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The fate of surface roots of citrus seedlings in dry soil

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Abstract

The top portions of the root system of deeply rooted plants are frequently in dry soil while deeper roots still have access to water. We expected that many surface roots would be shed when subject to localized soil drying. We further hypothesized that the cost of fine root construction per unit root length would be negatively correlated with the rate at which root length is shed. Seedlings of four citrus rootstocks that varied widely in specific root length (cm g^{-1} root) were used to test these hypotheses. Plants were grown for 4 months in a split-pot system divided into a top and bottom pot. After roots were well established in the bottom pot, water was withheld from the top pots of half of the plants; plants were harvested every 2 weeks thereafter. Sufficient water was supplied to the bottom pot to prevent shoots of droughted seedlings from experiencing significant water stress. All plants were labelled with $^{14}CO_2$ 48 h before harvesting, and autoradiographs made of the fine roots harvested from the droughted compartment. Comparisons of the autoradiographs with digitized images of the root system allowed us to assess root mortality and root sink activity. As expected, the proportion of ^{14}C-labelled photosynthate allocated to fine roots in the top pot declined with soil drying in all four genotypes; however, there was no genotypic effect on this decline. Contrary to our expectations, extensive root mortality was not apparent for any genotype, even after 60 d of localized soil drying. Apparently, selection for rapid shedding of roots in response to soil drying has not occurred in these *Citrus* species.

Key words: Carbon allocation, drought, root death, split root, root autoradiography.

Introduction

Temporal variation in soil water and nutrient availability is greatest in the top portions of most soils. For deeply rooted plants, the top portions of the root system will frequently be in dry soil while deeper roots still have access to water. Despite the widespread occurrence of dry surface soil, few studies have examined carbon allocation and root mortality in roots subject to localized soil drying. How have plants adapted to spatial and temporal heterogeneity in water availability?

Studies of root mortality following imposition of drought on the entire root system have found evidence of increased root cortical cell death and increased root shedding (Jupp and Newman, 1987; Marshall, 1986; Stasovski and Petersen, 1991, 1993). Little information is available on patterns of root mortality following imposition of drought on only a portion of the root system. Increased root mortality of shallow roots of non-woody species under drought stress has been observed in uncontrolled field rhizotron studies (Huck *et al.*, 1987; Hayes and Seastedt, 1987). In controlled studies of root mortality in dry soil compartments (Ferrier and Alexander, 1991; Portas and Taylor, 1976) root viability has not been critically evaluated.

Root growth, unlike root death, has been examined in partially droughted root systems for a number of plants, either by design or due to a deep-rooted growth habit in the field. Root growth in drying surface soil or in dry root compartments has been observed to slow or stop, while root growth in the moist portions of the soil continued (wheat, Blum and Johnson, 1992; black walnut, Kuhns *et al.*, 1985; desert shrubs, Fernandez and Caldwell, 1975; peanuts, Meisner and Karnok, 1992; cotton, Klepper *et al.*, 1973; Taylor and Klepper, 1974; sitka spruce, Coutts, 1982; Ferrier and Alexander, 1991).

There are distinct costs associated both with maintaining existing roots in dry soil and with shedding

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existing roots and growing new roots when conditions become more favourable. If roots are not shed, carbon may be expended to maintain roots without any immediate benefit in terms of nutrient or water acquisition (see, however, Caldwell and Richards, 1989); shedding roots eliminates this maintenance cost, but forces the plant to assume the future cost of regrowing roots when soil conditions are more favourable. If plants act to optimize resource capture per resource expended for each root, there should be a balance between the integrated lifetime costs of maintenance and construction of individual roots and the benefits gained during the root's life-span (Bloom *et al.*, 1985; Caldwell, 1979). In this case, when the costs of maintaining roots in a region of dry soil exceed the costs of constructing new roots in moister soil, the roots in the dry region should be shed. This prediction is based on the assumptions that no immediate benefit is gained from maintaining roots in dry soil, and that there is no advantage gained in resource acquisition subsequent to rewetting by maintaining these roots. The life-span of individual roots would, then, vary with the costs of their construction and maintenance (Eissenstat, 1992).

The experiments described here were designed to test this hypothesis. We addressed two questions. First, how do root growth, root life-span and carbon allocation to fine roots change in roots of citrus seedlings exposed to localized soil drying? We monitored these parameters in a vertical split-root system, allowing the top portion of the root system to dry out while applying water and nutrients to the bottom portion of the root system; this allowed us to avoid whole-plant drought and nutrient stress. Root growth and life-span were assessed by destructive harvests and by direct observations of roots growing against transparent windows. Root viability was assessed by comparison of autoradiographs of ^{14}C-labelled roots with digitized images of the roots; we are not aware of previous use of this technique.

Secondly, does the response to localized soil drying vary among citrus genotypes with different specific root length (cm g^{-1} root)? Because construction costs (Williams *et al.*, 1987) per gram of fine root are similar among the four genotypes studied (Eissenstat, unpublished data), we hypothesized that the genotype with the highest specific root length would shed root length most rapidly.

Materials and methods

Plant material

This greenhouse study complements an ongoing field study in a 17-year-old citrus rootstock trial in Avon Park, Florida (described in Eissenstat, 1991). Cultivated citrus trees are grown as a compound plant, with a scion grafted on to a rootstock. In the rootstock trial, the same scion material (Valencia orange) was grafted on to 14 different rootstock genotypes. Four of these genotypes were selected for the greenhouse study described here: three evergreen types—Carrizo citrange (*Citrus sinensis* × *Poncirus trifoliata*), Swingle citrumelo (*Citrus paridisi* × *Poncirus trifoliata*), sour orange (*Citrus aurantium*)—and one deciduous type, trifoliate orange (*Poncirus trifoliata*). These genotypes span the range of specific root lengths of the fine roots in citrus.

Growth conditions

Plants were grown from seed in the greenhouse, and maintained as intact, ungrafted seedlings throughout the study. Because the embryos in citrus seeds are predominantly nucellar (produced by a type of apomixis), most seedlings are, effectively, clones of the parent plant, thus reducing genotypic variation in the experimental populations. Seeds were started in sterilized soil (Astatula fine sand, typic quartzipsamments) from the Avon Park site in 100 ml pots (Conetainers, Stuewe and Sons, Corvallis, Oregon, USA). The pots were placed directly on top of a 10 cm-deep bed of sterilized soil, so that roots could grow out of the pots and into the soil bed. After approximately 4 months, plants were transplanted into a double-pot system (Deepots, Stuewe and Sons, Corvallis, Oregon, USA) and allowed to grow until roots were well established in the bottom pot (Fig. 1). We used unsterilized soil from the rootstock trial in the double-pot system, so that the greenhouse and field experiments would be more comparable. The soil in our field site is very sandy (about 98% sand), with correspondingly low water-holding capacity (Fig. 2).

Plants were selected for uniform size (±1 s.d. from the mean height) and randomly assigned to two treatment groups. During the experiment, control plants received water and nutrients in both the top and bottom pots; partially droughted plants received water and nutrients in the bottom pot only. Plants received a diluted nutrient solution (Premier 10–10–10 with micronutrients, Growers Fertilizer Corp., Lake Alfred, FL) providing 10 mol m^{-3} N, 2 mol m^{-3} P, and 3 mol m^{-3} K twice per day in a volume sufficient to flush out the pots. The system was flushed weekly with water to prevent salt build-up. Plants were drenched with 50 ppm metalaxyl every 40 d to suppress infestations of *Phytophthora nicotianae*. Air temperatures in the greenhouse ranged from 21 °C to 38 °C; relative humidity ranged from 40–100% on a daily basis. Soil temperatures in the pots ranged from 21–35 °C.

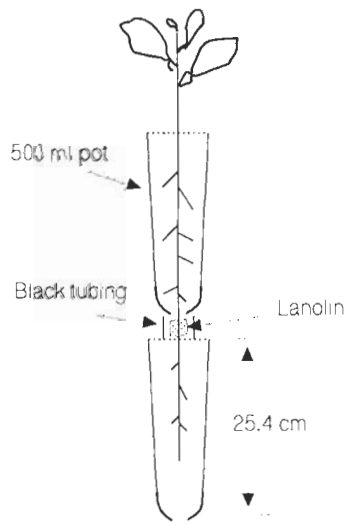

Fig. 1. Schematic diagram of the split-pot system.

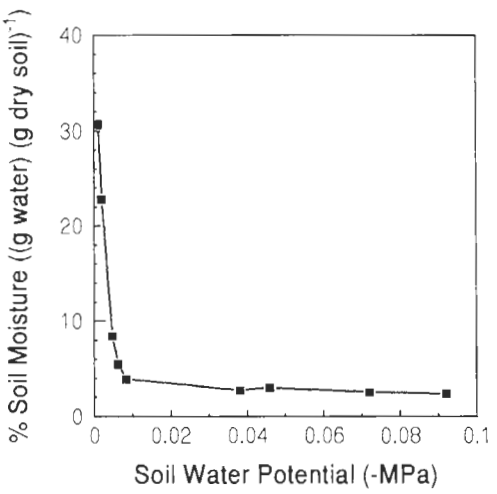

Fig. 2. Soil moisture release curve for soil used in this study: per cent soil moisture (w/w) as a function of applied soil water potential. Error bars are ± the standard error of the mean; small error bars are included within the symbol.

Experiment 1

Predawn leaf water potential: Predawn leaf water potential was measured about every 2 weeks with a Scholander pressure-bomb apparatus on leaves from three randomly chosen plants from the droughted and watered treatments for each genotype.

Growth and carbon allocation: Plants were harvested at regular intervals for assessing carbon allocation, root growth, and root death. Two days before harvesting, plants were labelled with $^{14}CO_2$ by exposing leaves to a 50 μCi pulse of $^{14}CO_2$ for approximately 10 min (Eissenstat *et al.*, 1992). At least four plants of each genotype were harvested each time. Soil samples were taken from the top pot of droughted plants to determine soil water content gravimetrically.

After harvesting, fresh roots were placed in a clear plastic cassette with an opaque back, and their digitized image recorded with a desktop scanner (H.P. ScanJet IIC). Roots were dried in the cassettes at 50 °C for 48 h and their image recorded again. Autoradiographs were then made of the dried fine roots from the top compartment by placing film (Kodak Xomat AR) in the cassette for 3 d. Comparison of the autoradiograph (Fig. 4A) with the image of the roots in the cassette (Fig. 4B) allowed us to determine if roots were acting as sinks for current photosynthate. Previous studies of root viability under drought typically involved microscopic examination of root sections for fluorescent nuclei after staining with acridine orange or other stains (Jupp and Newman, 1987; Ferrier and Alexander, 1991; Stasovski and Petersen, 1991, 1993; Lascaris and Deacon, 1991). Because of variation in cell permeability to the various stains and variable cell damage during sectioning, considerable care is required to avoid artifacts when using these methods (Wenzel and McCully, 1991). Autoradiography is less prone to artifacts, gives a view of the whole root system, and is fairly rapid, but does not provide information on the fate of individual cells.

^{14}C was measured on subsamples of the dried, ground fine roots from each compartment. Samples were combusted with a biological oxidizer (Harvey model OX300, Harvey Instrument Co., Hillsdale, NJ, USA, or Packard Tricarb oxidizer, Packard Instrument Co., Downers Grove, IL, USA), and the released $^{14}CO_2$ was trapped and analysed in a basic liquid-scintillation cocktail.

Root lengths were measured from digitized images using the program 'Rootlaw' (Pan and Bolton, 1991). The length of intensely labelled roots was measured from digitized images of autoradiographs by setting the program to read only the darkest pixels in the digitized image.

Statistical analysis of the data was done by analysis of variance, using the SAS GLM procedure (Freund *et al.*, 1986).

Percentage mycorrhizal infection: Randomly selected samples of fine root segments from the last harvest date were analysed for incidence of infection by vesicular-arbuscular mycorrhizae as described in Graham *et al.* (1991).

Experiment 2

Direct observation of root turnover: Plants were grown and transplanted into a double-pot system as above. The top pot had a viewing window where all roots within a 5 cm square were traced weekly. Roots were marked as dead when they disappeared from the window entirely or showed symptoms typical of decay (e.g. brown and translucent appearance). Except for brief periods when roots were traced, the window was covered with a flexible opaque plastic covering (Loretex T-4000, Research Plastics Inc.). We followed the cohort of roots produced in the 6 week period between transplanting and the start of the drought treatment for approximately 12 weeks in both watered and partially droughted plants.

Results

Time-course of plant and soil water status

In the droughted top pots, soil water potentials dropped below −0.1 MPa during the first 9 d of drought (Fig. 3). After this time, the soil was very dry, and could easily be poured from the pots when harvesting. Mean predawn

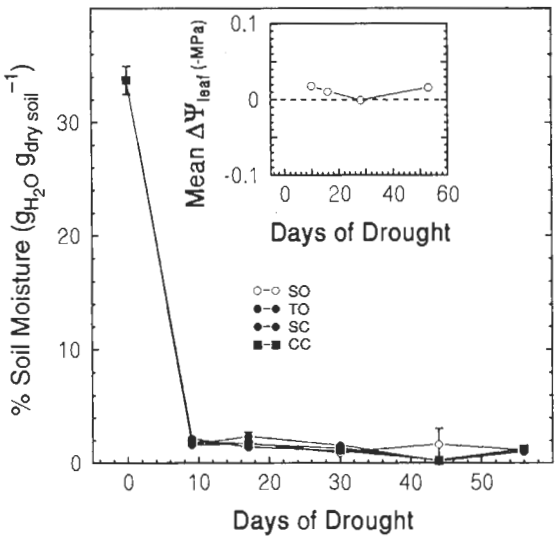

Fig. 3. Main graph: Relationship of per cent soil water content ($g_{water}g_{dry\ soil}^{-1}$; ±SE) in the top pot to drought duration (d). Comparison of these data to the soil moisture release curve for this soil (Fig. 1) indicates that soil water potential dropped from approximately −0.001 MPa to below −0.1 MPa during the first 9 d of drought for all genotypes. Inset: Mean difference in predawn leaf water potential (droughted plants − watered plants) as a function of drought duration.

Table 1. *Mean dry weight (g) for partially droughted and well-watered plants of each genotype at the last harvest date (±SE, n=4. * = significant difference between drought and water at P≤0.05; ** = significant difference at P≤0.1)*

Genotype	Treatment	Shoot wt.	Top pot fine root wt.	Bottom pot fine root wt.	Tap root wt.	Fine root wt. ratio (top/total fine roots)	Total plant wt.
Trifoliate	Drought	6.02±1.31	0.35±0.07	0.76±0.06	2.66±0.37	0.32±0.04*	9.80±1.88
	Water	5.28±0.88	0.36±0.06	0.46±0.07	2.16±0.21	0.44±0.05	8.26±1.15
Carrizo	Drought	7.63±1.09	0.35±0.04	0.81±0.14	3.95±0.42	0.30±0.03**	12.75±1.65
	Water	8.96±1.45	0.58±0.12	0.57±0.09	3.45±0.56	0.50±0.08	13.57±2.02
Swingle	Drought	9.91±1.67	0.46±0.07	0.75±0.15	4.35±0.75	0.35±0.04	15.46±2.14
	Water	13.30±0.83	0.71±0.10	1.09±0.19	4.93±0.50	0.40±0.06	20.03±1.40
Sour Orange	Drought	14.74±1.77	0.67±0.12	1.68±0.24	5.35±0.91	0.28±0.03*	22.44±2.98
	Water	14.18±1.57	0.92±0.06	1.14±0.23	4.00±0.49	0.46±0.06	20.25±2.22

leaf water potentials were typically greater than −0.4 MPa for the different species in both treatments. Seedlings in the partial-drought treatment had essentially the same predawn leaf water potentials as the watered control plants (Fig. 3 inset). Consistent with the absence of any difference in plant water potential, neither total root dry weight nor whole plant dry weight at the last harvest was significantly affected by the partial drought treatment for any genotype (Table 1, $P>0.1$).

Growth and carbon allocation

By comparing autoradiographs to images of the same roots made at the time of harvest, we determined that new, white laterals and root tips produced darker exposures on the autoradiographs than apparently older, more suberized roots (Fig. 4). This observation is consistent with increased sink strength associated with the carbon demands of growth and osmotic adjustment in the expanding portion of the root (Voetberg and Sharp, 1991). Roots that did not appear on the autoradiograph were intact, but inactive as carbon sinks, and were assumed to be dead. Direct measurement of ^{14}C in a sample of roots from the last harvest confirmed that roots which did not appear on the autoradiograph contained essentially no ^{14}C (data not shown). Little apparent root death was observed in harvests throughout the drought period (less than 1% at the first harvest date and 2%–8% at the last harvest date, as determined by comparisons of autoradiographs and root images; data not shown). In agreement with these findings, we observed little root shedding during a 12 week drought treatment in Experiment 2 (Table 2).

Root length in the top pot was not significantly affected ($P>0.05$) by the partial drought treatment for any genotype, with the exception of Swingle citrumelo at one date (Fig. 5A). Carbon allocation to roots in the dry soil decreased with increasing drought duration (Fig. 5B). There was no effect of genotype on this decline. The proportion of fine root weight in the top pot was significantly less in the drought treatment at the last harvest for trifoliate orange, sour orange, and Carrizo citrange (Table 1), a finding consistent with decreasing carbon allocation to fine roots in the dry soil. These changes in carbon allocation to fine roots in the top pot (Fig. 5B) were accompanied by significant declines in the portion of the root system that was intensely labelled (Fig. 5C). There were differences among genotypes in the rate of decline in intensely labelled root length (Fig. 5C), which may be explained in part by differences in quenching of beta-particle emission due to genotypic variation in specific root length.

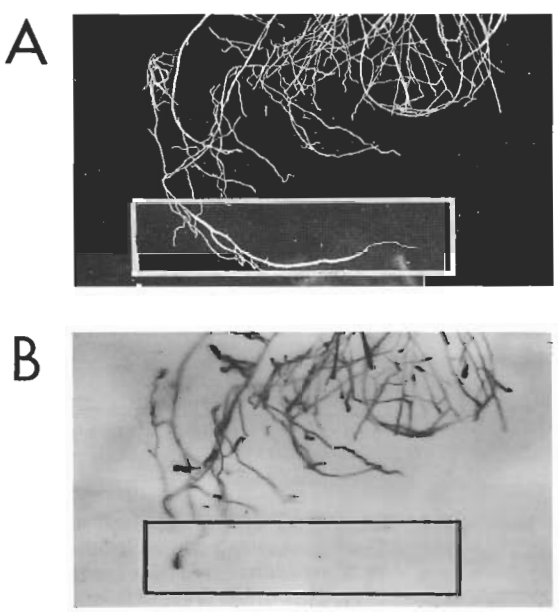

Fig. 4. (A) Image of a root system in the autoradiography cassette. (B) Autoradiograph of the same root system.

Table 2. *Percentage root mortality over a 12 week period for partially droughted and well-watered plants in Experiment 2 (number of roots in the observed cohort in parentheses)*

Weekly observations were made on roots growing against an acrylic window for 7 to 15 plants of each genotype.

Genotype	Mortality (%)	
	Watered	Drought
Trifoliate	4.3 (117)	1.8 (110)
Carrizo	14.0 (64)	2.5 (119)
Sour Orange	4.2 (189)	0.6 (157)

(±SE, n=4. Mycorrhizal infection

Roots from both the droughted and control plants were equally colonized by mycorrhizal fungi; the incidence of infection was greater than 80% for all genotypes except trifoliate orange (50% incidence—data not shown).

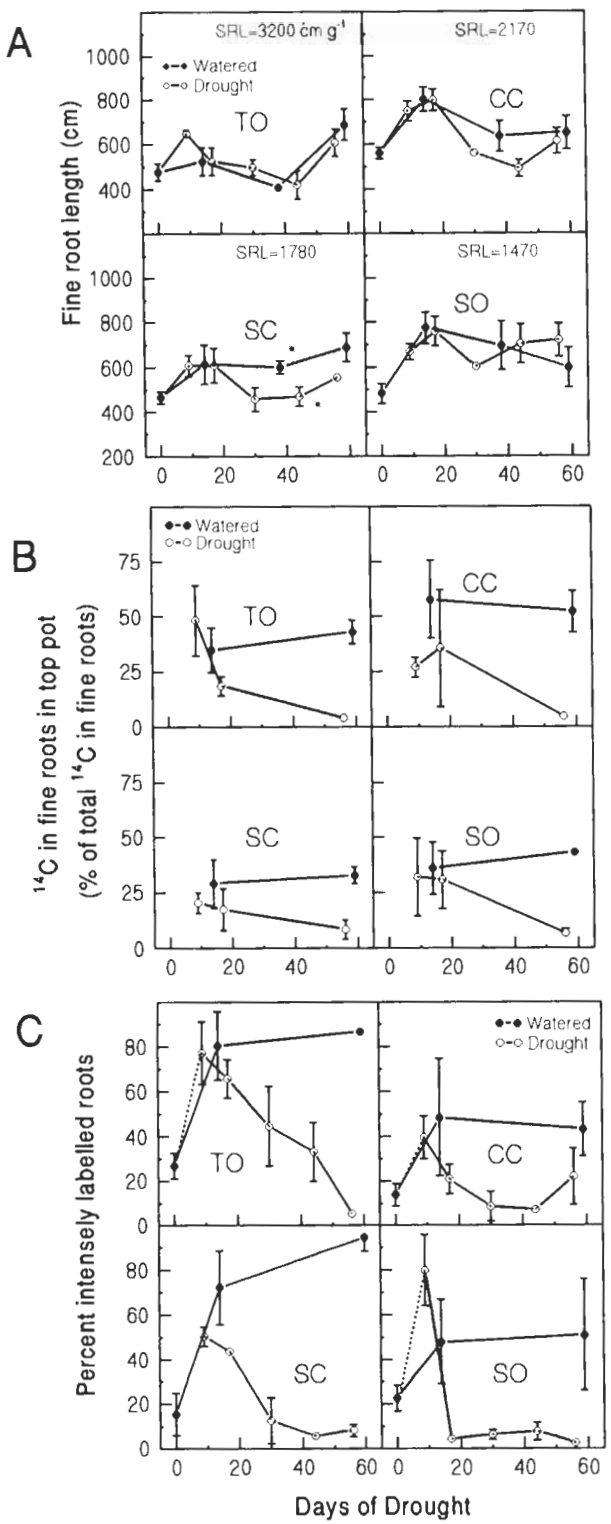

Fig. 5. Root length and carbon allocation as a function of drought duration in Carrizo citrange (CC), Swingle citrumelo (SC), sour orange (SO), and trifoliate orange (TO). Specific root length (SRL) values were derived from subsamples of roots from the last harvest. *Denotes differences that were significant at $P \leq 0.05$, Tukey's LSD. (A) Fine root length (cm, ±SE) in the top pot. (B) Ratio (±SE) of ^{14}C in fine roots from the top pot of the split root system to the total ^{14}C found in fine roots from both compartments. (C) Ratio (±SE) of fine root length that was intensely labelled (measured from autoradiographs) to total fine root length harvested from the top pot of the split root system.

Discussion

The most striking feature of this study was the notable lack of shedding of roots exposed to dry soil for over 60 d (Fig. 5A; Table 2). Our results clearly indicate that at least some plants with access to deeper soil supplies of water will not readily shed roots in dry surface soil. In Experiment 1, fine root length in dry soil remained similar to that in wet soil for the duration of the experiment (60 d; Fig. 5A). A small number of roots were harvested that did not act as carbon sinks, as indicated by the autoradiographs (Fig. 4). These roots, which comprised a relatively small portion of the root system, were either dead or supported metabolism with stored carbohydrates. In Experiment 2, little root turnover was observed in dry soil during the approximately 90 d drought treatment (Table 2); concurrent root shedding and regrowth are therefore insignificant factors in our analysis of growth patterns in Experiment 1. We are not aware of other studies that have critically examined root survivorship and carbon allocation under conditions of localized soil drying where leaf water status was not appreciably affected.

New white roots were occasionally observed growing in the dry soil throughout the drought period. There was, however, a large decrease in overall allocation of carbon to roots in the dry soil as the drought period continued past 20 d (Fig. 5B, C), accompanied by a decline in the proportion of fine root weight found in dry soil (Table 1). The shift in ^{14}C-carbon allocation was similar for all four genotypes we studied, and is consistent with the expectation that there was some degree of optimization in carbon allocation to fine roots. Root growth and carbon allocation patterns may have been influenced by the relatively small pot size used (Passioura, 1988), but this does not affect the conclusions drawn from the comparison between the droughted and watered treatments.

With declining carbon allocation to fine roots in dry soil, the rate of root respiration probably also declined. The respiration and growth measurements of Peng *et al.* (1993) indicate that integrated costs of maintenance respiration (less estimated costs of ion uptake) for roots of Volkamer lemon (mycorrhizal, high phosphate supply) would match the energetic costs of constructing those roots in approximately 22 d. Because root construction costs are similar among several citrus rootstock genotypes

(Eissenstat, unpublished data), this value may be taken as a rough guide for the expected time in which root construction costs are matched by maintenance respiration in the citrus genotypes we evaluated. If root maintenance respiration for roots in dry soil was to decline by an amount comparable to the observed decline of approximately 80% in percentage ^{14}C allocation (Fig. 5B), then the expected time at which maintenance respiratory costs equal construction costs would be increased from 22 d to 110 d. This contrasts markedly with the nodal roots of the desert succulent *Agave deserti*, which would require about 6.4 years for root respiration in dry soil at 20 °C to equal the costs of root construction (Nobel *et al.*, 1992). Clearly, the extent that root metabolism can be reduced under adverse conditions will affect tradeoffs between shedding and maintaining roots.

In deep-rooted plants, roots in dry soil may be able to acquire some nutrients due to the process of hydraulic lift (Richards and Caldwell, 1987, and references therein). Maintaining roots in dry soil may also be considered as an investment in future capacity for soil resource acquisition (Bloom *et al.*, 1985; Lerdau, 1992). In a competitive soil environment, plants that do not maintain the capacity to acquire water and nutrients rapidly from soil that becomes rewetted after a drought period may lose those future resources to other plants. Additionally, nutrient availability would be expected to be greatest immediately after a precipitation event in a seasonally dry soil, due to the increase in mineralization. In habitats where drought is normally a temporary phenomenon, *rapid* shedding of roots in response to drought, consequently, would not be advantageous.

Perennial plants that shed roots rapidly in response to soil drying should be found in habitats where prolonged drought is common (e.g. the desert succulent, *Agave deserti*, which grows new roots rapidly after rain, and then sheds them when the soil dries again; Huang and Nobel, 1992). We cannot readily make such predictions based on the native habitats of citrus species. Citrus has been cultivated for so long in China and north-east India, the presumptive centre of origin for citrus (Gmitter and Hu, 1990), that we do not know the pre-cultivation evolutionary conditions for the genotypes we studied. Drought frequency and duration would depend not only on rainfall patterns, but on local topography; topographic relief in the presumptive centre of origin is substantial.

Seedling fine roots may not necessarily respond to localized soil drying in the same manner as the fine roots of mature trees. Because of the multiple roles seedling roots may play in resource capture, structural support, and transport of water and nutrients, local conditions of resource availability may not be the predominant factors determining the fate of any given root. It remains to be seen if fine roots of mature trees are substantially different from the fine roots of seedlings in response to localized soil drying.

In conclusion, we found that the roots of citrus seedlings will tolerate prolonged periods of dry surface soil. There is, however, a reduction of about 80% in carbon allocation to surface fine roots exposed to localized soil drying.

Acknowledgements

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