8 The Efficiency of Nutrient Acquisition over the Life of a Root

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8.1 Introduction

Our understanding of root physiology and morphology has been strongly influenced by short-term studies of very young roots of seedlings in solution culture (Clarkson 1985). Few species have been studied in detail, and most of these are annual crop species. Consequently, our perception of root physiology is narrowly based on only a few economically important species grown under managed conditions. While short-term physiological and anatomical studies of seedling roots are important, these studies provide little insight into the amounts of nutrients acquired by a root over its lifetime.

Plants vary widely in their root life span. In some species including apple, kiwi and grape, a sizeable fraction (e.g., 30 %) of the roots may live only a few weeks (Reid et al. 1993; Comas et al. 2000; Wells and Eissenstat 2001). In other species, like sugar maple or citrus (Hendrick and Pregitzer 1992; Eissenstat et al. 2000; Bouma et al. 2001; Tierney and Fahey 2001), the fine roots may live about a year or more. Species with long-lived absorptive roots likely exhibit mechanisms of nutrient acquisition that differ from those of species with short-lived roots. How have plants evolved to use limited energy reserves for the acquisition of mineral nutrients?

Nutrient availability in soil is highly heterogeneous in space and time. Consequently, efficient deployment of roots for nutrient acquisition can be strongly influenced by the ability of the root system to constantly relocate its most absorptive elements in the most favorable soil. Under many circumstances, root life span is probably closely linked to root efficiency (Caldwell 1979; Yanai et al. 1995; Eissenstat and Yanai 1997). Short life spans would be expected for thin roots of high uptake capacity, high maintenance respiration, and occurring in soils with fairly short-lived patches or where depletion zones readily form. Mechanistic modeling using an optimization or cost-benefit approach can be a powerful tool in explaining patterns of variation of roots

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within a root system, among species, and in response to environmental changes.

In this chapter, we will review the current literature associated with nutrient acquisition efficiency over the life of the root. Root length and total absorptive surface area strongly influence nutrient acquisition, but do not completely explain differences among plants. As the root ages, changes in absorptive capacity, nutrient concentrations in the rhizosphere, as well as the costs to maintain the root length, root hairs, and mycorrhizal hyphae will influence the effectiveness of this absorptive surface area in nutrient acquisition. A complete study of root costs includes the energy required for root construction, growth, ion uptake and maintenance, as well as costs associated with the formation and maintenance of the mycorrhizal symbiosis. Benefits include acquisition of water and mineral nutrients by the root and its associated symbionts. Anatomical changes in roots over their life span will also be discussed. Lastly, we will illustrate the use of root efficiency modeling, and how this can be used to help explain different patterns of root foraging for nutrients. While our knowledge of root physiology as a function of root age is very limited, this information is critical to a better understanding of different plant strategies of nutrient acquisition in different environments.

8.2 Root Length and Absorptive Surface Area

8.2.1 Importance

The supply of water and ions to root surfaces can generally be increased by greater exploration of the soil by the roots and their associated mycorrhizal hyphae (Tinker and Nye 2000). Simulation models of solute transport to the root, and uptake kinetics at the root surface clearly indicate the importance of root length in explaining observed nutrient acquisition (Silberbush and Barber 1983). There also is considerable experimental evidence of the importance of root length for nutrient acquisition, especially in herbaceous plants. Nutrient mobility and the amount of root competition affect the extent that root length contributes to nutrient acquisition (Comerford, Chap. 1, this Vol.). For example, Andrews and Newman (1970) have demonstrated that, if some of the roots of all wheat seedlings in a pot are pruned, then P but not N uptake is diminished. If only some of the wheat plants are partially root-pruned, then the remaining plants take up more N but not P. These results indicate the importance of total root length for P acquisition (a relatively immobile nutrient), and the importance of N in plant competition, because of the broader depletion zones of N than of P. Similarly, root proliferation in patches was shown to be advantageous for nitrate uptake only when the plants were com-

peting with other plants (Robinson et al. 1999). These results lead to the prediction that immobile nutrients like P are more influenced by the total length of root than nutrients like nitrate under steady-state conditions of solute supply. Under non-steady state conditions where pulses of nutrients occur and plants compete, plants with more root length will acquire more nutrients (e.g., nitrate), all else being equal.

When nutrients are scarce or when root length density is low, root length alone may not be a good predictor of nutrient acquisition. Additional absorptive surface area may be contributed by root hairs and mycorrhizal hyphae. The importance of root hairs for P acquisition has been demonstrated by simulation modeling, and by comparing nonmycorrhizal species of different hair length (Itoh and Barber 1983a, b). In a recent study, Bates and Lynch (2000a) demonstrated the importance of root hairs more directly by comparing root hair mutants with wild-type *Arabidopsis thaliana* in soils of low P availability. There are also numerous examples, under controlled greenhouse conditions, of mycorrhizal colonization enhancing P acquisition (Smith and Read 1997). Factors affecting plant response to mycorrhizal colonization include plant demand for phosphorus, plant development of root surface area without mycorrhizas (root length, root hair length and abundance, root length density), and soil P supply. In the field, studies demonstrating improved P acquisition by mycorrhizas are often less compelling. This may occur only during relatively brief periods of a plant's life history, such as during flower or seedling establishment (Fitter 1986b; Wallace 1987). A notable exception is the bluebell (*Hyacinthoides non-scripta*), a vernal geophyte with a sparse, unbranched root system with relatively thick (0.5–1 mm) roots. Merryweather and Fitter (1996) found that reduced VA mycorrhizal colonization over a 2-year period caused a 35 % reduction of P concentration in roots, and a 42 % reduction in bulbs after 2 years . In fertile soil, mycorrhizas may have a negligible effect on nutrient uptake, leading to reductions in plant growth due to carbon consumption (see Sect. 8.3.3).

8.2.2 Inconsistencies Between Root Length, Mycorrhizal Colonization and Observed Nutrient Uptake

Some studies have indicated that root length, while probably important, cannot in itself describe variations in resource acquisition among species. For example, in a study of competition among two grass species and a shrub, Caldwell et al. (1991a, b) demonstrated that while the shrub *Artemisia tridentata* typically has less than half the root length density of the tussock grasses *Agropyron desertorum* and *Pseudoroegneria spicata*, the shrub can obtain as much P from enriched patches as *A. desertorum*, and considerably more P than *P. spicata*. Thus, factors other than absorptive surface area seem to be influencing competition for P.

8.2.3 Root Architecture and Variation Among Fibrous Roots in a Single Root System

Not all root length is equally effective in nutrient acquisition. A root system can be considered as being composed of interconnected modules, each having its own physiology and life history. The position of each root in relation to other roots in the plant, and in relation to soil solute supply affects the effectiveness of each element in nutrient acquisition. Traditionally, the root length of the "absorptive" portion of the root system is defined by choosing an arbitrary size limit (e.g., all roots <2 mm in diameter), with little consideration for position within the root system or developmental stage. Consequently, this definition treats roots of very different order, diameter, physiology and function as being equal. Because of branching, the position of a root relative to others in the root system can have a large influence on its function. Root order can be described using a topological system (Lynch, Chap. 7, this Vol.) similar to that used in streams; here, we use the convention where first-order roots are those that are external links with tips, and do not have laterals (Fitter 1986a; Berntson 1997). Using this scheme, second-order roots would be those that have first-order laterals only. In woody plants, most of the fine laterals that are produced each year tend to be determinate in length, growing no more than a few centimeters in perhaps a few days, and then remaining at this length the rest of their life. When they die, they often leave behind a scar on the higher-order root (Pregitzer et al. 2002). These roots typically do not undergo secondary thickening (Brundrett and Kendrick 1988; Eissenstat and Achor 1999) and so, over their lifetime, function almost entirely for water and nutrient acquisition. These are also the roots that typically form a symbiosis with mycorrhizal fungi. Herbaceous dicots and grasses may exhibit more indeterminate root growth, continually expanding through the soil until seed set, with much of the root system dying back at the end of the growing season. Often, the level of branching in herbaceous dicots and grasses is more limited, with only about three levels of branchings. The main portion of the absorptive root system, however, is still typically the first- and second-order roots.

In contrast to first- and second-order roots, higher-order roots that support lower-order laterals in perennial plants may be semi-permanent members of the root system, despite their relatively fine (i.e., less than 1 mm) appearance (Eissenstat et al. 2000; Wells and Eissenstat 2001; Pregitzer et al. 2002). The long life span of higher-order roots should not be a surprise, for if a higher-order root dies, then all the lower-order roots dependent on this higher-order root for transport of photosynthates also die. Thus, plants should allocate more energy for the defense of higher-order roots, as indicated by their accumulation of condensed tannins and periderm formation (Eissenstat and Achor 1999; Enstone et al. 2001). While these secondary compounds may be important for the defense of the root, they often impede water

and nutrient acquisition (Peterson et al. 1999), and probably mycorrhizal colonization. Thus, while the fine roots of woody plants are typically defined in terms of roots less than 1–2 mm in diameter, many of the higher-order fine roots probably play only a limited role in nutrient acquisition.

8.2.4 Variation in Root Life Span in Different Environments and Among Species

In general, data are limited on root longevity of different species and in different environments (reviewed by Bloomfield et al. 1996; Eissenstat and Yanai 1997, 2002; Gill and Jackson 2000). There remains much uncertainty on general patterns, partly because of shortcomings in methodology. Mechanisms of root shedding are unknown. No abscission layer has been clearly identified, as commonly found in leaf petioles. It is very hard to pinpoint an exact time at which a root is dead, as demonstrated by tetrazolium staining experiments (Comas et al. 2000). A small lateral root typically dies over its entire length in a fairly short time period (i.e., often on the order of days), and commonly leaves a scar on the surface of the mother root (Pregitzer et al. 2002). Root death may often be passive (Eissenstat and Yanai 1997). One hypothesis is that once the root has outlived its usefulness, the plant stops investing in defense compounds for that root, basically leaving the root vulnerable to herbivores and pathogens. In common bean, for example, root death was found to be minimal for plants grown in sand culture with limited soil fauna, even during pod fill and pod dry-down (Fisher et al. 2002). In the field, however, nearly 50 % of the bean roots died by pod dry-down in rich agricultural soil. Weak pathogens likely are able to parasitise roots once carbohydrates and defense compounds are low.

Several environmental factors have been associated with diminished life span, including temperature (Watson et al. 2000; Gill and Jackson 2000), parasitism and herbivory (Maron 1998; Eissenstat et al. 2000; Wells et al. 2002), and drought (Hayes and Seastedt 1987). Soil fertility has been shown to both increase and decrease root longevity, possibly suggesting that other factors interact with soil fertility to determine root longevity (reviewed by Eissenstat and Yanai 2002; also see Burton et al. 2000). Similarly, the myriad effects of elevated CO_2 on plant nutrition, plant water use, and rhizosphere soil chemistry complicate the interpretation of root life span responses in CO_2-enrichment studies. Compared to plants grown under ambient conditions, plants exposed to elevated CO_2 may exhibit increased (Johnson et al. 2000; Arnone et al. 2000), decreased (Fitter et al. 1997; Thomas et al. 1999), or no change (Gavito et al. 2001; Pritchard et al. 2001) in root longevity.

A cost:benefit approach can be used to integrate the effects of various environmental factors on root longevity, assuming that root life span can be predicted by the length of time required to reach maximum lifetime effi-

ciency (Yanai et al. 1995; Eissenstat and Yanai 1997, 2002). For example, roots of a fast- and slow-growing species of maple differ considerably in their root physiology, which influences the predicted time required to reach maximum root efficiency in different soil types (Fig. 8.1; Comas et al. 2002). Lifetime efficiency always increases when a root is young, as the initial construction cost is amortized over a longer period (Fig. 8.1). As the root ages, uptake typically declines, causing efficiency to decrease. The data in Fig. 8.1 show that in poorly buffered sandy soil (Lilly loamy sand), maximum root efficiency is reached in about 80–120 days, depending on the species. The main factor lowering the efficiency of older roots is decreased uptake caused by depletion of P in the rhizosphere. By contrast, in the more fertile loamy soil (Hagerstown silt loam) with its high buffering capacity, nutrient depletion in the rhizosphere is insufficient to cause a downturn in root efficiency with root age.

Consequently, we predict shorter root life spans in poorly buffered soils, especially in the fast-growing maple with its thinner roots, higher uptake capacity, and higher maintenance respiration. Ideally, root efficiency modeling requires information on root benefits in relation to root costs over the lifetime of the root, which was not available in the study by Comas et al. (2002). These data are only beginning to emerge, and there is still considerable uncertainty in these costs and benefits in natural soils of high temporal and spatial heterogeneity (see Sects. 8.3.2 and 8.4.4).

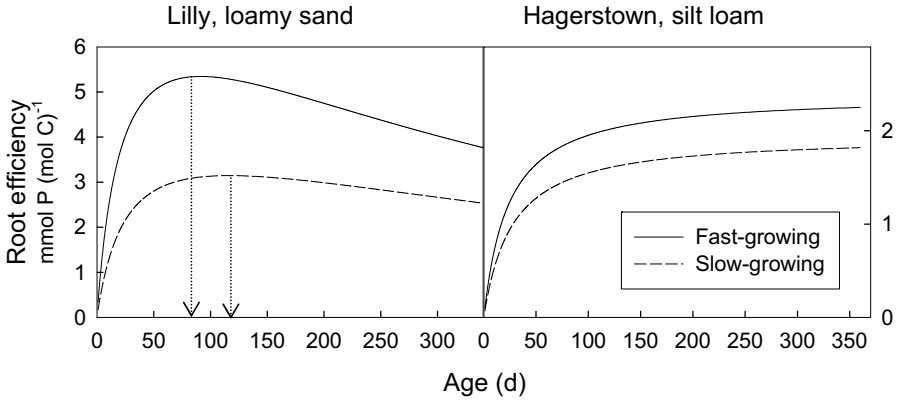

Fig. 8.1. Lifetime efficiency of first- and second-order roots of a fast- (*Acer negundo*) and slow-growing maple (*Acer sacharrum*; adapted from Comas et al., ~~unpubl. data~~) in two soils that differ widely in buffering capacity. *Arrows* indicate time to maximum efficiency where optimal life span is predicted. Root efficiency was calculated as cumulative P uptake per cumulative C cost, from root characteristics determined from seedlings in the greenhouse (Comas et al., ~~unpubl. data~~), and values for soil parameters from Kelly et al. (1992) and Bouma et al. (2001)

8.3 Costs of Root Production and Maintenance over a Root's Lifetime

8.3.1 Biomass Costs of Producing Root Absorptive Surface Area

8.3.1.1 Root:Shoot Biomass Partitioning

Typically, if soil resources such as nitrogen or phosphorus are limiting plant growth, plants increase the amount of root biomass allocation, and thus help maintain a "functional equilibrium" between shoot acquisition of C and root acquisition of mineral nutrients (Thornley 1972; Brouwer 1967, 1981; Gutschick and Pushnick, Chap. 4, this Vol.). At a whole-plant level, increasing the root:shoot ratio may enhance plant nutrient content, but it also increases biomass allocation to non-photosynthetic tissues. Therefore, it is not uncommon to find that while increased root-to-shoot ratios may help plant nutrient acquisition, the whole-plant relative growth rate is compromised (Gutschick and Pushnick, Chap. 4, this Vol.).

8.3.1.2 Specific Root Length

Root structure influences the allocation of root biomass for the production of root surface area. For example, species vary widely in their specific root length (SRL, root length:dry mass ratio; Eissenstat 1992), which strongly affects the amount of absorptive surface area for a given investment in root mass. There is also evidence that species of high SRL tend to more rapidly grow roots into disturbed soil or fertile soil patches (Eissenstat 1991; Fitter 1994; Bauhus and Messier 1999). Specific root length is controlled both by the length per unit volume (L/V; cm^{-2}) of the roots, and by the tissue density (root volume:dry mass ratio, V/M; g cm^{-3}) of the roots. Assuming cylindrical geometry, the L/V ratio is defined by the inverse of the square of the root radius. The radius of the terminal roots can vary an order of magnitude among species, from less than 0.05 mm in certain annual dicots, ericaceous species and grasses to greater than 0.5 mm among species in the Magnoliales, Cornaceae and Aliaceae (Fitter 1996). Tissue density can also vary widely among species, ranging from 0.09 to 0.14 in grasses (Ryser 1996; Bouma et al. 2003), and 0.05 to 0.20 in woody dicots (Wright and Westoby 1999; Eissenstat et al. 2000).

Specific root length varies widely with environmental conditions. However, the direction of change in SRL is not always predictable based on resource supply. Turf grasses, for example, can exhibit higher SRL in soil where water becomes less available (Huang and Fry 1998). Roots of *Festuca rubra*, by contrast, were found to have lower SRL when N was less available

(Paterson and Sim 2000). Because roots of different orders also vary widely in SRL, environmental effects on total root system SRL may be a result of differences in diameter or tissue density of the terminal laterals, or simply a result of greater production of new roots in a rapidly growing root system (Fitter 1985).

8.3.1.3 Root Hairs and Mycorrhizal Hyphae

Production of root hairs or extramatrical mycorrhizal hyphae can be a very efficient way by which a plant can increase absorptive surface for the same biomass allocation. While the diameter of the finest lateral roots of different plants may be typically on the order of 100–1,000 μm, root hairs are only 5–17 μm in diameter (Dittmer 1949), and the finest elements of extraradical mycorrhizal hyphal filaments are typically 2–7 μm (Smith and Read 1997). Assuming similar tissue densities among roots, root hairs and fungal hyphae, these differences in diameter suggest that for an equivalent biomass allocation, surface area production in the form of hairs and hyphae can exceed that of roots by factors on the order of 10–100.

As is the case for SRL, there is wide genotypic and phenotypic variation in the morphology of root hairs and fungal hyphae. Species vary widely in the density and length of root hairs. Root hairs range from less than 50 μm in length in onion and carrot to greater than 1,500 μm in spinach. Root hair density ranges from two hairs per millimeter of root in pine to about 100 hairs per millimeter of root in grasses and many annual dicots (Barber 1984; Tinker and Nye 2000). The frequency and size of root hairs also depend on environmental conditions. The direction of the response suggests increased foraging efficiency with greater limitation in soil nutrients. For example, root hairs are typically longer and denser at restricted supplies of P (Bates and Lynch 1996), nitrate (Bhat et al. 1979) and soil moisture (Mackay and Barber 1985).

Plants vary widely in the rate and extent to which their roots are colonized by mycorrhizal fungi (Smith and Read 1997; Finlay, Chap. 9, this Vol.). Environmental conditions that tend to depress colonization (and presumably extraradical hyphal growth) include high soil P, shade, and waterlogging. Vesicular-arbuscular (VA) mycorrhizal hyphal length can vary from 1 to 270 m^{-1} [redacted] length in field soil (Miller et al. 1995; Smith and Read 1997). Different fungi and different host plants produce different amounts of mycelium. Ectomycorrhizal hyphal production has been less well studied. Reported ECM hyphal lengths in *Salix viminalis* (100–300 m m^{-1} root; Jones et al. 1990) and *Pinus taeda* (504 m m^{-1} root; Rousseau et al. 1994) are at the high end of the range reported in the VA mycorrhizas cited above. Unlike VA mycorrhizas, ectomycorrhizal roots develop a fungal sheath that may represent as much as 30–40 % of the biomass of these roots (Smith and Read 1997).

8.3.2 Costs of Root Respiration

8.3.2.1 Construction Cost and Growth Respiration

The cost of tissue production is commonly referred to as construction cost, and includes the C or energy content of the root plus the energy or respiration involved in tissue formation (i.e., growth respiration). Often, root construction cost is assumed to be a one-time cost that occurs when the root is born (Yanai et al. 1995) – of course, an oversimplification. In reality, as a root ages, it becomes more lignified and suberized but, for the ephemeral fine root system, it is normally considered acceptable to treat the costs for this continued construction as negligible compared to the initial construction costs.

It is often assumed that high construction costs indicate a long life span, but this assumption may be incorrect. Tissues with shorter life spans may have less carbon invested in defense compounds such as tannins and lignins, but often have more proteins to support rapid nutrient acquisition. For example, Poorter et al. (1991) compared root construction costs for fast- and slow-growing grass species, and concluded that fast-growing species tended to have less defense compounds, but higher protein concentrations, making construction costs similar among the plant species tested. Similar results have been found in comparisons of fast- and slow-growing trees (Comas et al. 2002).

Growth respiration is the respiration involved in reducing carbon compounds to bring about the formation of new plant matter. Specific respiratory costs for growth depend on the chemical composition of the roots. The main compounds of plant biomass are proteins, carbohydrates, lipids, lignin, organic acids, soluble phenols, and minerals. Compounds such as proteins, lipids, and lignins have higher respiratory costs of construction than do carbohydrates such as cellulose and starch. Penning de Vries et al. (1974) calculated values of oxygen consumption associated with the costs of producing one unit of each of these compounds. Assuming an ADP:O ratio of 2.37 for 24 herbaceous species, Poorter and Bergkotte (1992) calculated the oxygen consumption needed for the production of 1 g root biomass for each species. The respiration rate varied between 5.5 and 8 mmol O_2 g^{-1} dry root mass. They also found that fast-growing species had higher respiratory costs for growth, due mainly to the higher protein contents of these roots. Thus, there is little evidence that slow-growing, well-defended root tissues are more expensive to produce than fast-growing tissues (on a gram dry weight basis). This is because of the high amounts of proteins in fast-growing tissues, which offset their lack of defense compounds.

Only a few studies have examined differences in root growth respiration or construction costs in relation to environmental conditions. In general, environmental effects on these costs are modest. Wullschleger et al. (1997)

reported that, compared to trees grown at ambient CO_2, *Lirodendron tulipifera* and *Quercus alba* trees exposed to elevated CO_2 exhibited less than 5 % lower root construction cost. In nonmycorrhizal Volkamer lemon seedlings, plants deficient in P exhibited about 6 % higher root construction costs than those sufficient in P (Peng et al. 1993). Mycorrhizal colonization increased construction costs of Volkamer lemon roots about 8 % for plants of equivalent P nutrition.

8.3.2.2 Maintenance Respiration

Maintenance respiration is that fraction of root respiration that is needed to maintain existing, mature cells in a viable state. Relatively little is known about the biochemistry and physiology of maintenance processes. Protein and carbohydrate turnover and maintenance of membrane potentials are considered major "maintenance" processes requiring energy. A more practical approach is to define maintenance respiration as the residual respiration not attributable to growth or ion-uptake processes, which includes respiration associated with the metabolism of exudates as well as respiration used to induce and maintain mycorrhizal infection. Bouma et al. (2001) estimated that belowground C expended for maintenance may be at least as large as that expended for root construction and growth respiration. In a study comparing protein turnover in fast- and slow-growing grass species, Scheurwater (1999) concluded that 22–30 % of maintenance respiration was used in protein turnover, regardless of species. This constituted 11–15 % of daily root ATP production.

Root hair production seems to add little additional cost to root maintenance, while mycorrhizal colonization can have a substantial additional maintenance cost. In a study of *Arabidopsis* root hair mutants, there was no clear pattern of greater respiration per unit root length for genotypes with abundant root hairs relative to those with no or very limited root hair development (Bates and Lynch 2000b). In citrus, mycorrhizal colonization caused maintenance respiration to increase by 39 % compared to nonmycorrhizal plants of similar P nutrition (Peng et al. 1993).

8.3.2.3 Ion-Uptake Respiration

Ion-uptake respiration is used to absorb and assimilate solutes. The absorption and assimilation of nutrients can account for 50–70 % of the respiratory energy in roots (Poorter et al. 1991). As much as 90 % of the respiration associated with ion uptake can be devoted to the uptake and assimilation of nitrogen ions (Veen 1981). Depending upon the form of solute, costs for ion uptake can vary. For example, Bloom et al. (1992) found different costs associated

with the uptake and assimilation of NH_4^+ and NO_3^- in barley. Costs associated with net N uptake (the balance of N influx and N efflux) can vary considerably between species, and appear to be linked to RGR. Costs associated with net N uptake were up to four times higher in slow-growing grass species than in fast-growing species (Poorter et al. 1991; Scheurwater et al. 1998). Scheurwater et al. (1999) found that N influx was similar between fast- and slow-growing species, but slow-growing species had higher rates of N efflux during periods of darkness. Thus, lower respiratory costs for N uptake do not necessarily mean that the plant has used less energy for nitrogen influx, but rather that it has retained a higher percentage of the N acquired (lower efflux).

8.3.3 Cost of Mycorrhizal Colonization and Maintenance

Most plants can benefit from forming a symbiosis with mycorrhizal fungi, at least at some periods of the year, when the demand for nutrients exceeds the amount that can be supplied by the roots alone. However, the symbiosis of mycorrhizal fungi with roots can have an appreciable C cost. For plants of similar size and P nutrition, belowground C costs may be on the order of 10–20 % higher in both VA and ectomycorrhizal compared to nonmycorrhizal plants (reviewed by Smith and Read 1997). Increased metabolic activity of the root, and respiration of the associated fungi both cause greater belowground expenditure (Peng et al. 1993; Rygiewicz and Anderson 1994). Costs of mycorrhizas are typically highest during the colonization phase when C demands for the fungus are high (Eissenstat et al. 1993). Costs vary widely as a function of, amongst others, the species of fungi, the mycorrhizal dependency of the host plant, and soil fertility. Indeed, mycorrhizal fungi can be parasitic on plants when the cost of the symbiosis exceeds the benefits (e.g., Johnson et al. 1997; Graham and Eissenstat 1998), which may be most common in soils of high fertility and when the fungus rapidly colonizes plants.

8.3.4 Changes in C Costs as the Root Ages

Not much is known about changes in tissue construction costs as the root ages. Bouma et al. (2001) reported that there was no change in C and N contents of fine apple and citrus roots as they aged. However, there was a dramatic decline in root respiration (Bouma et al. 2001; Fig. 8.2; also see Comas et al. 2000). The decline in root respiration without a corresponding decrease in N concentration might indicate that some of the N was used for other purposes such as the production of immobile defense compounds associated with root pigmentation. The effect of root age on root chemical composition may have a significant bearing on nutrient acquisition, and deserves further study.

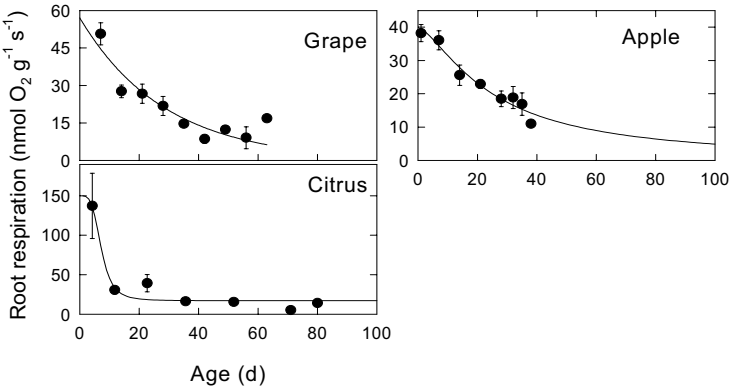

Fig. 8.2. Respiration of first- and second-order roots of Concord grape, apple (red chief delicious on M26 rootstock), and citrus (red grapefruit on sour orange rootstock) roots growing in the field. Roots of known age were collected from root boxes, and O_2 consumption (±SE) of the excised roots determined with an oxygen electrode. (Redrawn from Comas et al. 2000; Bouma et al. 2001)

Bouma et al. (2001) found that root respiration of fine citrus roots dropped to less than half of the initial levels within 10 days after the root was born (Fig. 8.2). Fine apple and grape root respiration also decreased rapidly; these were about half of the initial levels after approximately 20–30 days. Grape and apple respiration both exhibited an exponential decline with root age. However, citrus respiration remained quite stable after the initial decline (Fig. 8.2).

Mycorrhizal costs (and benefits) are likely to vary strongly with root age. The rapid colonization phase is a time of high C cost; transient whole-plant growth depression can occur at this time (Smith and Read 1997). In VA mycorrhizas, maintenance costs of mycorrhizal structures may decline with root age when arbuscules deteriorate and the root is occupied mainly by vesicles, the fungal storage organs. Older roots typically only have vesicles (Brundrett and Kendrick 1988). In ectomycorrhizal species, the fungus typically develops a more prominent hyphal sheath outside the root (Smith and Read 1997). Indeed, it is very likely that mycorrhizal fungi, especially ectomycorrhizal fungi, may have pronounced effects on the response curve of root costs as a function of root age and root longevity (e.g., Smith and Read 1997; Espeleta et al. 1999). Unfortunately, there is a notable lack of information on the costs (and benefits) of mycorrhizas as a function of root age, especially at the level of the individual root.

8.3.5 Other Costs

Other C costs involved with maintaining and expanding a root system include the exudation of C compounds from the roots, either through "active" exudation or sloughing of the cortex. Sloughing of the cortex has been known to increase microbial activity around the root, which may increase competition for nutrients between microbes and roots. Compounds that are exuded from the root can serve multiple functions – they can be used to decrease the pH around the root causing increased nutrient availability in calcareous soils (Hoffland et al. 1989; Grayston et al. 1997), to increase interplant root interference (alellopathy), to attract fungi/microbes (Grayston et al. 1997; Tarawaya et al. 1998; Yoder 2001), to improve nutrient uptake (chelation), and even to generate signals between plants or within root systems (Lambrecht et al. 2000). The quantity and quality of root exudates vary among life-forms (either herbaceous or woody), and with plant age. Seedlings have been reported to produce greater quantities and a more diverse range of carbohydrates than do mature trees, but mature trees exuded larger quantities of amino acids, amides and organic acids (Grayston et al. 1997). These differences suggest that root age may exert a strong effect on the type and amount of exudates from fine roots.

Marschner (1998) reviewed the role that root exudates can play in improving the efficiency of nutrient acquisition. Root exudates can facilitate the acquisition of P (via the release of acid phosphatases), Fe^{3+}, and other micronutrients (e.g., Zn^{2+}, Mn^{2+}, and Cu^{2+}). Other studies suggest that exudation increases when plants are grown under N-limited conditions. Paterson and Sim (2000) found that as much as 16 % of the total daily assimilate was lost in the form of root exudates when *F. rubra* plants were grown under low N supply. This value decreased to 1.6 % for plants grown under high N supply. These findings were supported by those of Hodge et al. (1996), who reported that 8.8 and 14 % of plant carbon was released as exudate by *Festuca ovina* seedlings grown at high and low N over a 34-day growth period, respectively. In the same experiment, they found percentages for *Plantago lanceolata* to be 5.6 and 15 % at high and low N, respectively. Other recent estimates also suggest that 7–15 % of net carbon fixation is exuded during plant growth (Johansson 1992; Swinnen et al. 1995). Thus, root exudates can represent an appreciable carbon cost over the lifetime of a root, especially for nutrient-deficient plants in infertile soil.

8.4 Uptake of Mineral Nutrients over a Root's Lifetime

8.4.1 Initial Advantages to Root Growth

Root growth allows the plant to explore new areas in the soil. Either root or soil properties, or both, may limit uptake (Williams and Yanai 1996). The factors that make new roots better than old ones include diminished uptake capacity in older roots, and the depletion of nutrients in solution around active roots. For example, Bar-Tal et al. (1994) found that root pruning and subsequent production of new roots resulted in a N uptake that was higher than that of undisturbed plants with intact root systems. Yanai (1994) simulated the contribution of new root growth to total nutrient acquisition using a modified steady-state model of solute uptake. She found that root growth was most important for fast-growing plants and immobile nutrients, which is consistent with earlier predictions (Caldwell 1979). Moreover, root production and rapid rates of resource acquisition may be very important aspects of resource competition, especially in nutrient patches of short duration (Robinson et al. 1999).

8.4.2 Importance of Mycorrhizal Colonization

Mycorrhizal colonization allows plants to increase the amount of nutrients captured by the root system (reviewed by Smith and Read 1997). For example, calculations by Sanders and Tinker (1971) show that roots infected with mycorrhizal fungi can transport phosphate up to four times faster than uninfected roots. Vesicular-arbuscular mycorrhizas are most noted for increased acquisition of P, whereas ecto- and ericoid mycorrhizas can also increase N acquisition. Mechanisms of enhancement also vary, with VA mycorrhizas being primarily associated with enhanced acquisition solely of inorganic phosphate. By contrast, ecto- and ericoid mycorrhizal fungi also have the ability to increase the mineralization and acquisition of organic sources of P and N. Soil conditions, such as temperature and aeration, can greatly influence the potentially beneficial role of mycorrhizal fungi in overall nutrient acquisition. Little is known about the mechanisms by which nutrients absorbed by these fungi are transferred into the plants. In ectomycorrhizal systems, the root cortical cells may simply absorb inorganic phosphate leaked from hyphae in the Hartig net (Ashford et al. 1989), but in VA mycorrhizal systems the situation may be more complex.

The contribution of mycorrhizas to root nutrient acquisition has an important age component. When new roots grow into undisturbed soil with an established hyphal network, colonization may be very rapid. For example, Smith and Read (1997) reported that over 70 % of tomato (*Lycopersicon escu-*

lentum) root length exhibited internal fungal colonization inside the root cortex 2 days after transplantion into soil with established mycorrhizal plants. Arbuscules, the fungal organ primarily associated with nutrient exchange, typically form soon after colonization and reach a peak about 6 days after transplantion. However, arbuscules are usually short-lived, with a life span of only about 7 days, although slow-growing plants may exhibit somewhat longer-lived arbuscules (Smith and Read 1997). Older roots typically contain internal hyphae, which are probably less effective in nutrient transfer than arbuscules. External hyphal development begins as main branches that may branch into fan-like networks. Most estimates of time for development of external mycelium have been made at the whole-root-system level, and not at the level of an individual root in undisturbed soil. A timescale of about 1–2 months is typical for potted plants (Smith and Read 1997). Similar to colonization, the rate and extent of external hyphal development are strongly influenced by fungus and host species type, and environmental conditions such as light intensity and soil phosphorus concentration (Smith and Read 1997; Henry and Kosola 1999). Longevity of external hyphae is another important unknown, but is recognized to be strongly influenced by soil organisms such as collembolas, which may not be present in typical pot-culture experiments (McGonigle and Fitter 1988).

Similar to VA plants, ectomycorrhizal plants can have their roots colonized within 2–4 days of contact by the ectomycorrhizal hyphae, and have a fully developed Hartig net and mantle within 7 days (Smith and Read 1997). In the majority of ectomycorrhizal angiosperms (e.g., *Alnus*, *Betula*, *Eucalyptus*), the formation of the Hartig net is confined to the epidermal layers. In ectomycorrhizal gymnosperms, the Hartig net typically encloses several cortical cell layers as well as the epidermis (Smith and Read 1997). Downes et al. (1992) grew seedlings of *Picea sitchensis* in 20 × 20 cm transparent root observation chambers to follow morphological and anatomical changes of known ~~root~~ age, and inoculated with either the ectomycorrhizal fungus *Paxillus involutus* or *Tylospora fibrillosa*. Mycorrhizal roots over 50 days old tended to have diminished extramatrical mycelium. Roots 30 days old exhibited 30–50 % cortical cell death with a linear decline in living cortical cells until, by 110–140 days, only 5–15 % of the cortex was still alive. Hartig net senescence generally followed soon after cortical cell senescence. The coupled loss of the extramatrical mycelium and the interface of the cortical cells with the Hartig net clearly indicated loss of uptake capacity in older roots. Downes et al. (1992) concluded from these anatomical studies that ectomycorrhizal *Picea* seedling roots exhibited a major decline in function after 85 days.

8.4.3 Longevity of Root Tissues

8.4.3.1 Overview

There is a large literature relating anatomical features of the root to nutrient acquisition, including the development of the endo- and exodermis, of root hairs and mycorrhizal fungi, and of vascular tissue (Clarkson 1996). It should be noted that most of this research has focused on the seminal root of developing seedlings; much less attention has been given to anatomical development in the fine laterals. Even more problematic is the lack of work on older roots in the field. When one evaluates nutrient acquisition over the life of a root, one needs to consider also the anatomical changes that typically occur over that root's lifetime. Many features of a root, such as root hairs, mycorrhizal arbuscules and cortical cells, may persist only for a certain portion of a root's life.

Traditionally, ecologists have characterized absorptive roots, especially those of woody plants, by some arbitrary diameter limit (e.g., all roots <2 mm). While most of these roots may serve some role in the absorption of water and nutrients, many no longer have an epidermis, or even a cortex. For example, in loblolly pine (*Pinus taeda*), only 53 % of the root length of roots less than 2 mm in diameter was in a primary stage of development with no secondary vascular tissue, and most of these were mycorrhizal short roots (McCrady and Comerford 1998). Kramer and Bullock (1966) found that growing root tips typically accounted for less than 1 % of the total root surface area in stands of loblolly pine and yellow poplar (*Lirodendron tulipifera*). Okano and Omae (1996) found that white rootlets constituted 30 % of the root system dry mass of the tea tree (*Camellia sinensis* L.), accounting for 60 % of root respiration and 75 % of total nitrogen uptake. Roots that have formed a periderm typically lose their cortex, and may have greatly reduced capacity for water and nutrient absorption (e.g., Sands et al. 1982; van Rees and Comerford 1990). They also have lost their ability to form a symbiosis with mycorrhizal fungi. Even among fine roots that exhibit no periderm formation, in many species substantial mortality of epidermal and cortical cells may have occurred.

8.4.3.2 Longevity of Root Hairs and Epidermis

From a physiological perspective, root hairs can be very important for nutrient acquisition. Root hairs have been shown to exhibit intense H^+-ATPase activity, and are involved in the uptake of most major nutrients, including Ca^{2+}, K^+, NH_4^+, NO_3^-, Mn^{2+}, Zn^{2+}, Cl^-, and $H_2PO_4^-$ (Gilroy and Jones 2000). Using ^{32}P, it has been estimated that root hairs can satisfy as much as 60 % of

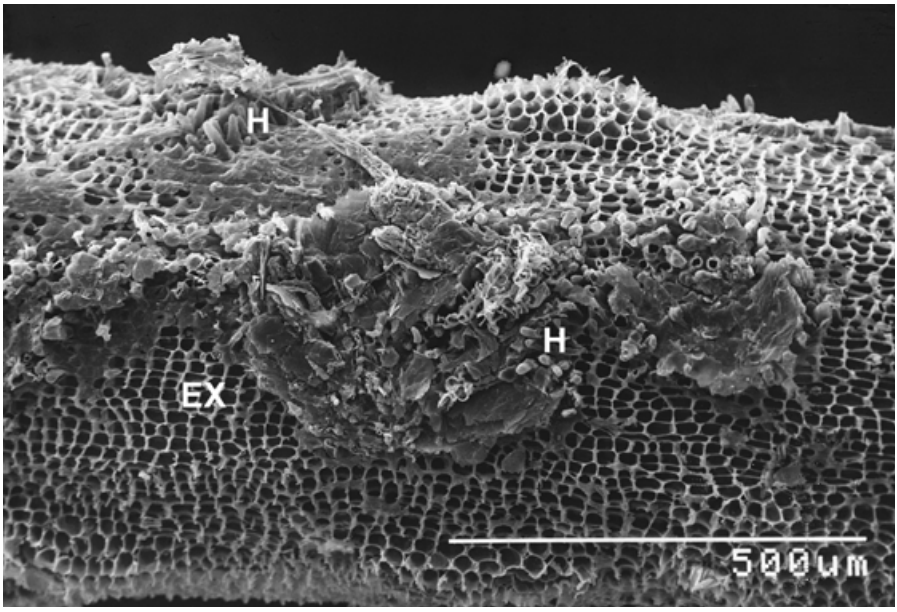

Fig. 8.3. Surface characteristics of typical sour orange roots collected from a Valencia orange rootstock trial (for details, see Eissenstat and Achor 1999). Most of the epidermis has sloughed away, exposing the radial walls of the exodermis (*EX*). The inner tangential walls of the exodermis are the effective barrier between the soil and the root. At this study site, citrus roots rarely have arbuscules, and only sparse portions of the root have root hairs (*H*), except in the very youngest roots. Presumably, most water and nutrient acquisition occurs from older roots, like the one illustrated here. Samples were fixed in glutaraldehyde and dehydrated in an ethanol series, critical-point dried with CO_2 and sputter coated with 80:20 gold:palladium for 90 s. Microscopy was performed with a Hitachi Model S530 at 100 ×

the plant P demand (Gahoonia and Nielsen 1998). From an ecological perspective, however, root hairs may be quite ephemeral and may not contribute greatly to the total nutrient acquisition over the lifetime of the root, especially for long-lived roots. In cereals, root hairs may live only from a few days to 2–3 weeks (Holden 1975; Henry and Deacon 1981; Fusseder 1987). Eventually the entire epidermis can die, especially for roots that form an exodermis. In citrus, healthy roots of the finest order often lack an epidermis (Fig. 8.3; Eissenstat and Achor 1999). Most northern hardwood species also typically do not have an epidermis on many of their fibrous roots (Brundrett and Kendrick 1988; Brundrett et al. 1990). Root hair death can be accelerated by exposure to dry soil (e.g., 10-day drought in *Cicer arietinum*; Spaeth and Cortes 1995). This is especially common in species such as corn (Stasovski and Peterson 1991), onion (Stasovski and Peterson 1993), and citrus (Eissenstat and Achor 1999), whose fine roots have a suberized exodermal layer just

below the epidermis that protects the inner cortex. If a soil sheath forms around the root, however, root hairs may live considerably longer (Vermeer and McCully 1982).

8.4.3.3 Longevity of Cortex

In many fine lateral roots less than 2 mm in diameter, the cortex is an ephemeral tissue that dies sooner than the entire root. While cortical cell death can result from natural developmental processes associated with the expansion of the vascular cylinder as the root undergoes secondary development, cortical cell death is also common in roots that have not undergone secondary thickening. Most wetland plants, for example, exhibit cortical cell death and formation of aerenchyma in adventitious roots soon after initiation following flooding (e.g., within 2 weeks in *Rumex* spp.; Visser et al. 1996). Drought can also accelerate cortical cell death, especially in species like perennial ryegrass (*Lolium perenne*; Jupp and Newman 1987), grape (Mapfumo et al. 1994) and chickpea (Spaeth and Cortes 1995), which lack heavily suberized outer layers of tissues. In species with a heavily suberized and lignified exodermis (onion, Stasovski and Peterson 1993; citrus, Eissenstat and Achor 1999) or epidermis (e.g., kiwi; Lemon and Considine 1993), however, little cortical cell death may occur in roots exposed to dry soil.

As new, white roots begin to turn yellow and brown (associated with the accumulation of condensed tannins; McKenzie and Peterson 1995), much of the cortex dies in some species (grape, Richards and Considine 1981; apple, Head 1967; spruce, Downes et al. 1992; pine, Peterson et al. 1999, but see McCrady and Comerford 1998). In other species, especially those with a heavily suberized epidermis and exodermis, the cortex may remain viable for the entire life span of the root (e.g., citrus, Eissenstat and Achor 1999; sugar maple, Brundrett and Kendrick 1988). Peterson et al. (1999) suggest that root maturation from white to yellow/brown in the condensed tannin zone should diminish uptake capacity, with limited symplastic uptake via the passage cells in the endodermis. In addition, the death of cortical cells also is typically followed by a loss of mycorrhizal fungal organs used for nutrient exchange (e.g., Downes et al. 1992). Formation of a cork periderm should result in a more complete barrier to water and nutrient absorption. Nevertheless, water and nutrient absorption can still occur in roots with a cork periderm, presumably through occasional cracks in this otherwise impermeable layer (Kramer and Bullock 1966). Because most of the fine root system may be brown and devoid of living cortex, at least in trees, roots with a cork periderm undoubtedly still play an important role in water, and perhaps also nutrient absorption (Kramer and Bullock 1966).

8.4.3.4 Longevity of Xylem Vessels

Actively growing roots may have immature xylem a considerable distance (i.e., 15–40 cm) from the root tip (McCully 1999). Living xylem vessels with cross-walls are not open conduits – consequently, they are not effective in conducting water. In the fine lateral roots of corn, for example, up to 40 % of the vessels are closed and nonconducting (McCully 1999). It is not known at what age xylem vessels in lateral roots typically mature, especially in dicots. In grasses, the transition from closed to open large xylem vessels is associated with decreases in the relative water content of the cortical tissues, and death of the epidermis (McCully 1999).

8.4.4 Changes in Nutrient Uptake Capacity as the Root Ages

Young roots are generally considered to have larger uptake capacities (capacity to take up nutrients at the root surface when nutrients are not limiting; i.e., V_{max}) than older roots, and thus the proportion of young roots in the whole root system can strongly affect overall plant nutrient uptake. A number of studies have compared "woody" or "suberized" roots with white roots in various tree species (Van Rees and Comerford 1990, and references cited therein). While white roots typically have higher rates of water and mineral nutrient uptake than do woody roots, the magnitude of the difference varies considerably. For example, white roots have 74 % faster K^+ uptake than do woody roots in *Prunus*, but only 22 % faster P uptake (Atkinson and Wilson 1980). In contrast to the relatively small effects of root age on nutrient acquisition, Kramer and Bullock (1966) found that water uptake in *P. taeda* white roots was on average about five times faster than that recorded in woody roots.

Several studies have measured nutrient uptake activity along a root axis of young seedlings. In these studies, it was found that the young region directly behind the meristem exhibits the greatest nutrient uptake activity (Russell and Sanderson 1967; Clarkson et al. 1968; Clarkson 1991). Gao et al. (1998) developed a method to calculate the age of a whole root system, and estimated that nitrogen uptake capacity was decreased to less than 50 % within 10 days. Root systems with an integrated age older than 10–15 days maintained a steady, slowly decreasing nitrogen uptake rate as a function of age. This would suggest that plants with higher fine root turnover rates would maintain a higher nutrient uptake capacity, as high turnover rates would decrease the integrated age of a root system.

Only few studies have directly measured nutrient uptake on differently aged, first-order roots in older plants (Bouma et al. 2001; Volder et al. 2005). Bouma et al. (2001) measured ^{32}P uptake rates of single, excised first- and second-order roots for two tree species, apple and citrus (Fig. 8.4). They found

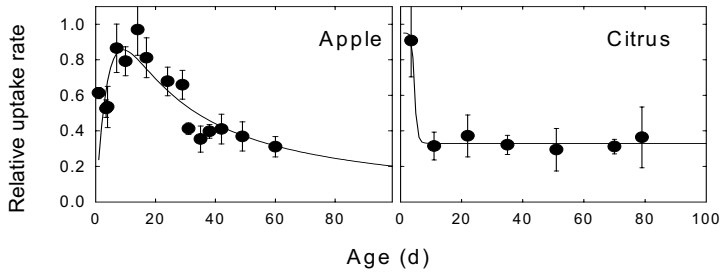

Fig. 8.4. Relative uptake rate of phosphorus as a function of root age in apple (red chief delicious on M26 rootstock) and citrus (red grapefruit on sour orange rootstock) roots growing in the field (from Bouma et al. 2001). Relative P uptake (±SE) was determined by measuring ^{32}P uptake from 1-cm excised root segments from mature trees at concentrations ranging from 1 to 1,000 μM P

marked differences between the two species, the longer-lived, coarser, citrus roots (median life span 300 days) showing a decreasing P uptake capacity about 4 days after birth, whereas apple roots (median life span 30 days) did not diminish P uptake capacity until they were about 25 days old. Maximum P uptake capacity was more than five times faster in apple than in citrus. After peak uptake capacity had been reached, citrus root values dropped to a stable level of about 35 % of maximum capacity that did not change further with root age, whereas apple roots exhibited a gradual but continuous decline with root age. A rapidly decreasing uptake capacity was also found for the uptake of NO_3^- in intact young roots of tomato (Volder et al., unpubl. data) and grape (Volder et al. 2005) seedlings grown in the laboratory, and 25-year-old mature grapevines in the field (Volder et al., unpubl. data). Within 5 days of root birth, N uptake was decreased by 50 % in all of these species. The pattern was best described by a logarithmic decrease with age for all the species, with very high NO_3^- uptake rates during the first 2 days and a rapid decline in uptake capacity thereafter.

In summary, nutrient uptake capacity typically diminishes with root age. The specific pattern of decline is affected by the type of mineral nutrient and the species of plant. Plants with long-lived roots likely have lower maximum uptake capacities than do plants with short-lived roots, but long-lived roots may exhibit less decrease in uptake capacity with age. Further study is needed to test these predictions.

8.5 The Efficiency of Nutrient Acquisition over a Root's Lifetime

8.5.1 Efficiency Concepts and Model Simulations

Root efficiency, *E*, can be defined as the rate of resource acquisition divided by the rate of carbon expenditure (Yanai et al. 1995; Eissenstat and Yanai 1997). Both daily efficiency (E_{daily}) and lifetime efficiency ($E_{lifetime}$) can be used to describe costs of nutrient foraging. The daily efficiency of the root, E_{daily}, represents the instantaneous efficiency at a single point in time, using appropriate rates of *uptake* (for example, mmol P g^{-1} root day^{-1}) and *cost* (mol C g^{-1} root day^{-1}). If daily costs and benefits are summed over time, then the integrated lifetime efficiency, $E_{lifetime}$, can be calculated. In our examples, cumulative *uptake* has units of mmol P or N/g root, while cumulative *cost* has units of mol C/g root. Both E_{daily} and $E_{lifetime}$, therefore, have units of mmol P or N/mol C. While $E_{lifetime}$ is theoretically most closely related to the overall efficiency of tissue deployment, E_{daily} can be a useful measure of instantaneous costs of nutrient uptake.

We have used the relationships between P uptake and root age (Fig. 8.4), and between respiration and root age (Fig. 8.2) to model E_{daily} and $E_{lifetime}$ of individual roots of citrus (Fig. 8.5; Bouma et al. 2001). Citrus groves are fertilized with P and other nutrients, and are commonly planted in sandy soils having low inherent fertility. If root P uptake does not deplete the soil, as might occur in a regularly fertilized grove, then efficiency remains high, and the optimal life span is infinite. Alternatively, if the P in the soil solution in the rhizosphere is depleted by the root over time, as predicted in the Candler fine sand, then E_{daily} of the root declines after about 35 days, and $E_{lifetime}$ peaks at about 120 days. The observed life span of citrus roots under low biotic pressure is about 300 days at this location (Eissenstat et al. 2000), suggesting that the roots remain effective in nutrient capture longer than predicted by the optimization model. Other factors not presently included in the efficiency model, such as P uptake by mycorrhizal fungi and P fertilization every 90 days, likely contribute to extend the P acquisition of older roots.

Some studies have also examined instantaneous or daily *E* levels. Scheurwater et al. (1998) measured the specific respiratory cost of nutrient uptake for a fast- (*Dactylis glomerata*) and a slow-growing species (*Festuca ovina*) in solution, where typically no depletion zones form. They found that the slow-growing grass had a respiratory cost per unit nitrogen taken up that was three times higher because of greater efflux. Clearly, there can be a considerable range in the efficiency of nutrient uptake among species grown in similar environments.

Volder et al. (2005) calculated E_{daily} in solution culture using nitrate uptake estimates from greenhouse-grown grape roots immersed in ^{15}N-labeled solu-

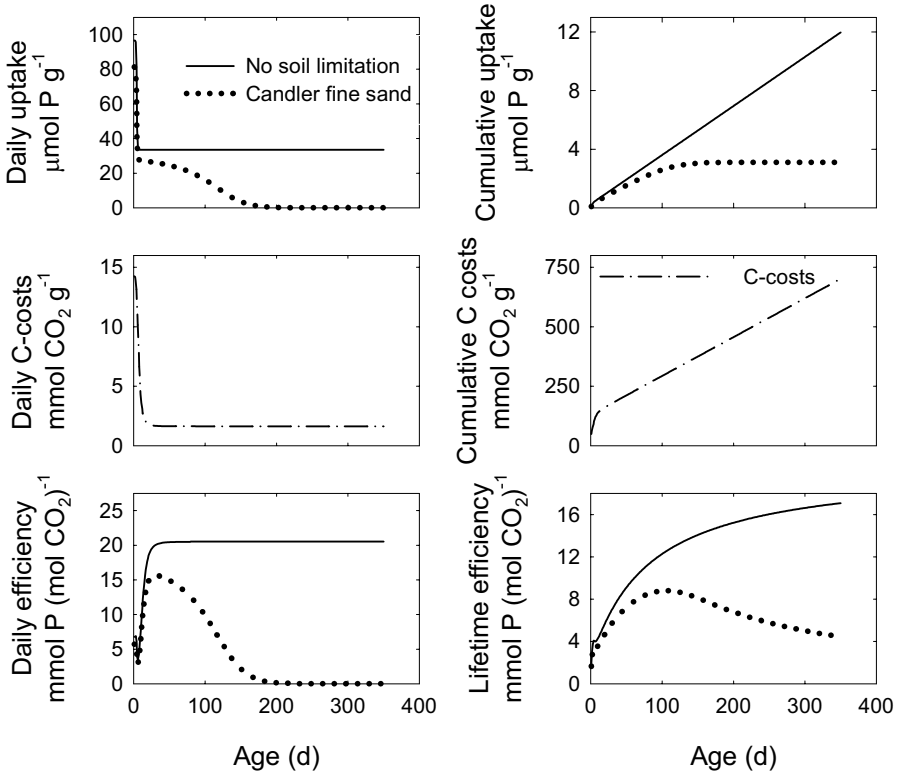

Fig. 8.5. Daily (E_{daily}) and lifetime efficiency ($E_{lifetime}$; mmol P mol^{-1} C) of citrus roots, based on C costs and P uptake. Carbon costs (*dashed line with one dot*) were calculated by multiplying the respiration rate (nmol O_2 g^{-1} s^{-1}) as a function of root age (Fig. 8.2) by a respiratory coefficient (RQ) of 1.1 mol CO_2 mol^{-1} O_2, and integrating over time with a time step of 1 day. Uptake capacity for P (i.e., I_{max}) was assumed to follow the age relationship shown in Fig. 8.4. Uptake affinity (K_m) was assumed not to change with root age. These data are slightly different from those published in Bouma et al. (2001) because of an incorrect effective diffusion coefficient in the original paper. The correct effective diffusion coefficient is 4.1×10^{-8} cm^2 s^{-1}. Carbon cost at age=0 is assumed to be equal to the carbon content of the root at age=1; the respiratory costs at day=1 are included. Soil P supply was assumed to be either not limiting (*solid line*) or limited by the soil characteristics of Candler fine sand where the trees were growing (*dotted line*). We assumed C costs were independent of P supply. Simulations suggest that unless soil depletion zones form around the root, limiting P uptake (see Candler fine sand simulation), $E_{lifetime}$ never reaches a maximum level and the root should not be shed. Thus, soil characteristics are at least as important as root characteristics in determining when $E_{lifetime}$ is maximized and when the roots should be shed

tion. Both N uptake and root respiration declined rapidly with root age (within 10 days, roots measured varied between 1 and 80 days in age). However, respiration declined slightly faster than N uptake, causing E_{daily} to increase with root age. In the field, these grape roots had median life spans varying in the range of 42–165 days, depending on year and time of birth (Anderson et al. 2003). The actual nitrate uptake rates from the soil are likely slower than those measured in solution culture. Respiration is largely a function of growth, ion uptake, and maintenance. For older first-order roots, growth respiration and ion-uptake respiration (based on low uptake capacity) are probably minor components of total root respiration. Thus, despite older roots having high efficiency, the large decrease in maintenance respiration suggests a gradual abandonment of the root by the plant, by way of not investing in defense compounds or in the energy required to maintain membrane potentials for an already ineffective root (in terms of nutrient uptake).

8.5.2 Problems Associated with Efficiency

8.5.2.1 Efficiency Versus Effectiveness

Higher efficiency does not always lead to higher plant fitness. In a competitive environment where resources are available only for short periods, rapid resource acquisition, rather than high efficiency, may be a key to plant success (e.g., Eissenstat and Caldwell 1988; Robinson et al. 1999). High expenditures for rapid resource acquisition may be an ecologically effective strategy if fitness of neighbors is diminished to a greater extent than is the fitness of the individual exhibiting rapid growth.

Plants may also overproduce tissues as a means of coping with herbivory, or as insurance against extreme events. The notion that plants might not be efficient in resource use was underscored in a review by Thomas and Sadras (2001). They argue that there may be many instances where plants may support large numbers of "unproductive" tissues that may provide secondary benefits for N storage, as a buffer against herbivory, and as a way of offloading excess C and other nutrients. For example, Thomas and Sadras (2001) speculate that plant species in fertile environments may exhibit high rates of leaf and root turnover, not in response to a reduced need for nutrient conservation (Berendse and Aerts 1987; Aerts 1990, 1999), but rather because of a greater need to offload excess resources associated with overproduction of carbohydrates. Consistent with the excess tissue hypothesis of Thomas and Sadras (2001) are the arguments that plants may use the alternative respiratory path as an "energy overflow" pathway (Lambers 1987), and the evidence from the elevated CO_2 literature that shows an average of 42 % enhanced soil respiration (root plus microbial respiration) in response to elevated CO_2 with-

out an increase in shoot growth (Zak et al. 2000). Our view is that while there may be times when plants appear "wasteful", especially over short time spans, maintaining redundant absorptive tissues to offset the risks of herbivory or extreme weather events still follows general concepts of optimization in an uncertain environment. Consequently, broad economic analogies (sensu Bloom et al. 1985) of plant resource acquisition and allocation may be useful tools as a first approximation for interpreting plant responses to multiple resource limitations and strategies for tissue deployment. More specific and quantitative models of nutrient use efficiencies are discussed by Gutschick and Pushnick (Chap. 4, this Vol.).

8.5.2.2 Problems of Currency

Ideally, efficiency should be unitless, so that both benefit and cost are defined by one and the same currency. There are many definitions of nutrient acquisition efficiency (e.g., Koide and Elliott 1989; Koide et al. 1999), and some use a mineral nutrient (e.g., N or P) for expression of both benefit and cost. We are particularly interested in a definition that embraces both costs of construction and costs of maintenance over the lifetime of individual roots. Costs of ion uptake may also be included in this definition (Veen 1981; Bouma et al. 1996). While costs associated with tissue construction are amenable to the use of mineral nutrients as a currency, the relationship of mineral nutrients to the costs of tissue maintenance and ion uptake is more problematic. In choosing a currency to assess costs of root production and maintenance under a wide range of conditions, an estimator of the energy allocated for nutrient acquisition (e.g., carbon) tends to have the widest utility. Even in what might be considered open habitats, there is evidence that energy limits growth and reproduction. For example, it has been shown that partial shading leads to a loss of plasticity in P uptake capacity (Jackson and Caldwell 1992) and root proliferation (Bilbrough and Caldwell 1995) of the perennial tussock grass, *Agropyron desertorum*. Taken together, these studies highlight the value of C as a broadly defined currency of costs of nutrient acquisition. While we recognize that C supply does not always constrain growth and reproduction (e.g., Arnone and Körner 1995), as a general tool, no other single currency is as effective as C (or glucose equivalents thereof) for estimating the costs of root construction, maintenance, and ion uptake.

It also is reasonable to express efficiency in units of C benefit/C cost. This can be done by determining the ratio of N or P acquisition over a given time interval to the C gain over the same time interval (measured by whole-plant gas exchange or estimated by whole-plant C increase in growth) to obtain the exchange ratio during that time interval. It should be emphasized that these estimates only approximate the exchange ratio of a mineral nutrient with C, as storage and costs of transport are not generally considered. The reader is

referred to Bloom et al. (1985) for a more complete discussion on exchange ratios of different currencies.

8.6 Heterogeneous Soil

8.6.1 Overview

Soil resources are unevenly distributed in space and time. New root growth is most advantageous when roots are deployed in the most favorable soil patches where soil nutrient availability is highest (Robinson, Chap. 3, this Vol.). Over the life of the root, soil nutrient availability can diminish for a number of reasons, including changes in temperature, soil moisture, and nutrient depletion by plants and microbes. A key to maximizing root efficiency is to reduce root costs as nutrients become less available, and to reallocate photosynthate to roots at more favorable soil locations. There are a number of studies that suggest that plants can adjust root activity to favor roots in patches of soil highest in nutrients, diminishing allocation of carbohydrates to those roots in less favorable soil (Huang and Eissenstat 2000). Pregitzer et al. (1993), for example, found that fine roots produced in hardwood forest lived longer in patches of water and water plus nitrogen than in untreated soil. The tendency to proliferate in patches varies among species, and is likely influenced by the costs of root construction. Consequently, nutrient acquisition over the life of the root is strongly affected by changes in soil nutrient availability, and root costs that may occur over the root's lifetime.

8.6.2 Effects of Water and Temperature

Water availability can dramatically affect soil nutrient availability, root physiology, and plant nutrient acquisition. If respiration does not decrease at a rate similar to those of water or nutrient uptake, then the roots become more costly to the plant. Moreover, dry surface soil is often associated with high soil temperature, potentially further increasing root costs. Plants can reduce root costs in dry soil by shedding roots quickly, or by reducing respiration. Desert succulents and many grass species cope with dry soil by rapidly shedding the fine lateral roots (Eissenstat and Yanai 1997). Immediately following drought, these species are capable of water uptake from main lateral roots and nodal roots (Lauenroth et al. 1987; Huang and Nobel 1993). New root growth soon follows, which in some species occurs within hours of rewetting (Lauenroth et al. 1987; Carmi et al. 1993); these roots may have a hydraulic conductivity three times higher than that of older roots (e.g., Huang and Nobel 1993).

Nutrient uptake also recovers quickly after drought in some species. For example, *Larrea tridentata* exhibited a fivefold increase in $\delta^{15}N$ as soon as 3 days after watering, compared to unwatered controls (BassiriRad et al. 1999). Nutrient uptake recovery in *Larrea* was attributed primarily to increased root growth, similar to that found in wheat (Brady et al. 1995) and barley (Shone and Flood 1983).

Some species rarely shed their roots in dry surface soil. Citrus roots, for example, when exposed to high temperatures and prolonged drought in sandy soil, strongly decrease respiration but exhibit little or no root shedding (Kosola and Eissenstat 1994; Bryla et al. 1997; Espeleta and Eissenstat 1998). In addition, citrus roots that were exposed to dry soil were unresponsive to an increase in soil temperature (i.e., respiration remained low, regardless of temperature), while roots in wet soil responded to changes in soil temperature by slowing rates at higher temperatures (roots exposed to temperatures>25 °C for more than 3 days had the same respiration rate as those at 25 °C; Bryla et al. 1997, 2001). Furthermore, citrus roots exposed to 43 days of drought were capable of rapidly resuming P and water uptake when watered and fertilized, indicating little or no loss of activity for P uptake by existing roots that could have been caused by exposure to dry soil (Eissenstat et al. 1999; also see Matzner and Richards 1996). Thus, we predict that species that construct coarse absorptive roots with a heavily lignified exodermis will tend to tolerate dry soils, reduce C losses by minimizing respiration at times of drought, and exhibit little loss in root activity after drought periods.

8.6.3 Effects of Nutrient-Rich Patches

In an extensive review of plant responses to non-uniform supplies of nutrients, Robinson (1994) found that two thirds of the measurements of root growth showed increased root proliferation in response to a localized nutrient supply. Overall root:shoot ratio generally increased (50 % of studies), or remained stable for heterogeneously supplied plants. Responses were dependent on time, plant species and nutrient, and plant nutrient status. Plants that were nutrient-deprived generally responded to localized nutrient enrichment by increasing uptake per unit root mass. Also, the extent to which a root system has access to patches of nutrients affects root uptake physiology – the smaller the fraction of the root system in the patch, the higher the uptake rate per unit root.

Not always does a higher proliferation rate in the patch equal a higher nutrient capture. For example, Hodge et al. (1998) found that capture of N from decomposing organic residue was not related to the degree of proliferation within the patch. Using two lupin species, *L. angustifolius* and *L. pilosus*, Dunbabin et al. (2001) found that only one species (*L. angustifolius*) had the capacity to increase nitrate uptake rate when locally supplied with high

nitrate, compared to a uniformly high nitrate supply. Plants grown singly in pots may mask some of the advantages of root proliferation. When plants compete with neighbors, the advantages of rapid root proliferation for nitrogen capture may become more apparent (Robinson et al. 1999; Hodge et al. 1999).

Root foraging in nutrient-rich patches can be energetically expensive. For example, Cui and Caldwell (1997) examined the effects of partial shading on nitrate and phosphate acquisition from soil patches in arid-land plants, using a shading-treatment designed to simulate the kind of light competition that can occur in shrub-steppe vegetation. The impact of shading on nutrient foraging was quite dramatic. For example, unshaded *Artemisia* seedlings acquired 54 % more P than did shaded plants in the uniform nutrient treatment, and 185 % more in the patchy nutrient treatment. If shading affected only plant demand, then one would expect that shading would diminish P uptake similarly in the uniform and patchy treatments. Other studies in this same environment have demonstrated that partial shading can diminish both root proliferation in nutrient-rich patches (Bilbrough and Caldwell 1995), and enhancement of nutrient uptake kinetics (Jackson and Caldwell 1992).

The higher efficiency in nutrient-rich patches should lead to longer root life spans in these patches. Eissenstat et al. (2001), for example, showed that apple roots grown in permanent high-nitrogen patches lived longer and had a higher total nutrient gain than those in low-nutrient patches. Similar results were found in northern hardwood forests with the addition of water and nutrients (Pregitzer et al. 1993; Fahey and Hughes 1994). Note that contrasting patterns of root longevity in fertile vs. unfertile patches, where competition for carbohydrates occurs among different axes of the same plant, are not likely to be equivalent to comparisons of plants at sites of different fertility (see Eissenstat and Yanai 2002).

Patch duration can of course influence the potential benefits of root proliferation. Cui and Caldwell (1997) varied pulse duration from 0.5 to 72 h but applied the same total amount of nitrate to an arid-land tussock grass (*Agropyron desertorum*) and shrub (*Artemisia tridentata*). Plants that had been exposed to longer pulses acquired significantly more nitrate from a 30-min tracer pulse than those plants exposed to shorter pulses. However, longer pulse durations did not increase root nitrate uptake activity for these two species. The higher nitrate acquisition capacity in the longer-pulse treatments was primarily due to the greater root mass that had developed.

From an economical point of view, it makes sense to maintain roots longer in patches of higher nutrient enrichment, as this maximizes nutrient capture. However, the duration of the patch also influences optimal root life span (Fitter 1985). If the patches are short lived, as they often are in low-nutrient habitats, construction costs of the roots may not be recovered by the additional nutrient gain of patch proliferation. One might predict that enhanced nutrient uptake kinetics (i.e., increased V_{max}, decreased K_m, or both) might be a more

viable option under these conditions (Fitter 1994; Eissenstat and Yanai 1997). In more permanent patches of high nutrients, one would expect plants to show a proliferation of roots, and to increase the life span of the roots.

8.7 Summary

Plants vary widely in root life span, which has important consequences for nutrient acquisition. The deployment of short-lived roots should correspond to a high surface area:mass ratio (small diameter, low tissue density), high nutrient uptake capacity, and a high respiration rate with a rapid decline in physiological capacity with age. The opposite traits should be associated with long-lived roots. Studies of patterns of nutrient acquisition and respiration over the life of a root are limited, but are generally consistent with this hypothesis. For long-lived roots, the importance of root hairs and possibly vesicular-arbuscular mycorrhizal fungi may be diminished if the epidermis and arbuscules persist only during a small fraction of the overall life of the root. Too much emphasis has been placed on the role of young roots of potted plants; the function of older roots in a fine root network deserves greater study.

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