13

Root Life Span, Efficiency, and Turnover

David M. Eissenstat
The Pennsylvania State University, University Park, Pennsylvania

Ruth D. Yanai
State University of New York, Syracuse, New York

I. INTRODUCTION

Like other plant organs, roots have a life history in which they pass from birth to death. The size and population structure of the root system is determined by the birth rate and death rate of the individual roots. The study of root demography is of interest to many disciplines, including crop science, physiology, ecology, and soil science. For example, a better understanding of root demography could enable agronomists and horticulturalists to increase yields while reducing agrochemical inputs. Severe root losses, such as those caused by drought or pathogens, clearly are not conducive to crop production. Growing too many roots, however, may also be undesirable, since large amounts of carbohydrates and mineral nutrients are needed for root growth and maintenance that otherwise might be allocated to photosynthetic organs or harvested parts. An optimization approach suggests that, other things being equal, total plant growth should be greatest when a root system maximizes water and nutrient acquisition per unit resource supplied from the shoot (e.g., Thornley, 1998). If roots are produced in the most favorable soil patches and shed when they are no longer efficient in water and nutrient absorption, then production, theoretically, should be maximized.

The birth and death of roots also influence plant competition. Root competition can be more intense than shoot competition (Wilson, 1988). Just as perennial structures aboveground can give plants a competitive advantage for light capture, there may be advantages to long-lived roots in the capture of limited soil resources. Resource preemption can be an important component of competitive success. For example, in climates with winter precipitation, perennial grasses with an established root system are much more effective than seedlings of perennial grasses at competing with annual grass species during the spring and summer (Harris, 1967). Clearly, root demography can have important consequences on species distribution and abundance.

The demography of roots also influences ecosystem processes associated with material and energy flows. Approximately 33% of global net primary production is used for fine-root production, based on fine-root biomass in 253 field studies in a wide range of ecosystems and assuming roots have a life span of 1 year, possibly a conservative estimate (Jackson et al., 1997). In other studies, belowground net primary productivity (BNPP) has been estimated to be at least as great as aboveground net primary productivity (Vogt et al., 1986; Caldwell, 1987). Clearly, the production and death of fine roots can have a substantial influence on ecosystem carbon and mineral nutrient cycling. Many ecologists have been concerned with understanding how BNPP varies among ecosystems and pre-

dicting how it may change in response to tropospheric ozone concentrations (Coleman et al., 1996), nitrogen deposition (Nadelhoffer, 2000), temperature (Gill and Jackson, 2000; Pregitzer et al., 2000a), drought (Joslin et al., 2000) and elevated CO_2 (Arnone et al., 2000; Tingey et al., 2000). We need a more mechanistic understanding of factors controlling root longevity if BNPP is to be incorporated into models of ecosystem response to global climate change (Norby and Jackson, 2000; Jackson et al., 2000).

The first roots of plants developing from seed are indeterminate, typically extending greatly in length as the taproot or other seminal roots develop. The major laterals that first emerge from these primary roots and the adventitious or nodal roots that emerge from the stem base are also typically indeterminate, often extending decimeters or more in length. These indeterminate roots form the basic framework of the root system and may live as long as the plant lives. This chapter focuses on the more ephemeral portion of the root system. Ephemeral roots are the fine laterals that may be replaced several times during a growing season and may have only a few orders of branching. In at least some woody species, these roots never undergo secondary development of the stelar tissue or the development of a periderm (Brundrett and Kendrick, 1988; Eissenstat and Achor, 1999).

In this chapter, we examine variations in root life span and causes for this variation. We discuss different methods of assessing root life span and root turnover. We describe a cost-benefit model of root deployment, which defines the root life span that maximizes the efficiency of resource acquisition. We review studies that have examined biotic and abiotic factors that influence root life span in the context of our hypothesis that plants modulate root life span to maximize root efficiency. Finally, we extend the model of individual root efficiency to describe a cohort of roots with a median life span, and we include allocation to defense in defining the optimal root life span.

II. VARIATION IN ROOT LIFE SPAN

A. Sources of Variation

Estimates of root life span vary widely. The median life span of the finest roots can range from <20 days in fast-growing trees and deciduous fruit crops to >1 year in slow-growing forest trees, according to studies using transparent windows in the soil (Eissenstat and Yanai, 1997). In a data set containing 190 studies in nonagricultural ecosystems, based mainly on changes in biomass from sampling soil monoliths, soil cores or ingrowth cores, average root life spans ranged from ~ 290 d in tropical ecosystems to ~ 3 years in high-latitude ecosystems, with considerable variation within each ecosystem type (Gill and Jackson, 2000). Recent studies based on tracer approaches have indicated that fine roots may live considerably longer—averaging 4–8 yr in some temperate forests (Matamala et al., 2000; Gaudinski et al., 2000). Although differences in methods contribute substantially to differences in estimates of life span, as we will discuss, undoubtedly much of the variation in reported root life span is caused by differences in environmental conditions and plant species.

B. Patterns of Variation Among Species

It is difficult to assess the relative importance of genetic and environmental variation on root life span. Few studies have tracked individual roots of more than one species under the same environmental conditions. In a greenhouse study of seedlings of four tree species, root life span varied from 26 d in *Prunus avium* to 86 d in *Picea sitchensis* (Black et al., 1998). In a Valencia orange citrus rootstock trial in central Florida, we measured a median root life span of 90 d in *Poncirus trifoliata* and 152 d in *Citrus volkameriana*. Weaver and Zink (1946) banded individual nodal roots of perennial range and pasture grasses. After 3 years, root survival ranged from 45% in *Bouteloua gracilis* to 10% in *Stipa spartea*. The fine laterals of the nodal roots presumably had shorter life spans, but they could not be followed with this approach.

The same theories that attempt to explain variation in leaf life span have been applied to roots (Grime, 1977; Chapin, 1980; Aerts, 1995). Plants that have slow growth rates and are adapted to chronically low-nutrient sites, for example, should have long life span of the absorptive organs compared to more fertile sites. Tissue retention in nutrient-poor sites allows nutrients to be retained as well, which is important if root and shoot growth rates are restricted by nutrient limitations. There is considerable evidence that leaf longevity is consistent with this hypothesis (Reich et al., 1997), but roots have been less well studied.

In the pot study of Black et al. (1998), the species with the shortest root life span, *Prunus avium*, had considerably faster growing root and shoot systems than the species with longest root life span, *Picea sitchensis*. In a study comparing grasses from nutrient-poor and nutrient-rich habitats in pots in the field, the grasses from the nutrient-rich habitat had lost a greater

percentage of their leaves and roots by the end of the second growing season (Ryser, 1996). Roots also lived longer in species adapted to more infertile soils among trees in mixed hardwood forests in Wisconsin (estimated by nitrogen budgeting; Aber et al., 1985; Nadelhoffer et al., 1985) and among heathland shrubs and grasses (estimated by minirhizotron and soil core sampling; Aerts et al., 1989, 1992). These results suggest that roots and leaves do have similar adaptations of longevity to resource availability. There are notable exceptions to this generalization, however. Desert succulents have long-lived leaves but short-lived "rain" roots (Huang and Nobel, 1992; North et al., 1993; see also Chapter 53 by Nobel in this volume). In seasonal dry climates, cluster roots of evergreen woody plants (Lamont, 1995) and ericoid mycorrhizal root hairs of plants in the Epacridaceae (Smith and Read, 1997) are shed during extended dry periods. Generalizations about the relationship of tissue longevity to resource availability may apply better to nutrients than water.

Long leaf life span has been associated with other leaf traits, including low specific leaf area (area/mass ratio), N concentration, maximum assimilation rate, high leaf thickness, toughness, lignin content, and tissue density (Reich et al., 1997). Similar suites of correlated traits may also occur in roots (Eissenstat, 1992; Reich et al., 1998), but the scarcity of observations makes patterns more difficult to detect. One such study by Ryser (1996) found higher tissue density in grasses with longer-lived roots. Similarly, in a comparison of apple and citrus, long root life span was associated with coarse root diameter and high tissue density (Eissenstat et al., 2000), low maintenance respiration, and a low P uptake capacity (Bouma et al., 2001).

III. METHODOLOGICAL CONSIDERATIONS

A. Difficulties and Definitions

The single greatest impediment to the study of root life span is the difficulty of studying roots in their natural environment. Many approaches have been taken with varying degrees of success. Often studies are not long enough to establish clear year-to-year variation or to have allowed the plants to fully adjust to installation of root measuring devices (e.g., minirhizotrons) or treatments. For example, fertilization studies are often conducted for only a few years, so they may not characterize steady-state responses to a new level of fertility.

The interpretation of estimates of root life span is hindered by inconsistencies in methods of reporting root dynamics. In many ecosystem studies, the main objective is to estimate BNPP (kg ha^{-1} yr^{-1}). The term "root turnover" has often been used synonymously with annual root production or annual root mortality and thus has units such as kg ha^{-1} yr^{-1}. Alternatively, root turnover may be used to describe the specific rate of root mortality, in units of yr^{-1}. One way to report the specific rate of root mortality is the rate constant in exponential decay (described in Section VII, below). Root turnover rate is also commonly reported as annual root production or annual root mortality divided by root standing crop. Studies differ in whether minimum (Hendrick and Pregitzer, 1993), average (Aber et al., 1985; Aerts et al., 1992), or maximum (Dahlman and Kucera, 1965; Gill and Jackson, 2000) root biomass are used to estimate standing crop. Gill and Jackson (2000) found that about one-third of root turnover studies report only the mean standing crop. An important disadvantage of using minimum or maximum standing crop is that the minimum or maximum value in any distribution is dependent on the number of samples collected and the sampling error associated with sample measurement. Nonetheless, Gill and Jackson (2000) found that maximum standing crop could be accurately estimated by mean standing crop by a regression approach ($r^2 = .90$), based on 20 data sets that included both maximum and mean root biomass.

Root life span is inversely proportional to root turnover rate, with the constant of proportionality dependent on the definitions of turnover rate and life span. Many recent studies that follow the fate of individual roots with minirhizotrons report only median life span (or similarly half-life of the cohort), partly because many of the roots in the study have not died by the end of the study and partly because the median is a better estimator of the central location of a highly skewed distribution—a condition common to survivorship curves. Clearly, average life span may be considerably longer than median life span if an appreciable fraction of the population lives a very long time. Studies that follow individual roots typically report median life spans of specific cohorts (roots born at the same point in time), because different cohorts may exhibit very different median life spans (Kosola et al., 1995).

B. Methods of Estimating Root Life Span

Early techniques estimated root turnover at ecosystem scales by measuring average standing crop and seasonal root production using sequential coring, root

ingrowth cores, and elemental budgeting (see reviews by Caldwell and Eissenstat, 1987; Vogt and Persson, 1991; Fahey et al., 1999). More recently, studies have used minirhizotrons (Cheng et al., 1990; Hendrick and Pregitzer, 1993) and other direct observational techniques (Fahey and Hughes, 1994), which focus on the fate of individual roots. In addition, tracer techniques hold considerable promise as an independent estimator of root longevity (Gaudinski et al., 2000; Matamala et al., 2000). No method of estimating root turnover has emerged as the best for all conditions.

In the 1970s and '80s, the most popular approach to estimating ecosystem BNPP was sequential coring. This approach involves collecting soil cores over the growing season (often monthly) and estimating BNPP based on changes in the mass of live and dead roots (e.g., Vogt et al., 1981). The advantages of sequential coring are that the roots being measured have not been altered in any way prior to coring, estimates can be scaled up to the ecosystem, and equipment costs are low. The labor required to separate roots from the soil core and to separate live from dead roots, however, is considerable (Bloomfield et al., 1996). The very finest roots, which may be very fragile, are probably never completely separated from the soil. Another limitation of this method is a lack of information on turnover of deeper roots; cores are commonly collected only to 20 cm depth.

There are also several sources of error in the calculations, which involve the differences between cores collected over time. Simultaneous birth and death of roots during a single sampling interval is not detected (Rytter, 1999). The very finest roots probably die within weeks, not months (Wells and Eissenstat, 2001). It is also difficult to separate spatial and sampling variation in root mass from the parameter of interest, temporal variation (Singh et al., 1984; Sala et al., 1988). Typically, soil-coring or soil monolith methods are used to estimate annual root production, and a steady-state assumption is required to equate annual root mortality with annual root production. Root turnover (yr^{-1}) is obtained by dividing production (kg ha^{-1} yr^{-1}) by some estimate of standing crop (kg ha^{-1}), which can introduce further errors. Various approaches have been used to improve biomass-based estimates using compartment-flow models (Santantonio and Grace, 1987; Mäkelä and Vanninen, 2000), but these methods require accurate information on fine-root decomposition, which is difficult to acquire (Fahey et al., 1999), especially for the very finest roots (Comas et al., 2000; Wells and Eissenstat, 2001).

The ingrowth-core technique for estimating root production and turnover assumes that root production in a soil volume initially devoid of roots reflects root production in the undisturbed soil (Fabião et al., 1985; Finér et al., 1997). It also assumes that no root mortality (or if dead roots are followed, no root decomposition) has occurred during a sampling interval. Like sequential coring, this method of estimating root mortality assumes steady-state conditions and requires an estimate of root standing crop. Ingrowth-core approaches are relatively inexpensive, requiring considerably less labor than either minirhizotron or sequential coring methods, because they do not involve distinguishing live roots from dead ones or removing them from soil organic matter. The biggest drawback is their artificiality. Soil disturbance can increase water and nutrient availability by increasing decomposition and reducing root competition (Eissenstat, 1991). Soil disturbance may also favor root growth by decreasing soil bulk density and impedance. For these reasons, root growth may be considerably higher in small volumes of disturbed soil than in surrounding undisturbed soil, biasing estimates of production and turnover.

Various elemental budgeting techniques have been used to assess root turnover (Nadelhoffer, 2000). The nitrogen budgeting approach estimates fine-root production as the difference between annual net mineralization and net N uptake into aboveground production (Aber et al., 1985; Nadelhoffer et al., 1985). This method depends on the accuracy of the estimate of net N mineralization, which is usually based on in situ soil incubations, and assumes that there is no change in ecosystem storage of mineralized N.

To estimate root turnover or root longevity further requires estimating the standing crop of roots and assuming a steady state, as for the other methods described above. The budgeting techniques are also subject to errors in other fluxes such as N deposition, denitrification, and leaching.

Another budgeting approach uses soil carbon fluxes to estimate root turnover. Soil respiration less root respiration and aboveground litterfall should equal fine root production (Raich and Nadelhoffer, 1989; Nadelhoffer and Raich, 1992; Haynes and Gower, 1995). This method depends on the accuracy of the estimates of soil and root respiration. It also assumes that soil organic matter is at steady state, unless the rate of change can be estimated (see Chapter 40 by Cramer in this volume).

Tracers of C and N have been used to estimate root turnover, typically by calculating the dilution of the

tracer in the structural tissues at various intervals after labeling (Caldwell and Camp, 1974; Milchunas and Lauenroth, 1992; Hendricks et al., 1997). The chief problems with this approach have been achieving uniform labeling of the structural tissue of the fine roots, estimating turnover rates of the very finest roots, which may be more rapid than the sampling intervals, and, for C, labeling whole trees. Recently, ^{13}C in free-air CO_2 exposure (FACE) experiments (Matamala et al., 2000) and the spike in atmospheric ^{14}C caused by bomb-testing in the 1950s (Gaudinski et al., 2000) have been used to provide estimates of root longevity for large trees.

There are some additional techniques that allow for the examination of factors influencing root demography. Tagging roots (Weaver and Zink, 1946) and following tillers of known age and root number (Shaver and Billings, 1975; Brundrett and Kendrick, 1988) permit estimation of the life span only of the major nodal roots, not the fine laterals. Root screens (Fahey and Hughes, 1994) can be useful for estimating the longevity of fine roots that form a readily accessible root mat.

The most versatile technique for the direct observation of root demography is to track roots growing against transparent windows. Large root observation windows, referred to as rhizotrons, were initially used to study root phenology (seasonal patterns of root growth), including root mortality, in relation to shoot phenology (Head, 1973). Rapid progress in our understanding of root demography has occurred with the development of minirhizotrons (transparent tubes typically 2–6 cm in diameter), which allow roots to be observed in diverse ecosystems with minimal disturbance and a reasonable degree of replication (Taylor, 1987; Fahey et al., 1999; see Chapter 18 by Polomski and Kuhn in this volume). This technique suffered in its early years from limitations in the quality of images and the amount of labor required to process thousands of root images. In the late 1990s, improvements in miniature cameras or borescopes, direct digital capture of images, fast low-cost computers with greater storage capacity, and more sophisticated statistical approaches have made this technique more powerful and accessible. Minirhizotron studies have provided detailed information about root life span, such as age-specific mortality rates, mortality rates of roots born at different times of year or at different depths in the soil, mortality rates among roots of different orders or diameters, and effects of localized soil conditions on root mortality (Hendrick and Pregitzer, 1993; Ruess et al., 1998; Arnone et al., 2000; Wells and Eissenstat, 2001).

Despite the widespread use of transparent wall techniques, they, too, have disadvantages. Transparent walls create an unnatural environment that may affect root production and longevity (Samson and Sinclair, 1994; Joslin and Wolfe, 1999). They can be difficult to use in rocky soils, shrink-swell soils, and clays that smear the tube surface, although various modifications have been devised (Gijsman et al., 1991; Meyer and Barrs, 1991; Lopez et al., 1996; Phillips et al., 2000). The biggest limitations are the cost of the camera equipment and the still considerable labor required to process the large numbers of root images.

C. Influence of Root Diameter and Root Order

The reported variation in root life span is partly due to the imprecise definition of the classes of roots under study. "Fine" roots are typically defined by an arbitrary diameter limit. The diameter limits for tree roots are generally large (1–5 mm) relative to the very finest roots. These finest roots can have much shorter life spans than the larger-diameter roots, which are still considered part of the fine-root system. For example, the median life span of apple roots 0.1–0.2 mm in diameter was only $\sim$ 40 d, while the median life span of roots 0.5–1.1 mm in diameter was longer than the observation period (211–240 d, depending on the year; Wells and Eissenstat, 2001). In peach, roots $\leq$0.25 mm in diameter had a median life span of 77 d while not a single root in the 0.5–1.7-mm class (n = 45) had died by the end of the study (369 d; Wells et al., submitted).

Root order, which describes the position of a root in the branching pattern, is also important to root life span. In sugar maple, among roots $<$0.25 mm in diameter, roots with dependent laterals lived $\sim$ 400 d longer than those with no laterals, which had a median life span of 319 d (Wells, 1999; Eissenstat et al., 2000). Similar effects of root order have also been found in peach (Wells et al., 2002).

Differences in longevity of roots of different diameter and order affect estimates of root turnover. For example, sugar maple roots $<$0.25 mm in diameter have a median life span of 319 d, with coarser roots (0.25–1.0 mm) living 694 d (Wells, 1999). Sugar maple has $\sim$ 50% of its fibrous root length, but only $\sim$ 20% of the mass, in the $<$0.25-mm-diameter class (Pregitzer et al., 1997). As a result, the average median life span is 503 d on a length-weighted basis but 616 d on a mass-weighted basis. Clearly, some of the variation in reported root life spans is associated with the size

and order of the roots being studied and the methods of reporting the data.

IV. MODELING ROOT LIFE SPAN

A. Value of Cost-Benefit Models Applied to Roots

The factors controlling root life span are not well understood. One way to explore hypotheses concerning the observed patterns in root life span is by constructing simulation models. The science of root life span is not so far advanced as to allow predictive modeling. The main value of our modeling efforts is heuristic, as we will illustrate: we compare predictions of our model to observations of root life span, and when inconsistencies occur we analyze the possible explanations.

Fine roots provide a service, which, from the point of view of the whole plant, comes at a cost. The service is the uptake of nutrients and water. While roots may have other important functions such as the supply of hormones, these are not included in an efficiency model based on resource acquisition. The cost is the material and energy required to build and maintain the roots. If a plant were deploying roots to maximize return on investment, then the ratio of benefit (defined by the uptake of the limiting resource, be it water or a nutrient element) to cost (defined by the carbon or nutrient expended) should be maximized. This cost-benefit approach is not limited to exploring the optimal life span of roots. It can be used to show the value of roots of small diameter (Yanai et al., 1995), proliferation of roots in new soil (Caldwell, 1979; Eissenstat et al., 2002), and mycorrhizal association (Eissenstat et al., 1993; Peng et al., 1993).

B. An Optimization Model for Root Life Span

We have used a cost-benefit analysis to describe the theoretically optimal life span that maximizes the efficiency of nutrient capture. We define the efficiency, E, as the ratio of nutrient uptake to carbon cost:

$$E = Uptake/Cost$$

The instantaneous efficiency of the root, E, can be calculated at a single point in time, using appropriate rates of *Uptake* (e.g., mmol P/g root/day) and *Cost* (mol C/g root/day). Alternatively, the costs and benefits can be summed over time to find the cumulative efficiency. Cumulative *Uptake* has units, in our examples, of mmol P/g root, while cumulative *Cost* has units of mol C/g root. The units of both instantaneous and cumulative E are therefore mmol P/mol C.

The optimal life span of a single root is defined as that with the highest cumulative efficiency. Plant carbon allocated to the root system will produce the highest possible rate of nutrient return if the roots live to the age with the highest cumulative *Uptake/Cost* ratio. The instantaneous efficiency always peaks at a younger age than the cumulative efficiency, which does not begin to decline until the instantaneous efficiency falls below the cumulative efficiency.

The carbon cost of the root includes the carbon in the root and the carbon respired in constructing and maintaining the root:

$$Cost = \text{carbon content} + \text{respiration}$$

The initial carbon investment in roots is high, because of the cost of constructing them. In our examples, the C content (42.5%) of a citrus root is 35.3 mmol C/g root (dry weight). The C content of the root is much higher than the daily maintenance respiration costs; in citrus, ~ 3 weeks of maintenance respiration costs (~ 2 mmol/g/d in young roots) equal the C content of the root (Eissenstat and Yanai, 1997; see also Chapter 32 by Lambers et al., in this volume). Respiration costs of roots are not constant; they are initially high because of the metabolic energy used during root construction, and they decline over time, because of minimal growth respiration in fully formed roots and because of the decreasing metabolic activity of living cells in the root (Comas et al., 2000). This decline in respiration with age is evident in the daily carbon cost of citrus roots (Fig. 1c) (Bouma et al., 2001).

A decline in C cost would tend to make a root more efficient over time, if uptake rates were constant. Cumulative efficiency always increases early in the life of a root, as the initial construction cost is amortized over a longer period (Fig. 1d). If the capacity of roots for nutrient uptake were not affected by age, then the theoretical optimal life span in a constant soil environment would be infinite (Yanai et al., 1995). Simply put, it would always be more costly to rebuild roots than to keep the old ones, if new ones were no better.

The factors that make new roots better than old ones include the declining uptake capacity of older roots and the depletion of the soil around active roots. Comparisons of uptake capacity between woody and nonwoody roots and along different regions of the new roots of seedlings (Clarkson, 1991; Van Rees and Comerford, 1990) have shown declines related to root age. Our previous simulations (Yanai et

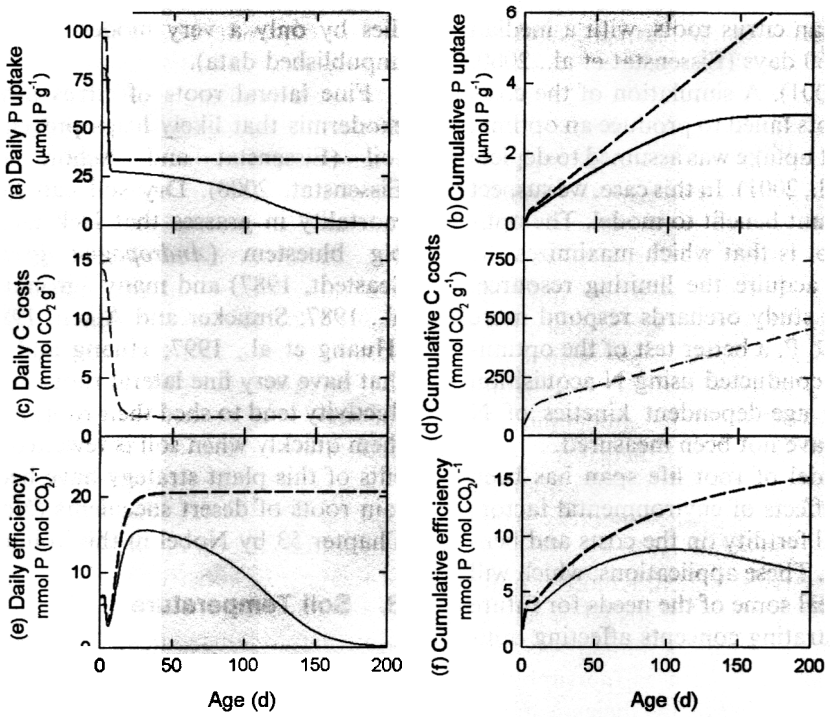

Figure 1 Daily P uptake (a), cumulative P uptake (b), daily C cost (c), cumulative C cost (d), daily efficiency (e), and cumulative efficiency (f) of citrus roots. Dashed line represents simulated uptake with no soil depletion. Solid line represents uptake with soil P depletion based on soil parameters of Chandler fine sand. (From Bouma et al., 2001.)

al., 1995; Eissenstat and Yanai, 1997; Bouma et al., 2001) assumed that uptake capacity declined with root age, although measurements were not yet available to parameterize that relationship. We now have measurements of nutrient uptake capacity in fine lateral roots of varying ages for citrus (Fig. 1a) and apple (Bouma et al., 2001). We used a model for uptake that described the effect of various root and soil properties on nutrient uptake (Yanai, 1994). Either root or soil properties, or both, may limit uptake (Williams and Yanai, 1996).

C. Optimization Model Applied to Individual Roots

The optimization model has been applied to individual roots of citrus and apple, using observed patterns of uptake capacity and respiration as a function of root age. Citrus groves are fertilized with P and other nutrients and are commonly planted on sandy soils with low inherent fertility. We simulated P uptake and carbon costs for citrus roots growing in Chandler soil in Florida (Fig. 1). We used age-dependent P uptake kinetics and C respiration measured on excised roots of known ages. The cumulative efficiency of P uptake increased initially, as P uptake increases and C costs decrease as the root develops. If the availability of P in the soil is assumed to remain high, as in a fertilized grove, then the efficiency remains high, and the optimal life span is infinite. Citrus roots are quite coarse and long-lived, but they do not live forever. Alternatively, if the P in the soil is assumed to be depleted by the root over time, then the efficiency of the root declines after ~ 35 days and the cumulative root efficiency peaks at ~ 50 days. This is much shorter than the observed life span of citrus roots (~ 300 days under low biotic pressure; Eissenstat et al., 2000), suggesting that the roots remain effective at nutrient capture for longer than predicted by the optimization model. The nutrient concentration in the soils is probably intermediate between the two cases illustrated; some depletion occurs, but not as much as if there were no nutrient supply to the soil. Mycorrhizal fungi may contribute significantly to the success of citrus in obtaining P from the soil. The effects of mycorrhizae on root longevity are discussed in a later section.

The most distal lateral roots of apple, in contrast to those of citrus, are very fine and widely spaced. They are

also more ephemeral than citrus roots, with a median life span of only ~ 30–60 days (Eissenstat et al., 2000; Wells and Eissenstat, 2001). A simulation of the costs and benefits of apple roots failed to produce an optimal life span, even when root uptake was assumed to deplete the soil of P (Bouma et al., 2001). In this case, we suspect that P is not the important benefit to model. The optimal life span of the root is that which maximizes the ability of the plant to acquire the limiting resource. Since apple trees in the study orchards respond more to additions of N than to P, a better test of the optimization model would be conducted using N acquisition as the benefit, but the age-dependent kinetics of N uptake by apple roots have not been measured.

This cost-benefit model of root life span has been applied to explore the effects of environmental factors such as drought and soil fertility on the costs and benefits of root deployment. These applications, which will be described below, reveal some of the needs for future research as well as illustrating concepts affecting optimal root life spans.

V. ABIOTIC FACTORS INFLUENCING ROOT LIFE SPAN

A. Soil Moisture

Changes in the soil environment may change the nutrient uptake efficiency of the root and hence the optimal longevity. For example, in citrus, carbon allocation to the roots and root respiration were slowed substantially when roots were in dry soil for more than a couple of weeks (Kosola and Eissenstat, 1994; Espeleta and Eissenstat, 1998; Espeleta et al., 1999; Bryla et al., 1997). Root respiration was only 10–20% of that in wet soil. Drought also affects the supply of nutrients from the soil to the roots, because of its effects on diffusion and transpiration rates. Phosphorus uptake by citrus in dry surface soil was reduced by 95–98% (Whaley, 1995); after the soil was rewetted, the roots recovered almost immediately, as indicated by water and P uptake rates. Sour orange seedlings whose surface roots were exposed to dry soil for > 40 d fully recovered their ability to take up water and P within the time interval of the first measurement (1–24 h; Eissenstat et al., 1999). Thus, while citrus roots have greatly diminished uptake in dry soil, they also have greatly diminished costs and essentially complete recovery, causing root efficiency to be only moderately affected by drought, according to model simulations (Eissenstat and Yanai, 1997). Not surprisingly, drought reduces citrus root life span in field studies by only a very modest amount (Akritas et al., unpublished data).

Fine lateral roots of citrus have a well-developed exodermis that likely helps prevent desiccation in dry soil (Eissenstat and Achor, 1999; Huang and Eissenstat, 2000). Dry soil can greatly increase root mortality in grasses that lack an exodermis, such as big bluestem (*Andropogon gerardii*) (Hayes and Seastedt, 1987) and many agronomic plants (Huck et al., 1987; Smucker and Aiken, 1992) and turf grasses (Huang et al., 1997; Huang and Fry, 1998). Species that have very fine lateral roots of high hydraulic conductivity tend to shed their roots in dry soil and regrow them quickly when soil is rewetted. The costs and benefits of this plant strategy have been described for the rain roots of desert succulents (Nobel et al., 1992; see Chapter 53 by Nobel in this volume).

B. Soil Temperature

The importance of soil temperature as a factor influencing root life span is difficult to assess. Experimental manipulations of soil temperature have shown either no effect or a decrease in root longevity with increased temperature (see Chapter 41 by McMichael and Burke in this volume). In a study of trembling aspen (*Populus tremuloides*) in temperature-controlled containers in the field, cooling soil temperature to about 13°C (±2°C) from roughly 20°C (±10°C, 3.5-d average) decreased cumulative root production and mortality, but had no clear effect on root longevity (King et al., 1999). Elevating soil temperature by 2.8°C at a 2 cm depth caused no clear change in root longevity in upland grassland in the United Kingdom (Fitter et al., 1999). In contrast, a growth chamber experiment with perennial ryegrass (*Lolium perenne*) found that grasses grown at 15°C exhibited 30% root mortality after 35 d, while grasses grown at 27°C had 84% root mortality (Forbes et al., 1997). Plants grown at 21°C exhibited intermediate root mortality.

Seasonal patterns and cross-site comparisons provide indirect evidence that high soil temperatures diminish root life span. Several studies have noted longer life spans of tree roots produced in the fall than those produced in the spring (Head, 1969; Hendrick and Pregitzer, 1993; Johnson et al., 2000; Wells and Eissenstat, 2001). Life spans of sugar maple roots were 75 d longer at the more northerly of two sites in Michigan, which corresponded with 2–4°C cooler soil temperatures at a 15-cm soil depth during the spring and summer months (Hendrick and Pregitzer, 1993). Life spans of fine roots of *Lolium*

perenne and *Trifolium repens* were ~ 30 d shorter in Italy (44 N latitude) than in the United Kingdom (57 N), which the investigators attributed primarily to differences in temperature (Watson et al., 2000). In a comparison of grassland sites along an altitudinal gradient in the United Kingdom where mean soil temperature at 2 cm ranged from 9.1°C to 4.5°C, root life spans were generally longer at the higher altitude sites except for roots produced in May, when they were shorter (Fitter et al., 1998). No differences were detected, however, in root life spans of aspen (*Populus*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*) forests between a southern (54 N latitude) and northern (56 N) site in Saskatchewan and Manitoba, Canada (Steele et al., 1997).

Global data sets can be used to suggest the effect of temperature on root turnover (Gill and Jackson, 2000). Mean annual temperature described more variation in fine-root turnover than any other variable, with an increase in mean annual temperature of 10°C causing a 40–90% decrease in root life span. One explanation is that soil temperature increases root respiration more than nutrient uptake and accelerates the rate at which root efficiency decreases with age, causing a decrease in optimal life span. Simulations of the effects of temperature on root costs (using $Q_{10} = 2$ for maintenance respiration and no change in root benefit), however, indicate only about a 15-d decrease in root life span with a 10°C increase in soil temperature (Eissenstat and Yanai, 1997). This clearly does not account for the approximately 0.5-year shift in root life span observed in the global data set of Gill and Jackson (2000). Unfortunately, studies of latitudinal and altitudinal variation in temperature and life span are readily confounded by covarying factors such as soil fertility, moisture, growing-season length, and herbivore and pathogen activity, making it nearly impossible to distinguish direct effects of temperature. Other factors, such as reduced root herbivory and parasitism in climates where soil freezes, may be a better explanation for the apparent effects of temperature on root longevity.

In summary, higher temperatures have occasionally, but not always, been associated with shorter root life span. It is difficult, however, to distinguish the direct effects of temperature on root life span from the numerous indirect effects that temperature can have on the abiotic and biotic factors that influence root longevity.

C. Soil Nutrients

Root life span is responsive to fertility, but the results have been inconsistent. Among studies that have tracked the fate of individual roots, increased N availability has been associated with decreased root life span in *Populus* (Pregitzer et al., 1995, 2000b) and *Picea abies* (Majdi and Kangas, 1997). However, greater root life span has been observed in surface roots of forests dominated by sugar maple (*Acer saccharum*) (Burton et al., 2000); in localized fertile patches created with water and N in a forest stand dominated by *Populus grandidentata*, *Prunus pennsylvanica*, and other second-growth hardwoods (Pregitzer et al., 1993); in a forest dominated by *Acer saccharum*, *Fagus grandifolia*, and *Betula alleghaniensis* (Fahey and Hughes, 1994); and in a nearly pure 60-yr-old *Acer saccharum* stand (Wells, 1999).

Information on variation in root life span among species along fertility gradients is sparse. Root life span is negatively correlated with plant potential growth rate in heathland species. *Molina*, which tends to dominate wet, moderately fertile heathlands, has median root life spans of ~160–220 d, whereas *Caluna*, which dominates low-nutrient heathlands, has a median root life span of ~ 570 d (Aerts et al., 1989, 1992). A comparison of 14 forest stands showed a strong inverse relationship between N availability and root life span using an N-budgeting approach, with average life spans ranging from 167 d in oak-cherry-maple forest on fertile soil to 1223 d in pine forest on very infertile soil (Aber et al., 1985; Nadelhoffer et al., 1985). Average root life span in coniferous forests ranged from ~80–580 d with no relationship with forest floor N (mean live root mass/root turnover; recalculated from Fig. 14 in Vogt et al., 1986).

Comparisons between species adapted to low and high fertility may differ from plastic responses to nutrient availability within species (Burton et al., 2000). In studies that examined the same species under different fertility regimes, sugar maple (using minirhizotrons; Burton et al., 2000) and Sitka spruce (*Picea sitchensis*) (using sequential coring; Alexander and Fairley 1983) exhibited increased root longevity with increased soil fertility. However, *Populus* (Pregitzer et al., 1995, 2000b) and *Picea abies* (Majdi and Kangas, 1997) exhibited the reverse response. Douglas fir (*Pseudotsuga menziesii*) exhibited similar mortality of root tips in fertile and infertile sites in Washington (determined by root observation windows; Keyes and Grier, 1981).

In an efficiency context, plants should optimize carbon expenditure for uptake of nutrients that limit growth. To predict how increased nutrient availability might affect optimal root life span requires informa-

tion on root respiration and uptake capacity as a function of root age. In some plants, roots of high metabolic activity associated with high root N concentrations might be expected to exhibit rapid declines in uptake capacity with age and therefore earlier mortality than roots of lower metabolic activity (cf. Pregitzer et al., 1998). Indirect effects may complicate the interpretation of N-gradient studies. For example, plants in more fertile soils may exhibit higher water use, causing their roots to be periodically exposed to drier soil.

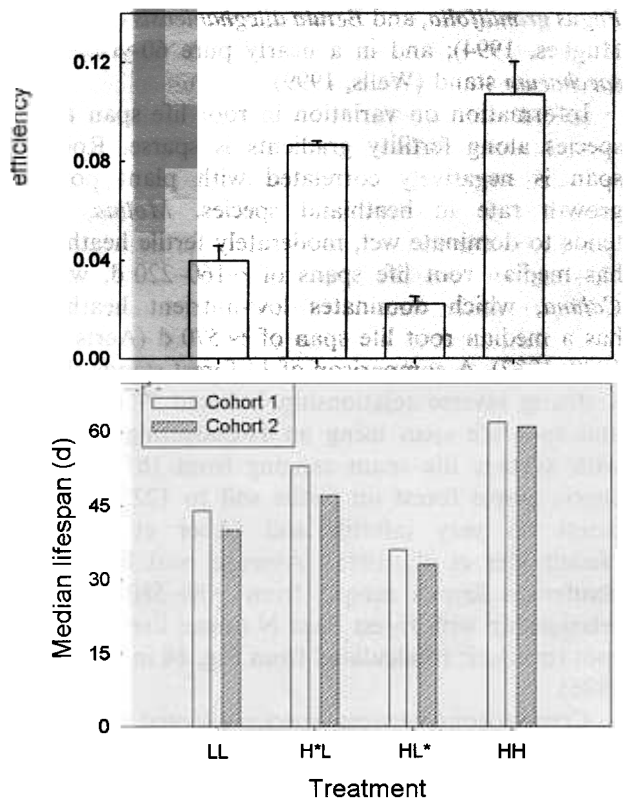

Figure 2 Daily root efficiency of nitrate acquisition and median life span of apple roots grown in split pots (Wang, Eissenstat, Flores-Alva, unpublished data). Plants received either high (H; 0.4 mmol) or low (L; 0.16 mmol) nitrate-N twice weekly in each pot separately. Treatments were: high N to both pots (HH), high N to one pot and low N to the other pot (HL), and low N to both pots (LL). The asterisk indicates the pot being measured (i.e., HL* indicates the low side of the high-low treatment is being measured). Root efficiency was determined by determining daily nitrate uptake at 75 d after transplanting using ^{15}N-nitrate and carbon costs by determining root construction cost (elemental analysis), root growth rates (minirhizotrons), and respiration (continuous gas exchange over 48-h period of the pot head space). Median life span was determined for two root cohorts using minirhizotrons and a rigid borescope.

Spatially localized nutrient enrichment can have different effects on root efficiency and root longevity than variation in site fertility, in which the whole root system is affected. Studies with trees in the field have demonstrated enhanced fine-root persistence in fertile patches (Pregitzer et al., 1993; Fahey and Hughes, 1994; Wells, 1999). Studies of potted herbaceous species have indicated both increases and decreases in root longevity in fertile patches (Gross et al., 1994; Hodge et al., 1999a,b). To maximize root efficiency, life span should be greater in fertile soil patches because root efficiency is higher where nutrients are more available. For example, in a split-root study using apple seedlings, root efficiency was considerably higher for roots receiving greater N additions, because root benefits were increased more than root costs in the fertile soil (Fig. 2). Consistent with the increased efficiency, median root life span was also increased in the high-nutrient side of the split-pot system (Fig. 2).

In summary, there are conflicting results on the effects of soil nutrients on root life span. Inconsistencies may be partially related to indirect effects of fertility and to differences in methodology. More direct observations of the survival of individual roots along fertility gradients, in long-term fertilization trials, and in response to nutrient patches are needed before we can generalize about the effect of soil fertility on life span.

VI. BIOTIC FACTORS INFLUENCING ROOT LIFE SPAN

A. Available Photosynthate and Competition with Other Sinks

Root mortality can be strongly affected by available photosynthate (Eissenstat and Yanai, 1997). Factors that reduce shoot carbon acquisition, such as canopy loss (Head, 1969; Eissenstat and Duncan, 1992) or shading (Marshall, 1986), can strongly diminish root longevity. For example, removal of the top third of the canopy of Valencia orange trees caused at least a 20% reduction in fine root length (Eissenstat and Duncan, 1992).

Strong carbon demands during reproduction have also been associated with high root mortality. Declines in total root length during and after flowering are common in annual crops (Eissenstat and Yanai, 1997). Farmers are concerned when their trees produce too many fruit, thereby "weakening" the root system. For

example, high root mortality has been associated with very heavy fruit crops of *Prunus* (Chandler, 1923) and *Citrus* (Smith, 1976; Graham et al., 1985).

B. Mycorrhizal Fungi

Approximately 90% of plants form mycorrhizal associations (Smith and Read, 1997). The primary benefit associated with vesicular arbuscular (VA) mycorrhizas is improved plant acquisition of P. Because plants may be more resistant to pathogens if not P deficient, many putative mycorrhizal benefits against pathogens may simply be an indirect result of improved P nutrition (Graham, 1988). There is, however, some evidence that mycorrhizae may enhance root longevity independent of P nutrition. Compared to nonmycorrhizal roots, root life span was extended in VA mycorrhizal roots exposed to dry surface soil (Espeleta et al., 1999), fungal pathogens (Benhamou et al., 1994; Newsham et al., 1995), and insect herbivores (Gange et al., 1994). Hooker et al. (1995), in contrast, found mycorrhizal colonization to diminish root longevity in *Populus*. In ectomycorrhizal associations, the fungal sheath that surrounds the roots probably protects the root from many forms of herbivory (Smith and Read, 1997).

The effects of mycorrhizal fungi on root life span can also be examined in the context of root efficiency (Eissenstat and Yanai, 1997). If the mycorrhizal roots of a plant are acquiring more nutrients for less carbon (including costs of construction and maintenance of extramatrical hyphae) than those that have not been colonized, then the plant may more actively maintain and defend the mycorrhizal roots. A root system differentially colonized by mycorrhizal fungi may behave similarly to one in patchy soil fertility, as described above.

C. Herbivores and Pathogens

Roots are constantly influenced by the myriad organisms that reside in the rhizosphere. Some soil organisms feed on roots directly, with obvious impact on plant communities (Weste, 1986). Others affect roots indirectly through root efficiency. Rhizosphere organisms may feed upon or compete with beneficial organisms such as mycorrhizal fungi and bacteria. They can also immobilize nutrients that would otherwise be available to the roots.

The extent to which root herbivory and parasitism influence root life span is poorly understood. In most cases roots probably are not actively shed but simply succumb to weak parasites and herbivores that reside in the rhizosphere. 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, as may occur following canopy loss or during heavy fruit set (Graham et al., 1985).

Wells (1999) examined the effects of selective pesticides on root life span by drenching pesticide monthly around minirhizotron tubes. In a 60-yr-old sugar maple stand, the fungicide metalaxyl (an inhibitor of protein synthesis in Oomycetes like *Phytophthora* and *Pithium*) caused an increase in median life spans from 270 d in water-drenched sites to 690 d in the fungicide treatment (Fig. 3). When both the fungicide and the insecticide chlorpyrifos (a broad-specturm cholinesterase inhibitor) were applied, median life spans were extended beyond the duration of the experiment (after 714 d, only 38% of the initial root population had died). The insecticide increased sugar maple root life span only when used in combination with the fungicide. In peach, chlorpyrifos also increased root life span, although the magnitude of the effect depended on the age of the roots when the insecticide was applied (Wells et al., submitted). For roots < 50 days old, drenching with insecticide increased median life span by > 250 d. For roots > 50 d old, median life span was

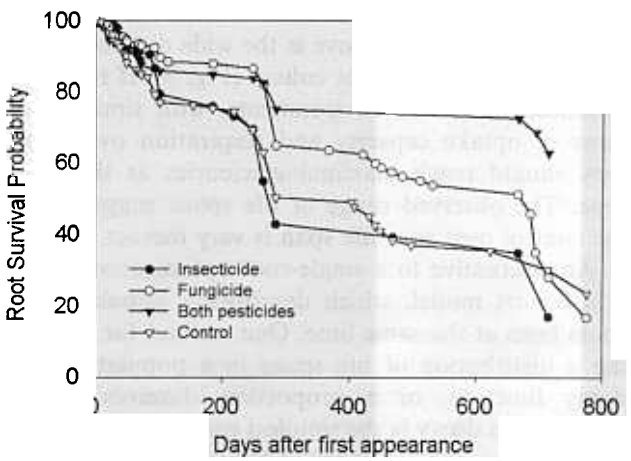

Figure 3 Survivorship of sugar maple roots following monthly drenches of metalaxyl fungicide (open circles), chlorpyrifos insecticide (closed circles), both pesticides (closed triangles), or the water control (open triangles). Survivorship was determined using the minirhizotron technique. Both the fungicide and the fungicide + insecticide roots were significantly different from the control roots ($P < .05$; Cox proportional hazards regression). (From Eissenstat et al., 2000.)

increased by only 44 d (from 56 d in control trees to ~ 100 d in treated) by the insecticide treatment.

In both the peach orchard and the sugar maple stand, the trees looked healthy and exhibited no root-related problems. Yet the influence of soil insects and fungi on patterns of root survivorship was clearly substantial. While we cannot say whether the pesticide treatments influenced root survivorship by directly removing root herbivores or fungal pathogens, we can conclude that root life span in many communities is likely to be strongly influenced by complex interactions with soil organisms. Factors controlling root life span likely include both biotic and abiotic factors.

VII. MODELING THE DEFENSE OF A COHORT OF ROOTS

A. Optimization Model Applied to a Cohort of Roots

The mechanisms controlling the shedding of fine roots are not clear. An optimization model does not specify how roots should be shed, but only when they should be shed. Roots in minirhizotron studies are commonly observed to disappear, rather than to die in place and decompose over time. If herbivory or parasitism cause the death of roots, then optimal life spans from the cost-benefit point of view might not be achieved.

Another observation in conflict with the optimization model described above is the wide distribution of life spans in a single root cohort (Fig. 3). If roots are produced in similar environments, with similar patterns of uptake capacity and respiration over time, they should reach maximal efficiencies at the same time. The observed range of life spans suggests that the control over root life span is very inexact.

An alternative to a single-root optimization model is a cohort model, which describes a population of roots born at the same time. One method for describing a distribution of life spans in a population is a decay function, or a proportional-hazards model. Exponential decay is the simplest example of a hazard model, in which the chance of failure is constant over time. In this idealized case, the number of roots dying is a constant proportion of roots living, and every root has an equal chance of failure at every point in time. Empirical root survivorship curves look roughly exponential, with seasonal variation in mortality causing important deviations (Wells and Eissenstat, 2001). We use a simple exponential model to illustrate our approach to analyzing the efficiency of a cohort, but more complex models could be developed to include factors such as climate, phenology, herbivore pressure, and the like.

In simple exponential decay, only one parameter describes the mortality rate:

$$A = A_0 \exp(k^* t)$$

where A_0 is the original mass, length, or number of roots in the cohort; t is the age of the root (d), and k is the decay constant (day^{-1}), which equals the fraction of the roots that die each day. This equation can also be described by the median life span, or half-life, which is the age at which half the roots have died, or $A = 1/2A_0$. At this point age = $\ln(1/2)/k$.

The cumulative efficiency of a cohort of roots is defined as the total cumulative uptake by all the roots divided by the total cumulative cost. This efficiency can be calculated by summing the costs and benefits over finite time intervals as the mass, length, or number of the roots decline. If the expressions for cost and benefit could be integrated, numeric integration would not be necessary.

To illustrate the efficiency of a cohort of roots, we use equations for uptake and respiration that have the convenient property of exhibiting an optimal life span even when soil depletion is not simulated. We used uptake rates from apple and respiration rates from citrus (Fig. 1c). The resulting behavior cannot be attributed to any species, but it is computationally simple, and it illustrates the value of an efficiency approach applied to a cohort of roots.

Because of the change in the number of roots present over time, the median life span of an optimal distribution does not coincide with the optimal individual life span. This point is illustrated in Fig. 4, using the equations for respiration and uptake described in the legend. In this illustration, the optimal life span for an individual root to maximize E is 86 days; the optimal half-life of the cohort using the same parameters is ~ 60 d, assuming exponential decline in number of roots.

From the point of view of the individual root, the exponential model means that there is a constant risk of root death from all sources. The plant could be imagined, however, to have some control over the magnitude of this risk. Root browning, for example, has been associated with reduced mortality in apple (Wells and Eissenstat, 2001) and peach (Wells et al., submitted). In addition, reduced insect herbivory was associated with delayed root browning (Wells et al., submitted). The optimization approach can explore what magnitude of investment in root defense is justified by an increase in root efficiency.

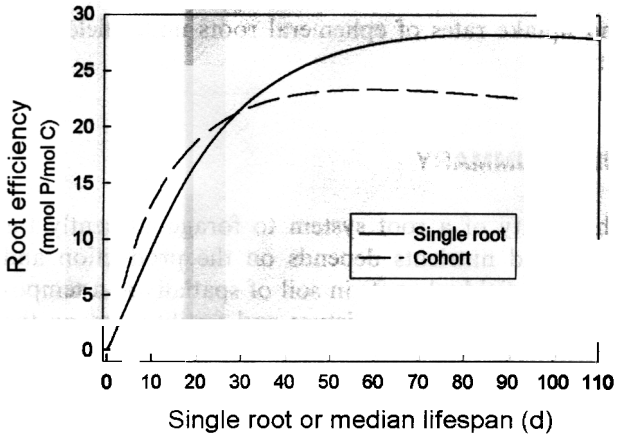

Figure 4 The cumulative efficiency of a single root as a function of age and the efficiency of cohort of roots as a function of the median life span, or $\ln(.5)/k$, assuming that the distribution of life spans in the cohort follows first-order kinetics, where the death rate is k times the pool of living roots. This illustration is based on Uptake (mmol P/g root/day) = 21.7 * age/(age^2 + 6.96 * age + 83.6) and Respiration (mol C/g root/day) = 14.3 + 12.6 * age$^{3.98}$/(age$^{3.98}$ + 2560), where age is in days.

B. Including Plant Defense and Herbivory in the Optimization Model

We can suggest an approach for determining whether allocation to defense is advantageous in terms of maximizing root efficiency. We should acknowledge at the outset, however, that to our knowledge, the data are not available to parameterize such a model for any species. We will illustrate the concept using respiration rates measured for citrus and uptake rates measured for apple, consistent with the demonstration of cohort efficiency, above.

We wish to describe how the allocation of C to defense (C_{def}) reduces the chance of mortality. A hypothetical relationship between C_{def} and the half-life of a cohort is illustrated in Fig. 5 (inset). This relationship will vary with the intensity of pressure from herbivores and pathogens. For simplicity, we assume a linear relationship between C_{def} and the median life span of roots. This life span is shorter in the case of higher pressures, for the same investment in C_{def}. In our example, in the case of lower pressure, an investment of 10 mmol C/g root decreases the chance of mortality by 29%, which corresponds to an increase in the median life span of 40%. In the case of higher pressure, the same investment in defense results in a 50% decrease in the risk of mortality or a doubling of the median life span. This sounds impressive, but still leaves the cohort with higher mortality and shorter life spans than the cohort under low pressure without any defense. We use these numbers for illustration, since we do not know specifically how much C associated with root construction is used for defense. Indirect evidence in support of C investment in defense is provided by the observation that coarser roots of longer longevity have higher tissue density and more lignified secondary walls (Eissenstat and Achor, 1999). In addition, as mentioned previously, older peach roots that have more condensed tannins and thicker secondary walls benefit less from insecticide application than young peach roots (Wells et al., submitted).

We can now compare the efficiency of cohorts of roots under different degrees of herbivore and pathogen pressure with different investments in defense (Fig. 5). The optimal allocation to defense in the scenario with lower herbivore and pathogen pressure is 5 mmol C/g root in this illustration; under higher pathogen pressure, a greater C allocation to defense is desirable to increase median life spans toward the optimum predicted in the absence of herbivory (Fig. 4). The efficiencies and life spans achieved are less than in the case without herbivory, where the optimal median life span was ~ 60 d, and the cohort efficiency was > 23 mmol

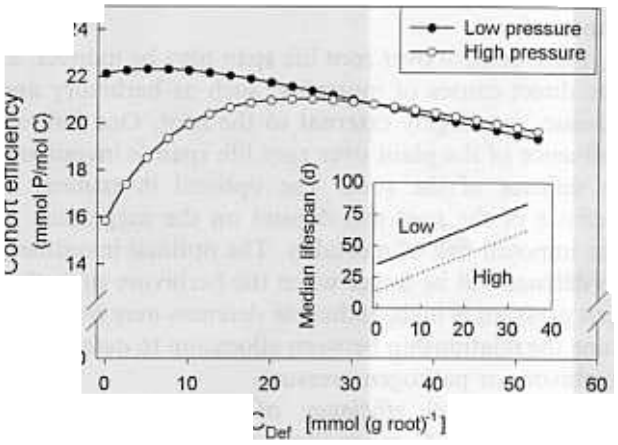

Figure 5 The efficiency of a cohort of roots as a function of C expended for defense (C_{Def}). The efficiency of the cohort is based on respiration and uptake rates of individual roots (see Fig. 1) and exponential decay at rates determined by the defensive C investment. The inset shows the assumed relationship between C expended for defense of the root and the resulting half-life of the cohort of roots, for scenarios of higher (High) and lower (Low) pressure from herbivores and pathogens.

P/mol C (Fig. 4). Under low pressure, where we assumed the median life span would be reduced to 35 d without an additional C investment, the optimal median life span was increased to 42 d by an additional C investment that resulted in 94% of the ideal maximum efficiency. With higher pressure, where we assumed the median life span would be only 14 d without the expenditure of C for defense, the optimal C investment was 25 mmol/g root, compared to only 5 mmol C/g root in the low-pressure case. This investment, according to our guess at the return on investment shown in Fig. 5 (inset), resulted in a median life span of 50 days, and a 10% loss in cohort efficiency, but a vast improvement over the efficiency achieved by the unprotected cohort.

We do not expect the quantitative relationships illustrated here to apply to any real situations in nature. The relationship between defensive C investment and median life span (Fig. 5, inset), upon which the optimal investment in defense depends (Fig. 5), was not based on data from any specific case. This illustration, however, serves to highlight some useful concepts and some needs for future research, as follows.

Applying a cost-benefit analysis to a cohort of roots with a distribution of life spans reveals that the optimal individual life span is not the same as the optimal median life span of the population. The relationship between the individual and population optima depends on the form of the survivorship curve or on its hazard function.

Plant control over root life span may be indirect, as the direct causes of mortality, such as herbivory and disease, are largely external to the root. One indirect influence of the plant over root life span is investment in defense of the root. The optimal investment in defense of the root will depend on the magnitude of the imposed risk of mortality. The optimal investment in defense will be larger when the herbivore or pathogen pressure is high. Inducible defenses may help fine-tune the relationship between allocation to defense and herbivore or pathogen pressure.

The maximal efficiency of the cohort will be reduced by the C expenditure for defense, compared to a situation without herbivore or pathogen pressure. Beyond the optimal expenditure, allocating additional C to root defense would increase life spans but reduce efficiencies, such that nutrient acquisition would be better served by constructing new roots than by defending old ones. The absence of data required to better quantify or test these relationships is due to the difficulty of collecting information on root demography, C allocation, and age-dependent C expenditures and uptake rates of ephemeral roots under field conditions

VIII. SUMMARY

The ability of a root system to forage efficiently for water and nutrients depends on the production and loss of individual roots in soil of spatially and temporally heterogeneous moisture and fertility and on the physiological activity of these roots, which changes with age. There is enormous variation in root life span, and sources for the variation are not well understood. We hypothesize that plant variation in root life span often relates to plant potential growth rate and the nutrient availability where the plant has evolved. More and wider species comparisons under common garden conditions are needed to test this hypothesis.

One of the difficulties in generalizing about factors controlling root life span is the lack of agreement among methods. No method has emerged as best for all conditions, although the minirhizotron approach seems to hold the most promise for developing a better understanding of root demography under a wide range of conditions.

Both abiotic and biotic factors affect root life span, and often these factors interact. Higher temperature, for example, may diminish root life span more by allowing for more root herbivores and pathogens than by directly affecting root maintenance costs. Reductions in available photosynthate for root maintenance, such as caused by grazing or pruning of the shoot or by high fruit production, often leads to greater root mortality.

We previously approached the cost-benefit analysis of root life span with the implicit assumption that plants controlled the life span of roots. Our current approach acknowledges the role of exogenous factors in root mortality, with the plant having indirect control through allocation to defense. A cohort analysis of root efficiency allows a distribution of life spans to be optimized. Additional studies examining factors influencing root life span combined with optimization modeling are needed to unravel the numerous controls and constraints on the life span of plant roots.

REFERENCES

Aber JD, Melillo JM, Nadelhoffer KJ, McClaugherty CA, Pastor J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availabil-

ity: a comparison of two methods. Oecologia 66:317–321.
Aerts R. 1995. The advantages of being evergreen. Trends Ecol Evol 10:402–407.
Aerts R, Berendse F, Klerk NM, Bakker C. 1989. Root production and rot turnover in two dominant species of wet heathlands. Oecologia 81:374–378.
Aerts R, Bakker C, De Caluwe H. 1992. Root turnover as determinant of the cycling of C, N and P in a dry heathland ecosystem. Biogeochemistry 15:175–190.
Alexander IJ, Fairley RI. 1983. Effects of N fertilization on populations of fine roots and mycorrhizas in spruce humus. Plant Soil 71:49–53.
Arnone III JA, Zaller JG, Spehn EM, Niklaus PA, Wells CE, Körner C. 2000. Dynamics of root systems in native grasslands: effects of elevated CO_2. New Phytol 147:73–85.
Benhamou N, Fortin JA, Hamel C, St-Arnaud M, Shatilla A. 1994. Resistance responses of mycorrhizal Ri T-DNA-transformed carrot roots to infection by *Fusarium oxysporum* f. sp. *Chrysanthemi*. Phytopathology 84:958–968.
Black KE, Harbron CG, Franklin M, Atkinson D, Hooker JE. 1998. Differences in root longevity of some tree species. Tree Physiol 18:259–293.
Bloomfield J, Vogt K, Wargo PM. 1996. Tree root turnover and senescence. In: Waisel Y, Eshel A, Kafkafi U, eds. Plant Roots: The Hidden Half. 2nd ed. New York; Marcel Dekker, pp 383–381.
Bouma TJ, Yanai RD, Elkin A, Hartmond U, Flores DE, Eissenstat DM. 2001. Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. New Phytol (in press).
Brundrett MC, Kendrick B. 1988. The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. Can J Bot 66:1153–1173.
Bryla DR, Bouma TJ, Eissenstat DM. 1997. Root respiration in citrus acclimates to temperature and slows during drought. Plant Cell Environ 20:1411–1420.
Burton AJ, Pregitzer KS, Hendrick RL. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia (in press).
Caldwell MM. 1979. Root structure: The considerable cost of belowground function. In: Solbrig OT, Jain S, Johnson GB, Raven PH, eds. Topics in Plant Population Biology. New York; Columbia University Press, pp 408–427.
Caldwell MM. 1987. Competition between roots in natural communities. In: Gregory PJ, Lake JV, Rose DA, eds. Root Development and Function. New York; Cambridge University Press, pp 167–185.
Caldwell MM, Camp LB. 1974. Belowground productivity of two cool desert communities. Oecologia 17:123–130.
Caldwell MM, Eissenstat DM. 1987. Coping with variability: examples of tracer use in root function studies. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC, eds. Plant Response to Stress—Functional Analysis in Mediterranean Ecosystems. NATO Adv Sci Inst Ser. New York; Springer-Verlag, pp 95–106.
Chapin FS III. 1980. The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260.
Chandler WH. 1923. Results of Some Experiments in Pruning Fruit Trees. Ithaca, NY; New York Agricultural Exp Sta Bull No. 415.
Cheng W, Coleman DC, Box, JE Jr. 1990. Root dynamics, production and distribution in agroecosystems on the Georgia Piedmont using minirhizotrons. J Appl Ecol 27:592–604.
Clarkson DT. 1991. Root structure and sites of ion uptake. In: Waisel Y, Eshel A, Kafkafi U, eds. Plant Roots: The Hidden Half. New York; Marcel Dekker, pp 417–453.
Coleman MD, Dickson RE, Isebrands JG, Karnosky DF. 1996. Root growth and physiology of potted and field-grown trembling aspen exposed to tropospheric ozone. Tree Physiol 16:145–152.
Comas LH, Eissenstat DM, Lakso AN. 2000. Assessing root death and root system dynamics in a study of grape canopy pruning. New Phytol 147:171–178.
Dahlman RC, Kucera RL. 1965. Root productivity and turnover in native prairie. Ecology 46:84–89.
Eissenstat DM. 1992. The costs and benefits of constructing roots of small diameter. J Plant Nutr 15:763–782.
Eissenstat DM. 1991. On the relationship of specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytol 69:870–873.
Eissenstat DM, Achor DS. 1999. Anatomical characteristics of roots of citrus rootstocks that vary in specific root length. New Phytol 141:309–321.
Eissenstat DM, Duncan LW. 1992. Root growth and carbohydrate responses in bearing citrus trees following partial canopy removal. Tree Physiol 10:245–257.
Eissenstat DM, Yanai RD. 1997. The ecology of root life span. Adv Ecol Res 27:1–62.
Eissenstat DM, Graham JH, Syvertsen JP, Drouillard DL. 1993. Carbon economy of sour orange in relation to mycorrhizal colonization and phosphorus stress. Ann Bot 71:1–10.
Eissenstat DM, Whaley EL, Volder A, Wells CE. 1999. Recovery of citrus surface roots following prolonged exposure to dry soil. J Exp Bot 50:1845–1854.
Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL. 2000. Building roots in a changing environment: implications for root longevity. New Phytol 147:33–42.
Eissenstat DM, Wells CE, Wang L. 2002. Root efficiency and mineral nutrition in apple. Acta Hort (in press).
Espeleta JF, Eissenstat DM. 1998. Responses of citrus fine roots to localized soil drying: a comparison of seedlings with adult fruiting trees. Tree Physiol 18:113–119.
Espeleta JF, Eissenstat DM, Graham JH. 1999. Citrus root responses to localized drying soil: a new approach to

Huck MG, Hoogenboom G, Peterson CM. 1987. Soybean root senescence under drought stress. In: Taylor HM, ed. Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. ASA Special Publ. No. 50. Madison, WI: Agronomy Society of America, pp 168–174.

Jackson RB, Mooney HA, Schulze ED. 1997. A global budget of fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94:7362–7366.

Jackson RB, Schenk HJ, Jobbagy EG, Canadell J, Colello GD, Dickinson RE, Field CB, Friedlingstein P, Heimann M, Hibbard K, Kicklighter DW, Kleidon A, Neilson RP, Parton WJ, Sala OE, Sykes MT. 2000. Belowground consequences of vegetation change and their treatment in models. Ecol Appl 9:470–483.

Johnson MG, Phillips DL, Tingey DT, Storm MJ. 2000. Effects of elevated CO_2, N-fertilization, and season on survival of ponderosa pine fine roots. Can J For Res 30:220–228.

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

Joslin JD, Wolfe MH, Hanson PJ. 2000. Effects of altered water regimes on forest root systems. New Phytol 147:117–129.

Keyes MR, Grier CC. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can J For Res 11:599–605.

King JS, Pregitzer KS, Zak DR. 1999. Clonal variation in above- and below-ground growth responses of *Populus tremuloides* Michaux: influence of soil warming and nutrient availability. Plant Soil 217:119–130.

Kosola, KR, Eissenstat DM. 1994. The fate of surface roots of citrus seedlings in dry soil. J Exp Bot 45:1639–1645.

Lamont BB. 1995. Mineral nutrient relations in Mediterranean regions of California, Chile and Australia. In: Arroyo MTK, Zedler PH, Fox MD, eds. Ecology and Biogeography of Mediterranean Ecosystems of Chile, California, and Australia. New York; Springer-Verlag, pp 211–238.

Lopez B, Sabate S, Garcia C. 1996. An inflatable minirhizotron system for stony soils. Plant Soil 179:255–260.

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

Mäkelä A, Vanninen P. 2000. Estimation of fine root mortality and growth from simple measurements: a method based on system dynamics. Trees 14:316–323.

Marshall JD. 1986. Drought and shade interact to cause fine-root mortality in Douglas-fir seedlings. Plant Soil 91:51–60.

Matamala R, Gonzalez-Meler MA, Schlesinger WH. 2000. How long do roots live? A ^{13}C tracer technique for assessing fine root longevity in a North Carolina pine forest. Abstracts of Ecological Society of America Annual Meeting, Snowbird, UT, p 154.

Meyer WS, Barrs HD. 1991. Roots in irrigated clay soils: measurement techniques and responses to root zone condition. Irrig Sci 12:125–134.

Milchunas DG, Lauenroth WK. 1992. Carbon dynamics and estimates of primary production by harvest, ^{14}C dilution, and ^{14}C turnover. Ecology 73:593–607.

Nadelhoffer KJ. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol 147:-131-139.

Nadelhoffer KJ, Raich JW. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147.

Nadelhoffer KJ, Aber JD, Melillo JM. 1985. Fine roots, net primary production and nutrient availability: a new hypothesis. Ecology 66:1377–1390.

Newsham KK, Fitter AH, Watkinson AR. 1995. Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. J Ecol 83:991–1000.

Nobel PS, Alm DM, Cavelier J. 1992. Growth respiration, maintenance respiration and structural-carbon costs of roots of three desert succulents. Func Ecol 6:79–85.

Norby RJ, Jackson RB. 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol 147:3–12.

North GB, Huang B, Nobel PS. 1993. Changes in the structure and hydraulic conductivity of desert succulents as soil water status varies. Bot Acta 106:126–135.

Peng S, Eissenstat DM, Graham JH, Williams K, Hodge NC. 1993. Growth depression of mycorrhizal citrus at high phosphorus supply: analysis of carbon costs. Plant Physiol 101:1063–1071.

Phillips DL, Johnson MG, Tingey DT, Biggart C, Nowak RS, Newsom JC. 2000. Minirhizotron installation in sandy, rocky soils with minimal soil disturbance. Soil Sci Soc Am J 64:761–764.

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

Pregitzer KS, Zak DR, Crutis PS, Kubiske ME, Teeri JA, Vogel CS. 1995. Atmospheric CO_2, soil nitrogen and fine root turnover. New Phytol 129:579–585.

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

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR. 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol 18:665–670.

Pregitzer KS, King JS, Burton AJ, Brown SE. 2000a. Responses of tree fine roots to temperature. New Phytol 147:105–115.

Pregitzer KS, Zak DR, Maziasz J, DeForest J, Curtis PS, Lussenhop J. 2000b. Interactive effects of atmospheric

CO_2 and soil-N availability on fine roots of *Populus tremuloides*. Ecol Appl 10:18–33.

Raich JW, Nadelhoffer KJ. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346–1354.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734.

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Func Ecol 12:395–405.

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

Ryser P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. Func Ecol 10:717–723.

Rytter, R-M. 1999. Fine-root production and turnover in a willow plantation estimated by different calculation methods. Scand J For Res 14:526–537.

Sala OE, Biondi ME, Lauenroth WK. 1988. Bias in estimates of primary production: an analytical solution. Ecol Model 44:43–55.

Samson BK, Sinclair TR. 1994. Soil core and minirhizotron comparison for the determination of root length density. Plant Soil 161:225–232.

Santantonio D, Grace JC. 1987. Estimating fine root production and turnover from biomass and decomposition data: a compartment flow model. Can J For Res 17:900–908.

Shaver GR, Billings WD. 1975. Root production and root turnover in a wet tundra system. Ecology 56:401–409.

Singh JS, Lauenroth WK, Hunt HW, Swift DM. 1984. Bias and random errors in estimators of net root production: a simulation approach. Ecology 65:1760–1764.

Smith PF. 1976. Collapse of 'Murcott' tangerine trees. J Am Soc Hort Sci 101:23–25.

Smith SE, Read DJ. 1997. Mycorrhizal Symbiosis. 2nd ed. San Diego, CA: Academic Press.

Smucker AJM, Aiken RM. 1992. Dynamic root responses to soil water deficits. Soil Sci 154:281–289.

Steele SJ, Gower ST, Vogel JG, Norman JM. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol 17:577–587.

Taylor HM, ed. 1987. Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. ASA Special Publ. No. 50. Madison, WI: American Society of Agronomy.

Tingey DT, Phillips DL, Johnson MG. 2000. Elevated CO_2 and conifer roots: effects on growth life span and turnover. New Phytol 147:87–103.

Thornley JHM. 1998. Modelling shoot:root relations: the only way forward? Ann Bot 81:165–171.

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

Vogt KA, Edmonds RL, Grier CC. 1981. Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer fine roots in 23- and 180-year-old subalpine *Abies amabilis* stands. Can J For Res 11:223–229.

Vogt KA, Grier CC, Vogt DJ. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Adv Ecol Res 15:303–377.

Vogt KA, Persson H. 1991. Root methods. In: Lassoie JP, Hinckley TM. Ecophysiology of Forest Trees. Vol. 1, Techniques and Methodologies. Boca Raton, FL: CRC Press, pp 477–501.

Watson CA, Ross JM, Bagnaresi U, Minotta GF, Roffi F, Atkinson D, Black KE, Hooker JE. 2000. Environment-induced modifications to root longevity in *Lolium perenne* and *Trifolium repens*. Ann Bot 85:397–401.

Weaver JE, Zink E. 1946. Length of life of roots of ten species of perennial range and pasture grasses. Plant Physiol 21:201–217.

Wells CE. 1999. Advances in the fine root demography of woody species. PhD thesis. Pennsylvania State University, University Park, PA.

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

Wells CE, Eissenstat DM, Glenn DM. Submitted. Soil insects alter fine root demography in peach (*Prunus persica*). Submitted to Plant Cell Environ.

Wells CE, Eissenstat DM, Glenn DM. 2002 Submitted 2 Changes in the risk of fine root mortality with age: a case study in peach (*Prunus persica*). Am J Bot.

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 EL. 1995. Uptake of phosphorus by citrus roots in dry surface soil. MSc thesis, University of Florida, Gainesville, FL.

Williams M, Yanai RD. 1996. Multi-dimensional sensitivity analysis and ecological implications of a nutrient uptake model. Plant Soil 180:311–324.

Wilson JB. 1988. Shoot competition and root competition. J Appl Ecol 25:279–296.

Yanai RD. 1994. A steady-state model of nutrient uptake improved to account for newly-grown roots. Soil Sci Soc Am J 58:1562–1571.

Yanai RD, Fahey TJ, Miller SL. 1995. Efficiency of nutrient acquisition by fine roots and mycorrhizae. In: Smith WK, Hinckley TM, eds. Resource Physiology of Conifers. New York; Academic Press, pp 75–103.