody plants during much of the favorable growing season. Older roots may contribute significantly to water and nutrient uptake. Although the water and nutrient uptake capacities of older roots are reduced, they are not negligible, and older roots represent by far the largest potential surface area for uptake. Alternatively, older fine roots may be important in supplying only a subset of below-ground resources. At present, it is difficult to evaluate these hypotheses. We are not aware of any study that has reported age-specific uptake rates for more than one or two nutrient ions in a woody species. Without such data, it is not possible to determine whether there are particular classes of nu-

trients whose uptake is especially restricted with root age. Studies that measure changes in both hydraulic conductivity and nutrient uptake are also lacking. Furthermore, among roots for which the age is known, nutrient uptake has only been determined in roots up to 60–80 days of age; the inclusion of much older fine roots in future studies would complete our understanding of changes in fine root function with age. Much more remains to be learned about the functional roles played by roots of different ages and orders. Such information is necessary if we are use minirhizotron observations of individual roots to make inferences about the functioning of the root system as a whole.

REFERENCES

Afek U, Rinaldelli E, Menge JA, Johnson ELV, Pond E. 1990. Mycorrhizal species, root age and position of mycorrhizal inoculum influence colonization of cotton, onion and pepper seedlings. J Am Soc for Horticultural Sci 115:938–942.

Allen M, Allen E, Friese C. 1989. Responses of the non-mycotrophic plant *Salosa kali* to invasion by vesicular-arbuscular mycorrhizal fungi. New Phytologist 111:45–49.

Anderson LJ, Comas LH, Lakso AN, Eissenstat DM. 2002. Multiple risk factors in root survivorship: a four-year study in Concord grape. New Phytologist *in press*.

Atkinson D. 1980. The distribution and effectiveness of the roots of tree crops. Horticult Rev 2:424–490.

Atkinson D, Wilson S. 1979. The root-soil interface and its significance for fruit tree roots of different ages. In: Harley J, Russell R, editors. The Soil-Root Interface. London: Academic Press, p 259–271.

Bartsch N. 1987. Response of root systems of young *Pinus sylvestris* and *Picea abies* plants to water deficits and soil acidity. Can J Forest Res 17:805–812.

Beyrouty C, Wells B, Norman R, Marvel J, Pillow J. 1987. Characterization of rice roots using a minirhizotron technique. Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. ASA Special Publication No. 50, pp 99–108.

Bouma TJ, Yanai RD, Elkin AD, Hartmond U, Flores-Alva DE, Eissenstat DM. 2001. Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. New Phytologist 150:685–695.

Box J, Ramseur E. 1993. Minirhizotron wheat root data: comparisons to soil core data. Agronomy J 85:1058–1060.

Chapman HD, Parker ER. 1942. Weekly absorption of nitrate by young, bearing orange trees growing out of doors in solution cultures. Plant Physiol 17:366–375.

Chen JH, Barbar SA. 1990. Soil pH and phosphorus and potassium uptake by maize evaluated with an uptake model. Soil Sci Soc Am J 54:1032–1036.

Cheng W, Coleman D, Box J. 1990. Root dynamics, production and distribution in agroecosystems on the Georgia Piedmont using minirhizotrons. J Appl Ecol 27:592–604.

Clarkson D. 1985. Factors affecting mineral nutrient acquisition by plants. Ann Rev Plant Physiol 36:77–115.

Clarkson D. 1991. Root structure and sites of ion uptake. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: the Hidden Half, 1st ed. New York: Marcel Dekker, p 417–454.

Clarkson D, Sanderson J, Russell R. 1968. Ion uptake and root age. Nature 220:805–806.

Clarkson DT. 1996. Root structure and sites of ion uptake. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: the Hidden Half, 2nd ed. New York: Marcel Dekker, p 483–510.

Coleman J. et al. 1986. Leaf development and leaf stress: increased susceptibility associated with sink-source transition. Tree Physiol 2:289–299.

Comas LH, Eissenstat DM, Lakso AN. 2000. Assessing root death and root system dynamics in a study of grape canopy pruning. New Phytol 147:171–178.

Crawford NM, Glass ADM. 1998. Molecular and physiological aspects of nitrate uptake in plants. Trends Plant Sci vol. 3:389–395.

Draye X. 2002. Banana roots. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: The Hidden Half, 3rd ed. New York: Marcel Dekker, p 261–277.

Drew M. 1987. Function of root tissues in nutrient and water transport. In: Gregory P, Lake J, Rose D, editors. Root Development and Function. Cambridge: Cambridge University Press, p 71–101.

Dunn R. 1979. Effect of *Xiphinema americanum* and *Rhizoctonia solani* on browning of apple roots. Fungicide and Nematicide Tests 35:214.

Eissenstat DM, Huang B. 2000. Linking hydraulic conductivity to anatomy in plants that vary in specific root length. J Am Soc Horticultural Sci 125:260–264.

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL. 2000. Building roots in a changing environment: implications for root longevity. New Phytologist 147:33–42.

Eissenstat DM, Yanai RD. 1997. The ecology of root lifespan. Adv Ecol Res 27:1–60.

Eissenstat DM, Yanai RD. 2002. Root life span, efficiency and turnover. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: The Hidden Half, 3rd ed. New York: Marcel Dekker, p 221–238.

Esau K. 1965. Plant anatomy, 2nd ed. New York: Wiley.

Eshel A, Waisel Y. 1972. Variations in sodium intake along primary roots of corn seedlings. Plant Physiol 49:585–589.

Fisher MCT, Eissenstat DM, Lynch JP. 2002. Lack of evidence for programmed root senescence in common bean (*Phaseolus vulgaris*) grown at different levels of phosphorus supply. New Phytol 153:63–71.

Fitter AH. 1987. An architectural approach to the comparative ecology of plant root systems. New Phytol 106:61–77.

Forbes PJ, Black KE, Hooker JE. 1997. Temperature-induced alteration to root longevity in *Lolium perenne.* Plant Soil 190:87–90.

Gao S, Pan WL, Koenig RT. 1998. Integrated root system age in relation to plant nutrient uptake activity. Agronomy J 90:505–510.

Glenn DM, Welker WV. 1993. Water transfer diminishes root competition between peach and tall fescue. J Am Soc Horticult Sci 118:570–574.

Grasmanis VO, Barley KP. 1969. The uptake of nitrate and ammonium by successive zones of the pea radicle. Aust J Biol Sci 22:1313–1320.

Grassi G, Millard P, Wendler R, Minotta G, Tagliavini M. 2002. Measurement of xylem sap amino acid concentrations in conjunction with whole tree transpiration estimates spring N remobilization by cherry (*Prunus avium* L.) trees. Plant Cell and Environ 25:1689–1699.

Hayward H, Blair W, Skaling P. 1942. Device for measuring entry of water into roots. Botanical Gazette 104:152–160.

Head G. 1966. Estimating seasonal changes in the quantity of white unsuberized root of fruit trees. J Horticult Sci 41:197–206.

Head G. 1969. The effects of fruiting and defoliation on seasonal trends in new root production on apple trees. J Horticult Sci 44:175–181.

Head GC. 1967. Effects of seasonal changes in shoot growth on the amount of unsuberized root on apple and plum trees. J Horticult Sci 42:169–180.

Hendrick RL, Pregitzer KS. 1992. The demography of fine roots in a northern hardwood forest. Ecology 73:1094–1104.

Hendrick RL, Pregitzer KS. 1993. Patterns of fine root mortality in two sugar maple forests. Nature 361:59–61.

Johnson MG, Tingey DT, Phillips DL, Storm MJ. 2001. Advancing fine root research with minirhizotrons. Environ Exp Botany 45:263–289.

Joslin JD, Wolfe MH. 1999. Disturbances during minirhizotron installation can affect root observation data. Soil Science Soc Am J 63:218–221.

Kosola KR. 1999. Laparascopic sampling of roots of known age from an expandable-wall minirhizotron system. Agron J 91:876–879.

Kosola KR, Dickmann D, Parry D. 2002. Carbohydrates in individual poplar fine roots: effects of root age and defoliation. Tree Physiol 22:741–746.

Kossiak RM, Chamberlin MA, Palmer RG, Bowen BA. 1997. Programmed cell death in the root cortex of soybean root necrosis mutants. The Plant J 11:729–745.

Kramer P. 1946. Absorption of water through suberized roots of trees. Plant Physiol 37–41.

Kramer PJ. 1983. Water relations of plants. New York, Academic Press.

Kramer PJ, Bullock HC. 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Am J Botany 53:200–204.

Liedgens M, Richner W. 2001. Minirhizotron observations of the spatial distribution of the maize root system. Agronomy J 93:1097–1104.

Liedgens M, Soldati A, Stamp P, Richner W. 2000. Root development of maize (*Zea mays* L.) as observed with minirhizotrons in lysimeters. Crop Sci 40:1665–1672.

Liljeroth E. 1995. Comparisons of early root cortical senescence between barley cultivars, *Triticum* species and other cereals. New Phytol 130:495–501.

Lopez FB, Nobel PS. 1991. Root hydraulic conductivity of two cactus species in relation to root age, temperature and soil water status. J Exp Botany 42:143–150.

Lyr H, Hoffman G. 1967. Growth rates and growth periodicity of tree roots. Int Rev Forest Res 2:181–236.

Maillete L. 1992. Seasonal model of modular growth in plants. J of Ecol 80:123–130.

Majdi H, Damm E, Nylund J-E. 2001. Longevity of mycorrhizal roots depends on branching order and nutrient availability. New Phytol 150:195–202.

Majdi H, Kangas P. 1997. Demography of fine roots in response to nutrient applications in a Norway spruce stand in southwestern Sweden. Ecoscience 4:199–205.

Majdi H, Nylund J. 1996. Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? Plant Soil 185:305–309.

McCrady R, Comerford N. 1998. Morphological and anatomical relationships of loblolly pine fine roots. Trees 12:431–437.

McCully M. 1999. Roots in soil: unearthing the complexities of roots and their rhizospheres. Ann Rev Plant Physiol Plant Mol Biol 50:695–718.

McKenzie BE, Peterson CA. 1995. Root browning in *Pinus banksiana* Lamb. and *Eucalyptus pilularis* Sm. 1. Anatomy and permeability of the white and tannin zones. Botanica Acta 108:127–137.

Mihail JD, Hung LF, Bruhn JN. 2002. Diversity of the *Pythium* community infecting roots of the annual legume *Kummerowia stipulacea.* Soil Biol Biochem 34:585–592.

Millard P, Thomson CM. 1989. The effect of autumn senescence of leaves on the internal cycling of nitrogen for the spring growth of apple trees. J of Exper Botany 40:1285–1289.

Nightingale G. 1935. Effects of temperature on growth, anatomy, and metabolism of apple and peach roots. Botanical Gazette 96:581–637.

Nobel PS. 1975. Effective thickness and resistance of the air boundary layer adjacent to spherical plant parts. J of Exp Botany 26:120–130.

Nobel PS, Schulte P, North G. 1990. Water influx characteristics and hydraulic conductivity for roots of *Agave deserti.* J Exp Botany 41:409–415.

Oosterhuis D. 1983. Resistances to water flow through the soil-plant system. South African J Sci 79:459–465.

Pages L. 2002. Modeling root system architecture. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: the Hidden Half, 3rd ed. New York: Marcel Dekker, p 359–382.

Palta JA, Nobel PS. et al. 1988. Root respiration for *Agave deserti*: influence of temperature, water status and root age on daily patterns. J Exp Botany 40:181–186.

Palta JA, Nobel PS. 1989. Influences of water status, temperature, and root age on daily patterns of root respiration for two cactus species. Ann Botany 63:651–662.

Persson H. 2002. Root systems of arboreal plants. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: The Hidden Half, 3rd ed.. New York: Marcel Dekker, p l87–204.

Perumalla CJ, Peterson CA. 1986. Deposition of Casparian bands and suberin lamellae in the exodermis and endodermis of young corn and onion roots. Can J Botany 64:1873–1878.

Peterson CA, Enstone DE, Taylor JH. 1999. Pine root structure and its potential significance for root function. Plant Soil 217:205–213.

Peterson CA, Murrmann M, Steudle E. 1993. Location of the major barriers to water and ion movement in young roots of *Zea mays* L. Planta 190:127–136.

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL. 2002. Fine root architecture of nine North American trees. Ecology 72:293–309.

Pregitzer KS, Hendrick RL, Fogel R. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytol 125:575–580.

Pregitzer KS, Kubiske ME, Yu CK, Hendrick RL. 1997. Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia 111:302–308.

Reid J, Bowden M. 1995. Temporal variability and scaling behavior in the fine-root system of kiwifruit (*Actinidia deliciosa*). Plant Cell Environ 18:555–564.

Reid JB, Sorenson I, Petrie RA. 1993. Root demography in kiwifruit (*Actinidia deliciosa*). Plant Cell Environ 16:949–957.

Richards D, Considine JA. 1981. Suberization and browning of grapevine roots. In: Brouwer R, editor. Structure and Function of Plant Roots. London: Dr. W. Junk, p 111–115.

Rogers WS. 1939. Root studies VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. J Pomol Horticult Sci 17:99–130.

Rogers WS. 1968. Amount of cortical and epidermal tissue shed from roots of apple. J of Horticult Sci 43:527–528.

Rogers WS, Head GC. 1969. Factors affecting the distribution and growth of roots of perennial woody species. In: Whittington W, editor. Root Growth. London: Butterworths.

Ruess RW, Hendrick RL, Bryant JP. 1998. Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forests. Ecology 79:2706–2720.

Russell R, Sanderson J. 1967. Nutrient uptake rates by different parts of the intact roots of plants. J Exper Botany 18:491–508.

Smethurst P, Commerford N. 1993. Simulating nutrient uptake by single or competing and contrasting root systems. Soil Science Soc Am J 57:1361–1367.

Snapp S, Shennan C. 1992. Effects of salinity on root growth and death dynamics of tomato, *Lycopersicon esculentum* Mill. New Phytologist 121:71–79.

Spaeth SC, Cortes PM. 1995. Root cortex death and subsequent initiation and growth of lateral roots from bare steles of chickpeas. Can J Botany 73:253–261.

Taylor JH, Peterson CA. 2000. Morphometric analysis of *Pinus banksiana* Lamb. Root anatomy during a 3-month field study. Trees 14:239–247.

Teo Y, Beyrouty C, Gbur E. 1995. Evaluation of a model to predict nutrient uptake by field-grown rice. Agronomy J 87:7–12.

Thomas P. 2001. Trees: Their Natural History. Cambridge: Cambridge University Press.

Tromp J, Ova J. 1973. Spring mobilization of protein nitrogen in apple bark. Physiol Plantarum 29:1–5.

Van Rees KCJ, Comerford N. 1990. The role of woody roots of slash pine seedlings in water and nutrient absorption. Can J Forest Res 20:1183–1191.

Waisel Y, Eshel A. 2002. Functional diversity of various constituents of a single root system. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: The Hidden Half, 3rd ed.. New York: Marcel Dekker, p 157–174.

Wang Z, Burch WH, Mou P, Jones RH, Mitchell RJ. 1995. Accuracy of visible and ultraviolet light for estimating live root proportions with minirhizotrons. Ecology 76:2330–2334.

Watkinson A, White J. 1986. Philosophical transactions of the Royal Society of London, Series B. Biol Sci 313:31–51.

Wells CE, Eissenstat DM. 2001. Marked differences in survivorship among apple roots of different diameters. Ecology 82:882–892.

Wells CE, Glenn DM, Eissenstat DM. 2002a. Changes in the risk of fine root mortality with age: a case study in peach (*Prunus persica*). Am J Botany 89:79–87.

Wells CE, Glenn DM, Eissenstat DM. 2002b. Soil insects alter fine root demography in peach (*Prunus persica*). Plant, Cell, Environ 25:431–439.