The Ecology of Root Lifespan

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I. SUMMARY

Theories of plant evolution and adaptation have posited relations between tissue deployment and environmental conditions which have yet to be substantiated below ground. Root production is quantitatively important, exceeding above ground productivity in a range of ecosystems. In addition, carbon expended for root maintenance often exceeds that used for root production. Root production and turnover have consequences for carbon and nutrient cycling, water and nutrient acquisition, competition between plants and the survival and reproduction of species under changing environmental conditions. Despite its importance, relatively few studies have examined factors controlling root lifespan.

This review identifies some competing theories of root lifespan and reviews the evidence available to support them. New methods of root observation and analysis produce data appropriate to testing these theories, but the results to date are few and often conflicting. Tentative generalizations include a suggestion that small diameter roots with low tissue density tend to have short lifespans. Root lifespan appears to be longest in cold environments, but data are lacking for tropical species. There is a strong seasonal variation in lifespan, with roots produced in the fall surviving longest, at least in temperate climates. Species differences are difficult to quantify because of seasonal and interannual variation, but root lifespans of deciduous fruit crops seem to be shorter than those of temperate deciduous forest trees or citrus, a broadleaf evergreen.

Until more data are available on root lifespan, simulation modeling offers an approach to developing testable hypotheses and identifying research needs. We applied a cost–benefit analysis to determine the lifespan that would maximize root efficiency, defined as the amount of nutrient acquired per unit of carbon expended. The analysis suggests that roots should have long lifespans if they have low maintenance respiration or are located in favorable patches of nutrient-rich soil. Shedding roots in dry soil may not be necessary for root efficiency if reductions in maintenance respiration can match reductions in uptake. Accurate predictions of optimal root lifespan are presently limited by insufficient information on the changing carbon costs and nutrient uptake capacity of roots with age. The costs and benefits of root hairs, root exudates and mycorrhizal fungi also need to be included.

The current model of root efficiency omits some important factors that may exert control over root lifespan. Fine roots have other functions in addition to absorption, including transport of water and nutrients. Seasonality of climate and the need for carbon and nutrient storage could constrain the root lifespan that optimizes plant fitness to differ from that which maximizes root efficiency. Roots compete for carbon and nutrients with other plant organs; roots may be shed when demands on roots are low relative to reproductive

demands or to the demands of new leaf production. Death of roots may not entail the loss of all the carbon and nutrients they contain, if material is resorbed from senescing tissues or if nutrient cycling is tight and the lost material eventually benefits the plant.

Finally, root herbivory and parasitism are probably much greater than generally appreciated. Young roots generally lack structural defenses and are at high risk of attack by soil organisms. The lifespan of stressed roots with low carbohydrate reserves is probably affected by weak pathogens and primary saprophytes that reside in the rhizosphere. Plant–animal (including plant–fungus) interactions are likely dominant factors influencing the lifespan of roots.

More long-term studies are needed, both to detect existing patterns of root lifespan with resource availability and plant strategy, and to progress beyond short-term responses to treatments, which may be misleading. Factors that should be included in studies of root lifespan in addition to resource availability include root age, plant carbon status, and pathogen pressure. Because root lifespan differs from leaf lifespan in many species, better knowledge of root lifespan may result in revision of current theories regarding plant adaptation and growth strategies.

II. INTRODUCTION

Root lifespan has important consequences for plant growth and productivity, plant competition, and carbon and nutrient cycling. Roots, like other plant organs, have a life history: they are born, age and die (Harper, 1977). The root system can be thought of as a population of foraging units of different ages responsible for acquiring water and nutrients. Growth of a root system, the ability of a root system to relocate in favorable patches, and the eventual architecture of a root system are largely determined by the birth and death of its parts. Root construction and maintenance also influence carbon (C) and mineral nutrient consumption, while root death influences the partial return of these resources to the soil.

The mass and energy involved in the birth and death of roots may be at least as great as that involved in the birth and death of leaves. Net primary production (NPP) is greater below ground than above ground in a range of ecosystems (Caldwell, 1987). Even in forests, which can have enormous above-ground biomass, below-ground NPP was consistently higher than above-ground NPP, especially early in stand development (Gower *et al.*, 1994). This greater allocation may reflect differences in the intensity of competition below and above ground. In shady as well as sunny environments, below-ground competition commonly has a greater influence on plant species growth and survival than above-ground competition (Donald, 1958; Wilson, 1988; Dillenburg *et al.*, 1993). Compared with the population dynamics of above-ground parts, however, very little is known about below ground

systems. Recent technological advances, especially video-imaging in mini-rhizotrons and video-processing with personal computers, have made it more possible to observe and quantify the demography of roots. In this review, we draw together current information on root lifespan, illustrate a cost–benefit modelling approach to predict root lifespan, reveal areas of ignorance, and provide direction for future demographic studies of roots.

III. ESTIMATING ROOT LIFESPAN

Accurately quantifying root turnover has been one of the most intractable problems in studies of terrestrial plant ecosystems. The most common method has been to collect soil cores periodically (usually monthly) and determine average mass of live and dead roots at each interval (Vogt *et al.*, 1986). The change in mass of live and dead roots through the season can then be used in various formulae to estimate root production and turnover. Average lifespan can be estimated by dividing production by the mean standing biomass. Estimates of root lifespan by soil coring have been reviewed by Schoettle and Fahey (1994) and Bloomfield *et al.* (1996). Other ways to estimate below-ground NPP include a nitrogen-balance approach (Nadelhoffer *et al.*, 1985; Nadelhoffer and Raich, 1992), C-isotope approaches (Milchunas *et al.*, 1985; Milchunas and Lauenroth, 1992; Nepstad *et al.*, 1994), root ingrowth techniques (Fabião *et al.*, 1985) and direct observation (Cheng *et al.*, 1990). There are several papers that discuss approaches for estimating annual root turnover (Milchunas *et al.*, 1985; Caldwell and Eissenstat, 1987; Hendrick and Pregitzer, 1992; Milchunas and Lauenroth, 1992; Hendricks *et al.*, 1993; Fahey and Hughes, 1994), which reveal no consensus on the best approach for estimating root turnover. This review focuses primarily on results of observational techniques in which roots are tracked individually, allowing specific demographic information on different cohorts of roots and direct estimates of root lifespan. In recent years, root tracking has been greatly facilitated by the use of miniature video cameras or borescopes inserted into transparent tubes (minirhizotrons) buried in the soil. Personal computers assist in processing the video images, allowing the fate of thousands of individual roots to be followed (Hendrick and Pregitzer, 1992, 1993). Direct observation avoids the assumptions used in ingrowth, budgeting, and isotope approaches. Direct observation also avoids important problems in the interpretation of root data collected by sequential coring, such as simultaneous birth and death of roots during a sampling interval and spatial and sampling variation being confounded with temporal variation. In addition, it is now realized that roots can disappear rapidly (in less than a few weeks), either by rapid decomposition or by herbivory (Hendrick and Pregitzer, 1992; Fahey and Hughes, 1994; Kosola *et al.*, 1995). Such rapid disappearance can cause serious overestimates of root longevity by sequential coring approaches. The most serious

problem associated with minirhizotrons and other direct observation approaches is the artificial environment at the surface of the observation windows, which may alter root behavior (see Harper *et al.*, 1991). For example, root length densities observed with minirhizotrons can be considerably lower than estimates based on soil coring (McMichael and Taylor, 1987). Care in the installation of the observation tubes or windows and subsequent protection from light and thermal gradients can help minimize this problem.

A difficulty in assessing root lifespan by any method is the definition of death. A fine root may exhibit signs of necrosis in portions of its length while the remainder of its length is still healthy. Moreover, in some species, roots continue to absorb water and nutrients after death of epidermal and cortical cells. Even portions of roots whose entire epidermis and cortex has sloughed may still provide important transport functions in the stele and be capable of new lateral formation from a viable pericycle (Spaeth and Cortes, 1995). Investigators usually use a combination of indicators in assessing death, such as color changes, loss of cortex and disappearance. Investigators who use nondestructive visual techniques such as minirhizotrons occasionally find that a root thought to be dead initiates new laterals upon continued observation. Vital staining, such as the use of tetrazolium dye, can be used to compare other methods of assessing death, such as ultraviolet fluorescence, color (dark brown, very dark brown or black), partial decay, and the presence of nonmycorrhizal fungal mycelia. Root death assessed by u.v. or visual approaches underestimated the number of dead roots by 12–15% (range 8–30%) compared to the tetrazolium method (Wang *et al.*, 1995). Root lifespan may therefore be overestimated with minirhizotrons.

IV. VARIATION IN ROOT LIFESPAN

Estimates of root lifespan using direct observation techniques are now quite numerous (Table 1). This table lists the median lifespan of different cohorts of roots of 14 plant species (seven of which are rootstocks of citrus) and five forest communities. Included in the table are the season the cohort was produced, the location of the study and the method of estimating lifespan.

Root lifespan of a given species may vary considerably among cohorts produced in different seasons. In temperate climates, lifespan is often shortest for roots produced in late spring. In England, median root lifespan was as little as 14 days in apple roots produced in June whereas roots produced in January lived an average of 84 days (Head, 1966). In this case, lifespan refers to the duration that roots remained white. Apparently, in apple and strawberry roots, the cortex is sloughed soon after the root turns brown (Atkinson, 1985). It is likely, however, that assessment of root death based on color change alone probably underestimates root lifespan compared with definitions of death based on root decay or disappearance. In Wisconsin, hybrid poplar roots

Table 1

Median lifespans (days to 50% mortality) of cohorts of roots determined by direct observation in a range of plants and communities

Plant species/community (treatment)	Cohort	Lifespan (days)	Location	Comments and References (*M* = minirhizotron; *R* = rhizotron)
Annual crops				
Grain sorghum (*Sorghum bicolor*)	Spring Summer	42–47 24–26	Georgia Piedmont	*M*, Data from Cheng *et al.* (1990) till and no-till combined. Spring: early vegetative phase. Summer: beginning seed fill
Groundnut (*Arachis hypogaea*)	All roots	24–31	Growth room study	Five cultivars. Grown in transparent tubes, 95 cm long, 5 cm diameter (Krauss and Deacon, 1994)
Perennial herbaceous crops				
Alfalfa (*Medicago sativa*)	22 June–20 July 3–17 Aug	58–131 47–92	St Paul, Minnesota	*M*, Four alfalfa germplasms (G.D. Goins, M.P. Russell, 1996) Lifespan increased with depth
Strawberry (*Fragaria* × *ananassa*)	All roots	17	Kent, England	*R*, East Malling Research Station. Dead roots defined as roots that turned 'brown' (from Figure 9 in Atkinson, 1985)
Woody fruit crops				
Apple (*Malus domestica*) M.VII rootstock	June–Sept	14–21	Kent, England	*R*, Dead roots defined in accordance with Atkinson (1985) as roots that turned 'brown' (East Malling Res. Station, Head, 1966)
	Oct–Nov	28–84		
Kiwifruit (*Actinidia deliciosa*)	All roots	28	Gisborne, New Zealand	*R*, No difference among cohorts produced in spring, summer, fall or winter (Reid *et al.*, 1993)
Citrus	Apr–Dec, 1992		Avon Park, Florida	*M*, Unhedged trees, Valencia sweet orange (*C. sinensis*) scion on range of rootstocks. Approximately monthly sampling (D.M. Eissenstat, unpublished data)
Trifoliate orange (*Poncirus trifoliata*)		90		
Sour orange (*Citrus aurantium*)		90		
Cleopatra mandarin (*C. reshni*)		116		
Volkamer lemon (*C. volkameriana*)		152		
Carrizo citrange (*P. trifoliata* × *C. sinensis*)		124		
Swingle citrumelo (*P. trifoliata* × *C. paradisi*)		99		

Table 1 *cont.*

Plant species/community (Treatment)	Cohort	Lifespan (days)	Location	Comments and References (*M* = minirhizotron; *R* = rhizotron)
Volkamer lemon (*C. volkameriana*)	May, 1993 Aug, 1993 Sept, 1993		Avon Park, Florida	*M* (0–17 cm depth, deeper roots lived about the same in May but 10–20 days longer in August and September) Differences in survival among cohorts during the season and between rootstocks related to infection by *Phytophthora nicotianae* (Kosola *et al.*, 1995)
Rough lemon (*C. jamibhiri*)	May, 1993 Aug, 1993			
Forest trees/communities				
Hybrid poplar (*Populus generosa inter-americana*) var. Beupre	All		Growth chamber	*M*, (20 cm diameter, 4.3 l pots) (Hooker *et al.*, 1995)
Arbuscular mycorrhizal		19		
Nonmycorrhizal		49		
Hybrid poplar (*Populus tristis* × *P. balsamifera*) cv. Tristis no. 1	May June July	62 118 130	Rhinelander, Wisconsin	*M*, M. Coleman, unpublished data
Pin cherry (*Prunus pensylvanica*) forest	21–31 July	59–67	Pellston, Michigan	*R*, Observations made every 2 days (Pregitzer *et al.*, 1993). Median life-span extrapolated after 82 days based on Figure 2
20–40 days pulse of water				
20–40 days pulse of water + N		82–90		
No addition of water or N (control)		42		
Sugar maple (*Acer saccharum*) forest	June–September 1989	200	N site, Michigan.	*M*, Sites 80 km apart, N site (Lat 44° 23′ Long 85° 50′), S site (Lat 43° 40′ Long. 86° 09′) otherwise very similar (Hendrick and Pregitzer, 1993; Figure 2).
	June–September 1989	125	S site, Michigan	
Sugar maple (*Acer saccharum*) forest	27 April		Michigan (N site)	*M*, (Hendrick and Pregitzer, 1992)
0–30 cm depth	11 June, 1989	340		
30–110 cm depth		250		
Sugar maple-Beech-Yellow birch forest (*Acer saccharum–Fagus grandifolia–Betula alleghaniensis*)	Late spring	180	Hubbard Brook, New Hampshire	Mesh-screen technique for tracking roots at the interface of the mineral soil surface (Fahey and Hughes, 1994)
Sugar maple–Beech forest	Late spring	195	South-central New York	Assumed mortality rate was constant with root age and extrapolated from 59% survivorship after 150 days (Fahey and Hughes, 1994)

produced in May typically only lived until July (62 days), whereas 50% or more of the roots produced in July lived past November (130 days) (Table 1). Similarly, in two sugar maple forests in northern Michigan, roots produced in the fall lived longer than those produced in the summer (Hendrick and Pregitzer, 1993), but in these forests, root lifespan was also long for roots produced in April through early June (Hendrick and Pregitzer, 1992).

In contrast to temperate species, in which roots produced in the fall seem to live the longest, citrus roots produced in September in subtropical Florida may have shorter lifespans than those produced in the spring (Kosola *et al.*, 1995). This result was linked to an increase in propagules of the parasitic root-rot fungus, *Phytophthora*. The variability in median root lifespans of different cohorts is further illustrated by our work on citrus. One rootstock, Carrizo citrange, in early May had a median lifespan of 141 days whereas a late July flush of Carrizo roots had a median lifespan of 348 days. Median lifespan of all the roots produced over the two-year period ranged from 90 days in the trifoliate orange rootstock to 152 days for Volkamer lemon (Table 1), a rootstock that had been specifically selected for resistance to the root-rot fungus, *Phytophthora nicotianae* (Kosola *et al.*, 1995).

Because of the variability in lifespan among different root cohorts, differences in the average lifespan of all the roots produced in a year can be difficult to detect between species. Nonetheless, it appears that other fruit crops have considerable shorter root lifespans than does citrus. In apple and in kiwifruit overall median lifespans of fine roots were only about 28 days (Atkinson, 1985; Reid *et al.*, 1993). Strawberry roots had average lifespans of only 17 days (Atkinson, 1985). Median lifespan of groundnut (*Arachis hypogaea* L.) is also only about 24–31 days (Krauss and Deacon, 1994).

Roots of temperate deciduous trees in mature forests have lifespans similar to citrus, a broadleaf evergreen, but longer lifespans than deciduous fruit trees. In a Michigan forest dominated by the late successional species *Acer saccharum*, median lifespans of the roots produced from June to September varied from about 125 to 200 days, depending on site (Hendrick and Pregitzer, 1993). However, if only the early spring flush of roots (roots before June) was considered, lifespans were much longer (about 250–340 days, depending on the depth of roots in the soil) (Hendrick and Pregitzer 1992). In forests dominated by the early successional species, *Prunus pensylvanica*, median lifespans were only 40–80 days (Pregitzer *et al.*, 1993). Roots in patches enriched with water or with water and nitrogen had significantly greater lifespans than those in unamended patches (Table 1).

In two northern hardwood forests, Fahey and Hughes (1994) estimated fine root survivorship by tracking surface roots that had grown into mesh screens just below the litter layer. In the Hubbard Brook forest in New Hampshire, which was dominated by *Acer saccharum*, *Fagus grandifolia* and *Betula alleghaniensis*, median lifespan of a late-spring flush of roots was about 180

days. Similar values were measured in a forest dominated by *A. saccharum* and *F. grandifolia* in south-central New York (59% of the roots had survived about 150 days). Both sites exhibited shorter lifespans than the spring cohort of roots (250–320 days) of Hendrick and Pregitzer (1993) but longer lifespans than their season-long average (80–120 days). There is some evidence that roots near the soil surface live longer than those deeper in the soil (Hendrick and Pregitzer, 1992; Schoettle and Fahey, 1994), which may also contribute to the differences found by the root screen method of Fahey and Hughes compared with the observation tubes used by Pregitzer and coworkers in Michigan.

In summary, although recent investigations have greatly increased the amount of reliable information on root lifespan, data are still too sparse to make many generalizations. The roots of woody species such as apple and kiwifruit may live no longer than those of annual herbaceous species. Roots in natural ecosystems such as northern hardwood forests seem to live longer that those in agricultural systems (also see Table 4). Within a species, cohorts of roots produced at different times of the year can differ greatly in lifespan.

V. ANALOGIES TO LEAF LIFESPANS

Leaves are more readily observed than roots, and theories concerning leaf lifespan are better developed than theories of root lifespan. Fine roots, whose primary function is the acquisition of water and nutrients with little role in storage and support, are in many ways similar to leaves, whose role is primarily acquisition of C. Like leaves, most fine roots typically exhibit determinant growth, extending only a few centimeters after emerging from woody laterals, and never undergo secondary thickening. Their ephemeral character is illustrated by the fact that fine roots often have shorter lifespans than leaves (Schottle and Fahey, 1994). The comparison of roots and leaves, however, is an imperfect analogy. Lateral roots arise internally from the pericycle, rupturing the cortex as they emerge. Branches and leaves, on the other hand, are born from external meristems and often die following formation of a distinct abscission layer, which has not been described in roots. Fine roots that branch extensively also serve important transport functions, causing their fate to affect the fate of all more distal segments; leaves have no such dependencies. Finally, a part of the function of roots can be consigned to symbionts, such as mycorrhizal fungi or nitrogen-fixing bacteria. The role of the root is then to exchange C for nutrients from the symbiont, rather than to absorb nutrients from the soil. Despite these differences in roots and leaves, analogies to leaves have provided much of the theory of root lifespan.

One organizing theme in the ecology of leaf lifespan is the influence of habitat resource availability on the evolution of a suite of interdependent plant characteristics, including leaf longevity (Grime, 1977; Chabot and Hicks,

1982; Coley *et al.*, 1985; Chapin *et al.*, 1993). For example, in a study of 23 Amazonian tree species, those with shorter leaf lifespan had higher specific leaf area (leaf area/leaf dry mass), leaf diffusive conductance, maximum net C assimilation rate, mass-based leaf nitrogen (N) and phosphorus (P) and lower leaf toughness (Reich *et al.*, 1991). Similarly, leaf lifespan in a lowland tropical rainforest in Panama was positively correlated with shade tolerance and plant defensive compounds such as tannins and lignins and negatively correlated with plant growth rate (Coley *et al.*, 1988). In leaves, short lifespan is thought to be important for rapid growth and morphological plasticity, whereas long lifespan is advantageous to nutrient conservation and nutrient-use efficiency (Monk, 1966; Chapin, 1980; Chabot and Hicks, 1982; Coley, 1988; Reich *et al.*, 1991, 1992; Grime, 1994). Root lifespan may be linked to a similar suite of traits as found in leaves (Eissenstat, 1992, 1997; Fitter, 1994; Grime, 1994). If so, plants of infertile habitats should produce coarse, well-defended, absorptive roots of long lifespan whereas plants from high-resource environments should produce short-lived roots with rapid potential rates of nutrient uptake (high V_{max}), rapid potential growth rates, and little allocation to certain kinds of defensive compounds such as lignins.

An important trait linked to lifespan in leaves and roots may be the morphological plasticity of the plant, that is, the ability to position leaves and roots in resource-rich patches. In unproductive habitats with unpredictable and short-lived pulses of resource supply, leaves and roots should have long lifespans and low morphological plasticity (Grime *et al.*, 1986). In more productive habitats, it is more advantageous to be able to grow rapidly in resource-rich patches (Grime, 1994). These generalizations are based on a comparison of the growth of species adapted to different habitats (Grime, 1994). Less is known about differences in selective mortality of tissues within plants or in plants adapted to different environments.

There have been some observations of selective mortality of branches and leaves in relationship to patchy distribution of light. For example, the light-demanding pioneer species, *Rosa canina*, selectively sheds shoots located in deep shade, which reduces maintenance costs and thus maintains a more favorable whole-plant C balance (Küppers, 1994). Selective mortality of shaded branches and leaves low on the bole of the tree is common in shade-intolerant species (Millington and Chaney, 1973). Shade tolerant, late-successional species tend to retain more leaves – an example of low morphological plasticity and long lifespan in low-resource environments. The analogous hypothesis below ground is that selective mortality of roots in unfavorable patches of soil is greater in plants from productive than unproductive habitats. Current information is inadequate to test this hypothesis.

The processes by which roots are shed are poorly understood. We know of no study showing that roots form a distinct abscission layer and thus are actively shed in the manner of leaves or stems. For example, B. Huang

(personal communication) found no evidence of abscission layer formation prior to death of rain roots in desert succulents (North *et al.*, 1993). Roots may die simply by restriction of the flow of carbohydrates until their reserves are exhausted. Alternatively, root death may be caused primarily by biotic factors extrinsic to the plant, such that root lifespan is a function of herbivore pressure in the rhizosphere and the degree of root defense. These alternative mechanisms of plant control of root lifespan are not easily separated experimentally.

VI. CONTROLS AND CONSTRAINTS ON ROOT LIFESPAN

A. Hypotheses

Many factors presumably shape the lifespan of a root. Below is a list of hypotheses that have received a certain degree of support, including some derived from hypotheses concerning the lifespan of leaves (Chabot and Hicks, 1982). While the hypotheses each describe a different aspect of root biology, they are not mutually exclusive. Some describe proximate causes of root death; others do not specify a mechanism.

(1) Root lifespan is a function of herbivore pressure and the degree to which roots are defended from herbivores and pathogens.
(2) Long lifespan is important in roots with functions other than water and nutrient acquisition, such as storage, transport, and structural support.
(3) Root lifespan is a function of competition for carbon among various plant parts.
(4) Root lifespan corresponds to the length of the favorable growing season.
(5) Long root lifespan is a form of mineral nutrient conservation.
(6) Root lifespan maximizes the efficiency of resource acquisition per unit C expended.

B. Root Herbivory and Parasitism

We suspect that extrinsic biotic factors contribute far more to root mortality than is generally recognized in the ecological literature. Examples of dramatic plant mortality associated with root pathogens are common in agriculture; root herbivory in natural ecosystems can also be substantial. Some data suggest that root-feeding nematodes can reduce net primary productivity in grasslands by 12–28% (Stanton, 1988). In Eucalypt forests in the Brisbane Ranges in Australia, *Phytophthora cinnamomi* has caused resistant species to expand at the expense of susceptible species such as *Eucalyptus* (Weste, 1986). Experimentally reducing root-feeding insects by applying insecticides to soil has been shown to enhance plant species richness and reduce seedling

mortality, especially of perennial forbs compared with grasses (Brown and Gange, 1991). Consequently, in studies using sterilized soil, root death might be substantially delayed by the absence of herbivores and pathogens.

Low levels of heterotrophic feeding on roots may be more the rule than the exception. In addition to root-feeding insects and nematodes, parasitic fungi may increase rates of root mortality, even in apparently healthy plants. For example, in Florida, healthy citrus trees had highest mortality of roots during periods when *Phytophthora* activity is greatest, such as late summer (Graham, 1995; Kosola *et al.*, 1995) Fine roots of the *Phytophthora*-susceptible rootstock (*Citrus jamibhiri*) had shorter median lifespans and supported larger populations of *Phytophthora* than the fine roots of the more tolerant rootstock (*Citrus volkameriana*) (Kosola *et al.*, 1995). Weak pathogens or primary saprophytes are also likely to be important in accelerating the death of stressed roots. For example, *Fusarium solani*, a fungus whose inoculum is ubiquitous in root tissues of citrus, is able to develop only when starch reserves in the citrus roots are depleted, for example following canopy loss or during heavy fruit set (Graham *et al.*, 1985).

A cost–benefit analysis of root retention and shedding would predict low mortality in young roots, with peak mortality at the optimal lifespan. But survivorship curves of roots indicate either fairly constant mortality with root age (Kosola *et al.*, 1995) or high mortality of young roots (Hendrick and Pregitzer, 1993; Pregitzer *et al.*, 1993). Young roots are generally more susceptible to parasitism and herbivory than older roots, which have developed thick secondary cell walls in the epidermis or hypodermis (Graham, 1995). Woody roots that have established a cork periderm have additional structural defenses against root-feeding organisms. Extrinsic biotic factors are probably a better explanation for mortality of young roots than active shedding by the plant.

Rates of root losses to herbivory and parasitism are not entirely beyond the control of the plant. Healthy roots typically produce a wide range of chemicals to defend against root-feeding organisms. Many of these organisms would not be considered pathogenic unless the roots were very stressed. The development of new pesticides routinely involves screening root compounds for insecticidal, fungicidal and nematicidal activity. Numerous compounds produced by plant roots have shown pesticidal efficacy, including phytoalexins, polythienyls, alkaloids, acetylenes and terpenoids (Veech, 1982; Chitwood, 1992). That C stress increases a root's susceptibility to biotic attack is well-accepted among plant pathologists (Dodd, 1980). Although roots may not be actively shed, reducing expenditures for root defense could be a mechanism whereby plants control root mortality.

Many factors influence the activity of soil herbivores, such as season, soil moisture, soil temperature and plant C status. Correlations of these factors with root lifespan may be mediated by the activity of soil organisms, which

are not usually considered in models of root foraging strategy. Roots of some species may live longer in dry or cold soil not so much because their maintenance expenses are lower, but because the activity of root-feeding organisms is less. The different lifespans of roots produced at different times of year, reviewed above, may likewise reflect the activity of soil organisms. A more indirect effect of plant and environmental factors on root lifespan acts through the strength of root defense. More research is obviously needed on the role of herbivores and pathogens in natural communities and the control plants have on root defense.

C. Roots with Multiple Functions

Fine roots have functions other than nutrient and water absorption, which are sometimes ignored in discussions of the costs and benefits of retaining or shedding roots. They serve as a reservoir of meristems, and they are involved to varying degrees not only in absorption but also in transport of water and nutrients. Roots may be classified in terms of external links which have no laterals and internal links which have one or more laterals (Fitter, 1991). Analyses of optimal root lifespan apply most clearly to external links, but root demographic studies include both internal and external links. The higher the order of branching of the fine roots of a plant, the more the survival of an internal link influences other root elements that depend on it for transport to and from the shoot. An external link should, consequently, have shorter lifespans than internal links, as found in kiwi (Reid *et al.*, 1993).

Certain roots emerging in seedlings eventually build the structural framework of the root system. Structural roots are often genetically distinct from the fine laterals and must have a very different life history. The well-studied seminal roots in cereals fall into this category. In citrus, 'pioneer' roots are produced which are quite different from the fine laterals. Pioneer roots are somewhat thicker, have a prominent root tip, and extend rapidly and indeterminately in the soil with typically little branching of laterals near the tip. These roots generally have little mycorrhizal infection, are not readily infected by fungal pathogens or nematodes and readily extend through dry soil (D.M. Eissenstat and J.H. Graham, personal observation). Thus, plants may have evolved special mechanisms to protect certain roots from early mortality even though they appear similar to the fine laterals at an early age.

D. Competing Sinks for Carbon

Whether it is advantageous to plants to retain roots should depend on the relative pay-off of other possible investments of the C. For example, reproduction is an important competing sink for C. In many annual plants, most root growth occurs prior to flowering and most root death occurs during and after

flowering. For example, total root length declines during and after flowering in wheat (Box and Johnson, 1987), sorghum (Cheng *et al.*, 1990), cotton (Klepper *et al.*, 1973) and soybean (Hoogenboom *et al.*, 1987). Cheng *et al.* (1990) did a minirhizotron study in the Georgia piedmont where they tracked individual roots. Lifespan of sorghum roots produced in the summer at beginning seed fill was only half of those produced in the spring (W. Cheng, unpublished data, Table 1). High root mortality has been associated with very heavy fruit crops in *Prunus* (Chandler, 1923) and *Citrus* (Smith, 1976; Graham *et al.*, 1985). Conversely, there is no evidence that root mortality is linked to seed fill in rice (Beyrouty *et al.*, 1987), groundnut (Krauss and Deacon, 1994), or dry bean (Snapp and Lynch, 1996), based on root length dynamics.

Carbon shortages in plants, such as those caused by defoliation, should affect C allocation to roots. Plants often respond to leaf loss by reducing root respiration (Culvenor *et al.*, 1989), slowing or ceasing root growth (Crider, 1955), or reallocating C to re-establish a functional equilibrium between roots and shoots (Brouwer, 1981). For example, 4 weeks after removal of the top third of the canopy in Valencia orange trees, there was at least a 20% loss of roots at a soil depth of 9–35 cm (Eissenstat and Duncan, 1992). In apple, leaf removal 6 weeks prior to natural leaf fall caused high root mortality within 2 weeks (Head, 1969). A similar response was observed in blackcurrant (Atkinson, 1972). Rapid root shedding following defoliation is less evident in grasses (Crider, 1955; Richards, 1984). The roots of two cold-desert tussock grasses differed in their responses to defoliation (Richards, 1984). In *Pseudoroegneria spicata*, roots of clipped plants continued to grow at the same rate as unclipped plants during the growing season but suffered greater mortality over winter. The expenditure of C for root growth in the clipped plants may have reduced the reserves available for root maintenance over winter. In a more grazing-tolerant species, *Agropyron desertorum*, root growth rates were slower in clipped than unclipped plants during the growing season, suggesting reduced draw on plant C reserves; there was little difference between clipped and unclipped plants in root survivorship over winter.

Carbon storage is another competing sink for plant resources. In strongly seasonal climates, stored C and nutrients are essential to the growth of roots and leaves at the beginning of the growing season. Stored C may be mobilized at other times for defense, repair, or replacement of tissues. Whether it is more advantageous to replenish storage or to increase growth of absorptive organs will depend not only on the costs and benefits of the tissue produced but also on the competing demands for stored C, including future risk of demand (Chapin *et al.*, 1990).

That root longevity is affected by the C status of plants is illustrated by experimental manipulation of C supply. Of the two studies found in the literature, however, the lifespan response reported has been in opposite directions. In a 2-year study of ponderosa pine (*Pinus ponderosa*), roots lived longer at

elevated than ambient CO_2 (D.T. Tingey, O.L. Phillips, M.G. Johnson, M.J. Storm and J.T. Ball, unpublished data). In contrast, in a study of hybrid poplar (*Populus* × *euramericna* cv. Eugenei), roots in low-N soil conditions lived longer under ambient than elevated CO_2 (Pregitzer *et al.*, 1995). In high-N soil, root longevity was not affected by increases in CO_2. The availability of C may interact with nutrient availability in controlling root dynamics in complicated ways that are presently poorly understood.

E. Seasonality

In strongly seasonal climates, the length of the growing season often dictates the lifespan of leaves (Harper, 1989); roots, however, often live less long. Although there is typically a strong flush of roots in the spring, often prior to leaf emergence (Lyr and Hoffman, 1967), these roots may live less than a month (Head, 1969). In droughty environments, cacti and many species in the Proteaceae have long-lived leaves that tolerate the dry period, but roots that are more ephemeral. North American desert cacti are noted for producing roots quickly after a rain event that die soon after the soil dries (Huang and Nobel, 1992; North *et al.*, 1993). In seasonally dry parts of western Australia and South Africa, many evergreen woody plants produce cluster roots which proliferate in the surface organic layers during the wet season but are shed by the time of the dry season (Lamont, 1995). Leaf and root longevity may differ so strongly in these environments because of the differences in timing of light and soil resource availability.

Thus, limited data suggest that in temperate climates, there is no strong relationship of root longevity to length of season with favorable temperatures, as commonly observed with leaves. Conversely, in very dry climates or climates of strongly seasonal rainfall, root longevity may be strongly linked to the length of time the soil is wet even though leaf longevity may not be. These conclusions are based on few data; more species comparisons are needed to better understand the relationship between length of growing season and root longevity.

F. Mineral Nutrient Conservation

Under nutrient-limited conditions, root foraging strategy should avoid unnecessary nutrient loss. Clearly, shedding roots is a pathway of nutrient loss, as nutrient resorption from dying roots is probably minimal (Nambiar, 1987; Dubach and Russelle, 1994). Long root lifespan in infertile environments could be a mechanism of nutrient conservation. In later sections, we explore the hypothesis that optimal root deployment should maximize the efficiency of nutrient uptake per unit C expended and review specific studies of root lifespan to soil fertility. In this section, we consider whether long lifespan

could be maximizing nutrient uptake relative to nutrient expenditure rather than C expenditure. Carbon may not be the best measure of 'currency' in strongly nutrient-limited environments where plant density is low and light availability is high. Under these circumstances, C may not be limiting or may be only weakly limiting, as indicated by a lack of growth responses or increased nutrient uptake when plants are exposed to elevated CO_2 (Arnone and Körner, 1995).

Observations above ground suggest that long tissue lifespan contributes to nutrient conservation in infertile environments. For example, in temperate deciduous forest regions, evergreen-dominated vegetation types such as pine forests and bog vegetation often occur in low-nutrient soils. In Mediterranean climates, very infertile regions support exclusively evergreen shrubs whereas more fertile regions have a mix of evergreen and drought-deciduous vegetation (Lamont, 1995). Across a wide range of ecosystems, annual nutrient losses in litterfall are smaller in species with lower leaf turnover rates and lower leaf nutrient concentrations (Vitousek, 1982). In addition, evergreen leaves are more resistant to decomposition than deciduous leaves, causing nutrients to be released more slowly to the soil solution. Polyphenols in long-lived leaves on infertile soils may inhibit mineralization of organic nitrogen (Northup *et al.*, 1995). The ectomycorrhizal and ericoid mycorrhizal plants common to these infertile soils may be able to break down this organic N and absorb the resulting amino acids, bypassing competition for mineral N with roots and other microbes (Chapin, 1995).

These patterns of nutrient retention and tight nutrient cycling in aboveground tissues may also occur in roots. The challenges are to understand the amounts and fate of nutrient losses from the root and whether nutrients are reabsorbed by the plant in a preferential manner. The 'tightness' of nutrient cycling back to the plant after the root dies may be higher in low-nutrient environments, which would diminish the advantages of long root lifespan in nutrient conservation. Recent literature suggests diverse means by which nutrients may be tightly cycled within a plant–soil system (Newman, 1988; Northrup *et al.*, 1995). In low-nutrient environments, slow mineralization rates and a lack of mixing can cause a thick organic layer to develop at the soil surface, which becomes the main source of N and P. Plants adapted to low-nutrient environments, such as ericoid and ectomycorrhizal plants, or plants that produce cluster roots, are particularly adapted to the proliferation of roots or hyphae in this organic surface horizon, excretion of extracellular enzymes, and uptake of N and P (Read 1993; Lamont, 1995). Because roots and mycorrhizal hyphae are concentrated in this layer, nutrients are more likely to be recaptured by other roots of the same plant when a surface root dies. This may occur directly by neighboring roots or by roots linked by shared mycorrhizal hyphae (Newman, 1988). In the latter case, nutrients are preferentially retranslocated from the dying root to other living roots via the hyphal

strands that link the roots, thus bypassing competition with soil microbes. The ability of ectomycorrhizal and ericoid fungi to take up organic N from soil, also bypassing microbes, further enhances nutrient return to the plant.

VII. TRADE-OFFS BETWEEN ROOT MAINTENANCE AND ROOT CONSTRUCTION

As in leaves, there are tradeoffs between maintaining old and growing new roots; C can be conserved or expended for lesser or greater gain in water or nutrients. One important factor in calculating such trade-offs is the relative cost of maintaining existing roots versus shedding roots and rebuilding them at a more favorable time or location.

In the previous section, we considered mineral nutrients as the currency for cost–benefit analyses of root lifespan. In the following sections, we examine root costs in terms of C. Carbon is the preferred currency in cost–benefit analyses and plant allocation models, perhaps because it describes the energy status of the plant. There are, however, some drawbacks to using C units for cost. First, estimating C losses from the roots by respiration, exudation, cell sloughing and mycorrhizal fungi can be difficult. Second, plants in infertile soils may not be very C-limited, according to results of CO_2 enrichment studies (Arnone and Körner, 1995); conserving C may not be important to these plants. Third, when the benefit is a resource other than C, such as a nutrient or water, the exchange value of that resource to C should be known; otherwise, it is difficult to compare plants in different circumstances (Bloom *et al.*, 1985). For example, a nutrient-limited plant can presumably afford to expend more C per unit of nutrient acquired, because C is less valuable to it than to a C-limited plant.

The costs of maintaining roots, which may include exuding organic compounds and constructing and maintaining mycorrhizas, is often as great or greater over the lifetime of the root than the cost of building the roots in the first place. One way to compare these costs is to calculate the age at which cumulative maintenance respiration equals construction cost. In well-watered citrus seedlings grown at high N supply, the time required for maintenance respiration to equal the cost of root construction ranges from 20 to 26 days, depending on P supply and mycorrhizal status (Peng *et al.*, 1993; Table 2). In a slash-pine ecosystem in Florida (Cropper and Gholz, 1991), root respiration rates measured at the soil surface would equal construction costs after 45 days, assuming that the roots were 45% C and the growth efficiency was 0.77. For desert succulents, which have quite slow maintenance respiration rates, it would take about 90 days for maintenance respiration of roots at 20°C to equal root construction costs (Nobel *et al.*, 1992). Because root respiration increases exponentially with temperature, the C expended in respiration exceeds that used in construction sooner in warmer soil. At 30°C, a common

Table 2

Summary of respiratory costs of Volkamer lemon colonized by *Glomus intraradices* (M) or uninoculated (NM). Plants were grown at either high-P supply (5P = 5 mM KH_2PO_4) or low-P supply (1P = 1 mM) (calculations made from Peng *et al.*, 1993. Copyright held by the American Society of Plant Physiologists.)

	Daily cost (μmol CO_2 d^{-1})			
	1P		5P	
	M	NM	M	NM
Construction cost, $CONST_t$	468	174	671	563
Total respiration, $R_{T(t)}$	555	234	820	600
Growth respiration, $R_{G(t)}$	114	40	153	117
Ion-uptake respiration, $R_{I(t)}$	111	56	109	111
Maintenance respiration, $R_{M(t)}$	330	138	559	372
$R_{M(t)}/CONST_t$	0.71	0.79	0.83	0.66
	Cost per unit root dry wt. mmol CO_2 (g new root)$^{-1}$			
Construction cost, $CONST_w$	48.7	44.7	45.3	42.0
	mmol CO_2(g whole-root system)$^{-1}$ d^{-1}			
Maintenance respiration, $R_{M(w)}$	2.46	1.77	2.05	1.62
	Days			
Number of days for maintenance respiration of 1 g of root ()$R_{M(w)}$) to equal the cost of constructing 1 g of root	19.8	25.3	22.1	

condition in the desert, it would take only 48 days for maintenance respiration to equal construction costs (Q_{10} = 1.9; Palta and Nobel, 1989). Using root maintenance respiration of a range of plant species (Amthor, 1984) and an average root construction cost of 45 mmol C (g dry wt)$^{-1}$ gives estimates of 13–32 days for maintenance respiration to equal the construction costs of roots.

Root lifespan commonly exceeds the point at which respiratory costs equal construction costs. In Volkamer lemon seedlings, the maintenance costs over the lifetime of the root are seven-fold greater than the construction cost for roots that live 152 days (Table 1). In slash pine, roots appear to live for an average of about 1.5 years (Schoettle and Fahey, 1994); thus, maintenance costs over the lifetime of the root are about 12-fold greater than the cost of root construction in this species. In desert succulents, maintenance respiration is 2.1- to 2.5-fold greater than root construction costs after the first year for nodal roots of *Agave deserti* and established roots of *Ferocactus acanthodes* and *Opuntia ficus-indica*; these roots can apparently live at least 2 years (Nobel *et al.*, 1992). Clearly, the C allocated for maintenance over the lifetime of a root often far exceeds the C allocated for root construction. Considering that annual root biomass production often exceeds 50% of total

NPP, the annual C costs associated with root maintenance are impressive. From the perspective of optimal lifespan, the high C requirements of maintenance respiration indicate the potential disadvantage of maintaining a root that is inefficiently acquiring water or nutrients.

VIII. MODELING OPTIMAL ROOT LIFESPAN

A successful theory of root deployment would explain the observed variation in lifespan with reference to environmental conditions, such as temperature, moisture and soil fertility, and plant factors such as life form, life stage, C status and symbioses. Such a theory is in its infancy, at best. The previous section illustrated some of the trade-offs, in terms of C costs, between ending the life of a root to construct a new one and maintaining existing roots for longer lifespans. A more comprehensive cost–benefit analysis would attempt to predict optimal root lifespan based on both C expended and resources gained.

Simulation models of root C expenditure and nutrient uptake provide a means to test specific hypotheses of optimal root strategies (Yanai *et al.*, 1995). Such models are not restricted to describing optimal behavior. Carbon costs and nutrient uptake can be simulated over time; optimal lifespan may be indicated by the maximal lifetime ratio between nutrient uptake and C costs. Departures of observed root longevity from theoretical predictions of maximal efficiency may provide insights into the trade-offs and constraints on both root and whole-plant function. There are many reasons, as discussed above, why root lifespan might not optimize the efficiency of nutrient acquisition.

In this section we introduce a model of root efficiency and describe how this model can be used to explore environmental conditions that might influence optimal lifespan. Previous models (McKay and Coutts, 1989; Fahey, 1992; Yanai *et al.*, 1995) have not included some factors important to root longevity, such as the variation in C expenditures and ion uptake rates with root age.

A. Root Efficiency

We define root efficiency, E, as the rate of resource acquisition divided by the rate of C expenditure for root growth and maintenance. Analysis of C cost and nutrient benefit should indicate the optimal lifespan for a root in a given soil environment; specifically, the lifespan that maximizes E.

$$E = (UPTAKE)(COST)^{-1} \tag{1}$$

where E = the efficiency of nutrient acquisition by roots [(mol nutrient)(mol C expended)$^{-1}$], $UPTAKE$ = nutrient gain [(mol nutrient) (g fine root)$^{-1}$ day^{-1}], and $COST$ = carbon cost [(mol C)(g fine root)$^{-1}$ day^{-1}].

The calculation of $COST$ includes the C contained in the root and C expended in growth respiration and maintenance respiration. Carbon costs are averaged over the lifespan of the root to obtain the cost per unit root per day.

$$(COST) = (C_{root} + R_{G(w)} + LR_{M(w)})\ L^{-1} \quad (2)$$

where C_{root} = root C content (mol C)(g root)$^{-1}$, $R_{G(w)}$ = growth respiration [(mol C)(g root)$^{-1}$], L = root longevity (days), and $R_{M(w)}$ = maintenance respiration [(mol C)(g root)$^{-1}$(day)$^{-1}$].

This equation does not separate mycorrhizal fungal construction and maintenance from that of the root proper; these costs are included in C_{root}, $R_{G(w)}$ and $R_{M(w)}$.

Likewise, root exudates that are rapidly metabolized are included in the maintenance component, according to the way $LR_{M(w)}$ is usually measured.

Root efficiency can be calculated using lifetime average values for root and soil properties or using shorter intervals, with cumulative costs and benefits determining lifetime efficiency. Previous efforts at exploring optimal lifespan of roots used only the lifetime averages of root and soil properties, producing a single average efficiency for each root considered (Yanai *et al.*, 1995). This approximation failed to simulate the effects of changes in root and soil properties over the lifetime of the root. In this paper, C costs and nutrient uptake are calculated on a daily timestep; efficiency is reported on a daily basis, and cost and uptake are accumulated to show changes in lifetime efficiency as the root ages. In addition to allowing parameters to be varied as the root ages, implementing the model on a daily timestep allows soil conditions to change over the life of the root.

In the following simulations, we varied the following parameters over time, depending on the simulation: inter-root distance, uptake kinetics, root respiration, radial water velocity, and soil moisture (which affects the effective diffusion coefficient). Importantly, we did not vary soil solution concentrations to simulate depletion of soil nutrients over time. We assumed that root radius and specific length were constant over the life of the root.

B. Carbon Costs

1. Construction Cost

Root construction cost is the sum of the C content of the root (C_{root}) and growth respiration ($R_{G(W)}$). In the model, root construction exacts a one-time cost, assessed for each day's growth. It is, of course, a simplification to assume that root construction ceases after root elongation. As roots age, the secondary walls become more lignified and suberized. The values of C_{root} and $R_{G(W)}$ depend on the age at which the roots were measured. Likewise, root construction costs may reflect mycorrhizal colonization and plant nutrient status. The effects of mycorrhizas on C costs are discussed under section XI, Further Considerations. The effect of plant nutrient status is illustrated by citrus seedlings (Table 2), in which low P conditions promote thinner roots, with a lower starch concentration and a higher percentage of the more lignified epidermal, hypodermal and stelar cells and fewer and smaller cortical cells (Peng *et al.*, 1993; D.M. Eissenstat, unpublished data).

High tissue construction cost is commonly assumed to indicate long lifespan, but this assumption may be unjustified. Short-lived leaves may have fewer defensive compounds than long-lived leaves but more proteins for rapid C assimilation. As a result, construction costs of tissues of different lifespans tend to be quite similar (Chapin, 1989; Poorter, 1994). Likewise, in roots, short-lived, highly absorptive roots with high V_{max} and high hydraulic conductivity may use C for energetically expensive proteins and enzymes associated with rapid ion uptake and assimilation, while well-defended roots may allocate similar amounts of C to defense. A refinement on the *COST* term of the efficiency equation would partition root construction costs into those associated with defense of the tissue (such as formation of a woody periderm, high C:N ratio, and high concentrations of phenolic compounds such as lignins, tannins and suberins), those associated with water and ion uptake (such as ATP, reductant, and carrier proteins) and those associated with storage (such as starch and fructans). Such a scheme has been proposed for leaves (Lerdau, 1992).

2. Ion-Uptake Respiration

Respiration associated with the uptake of nutrient ions is excluded from our estimates of root C costs. Respiration associated with ion uptake may represent a substantial portion of total root respiration (Veen, 1981; de Visser, 1985; van der Werf *et al.*, 1988; Johnson, 1990; Bloom *et al.*, 1992). For example, in barley mutants, about 14% and 23% of total root respiration was associated with ammonium and nitrate uptake, respectively (Bloom *et al.*, 1992). These values are similar to estimates derived by more indirect methods (references in Bloom *et al.*, 1992). Nitrogen uptake represents approximately 90% of the total ion uptake respiration (Veen, 1981). Little of the respiration for ion uptake is expended to acquire P. Under P-limited conditions, the respiration associated with N uptake should be treated as a whole-plant cost, and should not enter into the cost–benefit analysis of a particular root. Consequently, we exclude the costs of ion-uptake respiration in applying the model to optimize P uptake by citrus. In a system where N is the limiting resource, costs of absorption, transport and assimilation would need to be included and would depend on the form of N taken up. Nitrate assimilation can represent a substantial carbon cost. In some species, however, under high light conditions, nitrate is reduced in the leaves by photosynthetic electron transport, with minimal cost to plant carbon stores. The costs of N uptake are therefore not easily represented in a model of roots alone.

3. Maintenance Respiration

Maintenance respiration can be operationally defined as the respiration not attributable to growth or ion uptake. It is often determined from a regression of total root respiration as a function of root growth rate, where maintenance

respiration is the *Y*-intercept, or the respiration at zero growth (Szaniawski and Kielkiewicz, 1982). This approach assumes that maintenance respiration is constant and unaffected by root age, ion gradients, plant nutrient and water status or numerous other factors. An approach more amenable to roots in soil is to determine total root respiration and then subtract from the total the growth respiration (using estimates of root construction costs) and ion-uptake respiration (from measured rates of nutrient uptake and their theoretical costs) (Poorter *et al.*, 1991; Peng *et al.*, 1993). In both approaches, $R_{M(w)}$ represents residual respiration and, thus, includes root exudates that are metabolized by microbes and growth and maintenance respiration of the extramatrical hyphae.

4. Sensitivity of E *to Variation in Cost Parameters*

The sensitivity of E to values of the cost parameters is straightforward to analyze because the equation for cost is so simple (Eqn 2). Where construction costs ($C_{root} + R_{G(w)}$) are small relative to maintenance costs ($LR_{M(w)}$), changes or errors in these parameters will have little effect on the magnitude of E. Where L is very low, E will be more sensitive to construction costs. For the lemon seedling parameters used in these modeling illustrations (Table 3), a 50% change in $C_{root} + R_{G(w)}$ causes a 1% change in E if L is 10 days and a 0.1% change in E if L is 100 days. Maintenance respiration, $R_{M(w)}$, is much more influential, with E nearly inversely proportional to $R_{M(w)}$. Increasing $R_{M(w)}$ by 50% causes a 33% decrease in E at a longevity of 10 or 100 days. Alterations in L have little effect on E when L is large relative to construction costs, because the average daily cost will be nearly equal to $R_{M(w)}$ (L appears in both the numerator and the denominator of Eqn 2). Increasing L from 10 to 100 days increases E by only 2%. In the simulations we present, longevity is not a parameter estimated from measurements; we calculate E for any value of L. The cost–benefit analysis of root longevity is essentially an exploration of the sensitivity of E to L; we seek the L that maximizes E under various combinations of values of the other parameters. E varies strongly with L in our simulations due to changes in other parameters over the life of the root, such as V_{max}, soil moisture, or $R_{M(w)}$, not due to the structure of the cost part of the efficiency equation.

C. Uptake of Nutrients

In the model of cost-effectiveness of roots, nutrient uptake represents the benefit term in the equation. We estimate nutrient uptake using a steady-state model of solute uptake (Nye and Tinker, 1977; Yanai, 1994), which includes active uptake at the root surface and transport through the soil by diffusion and solution flow. The advantage of assuming a steady-state condition, in

Table 3

Parameter values used in simulating Volkamer lemon seedlings. Details of the uptake model can be found in the Appendix. Mycorrhizal (M) and nonmycorrhizal (NM) plants were grown in pots at two levels of P fertility for 92 days (Peng *et al.*, 1993). Soil was a Chandler series hyperthermic, uncoated Typic Quartzipsamment. Specific root length (λ) was calculated from measured dry weight and length of fine roots at 58 days for 1P plants and 65 days for 5P plants (Peng *et al.*, 1993) (Table 2). Root radius (r_0) was calculated from specific root length using a tissue density of 0.167 g cm^{-3} (Eissenstat, 1991). Maintenance respiration ($R_{M(w)}$) was measured at 25°C and excludes ion-uptake respiration; construction cost ($CONST_w$) is the sum of growth respiration ($R_{G(w)}$) and the carbon in the root (C_{root}) (Peng *et al.*, 1993). Construction cost was assessed on the first day. Uptake kinetics (V_{max} and K_m) were measured on excised roots using ^{32}P (K.R. Kosola and D.M. Eissenstat, unpublished data). Water uptake rate (v_0) was calculated from whole-plant transpiration and root surface area.

Parameters relating to root length and density were varied over time. Root mass was estimated from regression analysis of sequential harvests. Root length was calculated from root mass and λ. Inter-root distance, r_x, was calculated from root length and a pot volume of 130 cm^3. In the later simulations, r_x was 0.4 cm.

Soil parameters were held constant for the duration of the simulation. These include buffering capacity (b), diffusion coefficient of P in water (D_l), effective diffusion coefficient (D), solid-liquid partitioning coefficient (K_d), the impedance factor (describes tortuosity, f), and soil bulk density, ρ. In the pot study, P was added to soil weekly at concentrations of 1 mM (= 1P) and 5 mM P (= 5P); these concentrations were used for average solution concentration (C_{av}).

	NM 1 P	NM 5 P	M 1 P	M 5 P	Source
λ ($m\ g^{-1}$)	37.7	23.2	32.8	21.6	Peng *et al.* (1993)
r_0 (cm)	0.02249	0.02866	0.02411	0.02971	Eissenstat (1991)
$R_{M(w)}$ (mmol $g^{-1}\ d^{-1}$)	1.77	1.62	2.46	2.05	Peng *et al.* (1993)
$CONST_W$ (mmol g^{-1})	44.7	42.0	48.7	45.3	Peng *et al.* (1993)
V_{max} (pmol $cm^{-2}\ s^{-1}$)	2.3				K.R. Kosola & D.M. Eissenstat, unpublished data
K_m (mM)	36				K.R. Kosola & D.M. Eissenstat, unpublished data
v_0 ($cm\ s^{-1}$)	3.70×10^{-6}	3.90×10^{-6}	6.70×10^{-6}	3.70×10^{-6}	Peng *et al.* (1993)
b (unitless)	4.61				Barber (1984)
D_l ($cm^2\ s^{-1}$)	0.89×10^{-6}				
D ($cm^3\ s^{-1}$)	3.40×10^{-6}				
K_d	3				Ballard and Fiskell (1974)
θ_v ($ml\ cm^{-3}$)	0.17				Unpublished data
f	$3.13 * \theta^{1.72}$				van Rees *et al.* (1990)
C_{av} (mM)	1	5	1	5	Peng *et al.* (1993)
ρ ($g\ cm^{-3}$)	1.48				Unpublished data

which the rate of solute uptake equals the rate of transport to the root, is that a single rate of nutrient uptake can be estimated for a root in a given soil environment, without a dynamic simulation of the development of the concentration profile over time. Parameters in the model can be changed as the root ages to explore factors affecting optimal root lifespan.

1. Model Assumptions

When the model is applied to a whole root system, roots are assumed to be homogeneous and uniformly distributed; parameter values describe the average root. Alternatively, the model can be used to describe a single root. The soil is also assumed to be homogeneous, except for the variation radial to the root, which is the steady-state profile of solute accumulation or depletion around each root. Roots are characterized by the specific root length, λ, the root density (half-distance to the next root r_x), the radius of the root, r_0, the rate of water influx into the root, v_0, and the root uptake kinetics (the maximal rate, V_{max}, and the half-saturation constant, K_m). The soil is characterized by the average soil solution concentration, C_{av}, the buffer capacity, b, and the effective diffusion coefficient, D, which is a function of soil water content, soil bulk density, and the tortuosity of the path a nutrient ion must take to reach the root. The equations used to calculate uptake from these parameters are given in the Appendix. The parameter values used in our simulations are given in Table 3.

2. Model Sensitivity

The sensitivity of E to values of the uptake parameters is complex because the uptake equations are complex (Eqns 3, 4, and 5 in the Appendix). The importance of any parameter in determining uptake depends on the values of the other parameters. As a result, any exploration of model behavior must use appropriate values for all parameters. Williams and Yanai (1996) conducted a systematic exploration of model sensitivity across all parameters using statistical analysis of variance. They found that the most important variables in explaining variation across the parameter space defined by the ranges of parameter values reported in the literature were C_{av} and V_{max}. There were important interactions of two, three, and four parameters, which illustrates the need to conduct sensitivity analyses with the relevant values for other parameters. To show the nature of the main effects and the interactions, Williams and Yanai (1996) used a graphical approach, displaying five dimensions of parameter space by using rows and columns of graphs on multiple pages.

The results of this sensitivity analysis can be interpreted to indicate optimal foraging strategies for roots in different environmental conditions. Investment in increased uptake capacity (by increasing V_{max} or decreasing K_m) will have little effect on uptake if the rate of delivery to the root (limited by C_{av}, Db, and v_0) is limiting to uptake. In this case, adding to root length is a better strategy for increasing nutrient uptake. Conversely, when the rate of uptake at the root surface is limiting, then increased uptake capacity will be advantageous. In these circumstances, increased r_0 will also improve nutrient uptake per unit length of root, whereas in the transport-limited case, increased r_0 has less effect. In all cases, however, the same biomass invested in longer, finer roots rather than increased root thickness results in greater efficiency.

For the simulations that follow, representing lemon seedlings in fertilized sandy soil, uptake of P is most sensitive to D and b. Increasing Db results in decreased uptake, because the steady-state solution to solute transport and influx under these conditions results in an accumulation of P at the root surface, rather than a depletion zone. Diffusion is away from the root, and more rapid diffusion allows a lower C_0. Increases in each of the other parameters (r_0, v_0, C_{av}, V_{max}, K_m, λ, and r_x) cause at least proportional increases in uptake, with the greatest effects due to r_0 and v_0. In this parameter set, despite the accumulation of P at the root surface, V_{max} is not saturated, because K_m is high relative to C_0, in keeping with the linear uptake kinetics we observed in this concentration range (K. Kosola, unpublished data).

D. Other Factors

Root hairs, root exudates and mycorrhizal fungi influence nutrient uptake and C costs but have not been explicitly included in this model. The importance of these factors in influencing the costs and benefits of root deployment will be described later.

For illustration, we restrict our simulations in this paper to the acquisition of P, the limiting nutrient in our model system of citrus plants growing in sandy soil. Other resources, such as water, ammonium, or nitrate, could also be modeled as the primary benefit accruing from root deployment.

IX. MODEL APPLICATION

To illustrate the application of a cost–benefit analysis to optimal root lifespan, we parameterized the efficiency model with data based on our research in citrus. We tested the ability of the model to simulate P uptake by lemon seedlings over a two-month period as measured by Peng *et al.* (1993). Then we applied the model to roots over time from birth to six months, with nutrient uptake varying as a function of root age. Roots must be simulated from the time they are constructed to allow an analysis of optimal lifespan based on maximal efficiency. We use this simulation to introduce calculations of cumulative root uptake and root cost and lifetime average root efficiency. In the following sections, we further examine how morphological (root diameter) and environmental (fertility, soil temperature and drought) factors affect root uptake, cost, efficiency and optimal lifespan.

A. Validation of Simulated P Uptake

The experiment by Peng *et al.* (1993) using Volkamer lemon seedlings involved four treatments, with mycorrhizal and nonmycorrhizal plants and two levels of P fertilization. We simulated uptake from day 33 to day 92 of the experiment, the period for which data on root length were available. The

values of parameters used in the model are shown in Table 2. Average solution concentrations (C_{av}) were assumed to be constant at the concentrations added weekly to the pots. Uptake capacity of the roots was assumed to be constant with root age at the rate measured on seedling root systems (described by V_{max} and K_m). Phosphorus uptake per gram of root varied with treatment, because of differences in solution P concentration, specific root length, root radius, and water uptake rate, and decreased slightly over time because of root competition in the pot (average inter-root distance decreased). The simulated uptake summed over the 59 days agreed very well (within 5%) with the change in measured P content of harvested seedlings at days 33 and 92 for three of the treatments (Figure 1). The exception was the mycorrhizal plants at low P. The model underpredicted P uptake in this treatment by 23%, suggesting that the effect of mycorrhizal colonization, which was not included in the model, was important to P uptake. We did not calculate cumulative efficiency for these simulations because the first 33 days were not simulated (root length data were not available). Daily efficiency, given constant maintenance costs, is easily calculated from uptake.

B. Simulation with Root Age

To simulate lifetime average root efficiency, and thereby explore optimal root lifespan, requires simulating roots from the time they are constructed. The

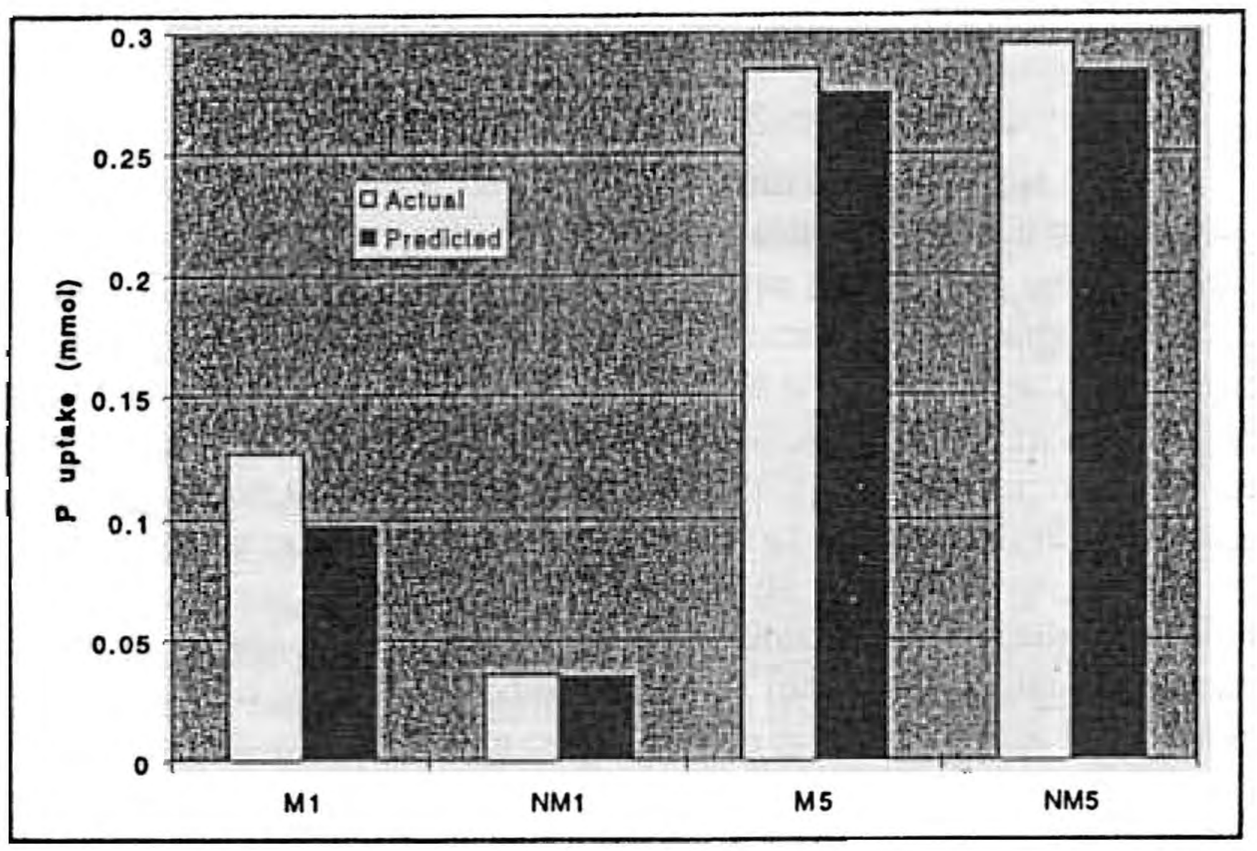

Fig. 1. Actual and predicted uptake of mycorrhizal (M) and nonmycorrhizal (NM) Volkamer lemon seedlings grown with weekly additions of 1 (M1, NM1) and 5 mmol P (M5, NM5) (from Peng *et al.*, 1993).

cost of constructing roots is one reason for plants to retain roots rather than build new ones: the average lifetime cost of a root decreases over time, if maintenance costs are constant, because the initial investment in constructing them is amortized over a longer period. In fact, if uptake were constant with root age, the optimal lifespan would be infinite. The decrease in nutrient uptake as roots age is presumably one of the primary reasons for root turnover. Declining nutrient uptake could be due to changes in the root or to changes in the supply of nutrient as the soil is depleted by uptake.

Estimates of changes in nutrient uptake capacity with root age come mainly from ion-depletion or ion-uptake techniques in solution culture. For a range of tree species, suberized woody roots typically have rates of nutrient absorption 30 to 80% of white roots (see references in van Rees and Comerford, 1990). When the cortex disintegrates, as is commonly found in older cereal roots in the field, phosphate uptake may be only 5% of that of roots where the cortex is still intact (Clarkson *et al.*, 1968). In 2-week old barley plants, P uptake 1 cm from the root tip was similar to that in basal portions of the root, suggesting that uptake capacity does not decline in the first two weeks (Clarkson *et al.*, 1968).

Although there are good indications that uptake rates are lower in older roots, uptake kinetics as a function of root age are not well known for citrus or for any other species. In our simulations, we assume a curve for V_{max} as a function of root age that starts at 60% of maximum at day 1, achieves maximum at 2 weeks, and declines asymptotically to 20%, passing 50% at about 3 months. For citrus seedlings, maximum V_{max} (3.8 pmol cm^{-2} s^{-1}) was calculated by determining the V_{max} (2.3 pmol cm^{-2} s^{-1}) of a population of roots (whose average age was determined by video analysis of sequential images taken with minirhizotrons). Other parameters were estimated as indicated from Table 2.

Simulated daily uptake per gram of root (Figure 2) is highest in the high-P treatments; other differences between treatments are due to differences in specific root length and water uptake rates. The changes in uptake with root age are driven by the relationship we assumed between V_{max} and root age. Cumulative uptake reflects the changes in daily uptake.

Daily costs are constant because maintenance respiration was assumed to be constant and the respiration associated with ion uptake is excluded from the model. Respiration is higher in mycorrhizal than nonmycorrhizal plants, and it is higher in the low-P treatment than in the high-P treatment. Cumulative cost, the sum of construction costs plus daily maintenance costs from zero to the age of the root, increases linearly because of the constancy of daily cost. Differences in construction costs are small compared with lifetime maintenance costs.

Daily efficiency shows a pattern with root age that is driven by the pattern of uptake with root age. Plants at high P are more efficient than plants at low P; the least efficient plant is the nonmycorrhizal low-P plant. Lifetime

efficiency is the cumulative cost divided by the cumulative efficiency; this shows the average efficiency of the root were it to die at the given age. The high-P treatments show maximal lifetime efficiency at a lifespan of 65–70 days. Simulated lifetime efficiency declines less steeply in the nonmycorrhizal treatments because the costs are lower. The optimal lifespan is sensitive to the assumed pattern of uptake with root age: if P uptake were not assumed to be so low in older roots, efficiency would not drop off as quickly and the optimal lifespan would be longer. The pattern of nutrient uptake with root age is an important uncertainty which deserves further experimental determination.

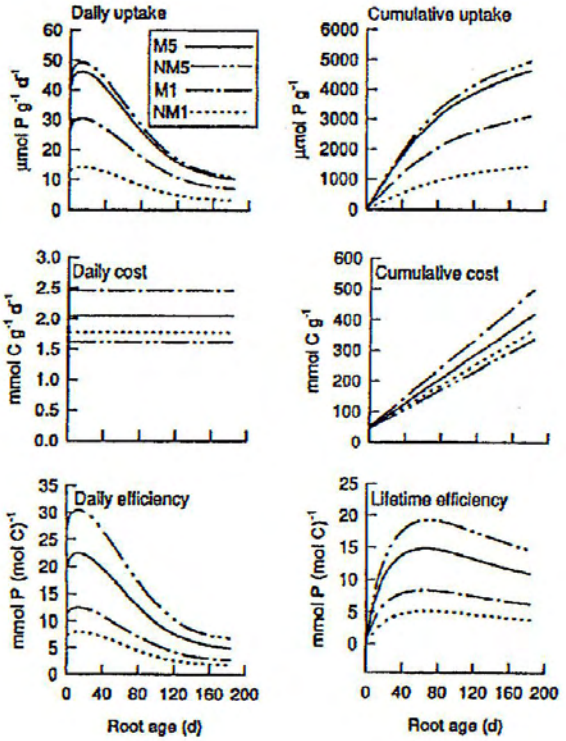

Fig. 2. Model simulations of daily and cumulative uptake, cost and efficiency of mycorrhizal (M1, M5) and nonmycorrhizal (NM1, NM5) Volkamer lemon seedlings at low (M1, NM1) and high (M5, NM5) phosphorus supply. Model parameterization is based on Table 3.

X. MORPHOLOGICAL AND ENVIRONMENTAL FACTORS AFFECTING ROOT COSTS AND BENEFITS

A. Specific Root Length, Root Diameter and Tissue Density

Specific root length (λ) is the ratio of root length to root mass. It has been used as a simple index of root benefit to root cost (Fitter, 1991), assuming that resource acquisition is proportional to length and root cost (construction and maintenance) is proportional to mass. Many studies equate λ with a measure of root fineness, assuming root density is constant. Here we discuss separately root diameter and tissue density and their relationship to root lifespan.

1. Root Diameter

Previous attempts using an earlier version of a cost–benefit efficiency model (Yanai *et al.*, 1995) failed to establish an optimal diameter of roots for maximum nutrient uptake efficiency. Thinner roots were always more efficient than coarser roots, because of the importance of root length and root surface area in nutrient uptake. The simulation assumed that finer roots had the same C cost as coarse roots per gram of root. This assumption may not be justified. Low-P nonmycorrhizal citrus roots are thinner than high-P mycorrhizal roots, and have about 6% higher construction cost and 9% higher maintenance respiration (Table 2). More importantly, thinner roots may place other constraints on root lifespan not represented in the present efficiency model, including increasing risk of herbivory and constrained axial water transport because of smaller xylem vessels. When C costs of fine roots were assumed to be higher than coarse roots, Yanai *et al.* (1995) found that optimal root diameter was no longer infinitely small. More accurate simulations of the effects of root diameter under different environmental conditions await more quantitative information on the relative costs of thin and thick roots.

Experimental evidence that root diameter is linked to root lifespan is limited. Obviously, roots that undergo secondary growth are normally longer-lived than absorptive roots that never undergo secondary thickening. The question is whether root longevity is related to root diameter among absorptive roots. Root diameter varies continuously within a plant's root system and can exhibit considerable morphological plasticity (Fitter, 1985). Absorptive roots typically decrease in diameter from internal to external links, with the terminal roots having the smallest diameter and shortest lifespan (Reid *et al.*, 1993). Root diameter also ranges widely among species and appears to be strongly influenced by plant phylogeny (Fitter, 1991; Eissenstat, 1992). The

diameter of the finest elements of the root system can be less than 100 μm in many graminoid species found in the Juncaceae, Cyperaceae and Poaceae, in ericoid mycorrhizal species in the Ericaceae and Epacridaceae and in many annual dicots such as the well-studied species *Arabidopsis thaliana* (Harley and Smith, 1983; Fitter, 1991; Eissenstat, 1992; D.M. Eissenstat, unpublished data). At the other extreme, the fine root elements of many woody species in the Magnoliaceae, Rutaceae and Pinaceae and herbaceous species in the Aliaceae are at least 500–1000 μm diameter. There is some evidence that species with thin roots have a shorter lifespan than those with coarse roots, as indicated by limited comparisons of cold-desert shrubs (Caldwell and Camp,

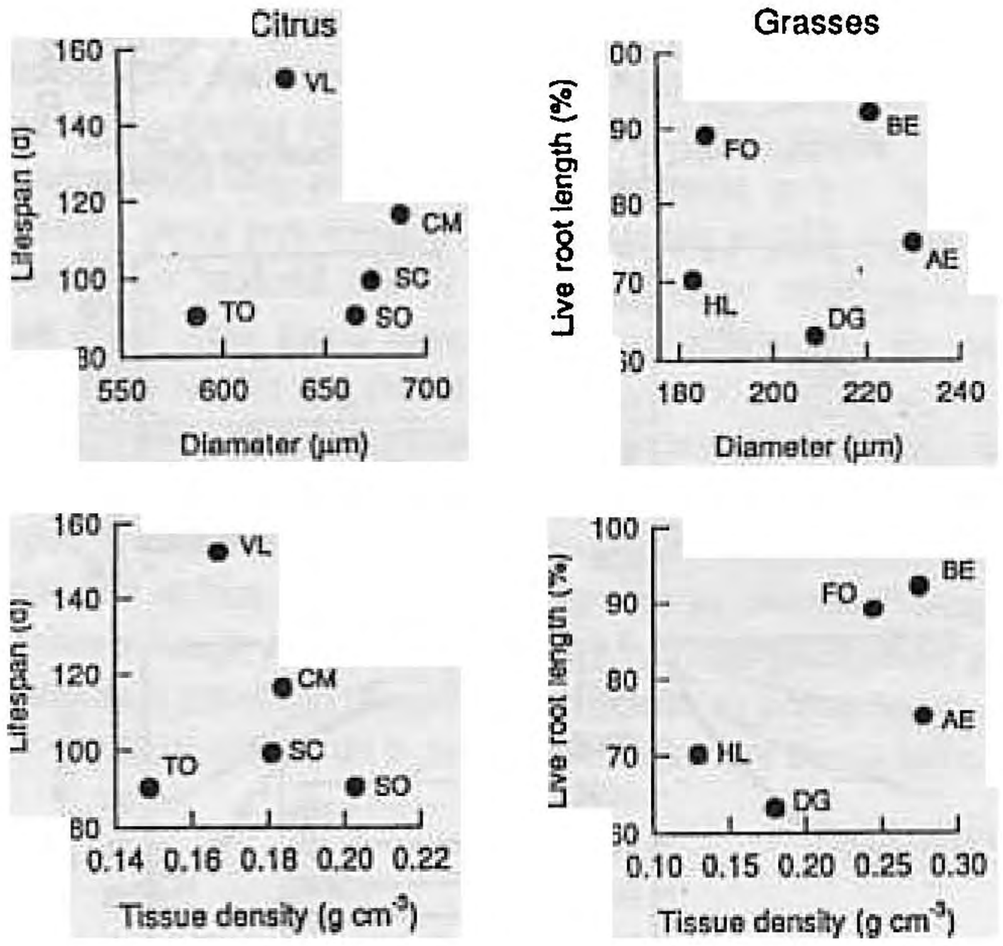

Fig. 3. The relationship of root diameter and tissue density to root longevity in citrus (Eissenstat, 1991) and perennial grasses (Ryser, 1996). Citrus roots were sampled in a Valencia orange rootstock trial. The perennial grasses were *Arrhenatherum elatius* (AE), *Dactylis glomerata* (DG), and *Holcus lanatus* (HL), species common to nutrient-rich grasslands, and *Festuca ovina* (FO) and *Bromus erectus* (BE), species characteristic of nutrient-poor grasslands. Citrus root diameters and tissue density are averages of roots about 70–90 days old. Citrus lifespan data and rootstock abbreviations are from Table 1. Grass root diameters and tissue density are from roots harvested at the end of the first growing season. Per cent live root was estimated from roots harvested at the end of the second growing season.

1974; Fernandez and Caldwell, 1975), chaparral shrubs (Kummerow *et al.*, 1978) and tundra species (Shaver and Billings, 1975). Among citrus rootstocks and perennial grasses, however, there was no relationship between mean root diameter and median root lifespan (Figure 3). Comparisons are needed of species with a broader range in root diameters before the relationship of root lifespan to genetic differences in root diameter can be fully assessed. Phenotypic variation in root diameter and its relation to root lifespan also deserves further study.

2. Tissue Density

Root tissue density is not constant and its variation may be ecologically important. Among citrus rootstocks, tissue density varied about 30%, tended to be lowest in rootstocks with the fastest root extension (Eissenstat, 1991), but exhibited no relationship to root lifespan (Figure 3). In perennial grasses, tissue density was again lowest in species with the fastest growth rates (Ryser and Lambers, 1995; Schläpfer and Ryser, 1996). Root density among these species differed by more than 100% and was positively correlated with the percentage of roots still alive after two growing seasons (Ryser, 1996; Figure 3). Root survivorship was determined by vital staining (triphenyl-tetrazolium chloride). These results are interesting but should be confirmed by methods that clearly separate root birth from death and that account for roots that are eaten or decomposed during the study period. Similar relationships between site productivity, growth rate, tissue density and lifespan have also been observed in leaves (Garnier and Laurent, 1994; Ryser and Lamber, 1995; Ryser, 1996; Schläpfer and Ryser, 1996). In leaves, tissue density has been related to high amounts of lignins and tanins and other secondary wall materials (Garnier and Laurent, 1994), which may affect tissue palatability and increase tissue toughness against adverse environmental conditions such as frost heaving.

B. Soil Fertility

Roots deployed in nutrient-rich soil will clearly be more efficient at nutrient uptake than roots in less fertile soil, if they acquire more nutrient for the same C expended (Bloom *et al.*, 1985). It is less clear how root lifespan should vary with soil fertility. Should roots be shed more rapidly in fertile or infertile soils? The effect of soil fertility on optimal root lifespan may depend on whether all the roots of the plant are exposed to uniformly fertile soil or whether a small portion of the roots are exposed to a fertile patch. This distinction is often overlooked when interpreting root responses to fertilization. If all the roots are supplied uniformly with nutrients, then competition for carbohydrates occurs principally between shoots and roots; for localized supply, carbohydrate competition will occur between roots in the nutrient-rich patches and roots in the

less-fertile bulk soil. Thus, optimal root lifespan is not only affected by nutrient supply but by the heterogeneity of supply among the root axes.

1. Uniform Nutrient Supply

Experimental investigations on the effect of fertility on root lifespan have mainly addressed community-level rates of root turnover in forested ecosystems. The evidence that habitat fertility is inversely related to root lifespan is conflicting (see review by Hendricks *et al.*, 1993). Much of the controversy may result from the different methods used to estimate root turnover. Aber *et al.* (1985) found decreasing root lifespan with increasing nitrogen availability when they estimated turnover using nitrogen-budgeting approaches (Table 4), but they found no relationship using a 'max-min' approach based on sequential harvesting of roots. This method assumes asynchronous birth and death and therefore probably underestimated root turnover on sites with low seasonal fluctuations. The nitrogen-budget approach, however, assumes that net mineralization is adequately estimated in buried bags, that all mineralized N is taken up, that N allocation above ground is accurately measured, and that the difference between uptake and above-ground allocation is used by fine roots and mycorrhizas. Although indirect, the method seemed to give reasonable estimates of whole stand rates of root turnover. For example, lifespan of sugar maple in Wisconsin ranged from 181 to 389 days by the N-budgeting approach (Table 4), which agrees well with lifespan of surface roots of sugar maple estimated from direct observation in Michigan, New York and New Hampshire (180 to 340 days, Table 1). Stands with high rates of nitrification had the highest N availability and shortest root lifespan (Aber *et al.*, 1985) (Table 4). These hardwoods were typically mixed, containing both ecto- (oaks, birch, hickory) and arbuscular mycorrhizal (maple, cherry) species. On Blackhawk Island, Wisconsin, ectomycorrhizal hardwoods had considerably longer root lifespan than those trees in the forest type in which arbuscular-mycorrhizal sugar maple was a major component. At the University of Wisconsin Arboretum, the main difference in root lifespan was between hardwoods and conifers, not between ectomycorrhizal and arbuscular-mycorrhizal species. Conifers tended to be on sites with the lowest N availability.

Few studies of the effect of soil fertility on lifespan have used direct observation techniques. In a study of hybrid poplar (*Populus* × *euramericna* cv. Eugenei), lifespan of a spring cohort of roots was significantly diminished in trees fertilized with nitrogen (Pregitzer *et al.*, 1995). Similar results were found in ponderosa pine (*Pinus ponderosa*). With no nitrogen addition 64% of the roots lived longer than 2 months; at 100 kg N ha^{-1} 51% lived past 2 months and at 200 kg N ha^{-1} 48% of the roots lived longer than 2 months (D.T. Tingey, D.L. Phillips, M.G. Johnson, M.J. Storm and J.T. Ball, unpublished data). Thus, direct

Table 4
The relationship of root lifespan to nitrification rate and nitrogen availability (after Aber *et al.*, 1985, and Nadelhoffer *et al.*, 1985). Lifespan = Standing fine root biomass/annual fine root production. Annual fine root production calculated by the nitrogen-budgeting approach

Forest Community	Nitrification (% of mineralization)	Nitrogen Availability (kg N ha^{-1} yr^{-1})	Average Lifespan (days)	Location	Comments and soil type
Black oak–White oak–Black cherry–Shagbark hickory–Red maple forest (*Quercus velutina–Q. alba–Prunus serotina–Carya ovata–A. rubrum*)	100	143	167	South-central Wisconsin University of Wisconsin Arboretum	Roots collected from 0–20 cm. Alfisol
Red oak (*Q. rubrum*)–White oak–Black cherry–Shagbark hickory–Sugar maple forest	100	133	188		Alfisol
White and black oak forest	100	107	301		Alfisol
Paper birch (*Betula paprifera*) forest	—	92	358		Alfisol
Sugar maple (*Acer saccharum*) forest	100	102	389		Alfisol
Red (*P. resinosa*) and white pine forest	—	69	507		Alfisol
White pine (*Pinus strobus*) forest	71	79	528		Alfisol
White Spruce (*Picea glauca*) forest	—	66	760		Alfisol
Red and jack pine (*P. banksiana*) forest	50	47	812		Alfisol
Sugar maple and red oak forest	100	133	181	Blackhawk Island, Wisconsin	Alfisol
White and red oak forest	30	86	553		Alfisol
Red and white oak forest	4	92	568		Alfisol
White pine, red oak, white oak forest	46	60	753		Spodosol
Red and white pine forest	82	36	1223		Entisol

observation lends greater support to the hypothesis that root longevity diminishes with increased soil fertility.

2. *Heterogeneous Nutrient Supply*

Studies of nutrient-amended patches on root lifespan have given mixed results. In mixed hardwood forests, roots that proliferated in response to additions of water or water and nutrients lived longer than roots in unamended patches of soil (Pregitzer *et al.*, 1993; Fahey and Hughes, 1994). Conversely, localized water and nutrient addition diminished root lifespan in a pot study using four old-field herbaceous species (Gross *et al.*, 1993). Dense populations of young roots resulting from local proliferation may be especially vulnerable to consumption by soil organisms (Graham, 1995). Citrus roots proliferating in zones of nutrient enrichment, for example, were more heavily infected with *Phytophthora* than roots outside the soil patches (K.R. Kosola and D.M. Eissenstat, unpublished data). Short lifespan in these conditions may not be optimal for nutrient uptake.

The duration of the fertile patch should also affect optimal root lifespan (Fitter, 1994). If the patches are very short-lived, nutrient uptake may not be sufficient to repay the costs of rapid root proliferation. In such a case, increasing the uptake capacity of existing roots may be a better foraging strategy (Grime, 1994). For example, roots of *Arrhenatherum elatius*, a plant associated with fertile environments, proliferated only in resource-rich patches if the patch was present for a day or more (Campbell and Grime, 1989). *Festuca ovina*, a low-nutrient-adapted species, was less responsive than *A. elatius* in root proliferation but had higher specific rates of N absorption for the nutrient pulses that were shorter than 1 day. This research led to the hypothesis that plants adapted to infertile soils where pulses tend to be short-lived should produce long-lived roots, whereas plants in fertile environments should produce short-lived roots which can be located in new patches as they become available (Campbell and Grime, 1989).

3. *Modeling Simulations of Soil Fertility*

The effects of soil fertility on optimal root lifespan were simulated in a previous application of the cost–benefit model of root efficiency (Yanai *et al.*, 1995). That earlier version of the model calculated lifetime efficiency based on lifetime average properties of roots; in contrast, the current version of the model calculates daily values of uptake and cost and sums them to calculate lifetime efficiency. As in the current model, some advantage of young roots over old roots had to be included to give a decrease in efficiency at long lifespan, otherwise, efficiency increased continuously with lifespan owing to the amortization of construction costs. The two presumed advantages of young roots are high water uptake rates and high nutrient uptake rates (Queen, 1967;

Chung and Kramer, 1975; Eissenstat and van Rees, 1994). The effect of soil fertility on optimal lifespan differed depending on which of these mechanisms was implemented. In all simulations, lifetime root efficiency was lower in infertile than in more fertile soils, because simulated uptake was lower. Clearly, in heterogeneous soil, roots should be deployed in fertile patches.

If nutrient uptake capacity was assumed to decline with lifespan (V_{max} decreased linearly with lifespan), maximal efficiency occurred at shorter lifespans in more fertile soil. In fertile soil (simulated by a higher average concentration of solute in the soil solution, (C_{av})), the rate of nutrient uptake was more limited by V_{max}, and the effect of lowered V_{max} with longer lifespan was disadvantageous: optimal lifespan was low. In infertile soils, uptake is more likely to be limited by the supply of nutrient than by V_{max}, and the disadvantage of retaining roots was lessened: optimal lifespan was longer.

In contrast, if nutrient uptake capacity was held constant but water uptake rates were dependent on root lifespan (decreased linearly with lifespan), the effect of soil fertility on optimal lifespan was different. The rate of water movement toward the root surface is more important in infertile than fertile soils in determining the rate of nutrient uptake (Yanai, 1994; Williams and Yanai, 1996). The advantage of short-lived roots, therefore, was greater in infertile soils, and the simulations showed optimal lifespan to be shorter in infertile than in fertile soils.

Current knowledge of water and nutrient uptake rates in roots of different ages and different lifespans is still too limited to distinguish which of the simulated mechanisms is more realistic. Certainly, uptake kinetics and water uptake rates will be more or less limiting to nutrient acquisition in different environments. Differences in the limitations to root efficiency in different circumstances may explain some of the variation observed in patterns of root lifespan with respect to soil fertility. The duration of fertile patches will also affect optimal root lifespan, with efficiency declining as nutrients are depleted.

C. Soil Temperature

Observations of native plants in the field suggest that roots may live longer in cooler environments. Roots tend to exhibit low mortality rates over winter (Head, 1969; Hendrick and Pregitzer, 1993). In a study by Hendrick and Pregitzer (1993), roots of sugar maple lived, on average, 75 days longer at the more northerly of two sites. The effect of soil temperature was also compared between two *Festuca* grasslands, one at an elevation of 845 m and the other at 170 m (Self *et al.*, 1995). There was a 5°C difference in annual temperature between the two sites. Root standing number and root production were greater at the low- than the high-elevation site and root longevity was greater at the high-elevation site. Increasing soil temperature with a heating grid at the high-

elevation site reduced root longevity. Except for these two studies, no one has examined root lifespan along either latitudinal or elevational gradients.

To simulate the effect of temperature on root costs and efficiency, we assumed an exponential increase in maintenance respiration with temperature, doubling $R_{M(w)}$ with each increase of 10°C (Ryan, 1991). We did not simulate the effect of increased temperature on uptake, although temperature may affect nutrient diffusivities and uptake kinetics. Above 30°C, uptake kinetics are usually much less affected by increases in temperature than is maintenance respiration (Barber, 1984; Marschner, 1986). We used parameters describing the nonmycorrhizal high-P treatment of the Volkamer lemon study (Table 3) because the effects of mycorrhizas are not included in this model and because the nonmycorrhizal low-P plants were P deficient and grew poorly.

Simulated lifetime efficiency, the ratio of cumulative uptake to cumulative cost, is highest at low temperature (Figure 4) because increased temperature was assumed to increase C cost without a corresponding benefit in increased uptake rates. The age at which lifetime efficiency is maximized is about 80 days at the lowest temperature and only about 50 days at the highest temperature. Thus, a 20-degree increase in soil temperature only resulted in a 30-day decrease in optimal root lifespan.

The results of this simulation suggest that differences in maintenance respiration alone can not account for the 75-day greater median lifespan at a 'northern' than 'southern' site in Michigan (Hendrick and Pregitzer, 1993), because the temperature difference between the two sites at a soil depth of 15 cm was only 2°C (growing season average). Secondary effects, such as greater activity of root pathogens and higher N mineralization at warmer temperatures may have contributed to differences observed in median lifespan.

D. Soil Dryness

In many ecosystems, a large fraction of the total root length is in the surface soil. For example, in pine ecosystems, 30–80% of root length may occur in the top 10 cm (Eissenstat and van Rees, 1994); in northern hardwoods, 50% of root length may occur in the top 7 cm (the forest floor) (Fahey and Hughes, 1994). This portion of the soil also experiences more fluctuations in moisture and more extreme dryness than deeper soil horizons, with consequent effects on root lifespan. In a rhizotron study, cotton root length declined by more than 50% at the 15-cm soil depth following exposure to dry soil for about 21 days (Klepper *et al.*, 1973). Fine roots of soybean also tended to die after about 20 days of drought (Huck *et al.*, 1987). In a tall-grass prairie dominated by big bluestem (*Andropogon gerardii*), root mortality was high in the top 10 cm in the first couple of weeks of drought (Hayes and Seastedt, 1987). In the following year when no drought occurred, mortality rates were fairly constant. Despite the frequency and importance of dry surface soil, the effects of local-

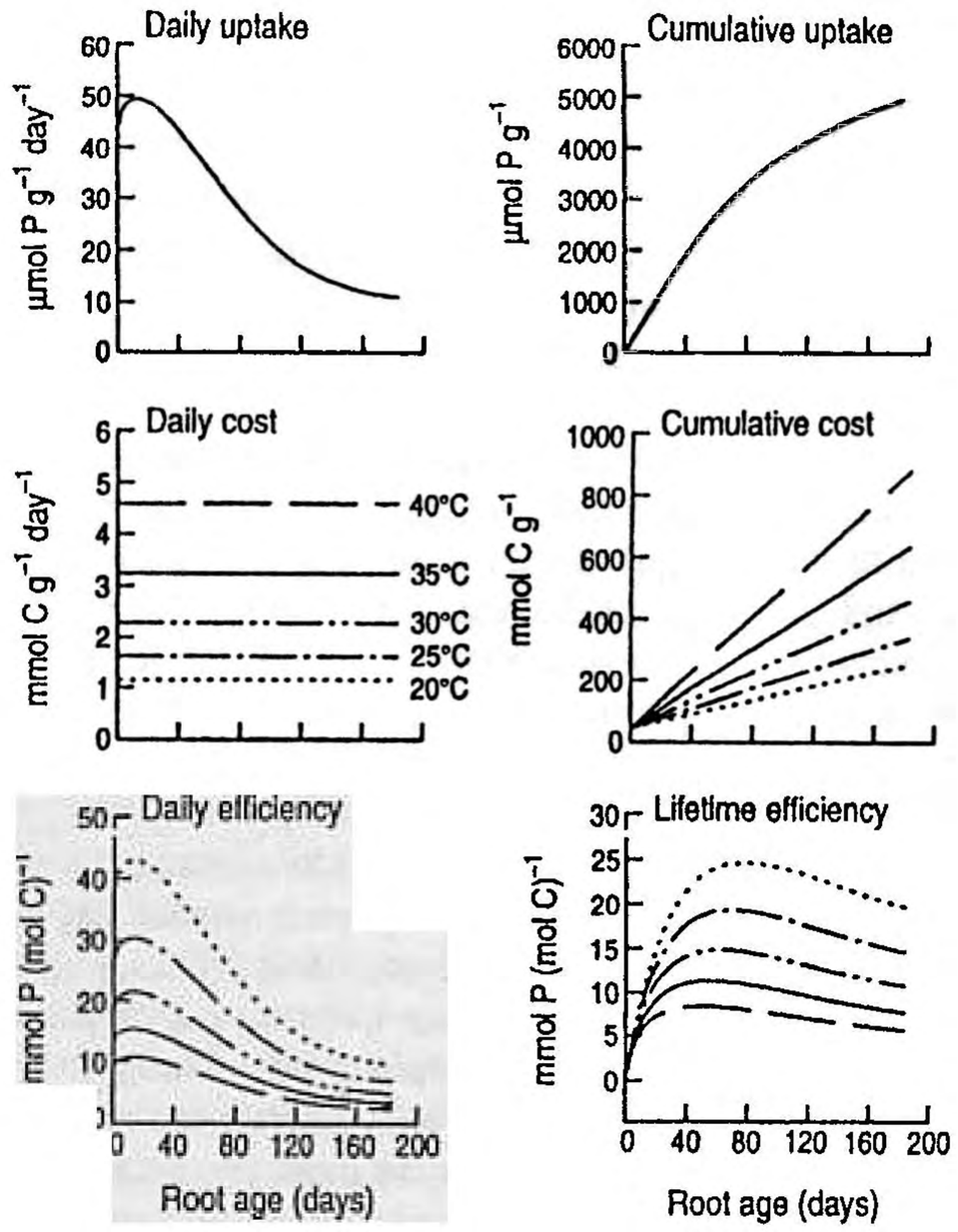

Fig. 4. The effects of increasing maintenance respiration on optimal lifespan. Model simulations of daily and cumulative uptake, cost and efficiency were for nonmycorrhizal (NM5) Volkamer lemon seedlings at soil temperatures that range from 20 to 40°C. For purposes of illustration, uptake was assumed constant at this range of temperatures whereas maintenance respiration was assumed to have a $Q_{10} = 2.0$.

ized drought on root behavior are poorly understood. The cost of retaining roots in dry soil should be compared with the benefits derived, both during and after the drought, to give an indication of optimal lifespan.

If optimal lifespan depends on the likely duration of drought, roots should be shed most readily in species adapted to conditions of prolonged drought. The desert succulent *Agave deserti* grows new roots rapidly after rain and then sheds them when the soil dries again (Huang and Nobel, 1992). Species not adapted to drought exhibit much greater tolerance of dry soil (Molyneux and Davies, 1983; Etherington, 1987; Jupp and Newman, 1987; Meyer *et al.*, 1990). Corn and tomato seedlings exhibited slow but continuous root growth

in quite dry soil (–4.0 MPa) (Portas and Taylor, 1976; root death is not mentioned in this report). Death of epidermal and cortical tissues, however, is quite common (Jupp and Newman, 1987; Stasovski and Peterson, 1991). In seminal roots of corn seedlings exposed to drought for 34 days, the extrastelar tissues died back radially, beginning with the epidermis (Stasovski and Peterson, 1991). Following rehydration, roots were generally able to produce new laterals despite having a collapsed cortex, if the whole plant had not been severely water stressed. These results are consistent with field observations that corn root length density (30 cm depth) does not diminish after exposure to dry soil for about 25 days (Taylor and Klepper, 1973). However, observations of population density do not reveal compensating shifts in birth and death rates.

Other factors may influence root death in dry soil, such as plant carbohydrate status or soil temperature. Mean root mortality increased from 8 to 16% in Douglas-fir seedlings exposed to 22 days of drought ($P > 0.05$; Marshall, 1986). Tree seedlings exposed to both drought and shade had four-fold faster rates of fine root mortality than well-watered, unshaded seedlings ($P < 0.05$), suggesting that the shaded plants, which were more C-limited, could less afford to retain their roots. Dry soils that are exposed to direct sunlight can reach temperatures of greater than 60°C (Ehleringer, 1985). Consequently, roots near the soil surface often experience both water and temperature stress, which may increase the advantages of shedding over maintaining the roots.

Plant age may also affect root shedding in dry soil. Citrus roots were grown in sandy soil in vertically split pots: irrigation was withheld from the top pot, while roots in the bottom pot supplied water and nutrients in quantities sufficient to prevent signs of stress. Six-month-old citrus seedlings exhibited less than 3% root mortality after exposure to dry soil for over 80 days (Kosola and Eissenstat, 1994). Roots of mature citrus trees, however, often live less than 80 days (Kosola *et al.*, 1995; Table 1: note that values in this table are for median lifespan, i.e. the time it takes for 50% of a population of roots to die). Consequently, a second study was established to compare death of fine roots in 1-year-old seedlings with those of 6-year-old bearing grapefruit trees (Espeleta, 1995). For the first 35 days of drought, root behavior was quite similar in juveniles and adults with neither exhibiting much mortality (about 2%). After 56 days, however, fine root mortality was 28% in adults but only 6% in juveniles; juvenile roots were also respiring more actively than those of adults, partly because of greater growth respiration. By 105 days, mortality was 33% in adults but only 8% in juveniles.

There are several differences between juvenile and adult citrus that could explain their different responses to dry surface soil. First, roots of adult citrus trees tended to be finer and less branched than the roots of juveniles (Espeleta, 1995). Juvenile fine roots may need to be thicker to serve additional functions, such as the transport of water and nutrients and the formation of the

future structural root system of the tree. Second, compared with adults, juvenile trees typically allocate proportionally more biomass to roots (Ledig, 1983); this allocation of C may inhibit shedding of inefficient roots. Finally, the adult trees at the time of rapid root shedding were in a period of high C allocation to the fruit. Whatever the reasons, it is clear that patterns of root lifespan exhibited by juveniles may contrast greatly with those of adults in response to environmental stress.

We simulated the effect of localized drought on optimal root lifespan, using parameter values for the nonmycorrhizal high-P treatment of Volkamer lemon seedlings, as in the illustrations of temperature effects (Table 3). Root costs were based on data from the experiment described above, where fine roots of grapefruit trees on Volkamer lemon rootstocks were exposed to moist and dry soil (Espeleta, 1995). Maintenance respiration was found to drop to 5% of predrought conditions after 30 days; we assumed this reduction was achieved linearly, beginning on the first day of drought. Nutrient-uptake kinetics (V_{max} and K_m) were assumed to be unchanged by drought, as found for sour orange roots exposed to dry soil for up to 43 days (Whaley, 1995). The effect of drought on P uptake was simulated, not through variation in uptake kinetics, but through the effects of drought on nutrient transport through soil. Drought increases soil resistance to diffusion by increasing soil tortuosity. We recalculated the effective diffusion coefficient (D) and the buffer power (b) assuming a volumetric water content of 1% (D changed from 3.42×10^{-8} to 2.0×10^{-8} cm s^{-1}; b changed from 4.61 to 4.54; see Appendix for equations). The rate of water movement towards the root (υ_0) also affects nutrient transport; this was set to zero during drought. In addition to simulating the effects of drought on nutrient transport and root uptake, we also simulated the effect of dry soil on P uptake per unit root length directly by diminishing uptake to 5% of that taken up by well-watered roots – the reduction Whaley (1995) observed in a study of sour orange seedlings using ^{32}P and ^{33}P. We assumed no residual effects of drought on respiration or uptake after soil moisture was restored.

We simulated various durations of drought at different stages of root development. Here we present simulations of an 80-day drought and an unremitted drought, both beginning when roots were 15 days old (Figure 5). We compare them to the case of no drought and to the case where uptake was fixed at 5% of normal.

Daily uptake shows the effect of drought on nutrient uptake. Of the three parameters that we modeled as affected by drought, the most important in limiting P uptake was the cessation of water movement toward the root, which is normally driven by the difference between root and rhizosphere soil water potential (in fact, under conditions of localized drought, water would tend to move from the root to the soil; υ_0 would be negative) The effect of drought on υ_0 alone would have reduced uptake by 68%. The drop in the

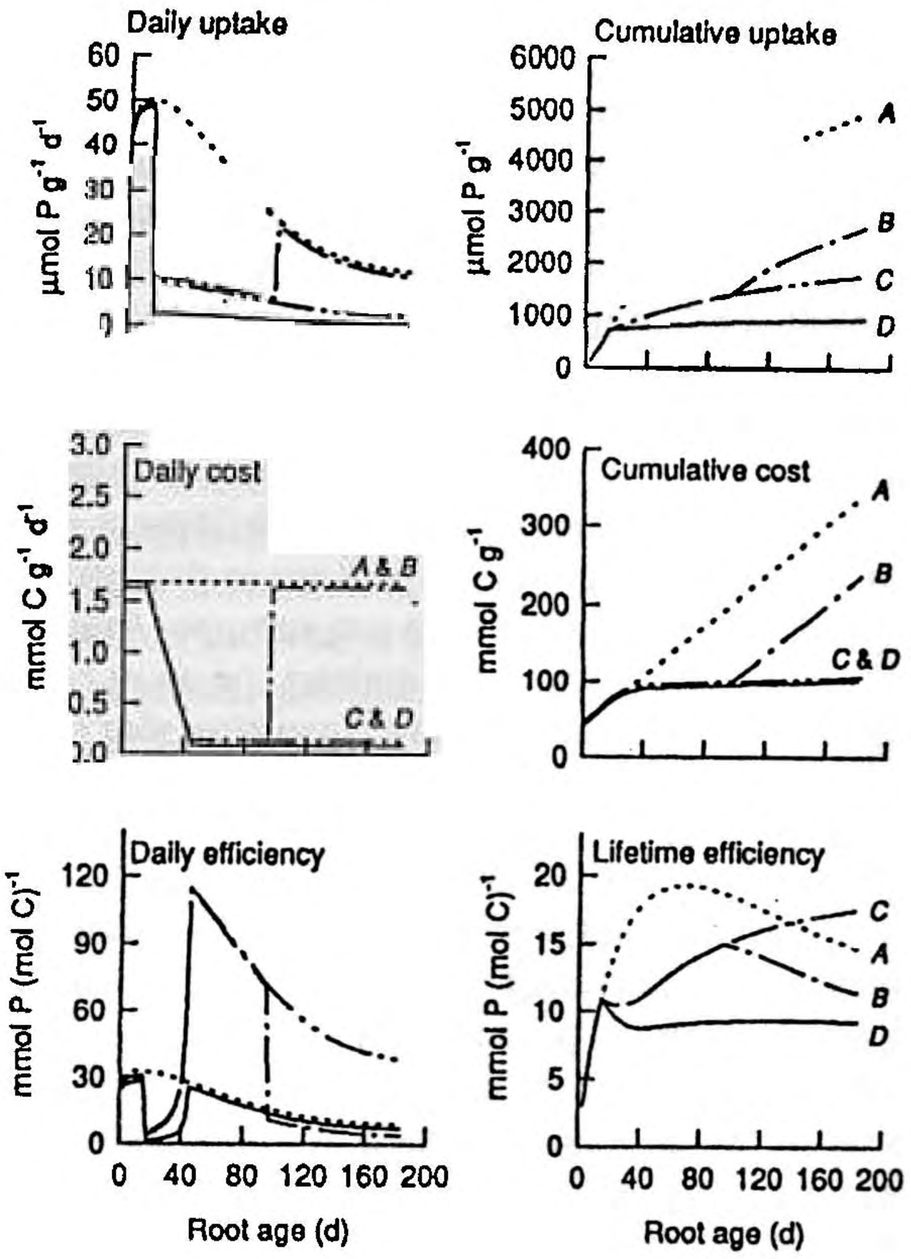

Fig. 5. The effects of drought on daily and cumulative uptake, cost and efficiency of nonmycorrhizal (NM5) Volkamer lemon seedlings. Model simulations were for conditions of no drought (*A*), 80 days of drought (*B*) beginning 15 days after the root was constructed, and continuous drought. For the continuous drought treatment, predicted responses are illustrated for P uptake in sandy soil based on the uptake model (*C*) and based on experimental data (*D*) (Whaley, 1995).

effective diffusion coefficient, D, accounted for an additional reduction of 11%; the drop in b caused only a 0.3% further reduction. The total 79% reduction in uptake was smaller than that observed using radioisotopes of P, where uptake in dry soil was only 2–5% of that in wet soil (Whaley, 1995); a 95% reduction is shown in simulation D.

The daily cost shows the assumed decline of maintenance respiration during the drought. Respiration recovers to normal rates at the end of the 80-day drought and remains low in unremitted drought.

Daily efficiency shows the combined effects of reduced respiration and reduced uptake. Daily efficiency drops sharply with the onset of drought because nutrient uptake was affected immediately by reduced soil moisture, whereas root maintenance respiration was assumed to respond to drought more slowly. Efficiency recovers rapidly during drought as maintenance respiration diminishes. Indeed, in simulations B and C, in which uptake declines by 79% during drought while respiration declines by 95%, daily efficiency is higher in dry than in moist soil. In simulation D, respiration and uptake both decline by 95%, and the daily efficiency of roots in dry soil is the same as those in moist soil. Clearly, the result of drought on root efficiency depends on the relative reductions of C costs and nutrient benefits.

Lifetime efficiency is generally greatest in roots never exposed to drought (simulation A). An exception is simulation C, where roots experience high daily efficiency, due to savings in respiration, that outweigh losses in uptake; these roots eventually overtake the non-drought roots in lifetime efficiency. The relatively more important savings in costs mean that efficiency declines when the drought ends (simulation B), implying that roots should be shed at the cessation of drought. If the loss in uptake were more severe than the savings in respiration costs, efficiency would decline during the drought and recover afterwards; whether roots should be shed at the onset of drought would depend on the likely duration of the drought. Where uptake and respiration were equally affected by drought (simulation D), lifetime efficiency never recovered; roots should have been shed at the onset of drought.

This simulation illustrates the importance of the relative reductions in costs and uptake to the efficiency of shedding roots in dry soil. Reduced maintenance respiration may be the reason that the roots of some plant species are so tolerant of dry surface soil.

XI. FURTHER CONSIDERATIONS

The lifespan of roots may be influenced by many factors beyond the scope of the efficiency model in its present form, such as seasonality, herbivore and pathogen pressure, competing sinks for carbohydrates in the plant, nutrient resorption and recycling, and other functions of roots such as transport and storage. In addition to these factors, which we discussed previously, there are other factors relating to root hairs, root exudates and mycorrhizal fungi that contribute to the C costs and nutritional benefits of roots. Costs and benefits will be discussed from the perspective of how they change with root age, especially for roots in a soil environment. Much is known about their costs and benefits in qualitative terms, but quantitative information is insufficient to include them explicitly in the current model.

A. Root Hairs

Root hairs are specially modified epidermal cells which develop in the elongation zone of the root, usually within a few centimeters of the root tip. An important benefit of root hairs is an increase in absorptive surface area beyond the depleted zone near the root surface (Bhat and Nye, 1973). Root hairs can be sites of extensive mucilage production (Dawes and Bowler, 1959), which has additional costs and benefits. The production of mucilage by root hairs can enhance the ability of the hair to attach to soil particles and thereby prevent air gaps from developing between the soil and root surface when the soil dries (Greaves and Darbyshire, 1972; Sprent, 1975). The prevention of air gaps and maintenance of a continuous film of water between the soil and root surface can strongly influence rates of water and nutrient uptake in soils of low moisture status (Newman, 1974).

Simulation models have provided some insights into the benefits of root hairs for P uptake (Itoh and Barber, 1983a, b). Root hairs can be included in the single-root model similar to that described above, where each hair is treated like a small root. Itoh and Barber found that root hair length, root hair radius and root hair density all influenced predicted P uptake, with root hair length being particularly significant. Prediction of P uptake without taking into account root hairs resulted in underpredictions of more than 50% in species with long root hairs such as Russian thistle and tomato; including root hairs resulted in a much closer fit to the 1:1 line of predicted with observed uptake (slope = 0.98, $r = 0.89$).

The costs of root hairs compared with unmodified epidermal cells have not been examined in detail. Despite the putative role of hairs in mucilage production, one study indicates that epidermal cells with hairs do not exude more C than older portions of the root without hairs (McCully and Canny, 1985). Once the cells develop heavily lignified and suberized secondary cell walls, rates of exudation would likely decrease. In *Arabidopsis*, cell volume of a root hair epidermal cell was about 50% greater than that of an unmodified cell (T.R. Bates and J.P. Lynch, unpublished data). The proportion of the cell that was vacuole, however, was not measured. It is not known if epidermal cells with hairs have higher respiration rates than those without hairs.

Longevity of root hairs does not coincide with longevity of the root. Root hair formation typically occurs within a few days of root formation, but root hair death can occur well before the root dies. Estimates of the lifespan of root hairs depends in part on whether the investigator defines death as loss of the viability of the root hair cell or as collapse of the skeletal cell wall structure, which may persist after the cell has died. In maize, Fusseder (1987) found evidence of cytoplasmic disintegration in hairs only 2 to 3 days old using electron microscopy, but by vital staining of nuclei, he concluded that hairs lived 1–3 weeks. Similar lifespans of root hairs have been reported for wheat (Henry and

Deacon, 1981) and barley (Holden, 1975) using the vital staining method. Consequently, the assumption that the nucleus dies at the same time as other cell organelles may lead to an overestimation of root hair lifespan. Investigators who define death by the loss of the entire root hair structure would produce even longer estimates of hair lifespan. Root hairs associated with soil sheath formation can have quite long lifespans (Goodchild and Myers, 1987; McCully and Canny, 1988). Some root hairs develop very thick walls that persist for many months after the cell has died (Head, 1973; Fusseder, 1987). These hairs may continue to function in helping bind soil particles to the root surface even though they are no longer living. Eventually, not only root hairs but the entire epidermis can be sloughed or abraded. In the primary roots of maize, epidermal senescence, which includes loss of root hairs, usually becomes extensive in the bare root portion beyond the soil sheath (McCully and Canny, 1988). In citrus roots, it is common to find sloughed epidermis in older fibrous roots that otherwise are quite healthy. For example, in Florida about 90% of the length of roots 2 to 3 months old had less than 30% of the epidermis still intact (D.M. Eissenstat and D. Achor, unpublished data).

Although there have been advances in quantifying the benefits of root hairs in short-term experiments, to model root lifespan we must understand the benefits of root hairs over the entire lifetime of the root. For many roots, root hairs may only exist for a small fraction of the root's lifetime. The costs of root hairs are poorly understood, even in a qualitative way.

B. Root Exudates

The costs of root exudation are better known than the benefits. Root exudates include water-soluble C compounds such as sugars, amino acids and organic acids and water-insoluble C compounds such as root cap cells, mucilage and limited cell wall debris (Lambers, 1987). Another term, rhizodeposition, has been used to express the loss of C from roots, but its meaning differs among investigators. Lynch and Whipps (1991) include dead roots and root respiration in rhizodeposition, whereas Newman (1985) did not. For purposes of C budgets, it is important neither to miss the C exuded nor to count it twice. Where cortical and epidermal walls are sloughed, these costs may already have been estimated in root construction costs. Mucilage and root cap cells, however, normally would not be included in construction costs. When maintenance respiration is calculated using total soil respiration and subtracting respiration attributable to growth or ion uptake, the remaining or 'residual' respiration includes not only root maintenance respiration but also respiration by soil microbes and mycorrhizal fungi. Some of the C thus respired can be assumed to have been exuded by roots.

Excluding root respiration and death, Newman (1985), in a review of the literature, estimated that from 10–100 mg of soluble exudates and

100–250 mg insoluble organic material, of which 60 mg was root cap cells and mucilage, was lost from young roots about 3 weeks old. This cost can be compared with estimates of 'residual' respiration (Table 2). If soluble C were metabolized at the rate at which it was exuded, it would represent about 1–10% of the 'residual' maintenance respiration of high-P nonmycorrhizal citrus plants. If the insoluble C were also metabolized, exudates could account for 12–38% of root 'residual' maintenance respiration or about 7–23% of total root respiration.

Some investigators have estimated higher rates of soluble C exudation. Two barley cultivars grown in sterile solution culture for 25 days had soluble C exudation rates of 390–465 μmol C (g root dry wt)$^{-1}$ day^{-1} (Xu and Juma, 1994) (this rate would comprise 14–17% of total root respiration in citrus; total respiration of barley seedlings was not measured). Cheng *et al.* (1993) estimated that microbial respiration of exudates represented nearly 60% of total root and soil respiration in 3-week-old barley plants. They used an isotopic dilution technique, in which unlabeled glucose fed to microbes allowed microbial respiration to be partitioned from root respiration; plant carbohydrates were uniformly labeled with ^{14}C. In a subsequent study with 3-week-old plants, Cheng *et al.* (1994) attributed 45% of the total root-soil respiration to microbial metabolism of root exudates in tall fescue and 31% in buffalo gourd. Although there are still several assumptions that need to be examined, this technique holds promise for estimating root exudation *in situ*. This work suggests that root exudation may be a substantial component of root C costs. Better estimates are needed of exudation by roots of different ages to define these costs more clearly.

Root exudation is not without benefit: it may enhance the ability of the plant to acquire P and other nutrients of low solubility such as iron. Some plants have specialized mechanisms to enhance P solubility in the soil solution. Certain arctic species produce extracellular phosphatases (Kroehler and Linkins, 1988). Species adapted to very low-P soils may exude chelating compounds such as citrate and piscidic acid (Gardner *et al.*, 1983; Ae *et al.*, 1990). Cluster roots in particular produce abundant exudates that promote P uptake in very infertile soils (Gardner *et al.*, 1983). Because of the extremely high value of P relative to C in these soils, this represents an efficient use of C to maximize the growth or fitness of the plant. Chelating compounds such as siderophores can also be produced by rhizospheric microorganisms that feed on root exudates. In alkaline soils, many plants can enhance P solubility by exuding protons and organic acids, which reduces rhizosphere pH (Nye, 1992). Lastly, colonization by mycorrhizal fungi is generally higher in roots with faster rates of exudation (Graham *et al.*, 1981; Schwab *et al.*, 1991).

C. Mycorrhizas

The roots of most plant species can form a symbiotic relationship with mycorrhizal fungi (Newman and Reddell, 1987). Although mycorrhizas are

widespread and known to have important effects on nutrient uptake and C costs of roots, they are rarely explicit in calculations of either nutrient or C fluxes. Incorporating mycorrhizal fungi in an analysis of root longevity is made difficult by our limited understanding of the processes by which the mycorrhizal symbiosis enhances nutrient uptake, the biomass, construction costs and turnover rates of mycorrhizal fungi, the age at which roots become colonized by mycorrhizas and the respiration associated with the colonization, and the changes in nutrient uptake and respiratory costs of mycorrhizal roots with root age. In addition, mycorrhizal fungi may have direct effects on root lifespan; there is some evidence that mycorrhizal roots live longer than uncolonized roots on the same plant (Harley and Smith, 1983; Espeleta, 1995; but see Hooker *et al.*, 1995). This observed effect on root longevity might be consistent with increased efficiency of nutrient acquisition, as nutrient uptake can be enhanced by mycorrhizal fungi. Alternatively, the mycorrhizal fungus may increase the root sink for C, extending root longevity beyond that optimal for the plant. Finally, mycorrhizal roots may be better defended against root pathogens than non-mycorrhizal roots (Gange *et al.*, 1994; Newsham *et al.*, 1995).

1. Nutritional Benefits

The nutritional benefits of mycorrhizas are well known, especially where the limiting nutrient is P. Mycorrhizal uptake of nutrients involves three distinct processes: uptake from the soil by extraradical fungal hyphae, translocation through the hyphae to the fungal structures within the root, and transfer from the fungus to the plant across the interface between them (Smith *et al.*, 1994). Any of these processes may limit nutrient uptake. Although the high absorptive surface area of the external hyphae certainly contributes to enhanced acquisition of nutrient by the plant, active extramatrical hyphal length alone is not a good predictor of nutrient acquisition. For example, the arbuscular mycorrhizal fungus, *Glomus caledonium*, transported 50 times more P per metre of hyphae than an ineffective species, *Scutellospora calospora*, in a study of cucumber plants (Pearson and Jakobsen, 1993a, b). Per unit of hyphal C expended, the more effective species was 38 times more efficient at P transport. The ineffective species contributed only about 7% of the total P taken up by the plant whereas the effective species contributed all of P uptake. For transfer from the fungus to the plant, Smith *et al.* (1994) found about four-fold differences between two species of arbuscular mycorrhizal fungi in the rate P was transported from the fungal arbuscules and intercellular hyphae to the cortical cells in the roots of the onion host. In addition to the added surface area for nutrient absorption, mycorrhizal fungi can enhance nutrient acquisition by the secretion of enzymes that transform organic N and P into more available forms (Read, 1993).

2. *Fungal Biomass*

To calculate the effect of mycorrhizas on optimal root lifespan requires information on the fungal biomass per gram of root. This biomass, however, is difficult to determine, both for fungal structures within the root and also for the extraradical hyphae. The arbuscular mycorrhizal fungus, *Glomus fasciculatum*, occupied 4.3% of onion root volume at 13 weeks; approximately 76% of the root length was colonized (Toth *et al.*, 1991). The per cent of the total fungal volume that was arbuscule was 37% in these same roots. Arbuscules degenerate rapidly; typically having a lifespan of about 8–10 days (Harley and Smith, 1983; Toth and Miller, 1984). It is not known whether the C is reabsorbed by the root or fungus after the arbuscules degenerate. The lipid-rich vesicles live much longer, develop after arbuscules, and are commonly abundant in older roots at high levels of colonization (Brundrett *et al.*, 1985). For the highly vesicular fungus, *Glomus intraradices*, construction costs of citrus roots were 8–9% higher in mycorrhizal than nonmycorrhizal roots 3 months after transplanting (Peng *et al.*, 1993); most of this cost difference was due to the presence of the vesicles. Thus, internal structures may represent an additional 5–10% of the cost of root construction.

The biomass of extraradical hyphae can be estimated indirectly from the hyphal length per length of root and some assumptions of tissue density and hyphal radius. Hyphal lengths vary widely. In tallgrass prairie and permanent pasture, for example, which have arbuscular mycorrhizas, extraradical hyphal lengths ranged from 60 to 270 cm (cm root)$^{-1}$ in the top 10 cm of soil (Miller *et al.*, 1995), which is in the range found by other investigators (Smith and Gianinazzi-Pearson, 1988; Sylvia, 1990; Miller and Jastrow, 1991). Miller *et al.* (1995) determined hyphal biomass and length. Standing biomass of extraradical arbuscular hyphae was estimated at 6–7% of root biomass in the top 10 cm of soil (Miller *et al.*, 1995). Deeper in the soil, the amount of hyphae per unit of root would likely diminish (Koide and Mooney, 1987).

Ectomycorrhizas show a similar range of fungal biomass per unit mass of root. For example, Jones *et al.* (1990) found ectomycorrhizal hyphal lengths associated with *Salix* roots to range from 100 to 300 cm (cm root)$^{-1}$, which amounts to 0.5–2% of the root biomass, assuming the density of fungal and root tissue are similar and that their diameters are 3 and 400 μm, respectively (Eissenstat, 1991; Eissenstat and van Rees, 1994). However, ectomycorrhizal fungi are probably longer-lived than arbuscular mycorrhizal fungi and the mass of the mycorrhizal mantle increases with root age. For a range of ectomycorrhizal fungi on *Pinus sylvestris*, Colpaert *et al.* (1992) estimated that between 2 and 6 months, the density of extramatrical mycelia increased two- to eight-fold. Fungal biomass at 6 months ranged from 8% to 44% of total root biomass. These results are consistent with data summarized by Harley and Smith (1983) where about 30–40% of the biomass of an ectomycorrhizal root may consist of fungal sheath.

In summary, in arbuscular mycorrhizal and young ectomycorrhizal plants, extraradical hyphal biomass probably represents less than 10% of root biomass. Importantly, much of this biomass may be dead, representing the tough chitin-impregnated fungal walls, not living tissue. For example, only about 20% and 10% of the external hyphae of *Glomus mosseae* and *Glomus intraradices* was active 6 and 13 weeks after planting *Paspalum notatum* in pots (Sylvia, 1988). The fraction of hyphae that is living has major implications in estimating mycorrhizal C costs, if the majority of hyphal cost is not due to hyphal construction but to the respiration associated with maintenance and ion uptake.

3. Carbon Expenditures

Mycorrhizas can increase below-ground C costs typically by 10–20% (see references in Peng *et al.*, 1993). Some of these host-plant expenditures on mycorrhizal fungi can be supported by neighboring plants. Approximately 5–10% of mycorrhizal root carbon may come from surrounding plants (Watkins *et al.*, 1996; Simard *et al.*, 1995). Host-plant C expenditure on mycorrhizal fungi depends on fungal biomass, construction costs, and respiration. Below-ground respiration can be 1.3–3 times higher in mycorrhizal plants than in nonmycorrhizal plants of equivalent nutritional status (Peng *et al.*, 1993; Rygiewicz and Andersen, 1994). Much of this increase may be due to the high respiration rates of extramatrical hyphae; ^{14}C pulse-chase experiments revealed that 50% more C was respired than retained in young, active ectomycorrhizal hyphae in ponderosa pine (Rygiewicz and Andersen, 1994).

The length of time that roots are mycorrhizal and the lifespan of hyphae are additional factors affecting the costs and benefits of mycorrhizas. Roots may take one or more weeks to be colonized by mycorrhizal fungi in disturbed soil or in pot cultures where root inoculum is used, but where roots are growing in an established hyphal network, colonization may take only a few days (Brundrett *et al.*, 1985). In the field, mycorrhizal colonization of the roots probably occurs very rapidly. The longevity of hyphae has not been determined, which greatly limits estimation of C costs. In the field, longevity of the hyphae may be diminished by grazing animals, especially fungal-feeding insects like *Collembola* and fungal-feeding nematodes (McGonigle and Fitter, 1988; Setälä, 1995).

Mycorrhizas can increase the fraction of whole-plant biomass allocated to roots (Peng *et al.*, 1993). Consequently, where mycorrhizas are not providing a nutritional benefit, these C costs can cause mycorrhizal plants to grow more slowly than nonmycorrhizal plants. Normally, however, the nutritional benefits of mycorrhizas outweigh the C costs, with consequent decreases in root: shoot allocation and specific rates of root respiration and increases in leaf C assimilation and overall plant growth (Ingestad and Agren, 1991; Eissenstat *et al.*, 1993; Peng *et al.*, 1993).

XII. FUTURE DIRECTIONS

The biomass of roots at the ecosystem scale indicates the magnitude of below-ground production, and physiological studies show that roots are expensive to maintain. Competition below ground influences plant survival and reproductive success. Despite these basic truths about their importance, we know very little about how the deployment of roots has evolved in an adaptive fashion.

In this paper we posed a number of hypotheses that may explain variation in root lifespan. Assessing the relative importance of these hypotheses is not yet possible because of important unknowns. Studies of individual plants have mainly focused on crop species. Observations of root productivity at the community or ecosystem level do not clearly indicate how different species have adapted root lifespan to their environment. It is also not known to what degree root death is under the control of the plant. If roots are mainly lost to root herbivory and parasitism, then selective root death may be accomplished more by limiting root defenses than by active shedding.

Recent developments in minirhizotrons, video imaging and computer processing have created new opportunities to address key questions associated with the ecology of root lifespan at the species level. For example, do species from low-nutrient habitats retain roots longer than species from fertile habitats? Is root lifespan correlated with leaf lifespan? If not, general theories on the relationship of tissue longevity to nutrient-use efficiency will require revision. Can plants optimize root foraging in a spatially and temporally heterogeneous environment not only by proliferating roots in favorable soil patches but also by shedding roots in unfavorable patches?

Observation of roots will always be more difficult than observation of leaves. For this reason, much of the theory regarding the ecology of root lifespan has been inspired by analogy to leaf lifespan. Modeling is another source of hypotheses about the adaptative advantages of root foraging strategies. In this review, we used an approach that treats C as cost and P as a benefit. Advances in this direction will require a better understanding of maintenance respiration and nutrient uptake kinetics, especially as they change with root age and environmental conditions. In addition, the costs and benefits of root hairs, mycorrhizal fungi and exudation in the natural environment must be clarified.

Other modeling approaches deserve consideration. A cost–benefit analysis that treats the limiting nutrient, rather than C, as the cost might prove fruitful. This approach would require information on the amount of nutrient recovery from roots after death. Above-ground sinks compete with roots for both carbon and nutrients; the optimal allocation of resources to leaves and roots can be explored with whole-plant models. The optimal root lifespan should do more than maximize nutrient uptake; it should maximize plant success in the

environments to which it is adapted. Given the difficulty of observing roots, simulation models will continue to be useful tools for selecting research questions and advancing understanding of the ecology of root lifespan.

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REFERENCES

Ae, N., Arihara, J., Okada, K., Yoshihara, T. and Johansen, C. (1990). Phosphorus uptake by pigeon pea and its role in cropping systems of the Indian subcontinent. *Science* **248**, 477–480.

Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A. and Pastor, J. (1985). Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* **66**, 317–321.

Amthor, J.S. (1984). The role of maintenance respiration in plant growth. *Plant Cell Environ.* **7**, 561–569.

Arnone, III, J.A. and Körner, Ch. (1995). Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. *Oecologia* **104**, 61–71.

Atkinson, D. (1972). Seasonal periodicity of black currant root growth and the influence of simulated mechanical harvesting. *J. Hort. Sci.* **47**, 165–172.

Atkinson, D. (1985). Spatial and temporal aspects of root distribution as indicated by the use of a root observation laboratory. In: *Ecological Interactions in Soil: Plant, Microbes and Animals* (Ed. by A.H. Fitter, D. Atkinson, D.J. Read and M.B. Usher), pp. 43–65. Special Publ. Ser. British Ecol. Soc. **4**. Blackwell Scientific Publications, Oxford.

Baldwin, J.P., Nye, P.H. and Tinker, P.B. (1973). Uptake of solutes by multiple root systems from soil. III. A model for calculating the solute uptake by a randomly dispersed root system developing in a finite volume of soil. *Plant Soil* **38**, 621–635.

Ballard, R. and Fiskell, J.G.A. (1974). Phosphorus retention in the Coastal Plain. *Proc. Soil Sci. Soc. Amer.* **38**, 250.

Barber, S.A. (1984). *Soil Nutrient Bioavailability: a Mechanistic Approach.* John Wiley and Sons, Inc., New York.

Beyrouty, C.A., Wells, B.R., Norman, R.J., Marvel, J.N. and Pillow, Jr., J.R. (1987). In: *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H.M. Taylor), pp. 99–108. ASA Special Publ. **50**, American Society of Agronomy, Madison.

Bhat, K.K.S. and Nye, P.H. (1973). Diffusion of phosphate to plant roots in soil. I. Quantitative autoradiography of the depletion zone. *Plant Soil* **38**, 161–175.

Bloom, A.J., Chapin, III, F.S., and Mooney, H.A. (1985). Resource limitation in plants: An economic analogy. *Annu. Rev. Ecol. System.* **16**, 363–392.

Bloom, A.J, Sukrapanna, S.S, Warner, R.L. (1992). Root respiration associated with ammonium and nitrate absorption and assimilation by barley. *Plant Physiol.* **99**, 1294–1301.

Bloomfield, J., Vogt, K. and Wargo, P.M. (1996). Tree root turnover and senescence. In: *Plant Roots: The Hidden Half* (Ed. by Y. Waisel, A. Eshel and U. Kafkafi), 2nd edn., pp. 363–382. Marcel Dekker, Inc., New York.

Box, J.E., Jr, and Johnson, J.W. (1987). Minirhizotron rooting comparisons of three wheat cultivars. In: *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H.M. Talor), pp. 123–130. ASA Special Publ. **50**, American Society of Agronomy, Madison.

Brouwer, R. (1981). Co-ordination of growth phenomena within a root system of intact maize plants. *Plant and Soil* **63**, 65–72.

Brown, V.K. and Gange, A.C. (1991). Effects of root herbivory on vegetation dynamics. In: *Plant Root Growth: An Ecological Perspective* (Ed. by D. Atlkinson), pp. 453–470. Blackwell Scientific, Boston.

Brundrett, M.C., Piché, Y. and Peterson, R.L. (1985). A developmental study of the early stages in vesicular-arbuscular mycorrhiza formation. *Can. J. Bot.* **63**, 184–194.

Caldwell, M.M. (1987). Competition between roots in natural communities. In: *Root Development and Function.* (Ed. by P.J. Gregory, J.V. Lake and D.A. Rose), pp. 167–185. Cambridge University Press, New York.

Caldwell, M.M. and Camp, L.B. (1974). Belowground productivity of two cool desert communities. *Oecologia* **17**, 123–130.

Caldwell, M.M. and Eissenstat, D.M. (1987). Coping with variability: examples of tracer use in root function studies. In: *Plant Response to Stress* (Ed. by J.D. Tenhunen, F.M. Catarino, O.L. Lange and W.C. Oechel), pp. 95–106. NATO ASI Series 15G, Springer-Verlag, Berlin.

Campbell, B.D. and Grime, J.P. (1989). A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytologist* **112**, 261–267.

Chabot, B.F. and Hicks, D.J. (1982). The ecology of leaf life spans. *Annual Rev. Ecol. System. 13*, 229–259.

Chandler, W.H. (1923). *Results of Some Experiments in Pruning Fruit Trees.* N.Y. Agricultural Exp. Sta. Bull. 415, Ithaca.

Chapin, III, F.S. (1980). The mineral nutrition of wild plants. *Annu. Rev. Ecol. Systemat. 11*, 233–260.

Chapin, III, F.S. (1989). The costs of tundra plant structures: Evaluation of concepts and currencies. *American Naturalist* **133**, 1–19

Chapin, III, F.S. (1995). New cog in the nitrogen cycle. *Nature* **377**, 199–200.

Chapin, III, F.S., Schulze, E-D and Mooney, H.A. (1990). The ecology and economics of storage in plants. *Ann. Rev. Ecol. System.* **21**, 423–447.

Chapin, III, F.S., Autumn, K., and Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *American Naturalist* **142**, S78–S92.

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

Cheng, W., Coleman, D.C., Carroll, C.R. and Hoffman, C.A. (1993). *In situ* measurement of root respiration and soluble C concentrations in the rhizosphere. *Soil Biol. Biochem.* **25**, 1189–1196.

Cheng, W., Coleman, D.C., Carroll, C.R., and Hoffman, C.A. (1994). Investigating short-term carbon flows in the rhizospheres of different plant species, using isotopic trapping. *Agron. J.* **86**, 782–788.

Chitwood, D.J. (1992). Nematicidal compounds from plants. In: *Phytochemical Resources for Medicine and Agriculture* (Ed. by H.N. Nigg and D. Seigler), pp. 185–204. Plenum Press, New York.

Chung, H.-H., and Kramer, P.J. 1975. Absorption of water and ^{32}P through suberized and unsuberized roots of loblolly pine. *Can. J. For. Res.* **5**, 229–235.

Clarkson, D.T., Sanderson, J. and Russell, R.S. (1968). Ion uptake and root age. *Nature* **220**, 805–806.

Coley, P.D. (1988). Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**, 531–536.

Coley, P.D., Bryant, J.P. and Chapin, III, F.S. (1985). Resource availability and plant anti-herbivore defense. *Science* **230**, 895–899.

Colpaert, J.V., van Assche, J.A., and Luijtens, K. (1992). The growth of the extramatrical mycelium of ectomycorrhizal fungi and the growth response of *Pinus sylvestris* L. *New Phytol.* **120**, 127–135.

Crider, F.J. (1955). Root-growth stoppage resulting from defoliation of grass. *USDA Tech. Bull.* **1102**. Washington D.C., 23 pp.

Cropper, W.P., Jr and Gholz, H.L. (1991). *In situ* needle and fine root respiration in mature slash pine (*Pinus elliottii*) trees. *Can. J. For. Res.* **21**, 1589–1595.

Culvenor, R.A., Davidson, I.A. and Simpson, R.J. (1989). Regrowth by swards of subterranean clover after defoliation. 2. Carbon exchange in shoot, root and nodule. *Ann. Bot.* **64**, 557–567.

Dawes, C.J. and Bowler, E. (1959). Light and electron microscope studies of the cell wall structure of the root hairs of *Raphanus sativus*. *Am. J. Bot.* **46**, 561–565.

de Visser, R. (1985). Efficiency of respiration and energy requirements of N assimilation in roots of *Pisium sativum*. *Physiol. Plant.* **65**, 209–218.

Dillenburg, L., Whigham, D.F., Teramura, A.H. and Forseth, I.N. (1993). Effects of below- and aboveground competition for the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar straciflua*. *Oecologia* **93**, 48–54.

Dodd, J.L. (1980). The role of plant stresses in development of corn stalk rots. *Plant Dis.* **64**, 533–537.

Donald, C.M. (1958). The interaction of competition for light and nutrients. *Aust. J. Agr. Res.* **9**, 421–435.

Dubach, M., Russelle, M.P. (1994). Forage legume roots and nodules and their role in nitrogen transfer. *Agron. J.* **86**, 259–266.

Ehleringer, J. (1985). Annuals and perennials of warm deserts. In: *Physiological Ecology of North American Plant Communities* (Ed. by B.F. Chabot and H.A. Mooney), pp. 162–180, Chapman and Hall, New York.

Eissenstat, D.M. (1991). On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. *New Phytologist* **118**, 63–68.

Eissenstat, D.M. (1992). Costs and benefits of constructing roots of small diameter. *J. Plant Nutr.* **15**, 763–782.

Eissenstat, D.M. (1997). Trade-offs in root form and function. In: *Agricultural Ecology* (Ed. by L.E. Jackson), Academic Press, Sand Diego (in press).

Eissenstat, D.M. and Duncan, L.W. (1992). Root growth and carbohydrate responses in bearing citrus trees following partial canopy removal. *Tree Physiol.* **10**, 245–257.

Eissenstat, D.M. and Van Rees, K.C.J. (1994). The growth and function of pine roots. *Ecol. Bull.* **43**, 76–91.

Eissenstat, D.M., Graham, J.H., Syvertsen, J.P. and Drouillard, D.L. (1993). Carbon economy of sour orange in relation to mycorrhizal colonization and phosphorus status. *Annals of Botany* **71**, 1–10.

Espeleta, J.F. (1995). The fate of citrus roots in surface dry soil: effects of tree juvenility and mycorrhizal status. M.S. Thesis, University of Florida, Gainesville.

Etherington, J.R. (1987). Penetration of dry soil by roots of *Dactylis glomerata* L. clones derived from well-drained and poorly drained soils. *Funct. Ecol.* **1**, 19–23.

Fabião, A., Persson, H.A. and Steen, E. (1985). Growth dynamics of superficial roots in Portuguese plantations of *Eucalyptus globulus* Labill. studied with a mesh bag technique. *Plant Soil* **83**, 233–242.

Fahey, T.J. (1992). Mycorrhizal and forest ecosystems. *Mycorrhiza* **1**, 83–89.

Fahey, T.J. and Hughes, J.W. (1994). Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *J. Ecol.* **82**, 533–548.

Fernandez, O.A. and M.M. Caldwell. (1975). Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.* **63**, 703–714,

Fitter, A.H. (1985). Functional significance of root morphology and root system architecture. In: *Ecological Interactions in Soil: Plant, Microbes, and Animals* (Ed. by A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher), pp. 87–106. Blackwell Scientific Publ., London.

Fitter, A.H. (1991). Characteristics and functions of root systems. In: *Plant Roots: The Hidden Half* (Ed. by Y. Waisel, A. Eshel and U. Kafkafi), pp. 3–25. Marcel Dekker, Inc., New York.

Fitter, A.H. (1994). Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: *Exploitation of Environmental Heterogeneity of Plants: Ecophysiological Processes Above- and Belowground* (Ed. by M.M. Caldwell and R.W. Pearcy), pp. 305–323. Academic Press, New York.

Fusseder, A. (1987). The longevity and activity of the primary root of maize. *Plant Soil* **101**, 257–265.

Gange, A.C., Brown, V.K. and Sinclair, G.S. (1994). Reduction of black vine weevil larval growth by vesicular-arbuscular mycorrhizal infection. *Entomol. Exp. Applic.* **70**, 115–119.

Gardner, W.K., Barber, D.A., and Parbery, D.G. (1983). The acquisition of phosphorus by *Lupinus albus* L. III. The probable mechanism by which phosphorus movement in the soil/root interface is enhanced. *Plant Soil* **70**, 107–124.

Garnier, E. and Laurent, G. (1994). Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist* **128**, 725–736.

Gholz, H.L., Hendry, L.C. and Cropper, W.P. Jr. (1986). Organic matter dynamics of fine roots in plantations of slash pine (*Pinus elliottii*) in north Florida. *Can. J. For. Res.* **16**, 529–538.

Goins, G.D. and Russelle, M.P. (1996). Fine root demography in alfalfa (*Medicago sativa* L.). *Plant Soil* (in press).

Goodchild, D.J. and Myers, L.F. (1987). Rhizosheaths – a neglected phenomenon in Australian agriculture. *Australian J. Agric. Res.* **38**, 559–563.

Gower, S.T., Gholz, H.L., Nakane, K. and Baldwin, V.C. (1994). Production and carbon allocation patterns of pine forests. *Ecol. Bull. (Copenh.)* **43**, 115–135.

Graham, J.H. (1995). Root regeneration and tolerance of citrus rootstocks to root rot caused by *Phytophthora nicotianae*. *Phytopathology* **85**, 111–117.

Graham, J.H., Leonard, R.T. and Menge, J.A. (1981). Membrane-mediated decrease in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhizae formation. *Plant Physiol.* **68**, 548–552.

Graham, J.H., Brylansky, R.H., Timmer, L.W. and Lee, R.F. (1985). Comparison of citrus tree declines with necrosis of major roots and their association with *Fusarium solani*. *Plant Dis.* **69**, 1055–1058.

Greaves, M.P. and Darbyshire, J.F. (1972). The ultrastructure of the mucilaginous layer on plant roots. *Soil Biol. Biochem.* **4**, 443–449.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Naturalist* **111**, 1169–1194.

Grime, J.P. (1994). The role of plasticity in exploiting environmental heterogeneity. In: *Exploitation of Environmental Heterogeneity of Plants: Ecophysiological Processes Above- and Belowground* (Ed. by M.M. Caldwell and R.W. Pearcy), pp. 1–20. Academic Press, New York.

Grime, J.P., Crick, J.C. and Rincon, J.E. (1986). The ecological significance of plasticity. In: *Plasticity in Plants* (Ed. by D.H. Jennings and A.J. Trewavas), pp. 5–29. Cambridge University Press, New York.

Gross, K.L., Peters, A., and Pregitzer, K.S. (1993). Fine root growth and demographic responses to nutrient patches in four old-field plant species. *Oecologia* **95**, 61–64.

Harley, J.L. and Smith, S.E. (1983). *Mycorrhizal Symbiosis*. Academic Press, New York.

Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, New York.

Harper, J.L. (1989). The value of a leaf. *Oecologia* **80**, 53–58.

Harper, J.L., Jones, M. and Sackville Hamilton, N.R. (1991). The evolution of roots and the problems of analyzing their behaviour. In: *Plant Root Growth: An Ecological Perspective* (Ed. by D. Atkinson), pp. 3–22. Blackwell Scientific Publications, Oxford.

Hayes, D.C. and Seastedt, T.R. (1987). Root dynamics of tallgrass prairie in wet and dry years. *Can. J. Bot.* **65**, 787–791.

Head, G.C. (1966). Estimating seasonal changes in the quantity of white unsuberized root on fruit trees. *J. Hort. Sci.* **41**, 197–206.

Head, G.C. (1969). The effects of fruiting and defoliation on seasonal trends in new root production on apple trees. *J. Hort. Sci.* **44**, 175–181.

Head, G.C. (1973). Shedding of roots. In: *Shedding of Plant Parts* (Ed. by T.T. Kozlowski), pp. 237–293. Academic Press, New York.

Hendrick, R.L. and Pregitzer, K.S. (1992). The demography of fine roots in a northern hardwood forest. *Ecology* **73**, 1094–1104.

Hendrick, R.L. and Pregitzer, K.S. (1993). Patterns of fine root mortality in two sugar maple forests. *Nature* **361**, 59–61.

Hendricks, J.J., Nadelhoffer, K.J. and Aber, J.D. (1993). Assessing the role of fine roots in carbon and nutrient cycling. *Trends. Ecol. Evol.* **8**, 174–178.

Henry, Ch.M. and Deacon, J.W. (1981). Natural (non-pathogenic) death of the cortex of wheat and barley seminal roots, as evidenced by nuclear staining with acridine orange. *Plant Soil* **60**, 255–274.

Holden, J. (1975). Use of nuclear staining to assess rates of cell death in cortices of cereal roots. *Soil Biol. Biochem.* **7**, 333–334.

Hoogenboom, G., Huck, M.G. and Peterson, C.M. (1987). Root growth rate of soybean as affected by drought stress. *Agron. J.* **79**, 607–614.

Hooker, J.E., Black, K.E., Perry, R.L. and Atkinson, D. (1995). Arbuscular mycorrhizal fungi induced alteration to root longevity of poplar. *Plant Soil* **172**, 327–329.

Huang, B. and Nobel, P.S. (1992). Hydraulic conductivity and anatomy for lateral roots of *Agave deserti* during root growth and drought-induced abscission. *Journal of Experimental Botany* **43**, 1441–1449.

Huck, M.G., Hoogenboom, G. and Peterson, C.M. (1987). Soybean root senescence under drought stress. In: *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H.M. Taylor), pp. 109–121. ASA Special Publ. **50**, Agronomy Society of America, Madison.

Ingestad, T. and Ågren, G.I. (1991). The influence of plant nutrition on biomass allocation. *Ecolog. Appl.* **1**, 168–174.

Itoh, S. and Barber, S.A. (1993a). A numerical solution of whole plant nutrient uptake for soil-root systems with root hairs. *Plant Soil* **70**, 403–413.

Itoh, S. and Barber, S.A. (1993b). Phosphorus uptake by six plant species as related to root hairs. *Agron. J.* **75**, 457–461.

Johnson, I.R. (1990). Plant respiration in relation to growth, maintenance, ion uptake, and nitrogen assimilation. *Plant Cell Environ.* **13**, 139–328.

Jones, M.D., Durall, D.M. and Tinker, P.B. (1990). Phosphorus relationships and production of extramatrical hyphae by two types of willow ecto-mycorrhizas. *New Phytol.* **115**, 259–267.

Jupp, A.P. and Newman, E.I. (1987) Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. *New Phytol.* **105**, 393–402.

Klepper, B., Taylor, H.M., Huck, M.G. and Fiscus, E.L. (1973). Water relations and growth of cotton in drying soils. *Agron. J.* **54**, 307–310.

Koide, R.T. and Mooney, H.A. (1987). Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi caused by formation of gopher mounds. *New Phytol.* **107**, 173–182.

Kosola, K.R. and Eissenstat, D.M. (1994). The fate of citrus seedlings in dry soil. *J. Exp. Bot.* **45**, 1639–1645.

Kosola, K.R., Eissenstat, D.M., and Graham, J.H. (1995). Root demography of mature citrus trees: the influence of *Phytophthora nicotianae*. *Plant Soil* **171**, 283–288.

Krauss, U. and Deacon, J.W. (1994). Root turnover of groundnut (*Arachis hypogaea* L.) in soil tubes. *Plant Soil* **166**, 259–270.

Kroehler, C.J. and Linkins, A.E. (1988). The root surface phosphatases of *Eriophorum vaginatum*: effects of temperature, pH, substrate concentration and inorganic phosphorus. *Plant Soil* **105**, 3–10.

Kummerow, J., Krause, D. and Jow, W. (1978). Seasonal changes in fine root density in the southern California chaparral. *Oecologia* **37**, 201–212.

Kuppers, M. (1994). Canopy gaps: competitive light interception and economic space filling – a matter of whole-plant allocation. In: *Exploitation of Environmental Heterogeneity of Plants: Ecophysiological Processes Above- and Belowground* (Ed. by M.M. Caldwell and R.W. Pearcy), pp. 111–144. Academic Press, New York.

Lambers, H. (1987). Growth, respiration, exudation and symbiotic associations: the fates of carbon translocated to the roots. In *Root Development and Function* (Ed. by P.J. Gregory, J.V. Lake, and D.A. Rose), pp. 125–145. New York: Cambridge University Press.

Lamont, B.B. (1995). Mineral nutrient relations in Mediterranean regions of California, Chile and Australia. In *Ecology and Biogeography of Mediterranean Ecosystems of Chile, California, and Australia* (Ed. by M.T.K. Arroyo, P.H. Zedler and M.D. Fox), pp. 211–238. New York: Springer-Verlag.

Ledig, F.T. (1983). The influence of genotype and environment on dry matter distribution in plants. In: *Plant Research in Agroforestry. International Council for Research in Agroforestry* (Ed. by P.H. Huxley), pp. 427–454. Nairobi, Kenya.

Lerdau, M. (1992). Future discounts and resource allocation in plants. *Functional Ecology* **6**, 371–375.

Lynch, J.M. and Whipps, J.M. (1991). Substrate flow in the rhizosphere. In: *The Rhizosphere and Plant Growth* (Ed. by D.L. Keister and P.B. Cregan), pp. 15–24. Kluwer Acad. Publ., Boston.

Lyr, H. and Hoffman, G. (1967). Growth rates and growth periodicity of tree roots. *Int. Rev. Forest. Res.* **2**, 181–206.

Marschner, H. (1986). *Mineral Nutrition of Higher Plants.* Academic Press, New York.

Marshall, J.D. (1986). Drought and shade interact to cause fine-root mortality in Douglas-fir seedlings. *Plant Soil* **91**, 51–60.

McCully, M.E. and Canny, M.J. (1985). Localisation of translocated ^{14}C in roots and root exudates of field-grown maize. *Physiol. Plant.* **65**, 380–392.

McCully, M.E. and Canny, M.J. (1988). Pathways and processes of water and nutrient movement in roots. *Plant Soil* **111**, 159–170.

McGonigle, T.P. and Fitter, A.H. (1988). Ecological consequences of arthropod grazing on VA mycorrhizal fungi. *Proc. Roy. Soc. Edin.* **94B**, 25–32.

McKay, H. and Coutts, M.P. (1989). Limitations placed on forestry production by the root system. *Aspect. Appl. Biol.* **22**, 245–254.

McMichael, B.L. and Taylor, H.M. (1987). Applications and limitations of rhizotrons and minirhizotrons. In: *Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics* (Ed. by H.M. Taylor), pp. 1–14. ASA Special Publ. **50.**

Meyer, W.S., Tan, C.S., Barrs, H.D. and Smith, R.C.G. (1990). Root growth and water uptake by wheat during drying of undisturbed and repacked soil in drainage lysimeters. *Aust. J. Agric. Res.* **41**, 253–265.

Milchunas, D.G. and Lauenroth, W.K. (1992). Carbon dynamics and estimates of primary production by harvest, ^{14}C dilution, and ^{14}C turnover. *Ecology* **73**, 593–607.

Milchunas, D.G., Lauenroth, W.K., Singh, J.S., Dole, C.V. and Hunt, H.W. (1985). Root turnover and production by ^{14}C dilution: implications of carbon partitioning in plants. *Plant Soil* **88**, 353–365.

Miller, R.M. and Jastrow, J.D. (1991). Extraradical hyphal development of vesicular-arbuscular mycorrhizal fungi in a chronosequence of prairie restorations. In: *Mycorrhizas in Ecosystems* (Ed. by D.J. Read, D.H. Lewis, A.H. Fitter and I.J. Alexander), pp. 171–176. CAB International, Wallingford, UK.

Miller, R.M., Reinhardt, D.R. and Jastrow, J.D. (1995). External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* **103**, 17–23.

Millington, W.F. and Chaney, W.R. (1973). Shedding of shoots and branches. In: *Shedding of Plant Parts* (Ed. by T.T. Kozlowski), pp. 149–204. Academic Press, New York.

Molyneux, D.E. and Davies, W.J. (1983). Rooting pattern and water relations of three pasture grasses growing in drying soil. *Oecologia* **58**, 220–224.

Monk, C.D. (1966). An ecological significance of evergreeness. *Ecology* **47**, 504–505.

Nadelhoffer, K.J. and Raich, J.W. (1992). Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology* **73**, 1139–1147.

Nadelhoffer, K.J., Aber, J.D. and Melilo, J.M. (1985). Fine roots, net primary production and nitrogen availability: a new hypothesis. *Ecology* **66**, 1377–1390.

Nambiar, E.K.S. (1987). Do nutrients retranslocate from fine roots? *Can. J. For. Res.* **17**, 913–918.

Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., da Silva, E.D., Stone, T.A., Trumbore, S.E., and Vieira, S. (1994). The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**, 666–669.

Newman, E.I. (1974). Root and soil water relations. In: *The Plant Root and its Environment* (Ed. by E.W. Carson). University Press of Virginia, Charlottesville.

Newman, E.I. (1985). The rhizosphere: carbon sources and microbial populations. In: *Ecological Interactions in Soil* (Ed. by A.H. Fittter, D. Atkinson, D.J. Read and M. Busher), pp. 107–121. Blackwell Scientific Publications, Oxford.

Newman, E.I. (1988). Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* **18**, 243–270.

Newman, E.I. and Reddell, P. (1988). The distribution of mycorrhizas among families of vascular plants. *New Phytol.* **106**, 745–751.

Newsham, K.K., Fitter, A.H., and Watkinson, A.R. (1995). Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *J. Ecol.* **83**, 991–1000.

Nobel, P.S., Alm, D.M. and Cavelier, J. (1992). Growth respiration, maintenance respiration and structural-carbon costs for roots of three desert succulents. *Funct. Ecol.* **6**, 79–85.

North, G.B., Huang, B., and Nobel, P.S. (1993). Changes in the structure and hydraulic conductivity of desert succulents as soil water status varies. *Botan. Acta* **106**, 126–135.

Northup, R.R., Yu, Z., Dahlgren, R.A. and Vogt, K.A. (1995). Polyphenol control of nitrogen release from pine litter. *Nature* **377**, 227–229.

Nye, P.H. (1992). Towards the quantitative control of crop production and quality. III. Some recent developments in research into the root–soil interface. *J. Plant Nutr.* **15**, 1175–1192.

Nye, P.H. and Tinker, P.B. (1977). *Solute Movement in the Soil–Root System.* Blackwell Scientific Publications, Oxford

Palta, J.A. and Nobel, P.S. (1989). Influences of water status, temperature, and root age on daily patterns of root respiration for two cactus species. *Ann. Bot.* **63**, 651–662.

Pearson, J.N. and Jakobsen, I. (1993a). Symbiotic exchange of carbon and phosphorus between cucumber and three arbuscular mycorrhizal fungi. *New Phytol.* **124**, 481–488.

Pearson, J.N. and Jakobsen, I. (1993b). The relative contribution of hyphae and roots to phosphorus uptake by arbuscular mycorrhizal plants, measured by dual labelling with ^{32}P and ^{33}P. *New Phytol.* **124**, 489–494.

Peng, S., Eissenstat, D.M., Graham, J.H., Williams, K., and Hodges, N.C. (1993). Growth depression of mycorrhizal citrus at high phosphorus supply: analysis of carbon costs. *Plant Physiol.* **101**, 1063–1071.

Poorter, H. (1994). Construction costs and payback time of biomass: a whole plant perspective. In: *A Whole Plant Perspective on Carbon-Nitrogen Interactions* (Ed. by J. Roy and E. Garnier), pp. 111–127.

Poorter, H., van der Werf, A., Atkin, O.K., and Lambers, H. (1991). Respiratory energy requirements of roots vary with the potential growth rate of a plant species. *Physiol. Planta* **83**, 469–475.

Portas, C.A.M. and Taylor, H.M. (1976). Growth and survival of young plant roots in dry soil. *Soil Sci.* **121**, 170–175.

Pregitzer, K.S., Hendrick, R.L. and Fogel, R. (1993). The demography of fine roots in response to patches of water and nitrogen. *New Phytol.* **125**, 575–580.

Pregitzer, K.S., Zak, D.R., Curtis, P.S., Kubiske, M.E., Teeri, J.A. and Vogel, C.S. (1995). Atmospheric CO_2, soil nitrogen and fine root turnover. *New Phytol.* **129**, 579–585.

Queen, W.H. (1967). Radial movement of water and ^{32}P through suberized and unsuberized roots of grape. Ph.D. Dissertation. Duke University, Durham, North Carolina.

Read, D.J. (1993). Mycorrhiza in plant communities. In: *Advances in Plant Pathology: Mycorrhiza Synthesis.* (Ed. by I.C. Tommerup), pp. 1–31. Academic Press, New York.

Reich, P.B., Uhl, C. Walters, M.B. and Ellsworth, D.S. (1991). Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia* **86**, 16–24.

Reich, P.B., Walters, M.B. and Ellsworth, D.S. (1992). Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecolog. Monogr.* **62**, 365–392.

Reid, J.B., Sorensen, I. and Petrie, R.A. (1993). Root demography of kiwifruit (*Actinidia deliciosa*). *Plant Cell Environ.* **16**, 949–957.

Richards, J.H. (1984). Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* **64**, 21–25.

Ryan, M.G. (1991). Effects of climate change on plant respiration. *Ecolog. Appl.* **1**, 157–167.

Rygiewicz, P.T. and Andersen, C.P. (1994). Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* **369**, 58–60.

Ryser, P. and Lambers, H. (1995). Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant Soil* **170**, 251–265.

Ryser, P. (1996). The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecol.* (in press).

Schläpfer, B and Ryser, P. (1996). Leaf and root turnover of three ecologically contrasting grass species in relation to their performance along a productivity gradient. *Oikos* **75**, 398–406.

Schoettle, A.W. and Fahey, T.J. (1994). Foliage and fine root longevity in pines. *Ecolog. Bull.* **43**, 136–153.

Schwab, S.M., Menge, J.A. and Tinker, P.B. (1991). Regulation of nutrient transfer between host and fungus in vesicular-arbuscular mycorrhizas. *New Phytol.* **117**, 387–398.

Self, G.K., Brown, T.K., Graves, J. and Fitter, A.H. (1995). Longevity and respiration rates of roots of upland grassland species in relation to temperature and atmospheric CO_2 concentration (Abstract). *J. Exp. Bot.* **46** (Suppl.), 25.

Setälä, H. (1995). Growth of birch and pine seedlings in relation to grazing by soil fauna on ectomycorrhizal fungi. *Ecology* **76**, 844–1851.

Shaver, G.R. and Billings, W.D. (1975). Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. *Ecology* **56**, 401–409.

Simard, S.W., Perry, D.A., Jones, M.D., and Durall, D.M. (1995). Shading influences net carbon transfer among ectomycorrhizal tree seedlings in the field. *Dynamics of Physiological Processes in Roots*, 8–11 Oct. 1995, Cornell University, NY (Abstract).

Smith, P.F. (1976). Collapse of 'Murcott' tangerine trees. *J. Amer. Soc. Hort. Sci.* **101**, 23–25.

Smith, S.E. and Gianinazzi-Pearson, V. (1988). Physiological interactions between symbionts in vesicular arbuscular mycorrhizal plants. *Ann. Rev. Plant Physiol. Molec. Biol.* **39**, 221–244.

Smith, S.E., Dickson, S., Morris, C. and Smith, F.A. (1994). Transfer of phosphate from fungus to plant in VA mycorrhizas: calculation of the area of symbiotic interface and of fluxes of P from two different fungi to *Allium porrum* L. *New Phytol.* **127**, 93–99.

Snapp, S.S. and Lynch, J. (1996). Phosphorus distribution patterns in mature bean plants: root retention and leaf remobilization to pods. *Crop Sci.* **36**, 929–935.

Spaeth, S.C. and Cortes, P.H. (1995). Root cortex death and subsequent initiation and growth of lateral roots from bare steles of chickpeas. *Can. J. Bot.* **73**, 253–261.

Sprent, J.I. (1975). Adherence of sand particles to soybean roots under water stress. *New Phytol.* **74**, 461–463.

Stanton, N.L. (1988). The underground in grasslands. *Annu. Rev. Ecol. System.* **19**, 573–589.

Stasovski, E. and Peterson, C.A. (1991). The effects of drought and subsequent rehydration on the structure and vitality of *Zea mays* seedling roots. *Can. J. Bot.* **69**, 1170–1178.

Sylvia, D.M. (1988). Activity of external hyphae of vesicular-arbuscular mycorrhizal fungi. *Soil Biol. Biochem.* **20**, 39–43.

Sylvia, D.M. (1990). Distribution, structure and function of external hyphae of vesicular-arbuscular mycorrhizal fungi. In: *Rhizosphere Dynamics* (Ed. by J.E. Bo Jr, and L.C. Hammond), pp 144–167. Boulder, Colorado: Westview Press.

Szaniawski, R.K. and Kielkiewicz, M. (1982). Maintenance and growth respiration in shoots and roots of sunflower plants grown at different root temperatures. *Physiol. Planta* **54**, 500–504.

Taylor, H.M. and Klepper, B. (1973). Rooting density and water extraction patterns for corn (*Zea mays* L.). *Agron. J.* **65**, 965–968.

Toth, R. and Miller, R.M. (1984). Dynamics of arbuscule development and degeneration in a *Zea mays* mycorrhiza. *Am. J. Bot.* **71**, 449–460.

Toth, R., Miller, R.M., Jarstfer, A.G., Alexander, T. and Bennett, E.L. (1991). The calculation of intraradical fungal biomass from percent colonization in vesicular-arbuscular mycorrhizae. *Mycologia* **83**, 553–558.

van der Werf, A., Kooijman, A., Welschen, R. and Lambers, H. (1988). Respiratory energy costs for the maintenance of biomass for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. *Physiol. Planta* **72**, 483–491.

van Rees, K.C.J. and Comerford, N.B. (1990). The role of woody roots of slash pine seedlings in water and potassium absorption. *Can. J. For. Res.* **20**, 1183–1191.

van Rees, K.C.J., Comerford, N.B. and Rao, P.S.C. (1990). Defining soil buffer power: implications for ion diffusion and nutrient uptake modeling. *Soil Sci. Soc. Am. J.* **54**, 1505–1507.

Veech, J.A. (1982). Phytoalexins and their role in the resistance of plants to nematodes. *J. Nematol.* **14**, 2–9.

Veen, B.W. (1981). Relation between root respiration and root activity. *Plant Soil* **63**, 73–76.

Vitousek, P. (1982). Nutrient cycling and nutrient use efficiency. *Amer. Naturalist* **119**, 553–572.

Vogt, K.A., Grier, C.C. and Vogt, D.J. (1986). Production, turnover and nutritional dynamics of above- and belowground detritus of world forests. *Adv. Ecol. Res.* **15**, 303–307.

Wang, Z., Burch, W.H., Mou, P., Jones, R.H., and Mitchell, R.J. (1995). Accuracy of visible and ultraviolet light for estimating live root proportions with mini-rhizotrons. *Ecology* **76**, 2330–2334.

Watkins, N.K., Fitter, A.H., Graves, J.D., and Robinson, D. (1996). Quantification using stable carbon isotopes of carbon transfer between C3 and C4 plants linked by a common mycorrhizal network. *Soil Biol. Biochem.* (in press).

Weste, G. (1986). Vegetation changes associated with invasion by *Phytophthora cinnamomi* of defined plots in the Brisbane Ranges, Victoria, 1975–1985. *Aust. J. Bot.* **34**, 633–648.

Whaley, E.L. (1995). *Uptake of Phosphorus by Citrus Roots in Dry Surface Soil.* M.S. Thesis, University of Florida, Gainesville, Florida.

Williams, M. and Yanai, R. (1996). Multi-dimensional sensitivity analysis and ecological implications of a nutrient uptake model. *Plant Soil* (in press).

Wilson, J.B. (1988). Shoot competition and root competition. *J. Appl. Ecol.* **25**, 279–296.

Xu, J.G. and Juma, N.G. (1994). Relations of shoot C, root C and root length with root-released C of two barley cultivars and the decomposition of root-released C in soil. *Can. J. Soil Sci.* **74**, 17–22.

Yanai, R.D. (1994). A steady-state model of nutrient uptake improved to account for newly-grown roots. *Soil Sci. Soc. Am. J.* **58**, 1562–1571.

Yanai, R.D., Fahey, T.J. and Miller, S.L. (1995). Efficiency of nutrient acquisition by fine roots and mycorrhizae. In: *Resource Physiology of Conifers* (Ed. by W.K. Smith and T.M. Hinckley), pp. 75–103. Academic Press, New York.

Appendix

Uptake equations

Solute uptake at the root surface depends on the concentration of solute in solution at the root surface. This concentration will differ from the average concentration in solution, due to gradients created by solute uptake by the root and movement of solute by diffusion and solution flow. The concentration profile around the root can be described by assuming that a steady state is reached. The concentration at the root surface can then be described as a function of the average concentration in solution.

$$C_0 = C_{av} v_0 \left[\alpha + (v_0 - \alpha) \left(\frac{2}{2-\gamma} \right) \frac{(r_x / r_0)^{2-\gamma} - 1}{(r_x / r_0)^2 - 1} \right]^{-1} \qquad (3)$$

where C_0 = concentration of substance at the root surface (mol cm^{-3}). C_{av} = the average solution concentration (mol cm^{-3}), α = root absorbing power (cm s^{-1}). v_0 = inward radial velocity of water at the root surface (cm), r_x = average radial distance to the next root's zone of influence (cm), r_0 = radius of the root (cm), and $\gamma = r_0 v_0 / (Db)$ (dimensionless), where D = diffusion coefficient (cm^2 s^{-1}) and b = buffer capacity of the soil, or the ratio between exchangeable and dissolved nutrient (dimensionless).

This expression for C_0 uses a linear representation of nutrient uptake kinetics, which is appropriate only at low concentrations. To modify the model to allow carrier saturation at high concentrations, we substitute Michaelis–Menten kinetics:

$$\alpha = V_{max} / (K_m - C_0) \tag{4}$$

where V_{max} = maximum rate of uptake (mol cm^{-2} s^{-1}), and K_m = concentration at the root surface at half of V_{max} (mol cm^{-3}). In addition, a C_{min} can be specified, such that uptake does not occur when $C_0 < C_{max}$.

When solute concentration at the root surface is obtained, solute uptake can be calculated from the root surface area, $2\pi r_0 L$, and the uptake kinetics.

$$UPTAKE = \lambda 2\pi r_0 \alpha C_0 \Delta t \tag{5}$$

where λ = specific root length (cm (g root)$^{-1}$) and Δt = the model timestep (s). Equations (3) and (5) are presented by Baldwin *et al.* (1973) and Nye and Tinker (1977) and were derived by Yanai (1994), along with equation (4). Calculations of b and D can be made sensitive to the volumetric soil water content, θ (van Rees *et al.*, 1990):

$$b = \theta + \rho K_d \tag{6}$$

where K_d is the solid-liquid partitioning coefficient.

$$D = D_l \theta f / b \tag{7}$$

where D_l is the diffusion coefficient in water (cm^2 s^{-1}) and f is the impedance factor, which describes soil tortuosity.