ROOT EFFICIENCY AND MINERAL NUTRITION IN APPLE

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Abstract

Among deciduous fruit crops, maximum sustained yields under ideal conditions reportedly range from 22 MT/ha in sweet cherry to 112 MT/ha in apple: about a 5-fold difference. Root length densities under fruit trees, however, range from about 0.2 km/m^2 in apple to about 12 km/m^2 in kiwifruit: a 60-fold difference. What causes these differences among the root systems of different fruit crops? Patterns of root growth and distribution are reviewed as well as recent work on root pigmentation and survivorship. These data illustrate the importance of recognizing fine roots as a heterogeneous population with different longevities and physiological functions. Both root costs and benefits need to be understood to evaluate root efficiency. The concept of root efficiency has been largely ignored in horticulture, despite the considerable cost of building and maintaining the root system. Plants expend carbon (photosynthate) on constructing new roots and maintaining existing roots. Root efficiency can be defined as the ratio of water or nutrient benefit to carbon cost over the lifetime of the root. Apple roots are readily shed when they become inefficient, as occurs when soil temperatures are elevated, soil becomes dry, or when roots are located in infertile patches of soil. For example, in a field experiment with 'Red Chief Delicious' on M.26 rootstock, only 23% of apple roots born in June were still alive in September when the soil was unirrigated and heated, whereas 45% were still alive in the irrigated and unheated treatment. In a split-pot study in the greenhouse, apple seedlings whose roots received 8 mM nitrate lived about 50% longer than its portion of roots that only received 1.6 mM nitrate. High root efficiency may partly explain why apple trees are able to produce relatively high yields despite their sparse root system.

INTRODUCTION

Fruit trees depend on their root systems for the acquisition of water and mineral nutrients. However, while tree canopies are carefully pruned and trained, few cultural practices are aimed at directly modifying the root system. If nutrient or water deficiencies are detected, growers may simply fertilize or irrigate as required. This strategy works some of the time, but not always. The status of the root system can compromise yield even in situations where drought or mineral nutrient deficiencies are not apparent.

Previous research suggests that the single most important factor influencing nutrient acquisition is the total length of the root system (Nye and Tinker, 1977; Barber, 1984). Uptake of immobile nutrients like phosphate and micronutrients like zinc and iron, is particularly dependent on root absorptive surface area, which is not only influenced by root length, but also by the length of root hairs and mycorrhizal hyphae. This might indicate that trees with greater

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root length densities would also have a greater capacity for nutrient acquisition and fruit production. Yet a comparison of various fruit tree species reveals no relationship between root length density and the potential for sustained fruit production under ideal conditions (Fig. 1). For example, apple produces a high yield per hectare despite its relatively sparse root system. What other aspects of the root system need to be considered if we are to understand and manage the root system for optimal fruit production?

In this paper we will review what is known about root distribution and seasonal root growth patterns in apple and discuss our work on the factors that affect apple root survival. We will then introduce the concept of root efficiency and discuss observations we have made on the root efficiency of apple and other fruit crops. Finally, we will discuss how root efficiency and lifespan may be connected to patterns of fruit yield.

PATTERNS OF ROOT DISTRIBUTION AND ROOT DYNAMICS

Seasonal Patterns of Root Growth and Distribution

An abundance of basic root information collected in the early decades of the twentieth century from excavations and rhizotrons at the East Malling Research Station in Kent, England has provided most of the basic information about roots appearing in horticultural textbooks today. For example, Rogers and Vyvyan (1934) found that 10-year-old Prince Albert trees on the dwarfing rootstock, M9, had a 4.6 m root spread and a ratio of root/canopy spread of 1.43. In contrast, the vigorous rootstock M1 had a spread of about 6 m and a root/canopy spread ratio of 1.71. In general, the ratio of stem weight (i.e., trunk and branches) to root weight was remarkably constant throughout the range of rootstocks examined on a given soil type.

Fine root growth of many fruit trees has been shown to occur during one or more distinct seasonal "flushes" that are followed by periods of lower root production (Rogers, 1939; Head, 1966, 1969a; Atkinson and Wilson, 1980; Glenn and Welker, 1993; Reid and Bowden, 1995). Rogers (1939) found that seasonal patterns of apple root growth were closely correlated with soil temperature. Limited root growth occurred during the winter when soil temperatures were between 2 and 7 C, and root growth commenced when soil temperatures rose above 7 C. The period of active root growth extended beyond that of aboveground vegetative growth, beginning before the leaves unfolded and continuing after shoot growth ceased. Later investigations by Rogers and others indicated that while the timing of apple root flushes was variable, an initial flush of new root production usually occurred in the late spring during, or immediately following, bloom (Rogers, 1939; Head, 1966, 1967; Rogers and Head, 1969). A second peak of new root growth in the late summer and early autumn was also frequently reported and was often of greater duration and magnitude than the initial spring peak (Rogers, 1939; Head, 1966, 1967, Rogers and Head, 1969). There was also evidence for asynchronous root and shoot growth in apple. Periods of vigorous root and shoot growth rarely overlapped (Head, 1969a; Atkinson and Wilson, 1980), perhaps reflecting competition for carbohydrates between aboveground and belowground organs (Priestley et al., 1976).

Seasonal trends in apple fine root production have been affected by rootstock (Head, 1966), tree age (Atkinson and Wilson, 1980), fertilization (Head, 1969b), aboveground pruning (Knight, 1934; Head, 1967; Hass and Hein, 1973) and fruit load (Head, 1969a; Weller 1967), making generalizations regarding root growth patterns difficult. Like apple, peach typically exhibits a spring root flush and further peaks in mid-summer and/or autumn (Crockroft and Olsson, 1972; Glenn and Welker, 1993). Grape (Freeman and Smart, 1976; Eissenstat, unpubl. data) and kiwi (Buwalda and Hutton, 1988; Reid and Bowden, 1995); however, may not exhibit peak root growth until mid to late summer.

Patterns of Root Mortality: a Case Study in 'Red Delicious' on M.26 rootstock.

While a moderate amount of information exists on the timing of fine root production in fruit trees, little is known about the timing of root mortality. Low numbers of fine roots observed during the winter suggest that most fine roots die at the end of one growing season and are

replaced during the next (Rogers, 1939; Atkinson, 1980; Wells and Eissenstat, 2001). However, the extent to which fine roots may survive and function in more than one growing season has not been investigated in detail.

We used minirhizotrons to follow the fate of apple fine roots produced during the fall root flush in a Pennsylvania apple orchard and to identify factors that influenced root survival over winter (Wells and Eissenstat, 2001). We asked the following questions: (1) what percentage of fine roots survives over winter? (2) Are all roots equally likely to survive over winter? (3) Is there significant production of new fine roots in the spring prior to bloom?

The study was conducted at the Russell E. Larson Agricultural Research Center in Rock Springs, PA using six 20-yr.-old 'Red Chief Delicious' trees on M.26 rootstock. Trees were about 2.5 m tall and planted at a 2-m spacing in a "Penn State four-wire low-hedgerow" trellis system with 3.7-m spacing between rows. Soil at this location is Hagerstown silt loam, a Typic Hapludalf. Eight root observation tubes ("minirhizotrons") were placed in the soil surrounding each tree and inclined 30 degrees from the vertical towards the center of the trellis row. Four outer tubes (2 on each side of the row) were 0.5 m in length with the top 1.3 m from the base of the trunk and four inner tubes were 1.0 m in length with the top 0.67 m from the base of the trunk. A miniaturized camera system and portable video cassette recorder (VCR) were used to record video images of roots that had grown against the surface of the minirhizotrons at bi-weekly or monthly intervals. In both 1994 and 1995, root videotaping began in late October and was continued at approximately monthly intervals until bud break in May of the following year.

The videotapes were played back in the lab, and images of all minirhizotron windows that contained roots were digitized, compressed and stored. Images of roots as they appeared on sequential video sampling dates were reviewed and used to construct a database of life history information for over 600 individual roots. Roots were classified as dead on the first date when they (a) disappeared or (b) appeared blackened and shriveled. The diameter, color and number of neighboring roots (the number of roots sharing a minirhizotron frame with a given individual) were also noted for each root in the study. The effects of these three covariates on root mortality were assessed using Cox proportional hazards regression (Cox, 1972; Allison, 1995; see Wells and Eissenstat, 2001 for details).

Most apple fine roots present in late October did not survive over winter (85% over-winter mortality in 1994-95; 81% in 1995-96; Fig. 2), and those roots that did survive were likely to be of larger diameter (Fig. 3). While roots less than 0.3 mm in diameter made up the majority of the fine root population in October of both years, only 3 to 12% of these roots survived until the following spring. Fine roots between 0.5 and 1 mm in diameter, while accounting for only 16% of the initial fine root population, exhibited approximately 50% over-winter survival in both years. As a result, the fine root population present in May of each year was enriched in larger diameter fine roots compared with the original October population. It should be noted that individual root diameters did not increase with time during the course of our study and that there was no evidence for woody secondary growth in any of the roots we observed.

Roots that survived overwinter also tended to be brown (Fig. 3). The development of brown pigmentation in roots is thought to be due to the accumulation of condensed tannins in root cortical cells, followed by cortical senescence and the persistence of the intact stele (Rogers, 1939; McKenzie and Peterson, 1995). Root pigmentation in apple has been observed to develop within 4 weeks of root production during the growing season, although browning may take considerably longer during the winter months. (Rogers, 1939; Head, 1969). While the onset browning has been used as a criterion for root death (see Wang et al., 1995), numerous studies indicate that brown roots are viable and capable of nutrient uptake (Crider, 1933; Chapman and Parker, 1942; Kramer, 1946; Atkinson and Wilson, 1979), although they are generally considered inferior to white roots in this regard (Head, 1966). Our proportional hazards regression analyses indicated that brown roots were less likely to die than white roots ($P < 0.053$ 1994-95; $P < 0.078$ 1995-96; Table 1), a phenomenon which is illustrated by the increased proportion of brown roots in the May fine root population.

Number of neighboring roots had a significant ($P < 0.0001$) positive effect on root mortality in 1994-95: roots with higher numbers of neighbors were more likely to die (Table 1). While regions of the soil with higher densities of roots also tend to be roots of smaller diameters, the statistical analysis used examines the effect of neighbor, controlling for root diameter. A significant relationship between number of neighbors and root lifespan was not observed in 1995-96. In 1994-95, there were a larger number of densely proliferated patches, and some roots had as many as 17 neighbors. It may be that the effects of neighboring roots do not become apparent until roots reach very high densities.

There was no significant production of new roots until after bud break and flowering in the both years of our study (personal observation). The production of flowers and the initiation of the next year's fruit crop occurred when the fine root system consisted predominantly of roots that had survived from the previous fall. While it is generally assumed that newly produced white roots are most competent at water and nutrient uptake, our results show that during a critical phenological stage (i.e. bloom and fruit set), the tree functions with a greatly reduced root system consisting primarily of brown, over-wintered roots.

The differences in survival reported here for fine roots of different diameters, colors and degrees of crowding underscore the heterogeneity of the fine root system and indicate that subsets of the fine root population may serve different physiological roles and experience different levels of risk of mortality. Functional differences among morphologically and demographically distinct groups of fine roots are an area of root biology that deserves further investigation.

ROOT EFFICIENCY

Defining Root Efficiency

Compared to leaves (Reich et al., 1997), there is only a limited understanding of factors controlling root lifespan. Root lifespan varies greatly with species and environmental conditions (Pregitzer et al., 1993; Watson et al., 2000). Yanai et al. (1995) described a cost-benefit model based on the efficiency of nutrient capture, where efficiency is defined as the ratio of nutrient gained (benefit) per unit carbon expended (cost). Maximum root efficiency would be the optimal root lifespan. Using this approach, roots are considered a population of individual modules of different ages, each with their own life history (Harper, 1977). In this way, the birth and death of individual roots may be a mechanism by which plants can more efficiently exploit the soil (Caldwell, 1979).

Root Costs

How much do root systems cost? One simple approach is to estimate annual dry matter production. Using whole-tree excavations, Fukuda *et al.* (1991) followed the biomass partitioning of 6-year-old 'Tsugaru' on M.9 rootstock for four growing seasons and 'Fuji'/M.9 for three growing seasons. The total annual dry matter production in 'Tsugaru' ranged from 5.5 to 8.7 kg tree^{-1} yr^{-1}. In 'Fuji', dry matter production ranged from 9.8 to 12.4 kg tree^{-1} yr^{-1}. Fruit production, expressed as a percentage of total annual dry matter production, was about 30% in both varieties the first year and about 65% in the last year. Fine root standing crop represented about 2-3% of this total. Assuming that the median lifespan (time required for 50% of the roots to die) of apple roots was about 4-6 weeks (Wells and Eissenstat, 2001; Eissenstat unpubl. data), then perhaps 6-10% of total annual dry matter production was associated with the fine roots.

Respiration of roots can also represent a substantial cost (Eissenstat and Yanai, 1997), although there is little information on how respiration varies over the lifetime of a root. One way to estimate root respiration is to measure the oxygen consumption of excised roots with a Clark-type oxygen electrode. We have found good agreement between the respiration of excised and intact apple roots when roots are measured within a few hours of excision (A. Volder and D.M. Eissenstat unpubl. data).

The age dependency of both respiration and elemental composition were determined on roots of the same trees described in section 2.2 ('Red Chief Red Delicious' on M.26 rootstock) (Bouma et al., 2001). Root segments of known age were extracted from root boxes buried in the soil containing an acetate window on the side of the box facing the tree. Apple root respiration was high when the roots were white and only a week old, but then declined rapidly with age (Fig. 4a). We can use these data to compare the amount of carbon respired over the lifetime of a root with the amount used in its construction (Fig. 4b). Apple roots cost approximately 42.3 mmol CO_2 g^{-1} dry wt. to construct based on elemental analysis of the tissue. Based on cumulative respiration with age and assuming a respiratory quotient of 1.1, by the time a root was approximately 14.5 days old, the plant would have expended as much carbon on root respiration as on root construction. If we assume that roots were not fully constructed until they were one week old, that all respiration during the first week was growth respiration, that growth respiration plus root C content estimated root construction costs and that respiration after 1 week was maintenance respiration, then it took 30 d in apple before the carbon used in maintenance respiration exceeded that used in root construction. Using either approach, clearly a substantial cost of roots is the respiration associated with their continued maintenance. A cost-benefit model of root turnover would therefore predict that roots in unfavorable soil or roots that have lost the ability to take up nutrients should not be maintained but instead replaced with roots more capable of water and nutrient uptake.

Root Benefits

One of the chief functions of a fine root is mineral nutrient acquisition. In order to evaluate the efficiency of a root system, one must therefore evaluate how well roots acquire nutrients over time. When a root first grows into new soil, nutrients have not yet been depleted. With time, uptake of nutrients at the root surface often exceeds the rate that nutrients diffuse through the soil solution to the root surface, creating a depletion zone of varying magnitude and breadth (Nye and Tinker, 1977; Barber, 1984).

The physiological affinity and capacity of roots to take up nutrient ions at the root surface can also change with root age. In various agricultural herbaceous species, nutrient uptake kinetics at different positions along root axes have been studied using labeled nutrient solutions (Clarkson, 1991). These studies show that ion uptake is not just restricted to the root zone behind the root tip but widely distributed over much of the root surface. Development of suberin lamellae and tertiary walls in the endodermis can restrict apoplastic movement of ions into the xylem.

Studies in trees that compare white roots with older, pigmented, and often woody roots generally indicate that white roots have faster rates of ion uptake (reviewed by Van Rees and Comerford, 1990). For example in cherry seedlings, potassium (^{86}Rb) uptake by white roots was 74% faster and phosphorus (^{32}P) uptake was 22% faster than that observed in pigmented roots (Atkinson and Wilson, 1979; 1980).

While clearly there can be a decline in nutrient uptake capacity as the fine roots get older, the shape of the decline with root age has never been defined. Recently, Bouma et al. (2001) examined the capacity of excised apple roots of known age to take up phosphorus (^{32}P) using the tea-bag technique (Epstein et al., 1963). Roots of all ages had fairly similar uptake kinetics with P saturation occurring at about 200-µM phosphorus concentration (Fig 5a). In order to plot P uptake as a function of root age, for any P concentration, we determined the age where maximum uptake occurred and then expressed uptake at any age relative to the maximum at that solution concentration. We then calculated the mean (±SE) of the relative P uptake over all P concentrations to derive a general relationship of P uptake with age (Fig. 5b). Uptake capacity was moderate when roots were first born, highest when roots were between 7 and 17 days old, and declined rapidly thereafter.

Diminished uptake capacity is only one factor that can influence P uptake by the root. Diffusion of P to the root surface can also limit P uptake, and this limitation may be greater for new roots that rapidly deplete P in the rhizosphere soil solution. The decline in P uptake as a function of root age was modeled (1) with no soil limitation, (2) with a soil limitation

determined using a solute transport model parameterized with soil characteristics of a relatively fertile Pennsylvania silt loam, and (3) with a hypothetical nutrient-poor soil where soil solution P concentration at the root surface declined linearly from a maximum value to zero in 50 days (Fig. 6; Bouma et al. 2001). In these simulations, P uptake from a Pennsylvania soil was only slightly reduced compared to that from soil with no P limitation. Most of the reduction in P uptake over time occurred because of reduced physiological capacity of the root (Fig. 5). However, when the soil became severely depleted in the 50-d depletion scenario, there was clearly a profound impact on P uptake. These simulations underscore the importance soil properties and soil P availability have on changes in P acquisition with root age.

Not included in this model was the influence of mycorrhizae on P acquisition, which can be substantial in apple (Covey et al. 1981; Plenchette et al., 1981). Unfortunately, it is not yet possible to quantitatively estimate the costs and benefits of a specific amount of mycorrhizal fungi with root age. However, we might speculate that the benefits of mycorrhizae might not compensate for their costs in the Pennsylvania silt loam because root acquisition of P is only slightly limited by diffusion in this soil.

Simulation of Root Efficiency

A cost-benefit approach can also be used to estimate daily and lifetime efficiency of single roots as a function of root age (Bouma et al., 2001; Fig. 7). Daily efficiency (mmol P/mol CO_2) is initially low because the daily costs of root respiration are high relative to initial root acquisition of P (Fig. 7a). Daily efficiency increases rapidly between 7 and 14 d and then continues to increase in the no-soil-limitation and Pennsylvania soil scenarios at a slow but steady rate. In the simulation where soil P is depleted linearly over a 50-d period, daily efficiency reaches a maximum when roots are about 10 d old and then declines quite rapidly thereafter as soil P is depleted (Fig. 7a). Lifetime efficiency never reaches a maximum in the first two simulations (no-soil-limitation and Pennsylvania soil); only in the soil where we imposed a linear depletion over 50-d did a clear maximum lifetime efficiency occur (Fig. 7b). This example illustrates the importance of using solute transport models to estimate rates of nutrient depletion around the root surface because of its importance on the simulated efficiency of nutrient capture. These results also indicate that diminished nutrient acquisition as roots age probably influence root efficiency more than changes in root respiratory costs.

EVIDENCE THAT APPLE MODULATES ROOT LONGEVITY TO INCREASE ROOT EFFICIENCY

General Patterns

The preceding section on root efficiency assumes that plants can shed roots when they become inefficient. However, roots are not shed in a manner analogous to leaves. No abscission layer is typically formed when a root dies, and the specific physiological controls over which roots die and which roots live are poorly understood (Eissenstat and Yanai, 1997). There is general evidence to suggest that plants exhibit coarse control over root longevity. For example, when apple trees are completely defoliated, substantial root death may occur within two weeks (Head, 1969a). Heavy fruit production has also been associated with high root mortality (Eissenstat and Yanai, 1997). Besides high shoot or fruit demand for photosynthate, apple may also exhibit finer control of root longevity caused by different levels of root efficiency in heterogeneous soil.

Localized Nitrate Addition

To maximize root efficiency, lifespan should be greater in fertile soil patches of otherwise infertile soil because root efficiency is higher where nutrients are more available. We tested this hypothesis using apple trees from open-pollinated seed of ‘Red Chief Delicious’(L. Wang, D.M. Eissenstat, D.E. Flores-Alva, A. Volder, unpubl. data). Seedlings were grown in the greenhouse in unsterilized soil medium in split-pot containers in a completely randomized design. Plants

either received uniform low nitrate (L/L; 1.6 mM; 0.1-strength Hoagland's N, supplied as 0.5 mM $Ca(NO_3)_2$, Hoagland and Arnon, 1939), uniform high nitrate (H/H; 8 mM; half-strength Hoagland's N, supplied as 3.5 mM $Ca(NO_3)_2$) or where initially half the roots receiving high nitrate and the remaining half receiving low nitrate addition (H/L) with six replications per treatment for each of four harvests. We purposely used unsterilized soil to increase the potential for soil organisms to feed on poorly-defended apple roots. Soil (Hagerstown silt loam) was collected directly from the orchard. Whole-plant growth rates were determined by destructive harvests, root growth and survivorship using mini-rhizotrons, specific rates of nitrogen uptake using ^{15}N, root respiration using gas exchange techniques and root construction costs by elemental analysis. These measurements were used to determine the daily efficiency of nitrate uptake for roots from different treatments.

Root efficiency was considerably higher for apple roots receiving high rates of N addition in one half of the split pot because root uptake increased to a greater extent than did root cost (Fig. 8a). Consistent with their increased efficiency, roots from the high nutrient side also had a longer median lifespan (Fig. 8b). The data suggest that a plant can extend the longevity of its most efficient roots, presumably by greater carbohydrate allocation and greater defense production for roots that operate at higher efficiency.

Localized Irrigation and Elevated Temperature

Apple control of root longevity to increase root efficiency was also exhibited in a field experiment where 'Red Chief Delicious' trees on M.26 rootstock were exposed to four soil treatments (D.M. Eissenstat, L. Wang, D.E. Flores-Alva, unpubl. data). Trees were about 2.5 m tall and planted at a 2-m spacing in a "Penn State four-wire low-hedgerow" trellis system with 3.7-m spacing between rows. Soil at this location is Hagerstown silt loam, a Typic Hapludalf. Apple trees had not been fertilized with either N or P for several years prior to the study. Soil (at the 5 cm depth) on one side of each of six trees was heated approximately 5^oC above ambient by circulating hot water from a water heater through the tubing [see Hillier et al., (1994) for technical details]. The other side of the tree was left unheated. Half of each root system (north or south side) was also allowed to dry using rainout shelters (1.8 x 1.2 m), while the other half was irrigated with about 10 mm of water once per week using a soaker line. Soil water content was monitored by time domain reflectrometry. During a dry period, soil water content was about 30-35% in the irrigated treatment and 20-25% in the non-irrigated treatment at 5-30 cm depths. All together, there were four soil treatments beneath each tree: 1) ambient temperature and irrigated, 2) ambient temperature and dry, 3) heated and irrigated, and 4) heated and dry. Temperature and moisture treatments beneath each tree were randomly assigned.

Root dynamics were measured with minirhizotrons as described previously (Wells and Eissenstat, 2001) with a total of 12 minirhizotron tubes per treatment. Root/soil respiration was measured every 2 weeks in each treatment (6 replicates per treatment) by trapping CO_2 evolving from the soil surface over a 24-h period in 20 cm^3 of 0.2 *M* NaOH solution and titrating with 0.1 *M* HCl and Thymol blue as a pH indicator (Raich et al., 1990).

During the dry period in August and September, root-soil respiration was somewhat faster in irrigated soil and at elevated soil temperatures (Fig. 9a). These data suggest that root carbon costs were higher for roots in the heated soil. Lower soil water content is associated with slower diffusion of nutrients to the root, and it is likely that nutrient acquisition was lower in the dry soil treatment. We would therefore predict root efficiency to be lowest in the elevated temperature-dry soil treatment and highest in the ambient temperature-wet soil treatment. Consistent with this prediction, root survival during the drought was highest in the ambient temperature-irrigated soil condition and lowest in the heated-dry soil condition (Fig. 9b). These patterns of root survival are again consistent with the hypothesis that the tree has some ability to maximize root efficiency by shedding inefficient roots and prolonging the longevity of more efficiency roots.

CONCLUDING REMARKS

Apple is noted for producing large quantities of fruit per hectare. Compared to other fruit crops,

apple fruit production apparently occurs with a low amount of root length. Apple trees exhibit efficient root dynamics, causing more nutrients and water to be acquired per unit carbon invested belowground. Assessing root costs involves estimates of root growth, longevity and respiration over the lifetime of the root. Nutrient uptake over the lifetime of the root can also be estimated based on soil nutrient transport models and an understanding of nutrient uptake kinetics over the lifetime of the root. Together, these data on root costs and benefits can be used to calculate root efficiency. Data are presented to illustrate how daily and lifetime root efficiency changes in apple based on how root physiology changes with root age. We hypothesize that within the root system of a tree, root longevity should be shortest for roots of low efficiency and longest for roots of high root efficiency. Patterns of apple root longevity in relation to soil nitrate availability, water content and elevated temperature are shown to be consistent with this hypothesis.

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Tables

Table 1. Results of proportional hazards regression[1] (SAS PROC PHREG) for root survivorship data collected in 1994-95 and 1995-96 (Wells and Eissenstat, 2001).

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-square	Pr > Chi-Square
1994-95					
Diameter	1	-2.262529	0.4169229.44979	0.0001	
Neighbors	1	0.068305	0.0142722.90875	0.0001	
Browning	1	-0.491416	0.25443 3.73041	0.0534	
1995-96					
Diameter	1	-2.003237	0.923994.700350.0302		
Neighbors	1	-0.044616	0.051630.746790.3875		
Browning	1	-0.535815	0.304273.101010.0782		

[1]PROC PHREG employs the method of partial likelihood (Cox 1972) to estimate the β coefficient (or "parameter estimate") associated with each covariate in a proportional hazards model and calculates a chi-square statistic used to test the null hypothesis that each β is equal to zero. When interpreting the results of a PHREG analysis, a negative parameter estimate indicates that increasing values of the covariate are associated with a decreasing risk of mortality. Likewise, a positive parameter estimate indicates that increasing values of a covariate are associated with an increasing risk of mortality.

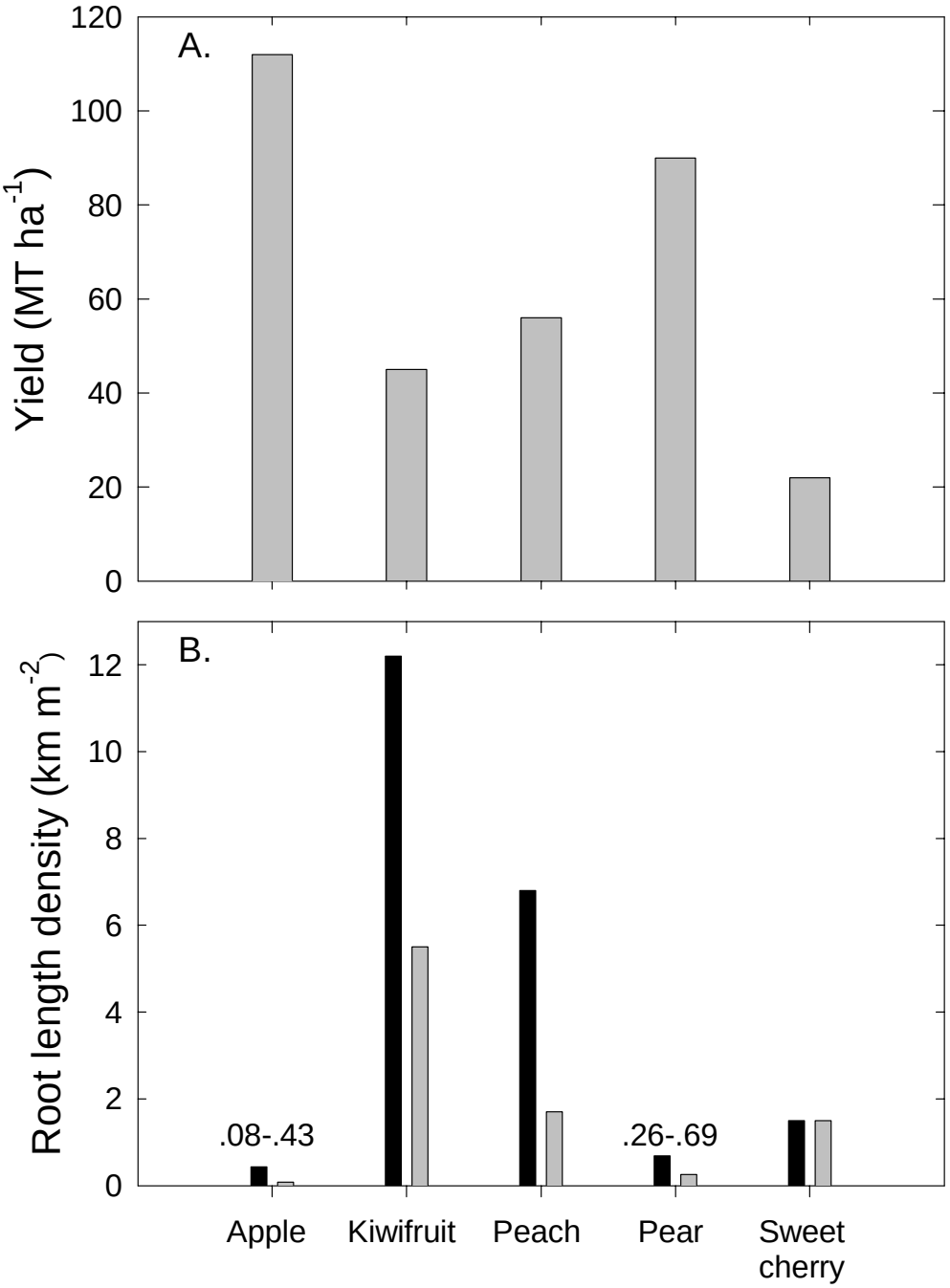

Fig. 1. Comparison of fruit production to root length in orchards of various fruit crops. A. Maximum sustained yields under ideal conditions of fruit crops (from Westwood, 1993). B. Maximum and minimum root length per unit orchard area at crop maturity (from Buwalda, 1993).

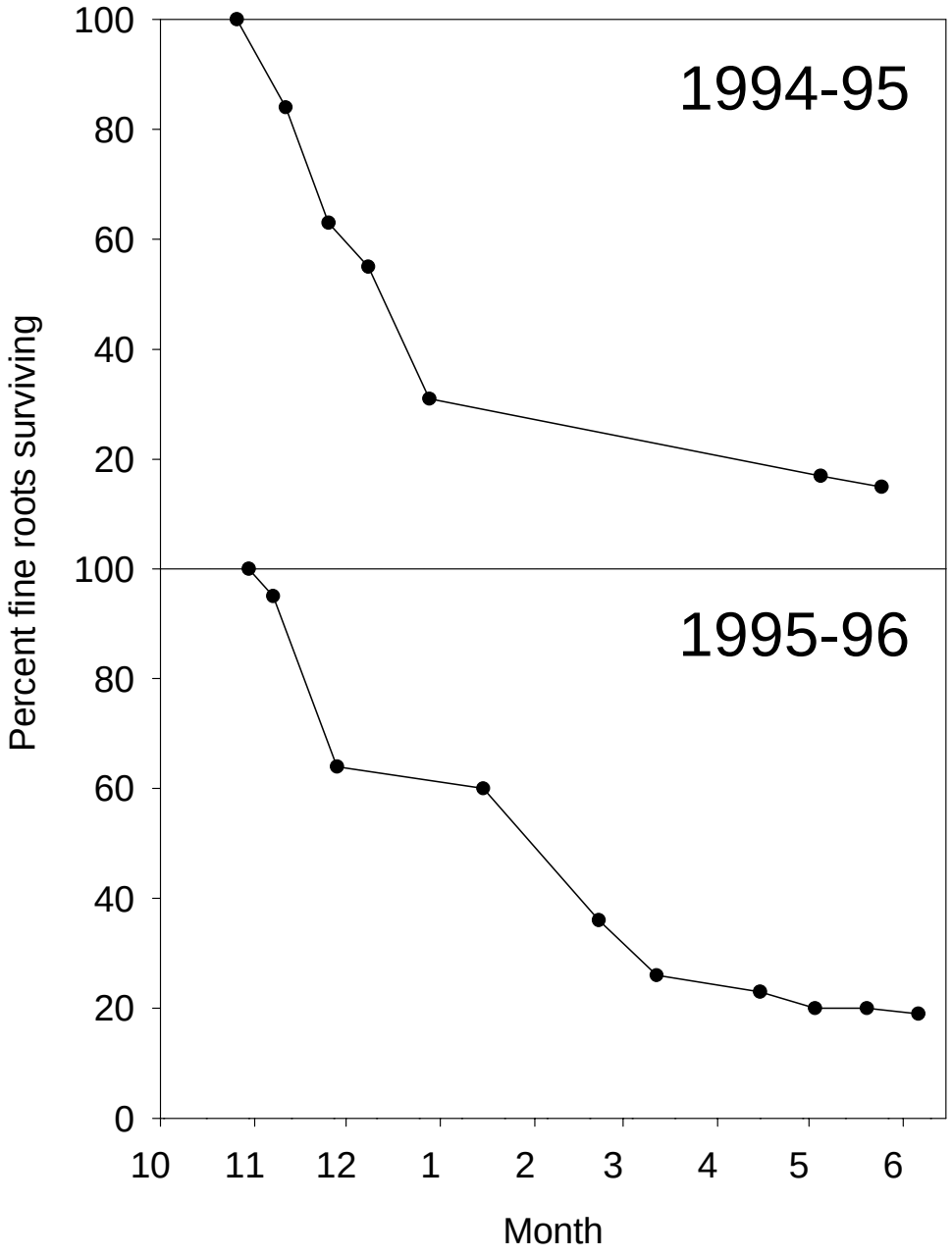

Fig. 2. Survivorship curves for the standing crops of apple fine roots present on October 26, 1994 and October 30, 1995 (adapted from Wells and Eissenstat, 2001). The percentage of fine roots surviving on successive minirhizotron sampling dates from October through May is shown.

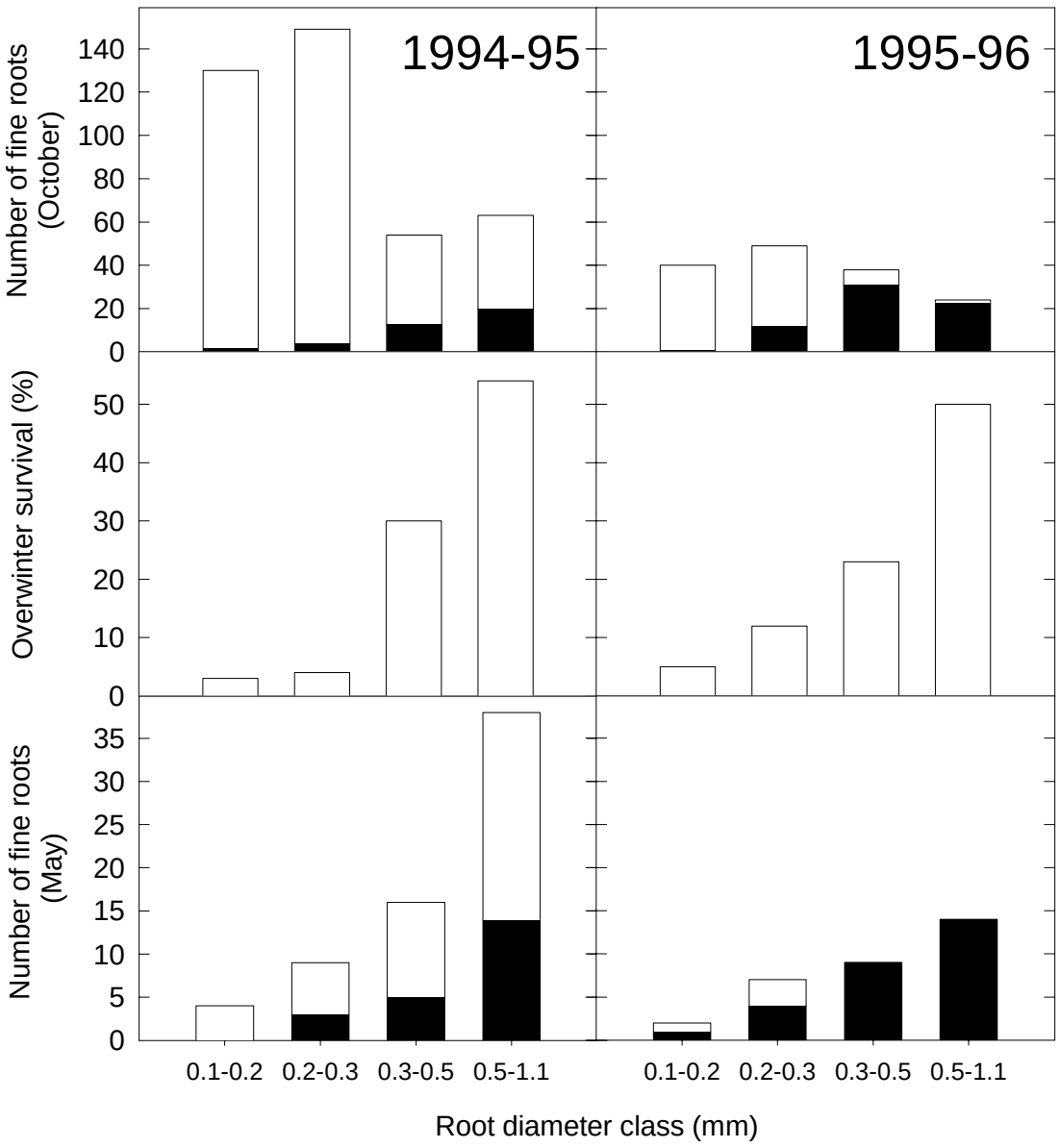

Fig. 3. A. Frequency distribution of fine roots from four diameter classes present in late October of 1994 and 1995 (adapted from Wells and Eissenstat, 2001). Dark portions of bars represent brown roots. B. Percent of fine roots from four diameter classes that survived from October through May in 1994-95 and 1995-96. C. Frequency distribution of fine roots from four diameter classes present in May of 1995 and 1996. Dark portions of bars represent brown roots.

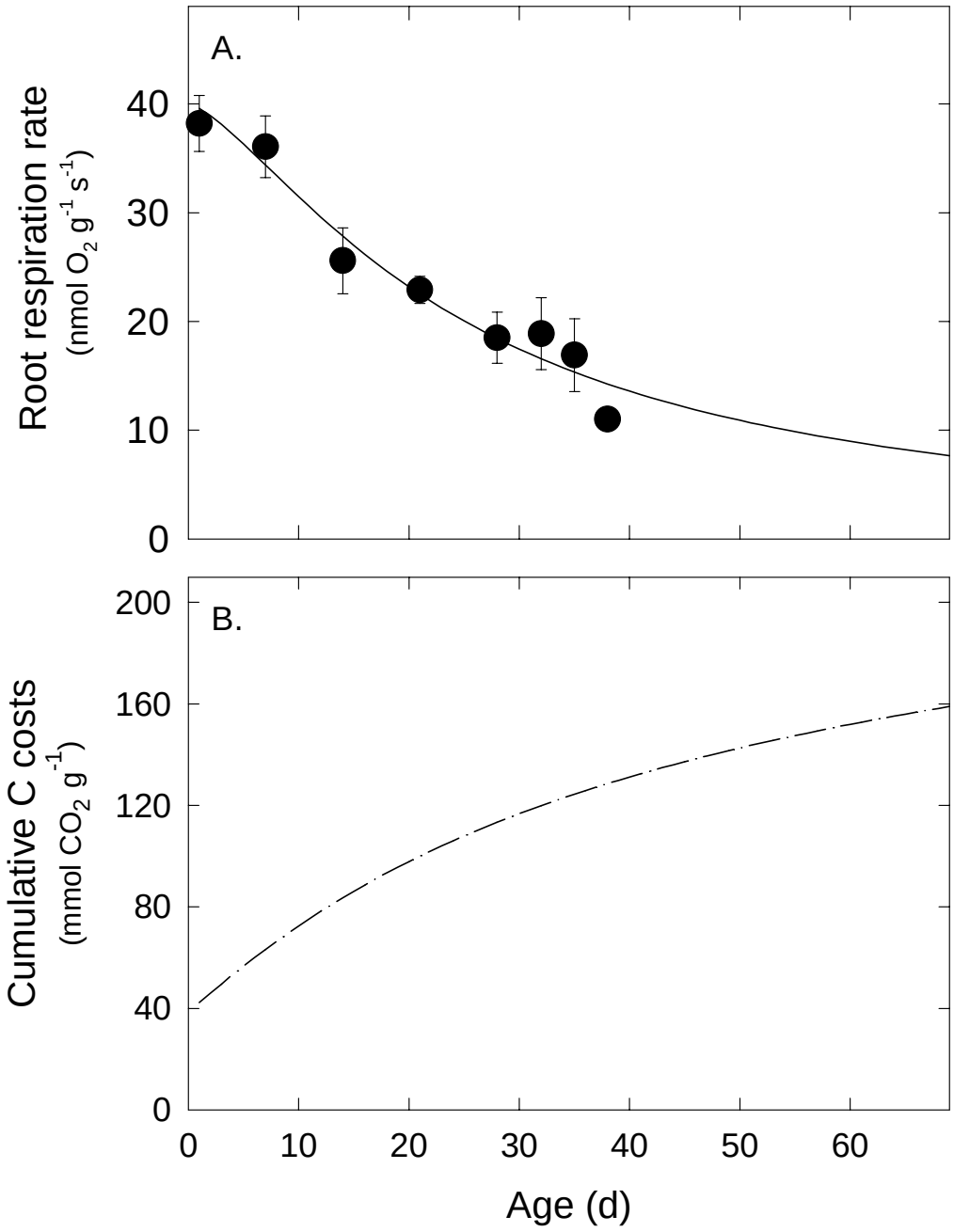

Fig. 4. Carbon costs as a function of root age in apple (from Bouma et al., 2001). A. Respiration rates (nmol CO_2 g^{-1} s^{-1}) (± SE) as function of root age (days). Respiration was measured on 1-cm excised root segments from mature trees, using a Clark-type electrode to determine O_2 consumption (r^2 = 0.95). B. Carbon costs (mmol CO_2 g^{-1}) were calculated by multiplying the respiration rate (nmol O_2 g^{-1} s^{-1}) as a function of root age with a respiratory coefficient (RQ) of 1.1 mol CO_2 [mol O_2]$^{-1}$, and then integrated over time.

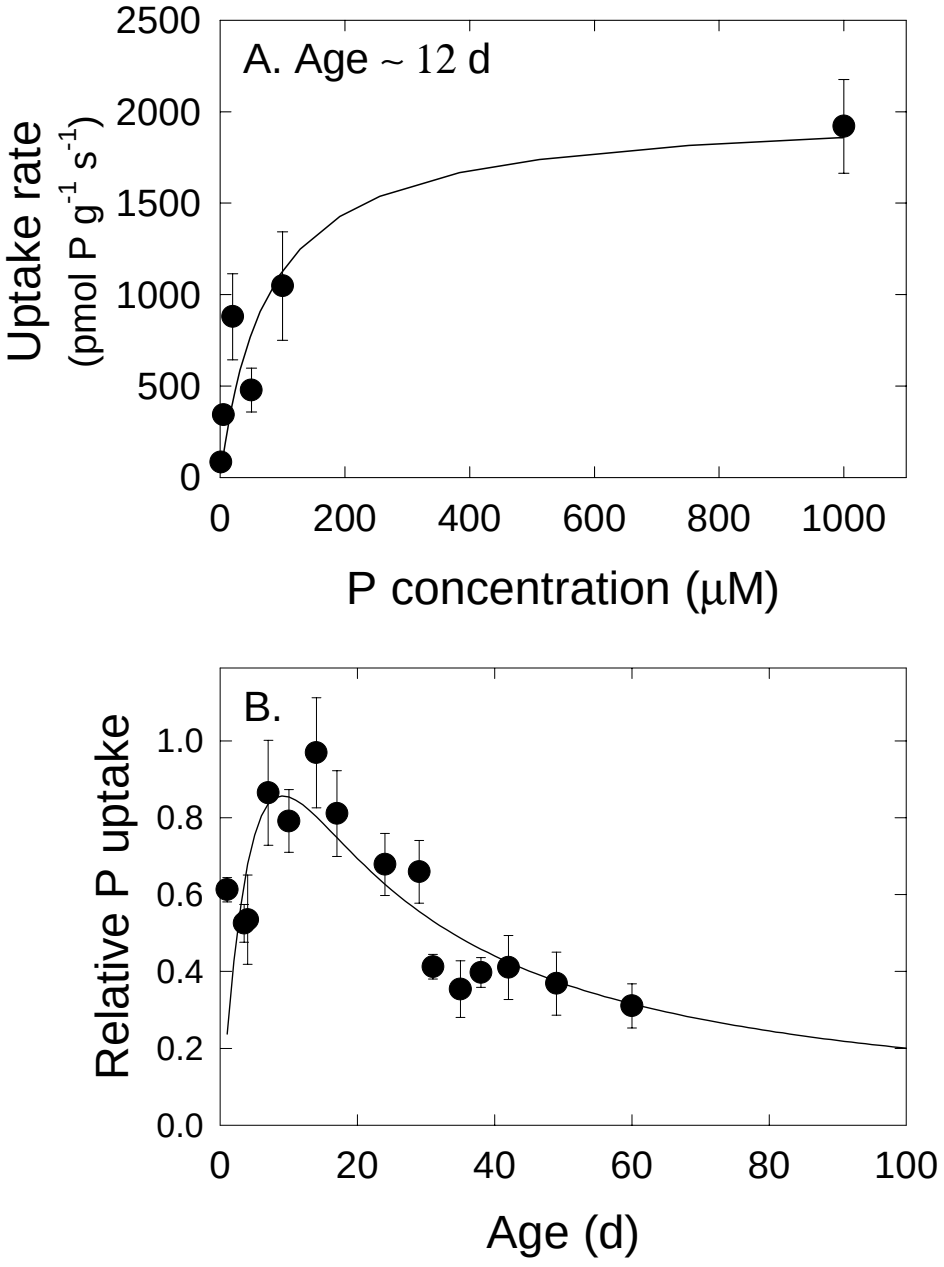

Fig. 5. Fig. 5. Phosphorus uptake kinetics and uptake capacity as a function of root age in apple (from Bouma et al., 2001). A. Uptake rates (pmol P g^{-1} s^{-1}) (± SE) as a function of the concentration of P in solution (µM). Average uptake rates were calculated by pooling roots about 12 days old. Data were fitted to the equation: $U_A = I_{max}$ x [P] x $(K_m + [P])^{-1}$, where I_{max} = 2001 pmol P g^{-1} s^{-1} and K_m = 77 µM (r^2 = 0.86). B. Relative rates of P uptake (U_R, -) (± SE) as function of root age (days). Uptake of ^{32}P was measured over a range of concentrations from 1 to 1000 µM, using 1-cm excised root segments from mature trees (r^2 = 0.60).

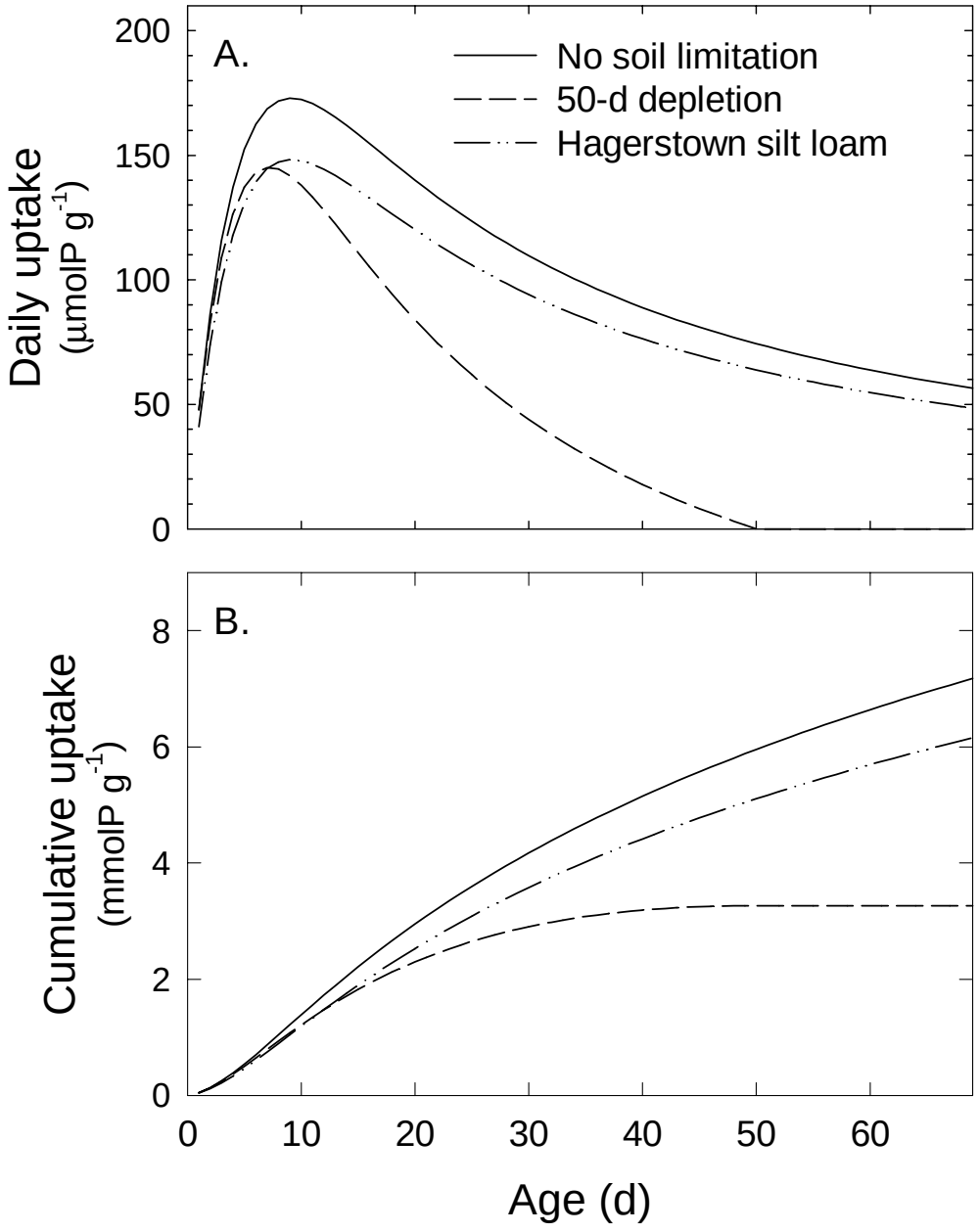

Fig. 6. Simulated phosphorus uptake of apple roots as a function of root age in (1) soil that was not limiting P diffusion, (2) soil assumed to be depleted at a linear rate over 50 days and (3) Hagerstown silt loam using a steady-state model of solute uptake (Nye & Tinker, 1977; Yanai, 1994) (from Bouma et al., 2001). The calculation of P uptake (µmol P g^{-1}) was based on the assumption that I_{max} (pmol P g^{-1} s^{-1}), which was determined for a single age class, changed with root age according to the curve fitted for the relative uptake rate (Fig. 5). The K_m (µM) was assumed to remain constant. Overall P uptake was obtained by integrating over time (days).

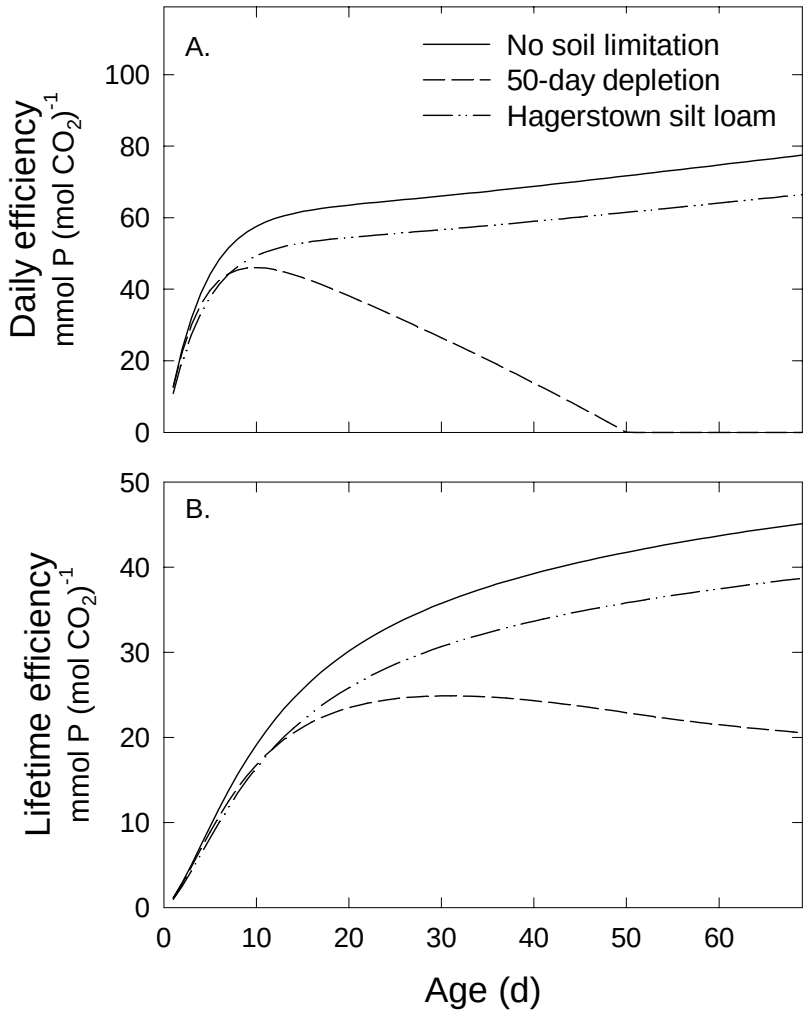

Fig. 7. Daily and lifetime root efficiency of apple roots in (1) soil that was not limiting P diffusion, (2) soil assumed to be depleted at a linear rate over 50 days and (3) Hagerstown silt loam using a steady-state model of solute uptake (Nye & Tinker, 1977; Yanai, 1994) (from Bouma et al., 2001). Root efficiency was based on the ratio of benefits (Fig. 6) to costs (Fig. 4). Optimal root lifespan is predicted to occur where lifetime root efficiency is maximized.

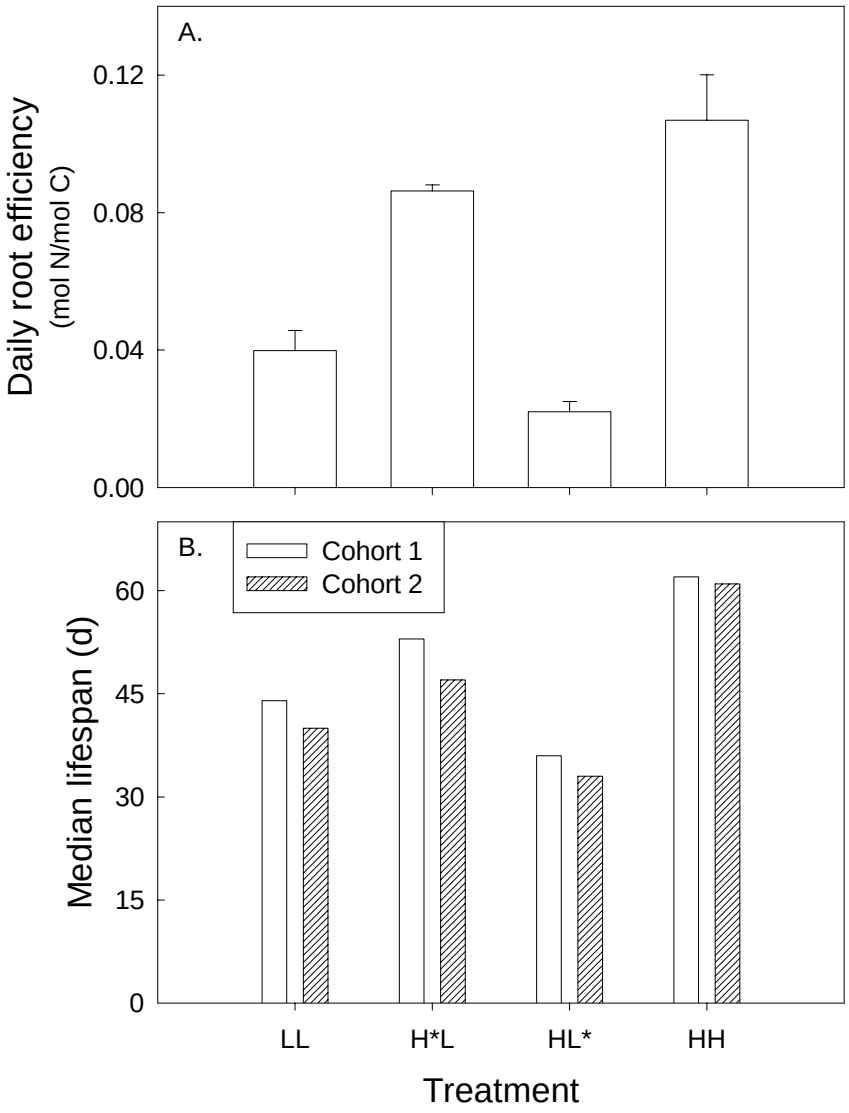

Fig. 8. Daily root efficiency of nitrate acquisition and median lifespan of apple roots grown in split pots (L. Wang, D.M. Eissenstat, D.E. Flores-Alva, A.Volder unpubl. data). Plants received either high (H; 8.0 mmol) or low (L; 1.6 mmol) nitrate-N twice weekly in each pot separately. Treatments were: 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). A. Daily 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-hr period of the pot head space). B. Median lifespan was determined for two root cohorts using minirhizotrons and a rigid boroscope. The first cohort represents roots born before the first harvest (112 days after transplanting, DAT) and the second cohort represents roots born between the first and second harvest (112 – 127 DAT).

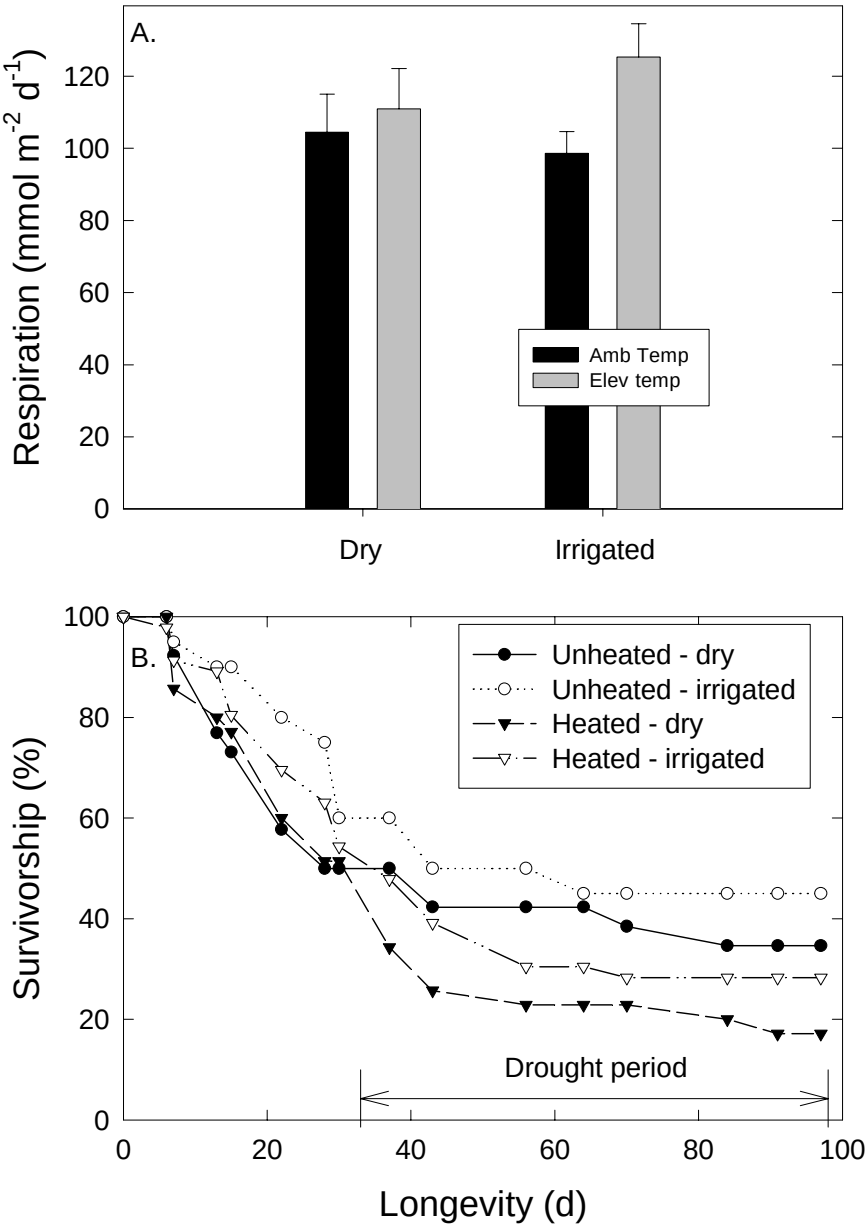

Fig. 9. Root/soil respiration and root survivorship of 'Red Chief Delicious' on M26 rootstock trees in an elevated soil temperature x drought experiment (D.M. Eissenstat, L. Wang, D.E. Flores-Alva, unpubl. data). Each tree was exposed to four different soil treatments: (1) heated soil (5 C above ambient at 5 cm soil depth) and irrigated; (2) heated soil and not irrigated; (3) unheated and irrigated; and (4) unheated and not irrigated. A. Root/soil respiration determined with a 24-alkaline trap during a drought period in August - September, 1997 (+SE). B. Root survivorship determined with minirhizotrons for roots born in June 1997. Period of drought indicated. Roots that had the highest respiration and the lowest nutrient uptake (because of dry soil) tended to have the lowest survivorship.