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Research review

Building roots in a changing environment: implications for root longevity

D. M. EISSENSTAT[1]*, C. E. WELLS[1], R. D. YANAI[2] AND J. L. WHITBECK[3]

[1]*Department of Horticulture and Intercollege Graduate Program in Plant Physiology, The Pennsylvania State University, 103 Tyson Building, University Park, PA 16802–4200, USA*
[2]*Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA*
[3]*Department of Ecology, Evolution and Organismal Biology, Tulane University, 310 Dinwiddie Hall, New Orleans, LA 70118, USA*

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SUMMARY

Root turnover is important to the global carbon budget as well as to nutrient cycling in ecosystems and to the success of individual plants. Our ability to predict the effects of environmental change on root turnover is limited by the difficulty of measuring root dynamics, but emerging evidence suggests that roots, like leaves, possess suites of interrelated traits that are linked to their life span. In graminoids, high tissue density has been linked to increased root longevity. Other studies have found root longevity to be positively correlated with mycorrhizal colonization and negatively correlated with nitrogen concentration, root maintenance respiration and specific root length. Among fruit trees, apple roots (which are of relatively small diameter, low tissue density and have little lignification of the exodermis) have much shorter life spans than the roots of citrus, which have opposite traits. Likewise, within the branched network of the fine root system, the finest roots with no daughter roots tend to have higher N concentrations, faster maintenance respiration, higher specific root length and shorter life spans than secondary and tertiary roots that bear daughter roots. Mycorrhizal colonization can enhance root longevity by diverse mechanisms, including enhanced tolerance of drying soil and enhanced defence against root pathogens. Many variables involved in building roots might affect root longevity, including root diameter, tissue density, N concentration, mycorrhizal fungal colonization and accumulation of secondary phenolic compounds. These root traits are highly plastic and are strongly affected by resource supply (CO_2, N, P and water). Therefore the response of root longevity to altered resource availability associated with climate change can be estimated by considering how changes in resource availability affect root construction and physiology. A cost–benefit approach to predicting root longevity assumes that a plant maintains a root only until the efficiency of resource acquisition is maximized. Using an efficiency model, we show that reduced tissue N concentration and reduced root maintenance respiration, both of which are predicted to result from elevated CO_2, should lead to slightly longer root life spans. Complex interactions with soil biota and shifts in plant defences against root herbivory and parasitism, which are not included in the present efficiency model, might alter the effects of future climate change on root longevity in unpredicted ways.

Key words: root turnover, root morphology, specific root length, elevated CO_2, climate change, root respiration, root herbivory, tissue density.

INTRODUCTION

Plants expend a substantial proportion of photosynthate below ground in the annual production of fine roots (Caldwell, 1987). Global change, and particularly increased atmospheric CO_2, is expected to affect rates of root production and decomposition, which might in turn influence the amount of C sequestered in soil. Root life span is highly variable, from a few weeks in some plants to a few years in others (Eissenstat & Yanai, 1997). Root longevity can also vary widely within an individual species. For example, median life spans of the citrus rootstock Volkamer lemon are typically about 150 d (Eissenstat

*Author for correspondence (fax +1 814 863 3371; e-mail dme9@psu.edu).

& Yanai, 1997), but can be as little as 16 d in the fall when populations of the root rot fungus *Phytophthora nicotianae* are high (Kosola *et al.*, 1995).

In cases where a specific root pathogen is present, the cause of root death can be readily identified. Unfortunately, under most conditions the factors that influence patterns of root mortality are poorly understood. Consequently we have only limited ability to predict how changes in climate might influence root dynamics and below-ground C sequestration.

In this paper we examine factors that might influence root longevity within individual root systems and among different species. Because the study of root longevity is often slow and labour-intensive, it is useful to identify more readily measured variables that might be correlated with root longevity, such as root diameter, tissue density and specific root length (SRL). Such patterns of correlated traits have previously been described in leaves. However, there are clear differences between the functions of fine roots and leaves that make an analogy imperfect, and these differences should be considered when taking a functional approach to understanding root life span. Last, we consider how changing climate and CO_2 might affect suites of root characteristics that are likely to influence root life span.

VARIATION IN ROOT TRAITS WITHIN ROOT SYSTEMS

One of the problems of comparing specific root length (SRL, length : d. wt ratio), diameter and tissue density (d. wt : turgid volume ratio) among species is that there is typically no control for root order (the position of a root within the branched hierarchy of the root system). Roots of different orders and diameters are likely to have different functional roles within the plant. Small-diameter, unbranched roots function primarily in water and nutrient uptake, while larger roots with many lateral branches might serve additional functions of transport, storage and lateral root production. The multifunctional nature of higher-order roots suggests that first-order roots might be most analogous to leaves, and that care should be taken to compare roots of similar order when relating root longevity to root morphology and physiology.

Both root order and root diameter can have strong effects on root survivorship (Table 1). In a 60-yr-old sugar-maple plantation, unbranched roots <0.25 mm in diameter had median life spans of less than 300 d, whereas unbranched roots >0.25 mm had median life spans of >600 d (Wells, 1999). The effect of branching order on root survivorship was also significant: among roots <0.25 mm in diameter, the median life span of roots with dependent laterals was 400 d longer than that of unbranched roots.

Root order was positively correlated with diameter and negatively correlated with N concentration (Pregitzer *et al.*, 1997, 1998; Wells, 1999). Maple roots harvested at this site had average tissue N concentrations of 18.5, 13.8 and 10.2 mg N g^{-1} d. wt for first-, second- and third-order roots, respectively, while SRL averages were 72.3, 46.5 and 27.1 m g^{-1}. Root respiration has been reported to increase with root N concentration in sugar maple (Fig. 2; Pregitzer *et al.*, 1998). These patterns are similar to those observed in leaves (Reich *et al.*, 1997), where longevity is negatively correlated with N concentration and respiration, and positively correlated with thickness and mass : area ratio.

INTERSPECIFIC VARIATION IN ROOT TRAITS

Parallels between roots and leaves

Leaves are more readily observed than roots, and theories concerning leaf life span are consequently

Table 1. *Results of a Cox proportional hazards regression performed on pooled root life span data* (n = *629*) *collected March 1997–1999 in a 60-yr-old sugar-maple stand*

Variable	df	Parameter estimate	SE	Wald chi-square	$P>$chi-square
Depth*	1	−0.25	0.13	3.49	0.06
Diameter	1	−1.76	0.55	10.28	0.001
Order	1	−0.78	0.30	6.76	0.01
Browning	1	−0.09	0.16	0.35	0.55
Fungicide	1	−0.38	0.17	4.69	0.03
Insecticide	1	−0.18	0.18	1.00	0.32
Fungicide × insecticide	1	−0.72	0.29	6.09	0.01

For details on use of Cox proportional hazards regression see Cox (1972); Allison (1995); Wells & Eissenstat (2000). Parameter estimates (β) can be interpreted as follows: for quantitative covariates such as diameter and order a one-unit change in the covariate is associated with a $100(\exp(\beta)-1)$ percentage change in the hazard of mortality, controlling for other covariates. For variables that can take on only one of two values, the ratio of the hazard of an individual coded '1' (e.g. added insecticide) to that of an individual coded '0' (e.g. no insectide) is $\exp(\beta)$, controlling for other covariates. The data were stratified by cohort in order to control for the effects of production date on the hazard of mortality.
*Depth interval was 0–25 or 25–50 cm.

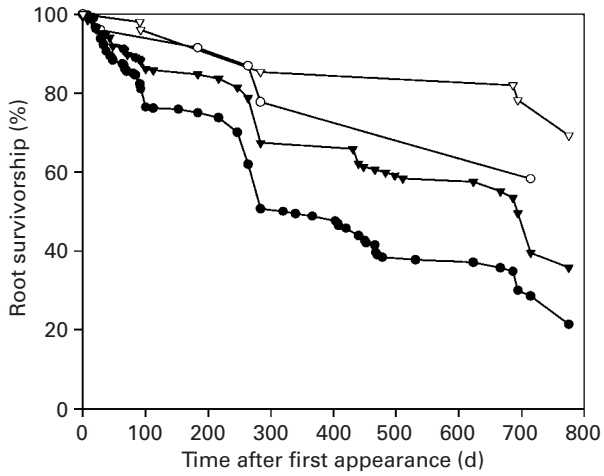

Fig. 1. Effects of root diameter and root branching order on root survivorship in sugar maple (from Wells, 1999). Each curve represents data from three trees, one tube per tree. Categories of diameter and order: roots <0.25 mm in diameter and first order (filled circles); roots <0.25 mm and higher order (open circle); roots >0.25 mm and first order (filled triangles); roots >0.25 mm and higher order (open triangles). Both order and diameter significantly affected survivorship (Table 1).

more advanced than those concerning roots. Parallels between leaves and roots are numerous. Both leaves and the finest roots of a root system are ephemeral and function primarily in resource acquisition, with lesser roles in storage, transport and support. Like leaves, most fine lateral roots exhibit determinant growth, extending only a few centimetres after emerging from the parent root. In woody plants most fine absorptive roots never undergo secondary thickening and do not increase in diameter with age (Eissenstat & Achor, 1999), making them more like leaves than twigs or branches.

By contrast with the hundreds of species for which leaf life span and associated morphological and physiological traits have been characterized, root life span and associated morphological traits have been characterized in perhaps only 10 species. Although technological improvements will increase this number, it is unlikely that the volume of data available for leaves will ever exist for roots. Thus, as a starting point, it is useful to refer to research on leaves when considering how root morphology might be linked to root longevity.

Leaves exhibit enormous interspecific variation in traits such as photosynthetic rate, respiration rate, life span, N concentration and specific leaf area (SLA), from 10- to 100-fold among species. For example, Reich *et al.* (1997) found that net photosynthesis, dark respiration, leaf N concentration and SLA were negatively correlated with leaf life span for 111 plant species from six biomes and for 170 species in a global data set: R^2 ranged from 0.62 to 0.88 using equations of the form $\log Y = a + b^*$ log(life span). The strong correlations are quite remarkable considering the differences in evolutionary history and selection pressures represented by these distantly related taxa from across a wide range of biomes.

Although there are few studies linking root morphology and physiology directly to root longevity, the limited data suggest that suites of correlated traits also exist in roots. For example, Reich *et al.* (1998) found root respiration and N uptake to be highly correlated with SRL among nine boreal tree species (Fig. 3). Nitrogen concentration and root respiration are also correlated both between (Reich *et al.*, 1998) and within a species (Pregitzer *et al.*, 1998) (Fig. 2). The morphology and physiology of leaves and roots might be closely coupled, such that roots that exhibit high SRL, high respiration, and high absorptive capacity are also short-lived (Eissenstat, 1992).

Specific root length, root diameter and tissue density

Specific root length is analogous to SLA, and is determined by the density of the root tissue and by the root length per unit root volume, which depends on the diameter of the root. Among citrus rootstocks, SRL has been positively correlated with root proliferation in disturbed soil (Eissenstat, 1991) and root hydraulic conductivity (Eissenstat, 1997; Huang & Eissenstat, 2000), and negatively with secondary wall thickening in the exodermis (Eissenstat & Achor, 1999). A well developed root exodermis has been linked to increased desiccation tolerance in onion (Stasovski & Peterson, 1993) and citrus (Eissenstat & Achor, 1999), and pathogen resistance in asparagus (Kamula *et al.*, 1994), but also to reduced root hydraulic conductivity in onion (Peterson & Waite, 1996) and citrus (Eissenstat, 1997; Huang & Eissenstat, 2000). However, variation in root longevity among citrus rootstocks was not strongly related to differences among rootstocks in SRL, tissue density or root diameter (Eissenstat & Yanai, 1997).

The lack of a relationship between root life span and other root traits in citrus might be partly due to the relatively narrow range of variation examined. Again, leaves provide a useful analogy. Within plant communities, where species could exhibit relatively similar traits, leaf life span might be poorly correlated with leaf morphology and physiology (Reich, 1993). But when broad gradients of species that vary widely in life span, SLA, leaf N concentration and net photosynthetic rate are compared, overall patterns can emerge (Reich, 1993; Reich *et al.*, 1997).

The importance of looking at traits that vary widely can be illustrated by comparing apple (*Malus*) and citrus, which differ dramatically in roots as well as fruits. The morphology of nonwoody apple and citrus roots was examined in rootstock trials where the same scion (shoot) was grafted to different

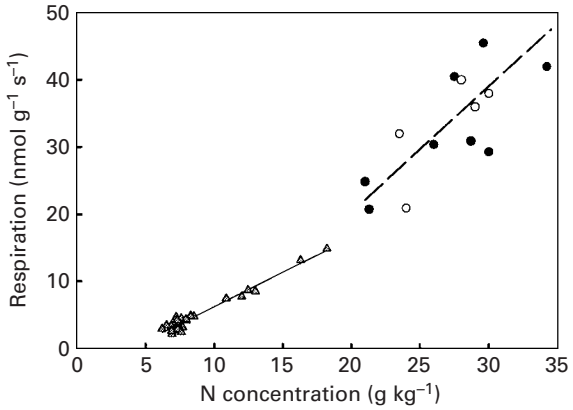

Fig. 2. Relationship of root respiration to root N concentration. Bottom curve (shaded triangles) shows sugar-maple roots of various diameter classes and soil depths collected from two sugar-maple forests (approx. 85 yr old) in northern Michigan, USA in late August (from Pregitzer *et al.*, 1998). Roots of smaller diameter and shallower depths had higher N concentrations. Respiration (O_2 consumption at 24°C) was determined using O_2 electrodes. Top curve, roots from seedlings of nine boreal species grown at either 5% (open circle) or 25% (filled circle) of full sunlight (from Reich *et al.*, 1998). Respiration (CO_2 evolution at 23.5°C) was determined with an infrared gas analyser.

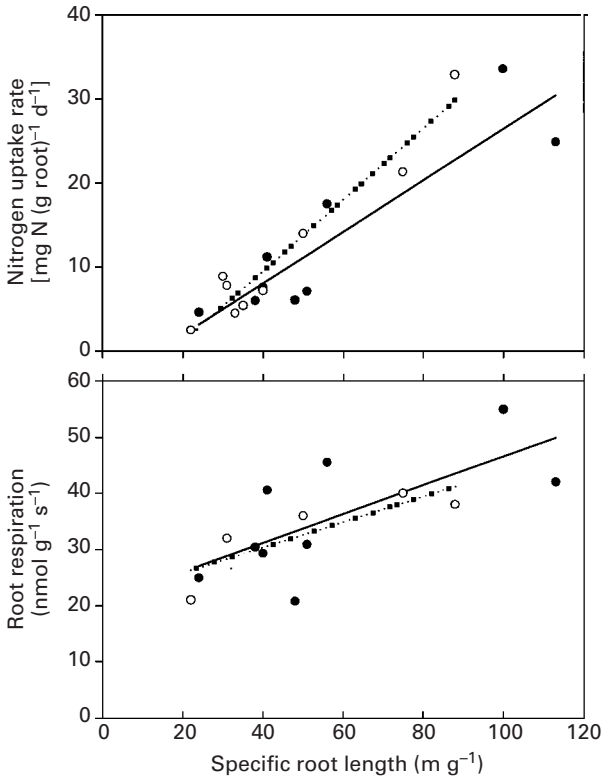

Fig. 3. Relationship of N uptake rate and root respiration to specific root length for seedlings of nine boreal species grown at either 5% (open circle) or 25% (filled circle) of full sunlight (from Reich *et al.*, 1998). Nitrogen uptake was determined by growth analysis of harvested plants. Root respiration was determined after keeping plants in the dark for 1 to several h, extracting plants from soil, separating the roots from shoot, and estimating root respiration (CO_2 evolution at 23.5°C) with an infrared gas analyser.

rootstocks. Citrus data were collected from four rootstocks that varied in SRL in a rootstock trial of approximately 17-yr-old Valencia sweet orange in Florida (Eissenstat, 1991; D. M. Eissenstat and R. Crawford, unpublished). The apple data were collected from three 11-yr-old 'Starkspur Supreme Delicious' rootstocks (Budagovski 9, EMLA 26 and domestic seedling) in Arkansas, Kentucky, Pennsylvania and Ontario (NC–140, 1996; J. L. Whitbeck and D. M. Eissenstat, unpublished). In apple, traits such as SRL, mean root diameter and tissue density showed significant plasticity in response to environmental conditions. For example, apple SRL was strongly affected by soil type in Arkansas, but not in Pennsylvania, whereas among citrus rootstocks, SRL in an organic medium or a sandy soil was generally similar (Fig. 4). Despite these differences in SRL plasticity between fruit crops, it is clear that apple rootstocks generally achieved much greater length per unit biomass than those of citrus (Fig. 4). In addition, tissue density and diameter were consistently less in apple than in citrus, despite the fact that apple exhibited fairly large variation in tissue density and root diameter among the different sites (Figs 5, 6). Consistent with their small diameter, and succulence and fragility, apple roots generally have much shorter life spans than those typical of citrus, except in conditions of high parasitism (Fig. 7).

Other workers have made limited species comparisons of root structure with root life span. Because the finest lateral roots, which often have the shortest life spans (Wells & Eissenstat, 2000), were not followed, the results of indirect methods used to estimate root longevity in the following studies might be somewhat inflated. It should also be noted that the physiology, morphology and longevity of different root orders were not independently determined in these studies; this might be critical in revealing potential relationships of root morphology to longevity in an interconnected, branched system of roots. Nonetheless, given the small number of studies that compare root morphology with longevity of different species, these observations are noteworthy.

In wet-tundra graminoids, tissue density (estimated by d. wt : f. wt ratio) was positively related to the maximum potential root life span (estimated by tiller longevity) and negatively related to root respiration (Table 2). The capacity for phosphate uptake (V_{max}) was not related to either SRL or tissue density. Diameter and SRL were not clearly associated with root physiology or maximum potential root life span in this group. *Eriophorum angustifolium*, the species with the coarsest roots, produces unbranched roots, by contrast with *Dupontia fischeri* and *Carex aquatilis*, which produce many fine, lateral roots off the nodal roots (Shaver &

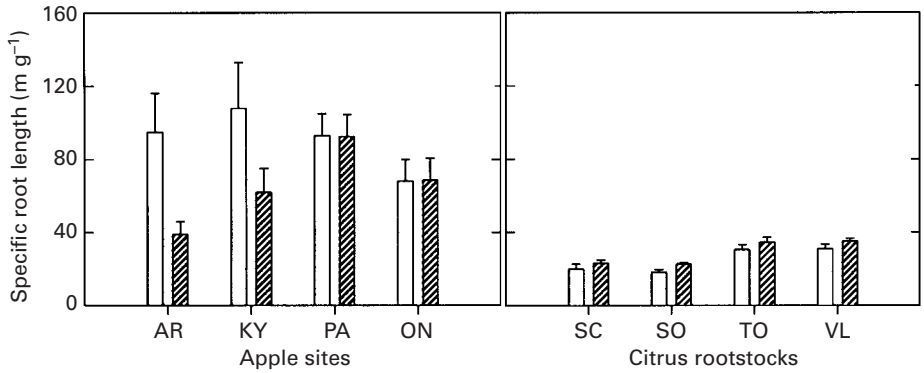

Fig. 4. Specific root length of apple and citrus. Apple roots collected from ingrowth containers were placed in the soil by each tree and filled either with surrounding topsoil of the site (soil, open bars) or fine quartz sand (sand, hatched bars). There were three to five replicate trees per rootstock for each location. Apple sites were Arkansas (AR), Kentucky (KY), Pennsylvania (PA) and Ontario (ON). Citrus rootstocks were Swingle citrumelo (SC), Sour orange (SO), Trifoliate orange (TO) and Volkamer lemon (VL). Ingrowth containers were placed in the soil in the spring and filled with either a high organic potting mixture (organic matter, open bars) previously observed to encourage root-hair development (Metro Mix 500 potting media, The Scotts Company, Marysville, OH, USA) or surrounding mineral topsoil (mineral soil, Astatula fine sand, hatched bars). For both citrus and apple, roots were sampled 8 wk after installing the ingrowth tubes. Bar, 1 SE.

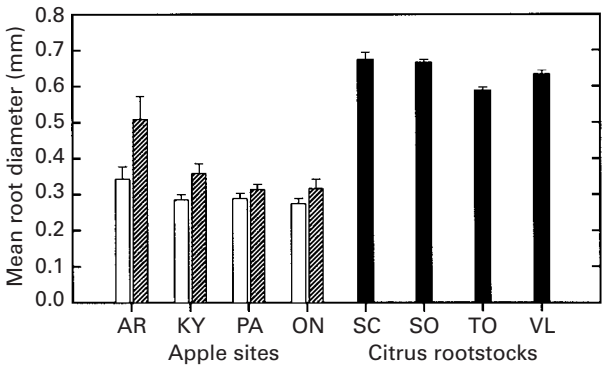

Fig. 5. Mean root diameter of apple and citrus. Apple roots were collected as described in Fig. 4 (open bar, soil; hatched bar, sand). Citrus data are from Eissenstat (1991). Rootstocks are as in Fig. 4. For apple, root diameter was determined with a desktop scanner and special software (DELTA-T SCAN, Dynamax, Houston, TX, USA). In citrus (solid bar), root diameter was determined with an ocular micrometer at 40 × magnification. Bar, 1 SE.

Billings, 1975). The longevity of these fine laterals was not followed. In wetland species where soil oxygen might limit species growth and survival, aerenchyma formation in the roots might confound potential relationships of root diameter and SRL with root physiology and longevity. However, the lack of a correspondence of root SRL with longevity and physiology might not be restricted to wetland species.

In other studies that have examined grasses and forbs of different potential growth rate, the primary factor associated with root longevity was found to be tissue density, not SRL or root diameter (Ryser, 1996; J. Crane, D. Wedin, P. Reich, T. Chapin and D. Tilman, unpublished). Indeed, Ryser (1996, 1998) argues that tissue density is much more important than SRL or diameter as a predictor of root life span. Specific root length might not be as useful as SLA in predicting root longevity and plant potential growth rate in leaves, because of the greater importance of transport in roots and the consequent importance of xylem vessel diameter (Ryser, 1998). For example, a doubling of xylem-vessel diameter will increase xylem conductive capacity about 16 times. In addition, thickness has a greater influence on SRL in roots than on SLA in leaves, because there is a linear relationship of thickness to volume in leaves whereas in roots the relationship is quadratic.

Table 2. *Interspecific variation in root morphology, respiration and longevity among three arctic graminoids*

Trait	*Eriophorum angustifolium*	*Dupontia fischeri*	*Carex aquatilis*
SRL (m g^{-1})	37.5	42.9	8.6
Root diameter (μm)	840	510	620
Tissue density* (g g^{-1})	0.11	0.15	0.27
Root respiration† (mg g^{-1} h^{-1})	4.9	3.7	3.0
Phosphorus uptake capacity‡ (pmol g^{-1} s^{-1})	97	53	92
Maximum root longevity (yr)	1	4–6	5–8

Data from Shaver & Billings, 1975; Billings *et al.* 1977; Chapin, 1978. SRL, specific root length.
*Estimated by the ratio of d. wt : f. wt. †Measured at 5°C. ‡Measured at 10°C on f. wt basis, corresponds to V_{max}.

If root diameter (thickness) is less directly related to organ longevity than tissue density, then SRL is less useful than tissue density for predicting root longevity (Ryser, 1998). However, from an evolutionary perspective, selection pressures in trade-offs between rapid acquisition and long life span should operate on SRL, not tissue density, if construction costs of tissue dry mass are similar, and root length or surface area more directly influence resource acquisition than mass or volume (Eissenstat, 1992). Otherwise, it is difficult to explain from a cost–benefit perspective why the finest roots of some plants are still relatively coarse. Other factors, such maintainence of a viable cortex through development of a well defined exodermis, probably play a role in determining both root diameter and root longevity.

It is premature to draw conclusions about the relative merits of diameter, tissue density and SRL as predictors of root longevity among species. Broader patterns of association might emerge from examination of a wider range of inter-species variation in these traits. Diameters of the finest root elements can range from 0.04 mm in some grasses, annuals and ericoid species to as much as 0.5–1 mm in species in the Magnoliaceae and Alliaceae (Fitter, 1991; Eissenstat, 1992). Variation in tissue density among species has not been as well characterized, but it includes a range of 0.06 g cm^{-3} in apple and 0.20 g cm^{-3} in sour orange (Fig. 6). To determine the potential of using easily measured parameters such as tissue density and SRL to predict root longevity, species that vary widely in root morphology need to be compared.

BIOTIC INTERACTIONS

Mycorrhizas are often associated with improved acquisition of nutrients, especially P. Mycorrhizal fungi colonize approximately 80% of all plant species, are extremely important to root function and might also help reduce the deleterious effects of

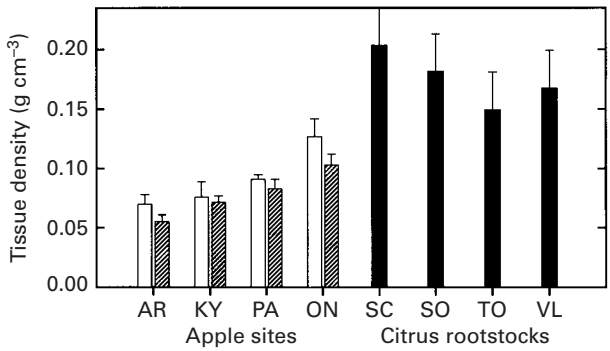

Fig. 6. Tissue density of apple and citrus. Apple roots were collected as described in Fig. 4 (open bar, soil; hatched bar, sand). Citrus data (solid bars) are from Eissenstat (1991). Rootstocks are as in Fig. 4. Tissue density was determined by dividing the length : volume ratio (calculated using root diameter and assuming cylindrical geometry) by SRL (length/d. wt). Bar, 1 SE.

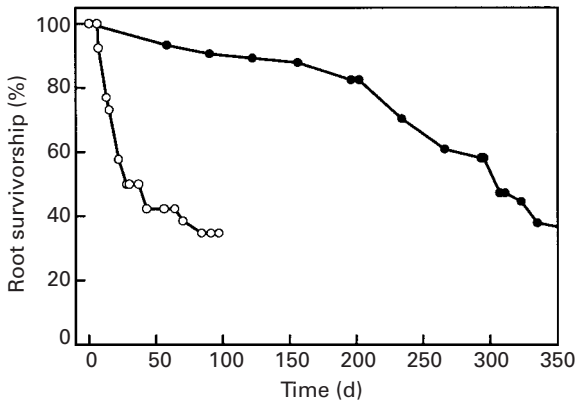

Fig. 7. Root survivorship in apple and citrus was determined with the mini-rhizotron technique. Apple root survivorship (open circles) was determined near State College, Pennsylvania, USA using 'Red Chief Delicious' on EMLA26 rootstock and a root cohort born in June (D. M. Eissenstat, L. Wang and D. Flores, unpublished). Citrus root survivorship (filled circles) was determined near Lake Alfred, Florida, USA using Red grapefruit on Sour orange rootstock and a root cohort born in April (D. M. Eissenstat, U. Hartmond and D. Flores, unpublished). Each curve represents data from six trees with two mini-rhizotron tubes per tree.

pathogens and herbivory on roots, independent of plant nutrition (Benhamou *et al.*, 1994; Gange *et al.*, 1994; Newsham *et al.*, 1995), and influence tolerance to drought (Espeleta *et al.*, 1999). By contrast, Hooker *et al.* (1995) found that vesicular–arbuscular mycorrhizal colonization decreased longevity of *Populus* roots. In citrus, we found that mycorrhizas improved root survivorship of surface roots after 15 wk exposure to dry soil in conditions where improved plant nutrition was not a possible explanation (Fig. 8). Mycorrhizas also decreased the SRL of fibrous roots in both top (droughted) and bottom (irrigated) pots, which might have influenced root tolerance to dry soil. Although the available evidence appears to favour improvement of root longevity by mycorrhizas, studies are too few to allow strong conclusions to be drawn.

Roots are surrounded by a matrix of soil organisms, in addition to mycorrhizal fungi, that might influence root function and survivorship in complex ways. We studied the effects of soil biota on root survivorship through the application of selective pesticides in a sugar-maple plantation. Each of four mini-rhizotrons around each of seven trees received a different treatment: chlorpyrifos insecticide (a broad-spectrum cholinesterase inhibitor; Dow Elanco, Indianapolis, IN, USA), metalaxyl fungicide (an inhibitor of protein synthesis in Oomycetes; Novartis, Greensboro, NC, USA), both pesticides, or a water control. We treated the soil around the tubes at monthly intervals May–October 1996–1998.

There was no significant effect of soil-insect suppression alone on sugar-maple root survival, while suppression of Oomycete fungi significantly increased root longevity (Table 1; Fig. 9). The

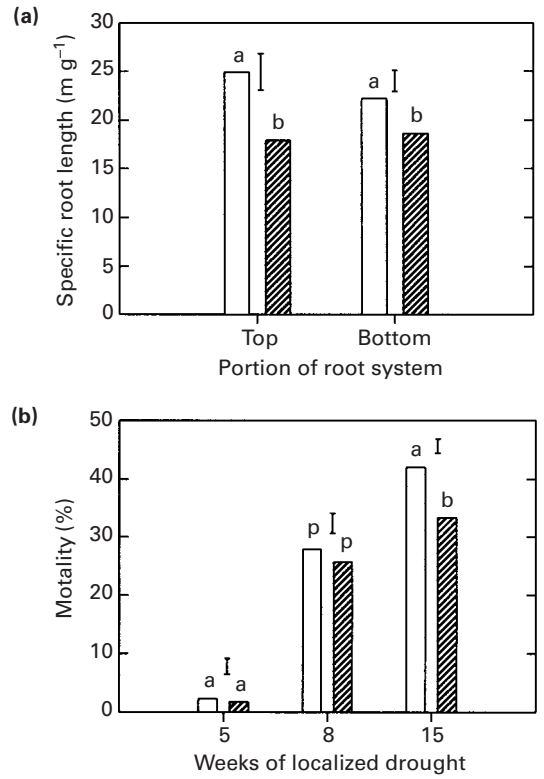

Fig. 8. The effects of vesicular–arbuscular mycorrhizas on (a) specific root length and (b) mortality of fibrous roots of 6-yr-old Red grapefruit on Volkamer lemon rootstock (from Espeleta *et al.*, 1999; hatched bars, mycorrhizal; open bars, nonmycorrhizal). Roots approximately 5 mm in diameter were excavated and fine laterals were removed, the surface of the woody root sterilized (NaOCl 5% for 2 min) and the root was passed through two vertically arranged plastic pots. A window in the upper pot enabled root longevity to be tracked. Pots were filled with autoclaved sandy soil (Astatula fine sand). Mycorrhizal roots were treated in the same way, but the soil was first inoculated with approximately 100 g air-dried fragments of mycorrhizal Sudan grass colonized by *Glomus etunicatum* and *Glomus intraradices*. Upper pots were allowed to dry for up to 15 wk, while the bottom pots were irrigated and fertilized twice weekly. Specific root length (SRL) was determined from roots harvested at 8 and 15 wk of localized drought. Means for SRL were compared by Duncan's test after analysis by two-way ANOVA. Root mortality (percentage cumulative dead to total length) was analysed by a paired *t*-test for each date. Different letters indicate differences significant at $P<0.05$.

combination of fungicide and insecticide increased longevity even further, more than doubling median life span over that of the control (Fig. 9). The pronounced interaction between insecticide and fungicide treatments suggests that the activities of soil insects and fungi might limit root life span in a synergistic manner.

Relationships among roots, mycorrhizal fungi, nonmycorrhizal fungi and insects have been shown to be extremely complex (Klironomos *et al.*, 1992; Klironomos & Kendrick, 1995a). In sugar maple, soil micro-arthropods can increase plant growth by preferentially feeding on the hyphae of nonmycorrhizal fungi, but can decrease plant growth by feeding on mycorrhizal fungi when other types of fungi are absent (Klironomos & Kendrick, 1995b). Some mycorrhizal-feeding micro-arthropods can increase in number following soil insecticide application, presumably because they benefit from reduced competition resulting from the death of more vulnerable organisms (Wilson *et al.*, 1995). Insect feeding might also provide wound sites through which fungal pathogens can colonize root tissue (Granett *et al.*, 1998). Application of pesticides undoubtedly altered a complex suite of below-ground interactions in this study, and the observed changes in root longevity represent a response to the sum of these alterations. Interactions with the soil biota can clearly exert a strong influence on root longevity, and the effects of climate on root turnover might be mediated through changes in the soil biotic community.

CLIMATE CHANGE, ROOT TRAITS AND ROOT LIFE SPAN

The effects of global atmospheric and climatic change on roots might be profound, but are difficult to predict. Some of the expected effects of global change on roots will be mediated indirectly through changes in shoot physiology. Increased C gain under elevated CO_2 might increase root length density, promote shallower root systems by stimulating lateral root production over primary root elongation, increase mycorrhizal colonization, and decrease tissue N concentrations, while at the same time whole-plant nutrient acquisition is increasing (Rogers *et al.*, 1999; Pritchard & Rogers, 2000; Tingey *et al.*, 2000). Roots can also be directly affected by changes in environment. Global temperatures are increasing, precipitation patterns are changing, and the availability of soil nutrients is expected to decrease (Rastetter *et al.*, 1997). Root mortality might be accelerated by decreases in soil moisture (Klepper *et al.*, 1973; Hayes & Seastedt, 1987; Huck *et al.*, 1987) or by increases in soil temperature (Fitter *et al.*, 1998). However, it might be reduced by decreased availability of nutrients (reviewed by Eissenstat & Yanai, 1997). The myriad effects that climate change could have on plants and their soil environment make simple predictions difficult. One approach is to examine how changes in the soil and atmospheric environment might affect root architecture, morphology and physiology, then use these traits to make predictions of root longevity using simulation modelling.

In theory, root longevity can be predicted through the analysis of the costs and benefits of constructing and retaining roots. The costs are calculated in units of C expended by the plant, and include growth and maintenance respiration. The benefits are calculated in units of the limiting nutrient taken up by the plant

(Yanai, 1994), or in water uptake if water is limiting. We define root efficiency as the ratio of benefit to cost, and the optimal root life span is that at which efficiency is maximized.

One limitation of this approach is the absence of physiological constraints in the model: for example, the optimal diameter of roots predicted to maximize nutrient uptake efficiency is infinitesimal (Yanai *et al.*, 1995). In addition, root herbivory and parasitism might truncate root life span below the optimal values (Eissenstat & Yanai, 1997); these influences are not readily incorporated into a cost–benefit analysis unless C allocation to root defence is predictably effective. Finally, the analyses presented here consider each of the possible influences independently, while interactions might well be important.

Temperatures are expected to increase by 1–3.5°C by the year 2100 (Houghton *et al.*, 1995). Respiration is sensitive to temperature, and we expect the optimal root life span to decrease when soil temperature increases (Eissenstat & Yanai, 1997). The magnitude of the transient response in respiration can be approximated using a Q_{10} of 2: each degree of temperature increase should cause respiration to increase by 7%. The increase in respiration due to soil warming is likely to be short-lived in many species, however, because plants can often acclimatize fairly rapidly to changes in temperature (Atkin *et al.*, 2000). In citrus, for example, a 5°C increase in soil temperature at a depth of 5 cm caused only a transient increase in root respiration and had no effect on root longevity (Bryla *et al.*, 1997; Eissenstat, 1998).

The other, opposing, influence on root respiration is the effect of changing N concentrations in roots. The magnitude of reduced N concentration in roots under elevated CO_2 is typically 10–25% (Rogers *et al.*, 1999). Because root respiration decreases proportionately with root N (Fig. 2), root respiration could also be reduced by 10–25%. This is similar in magnitude to the increase in respiration induced by soil warming, but it is likely to be lasting rather than transient. Using the construction and maintenance rates of citrus roots (Peng *et al.*, 1993) and an estimated relationship of P uptake with root age (Eissenstat & Yanai, 1997) we found that optimal life span increased by approximately 1 wk, or 10%, when we reduced root maintenance respiration by 25%. This prediction is consistent with the generalization that organisms with lower metabolic rates live longer. The magnitude of the effect is sensitive to the characteristics of the root, and could be more or less for other species in other limiting conditions.

Root length density will increase, and the average distance between roots will decrease, if the C allocation below ground increases in response to rising atmospheric CO_2. This response is related to the predicted decrease in available soil nutrients, as more nutrients are sequestered above ground (Rastetter *et al.*, 1997). We expect optimal life spans to increase if construction costs are high relative to maintenance, and uptake rates are low. The benefits of short root life span are reduced in soils of low fertility, because the benefit of growing into new soil is low. This effect should be amplified by the predicted increase in root length density (Williams & Yanai, 1996). In summary, our simulations predict modest increases in root life span resulting from both changes in C availability to the plant and changes in the soil environment.

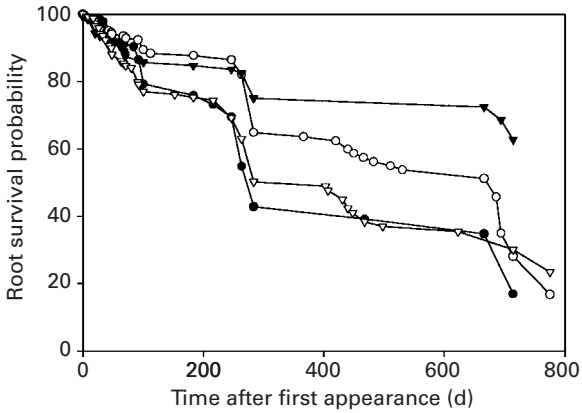

Fig. 9. Survivorship of sugar-maple roots following monthly drenches of metalaxyl fungicide (open circles), chlorpyrifos insecticide (closed circles), both pesticides (closed triangles) or the water control (open triangles) (from Wells, 1999). Survivorship was determined using the mini-rhizotron technique. Both the fungicide and fungicide + insecticide roots were significantly different from the control roots (Table 1).

Investigation of the theoretical optimal root life span is limited by the lack of age-dependent information on root uptake and respiration rates. Although woody and nonwoody roots have been compared, these data are not particularly useful in defining how the physiological activity of ephemeral roots changes with age. Recent investigations in apple, for example, indicate that P uptake capacity (V_{max}) decreases from 900 pmol g^{-1} s^{-1} in 2-wk-old apple roots to 300 pmol g^{-1} s^{-1} in 6-wk-old roots (T. J. Bouma *et al.*, unpublished). More information on how root respiration and uptake kinetics change with root age will improve estimates of optimal root life span. Whether elevated atmospheric CO_2 or changes in the soil environment alter the relationship of root physiology with root age is unknown, but the implications for root longevity could be substantial.

Another important unknown is the interaction of roots with the soil biota. Elevated CO_2 might increase mycorrhizal colonization (Tingey *et al.*, 2000), reduce root palatability by decreasing N concentration, and cause large changes in the soil biota (Zak *et al.*, 2000). As shown by the application of selective pesticides (Fig. 9), shifts in soil organisms can

profoundly influence root life span in a complex fashion. These effects would not be readily included in a cost–benefit model.

The relationships between root life span and simple metrics such as tissue density or SRL have some appeal for predicting the responses of root life span to climate change. However, interactions with soil biota could cause root life span in ecosystems to exhibit unforeseen responses to climate change not predicted by general relationships between root properties or models of root efficiency. More research is needed on the interactions of roots with the soil biota, even in the absence of changes in the global environment.

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