

Modeling Carbon Allocation below Ground

David M. Eissenstat and Xuming Huang
Department of Horticulture
The Pennsylvania State University
University Park, PA
USA

Alan N. Lakso
Department of Horticultural Sciences
New York State Agricultural
Experiment Station
Cornell University
USA

Keywords: *Vitis labruscana*, *Citrus*, Concord grape, citrus, root growth, root respiration, root mortality, minirhizotrons

Abstract

Belowground carbon expenditure has been difficult to measure, and even more so to predict. Root growth is influenced by both direct effects on plant metabolism and indirect effects of soil drying and interactions with soil organisms. In Concord grape, crop load may compete with root growth when soil moisture is not limiting. Root lifespan also is difficult to predict but some success can be achieved by taking a cost-benefit perspective to unraveling some of the processes affecting root lifespan. Root respiration is affected by both short- and long-term temperature conditions. Short-term studies suggested that elevated soil temperature may have direct effects on root respiration that follow a Q_{10} response of about 1.7 - 2. More recent work indicates that plant respiratory responses to soil temperature may be a function of plant growing temperature and soil moisture. Citrus and grape roots exposed to increasing temperatures above 20 °C for more than three days exhibited homeostatic respiratory responses, presumably to avoid excess carbohydrate metabolism. Moreover, citrus roots in dry soil exhibited no temperature response but maintain respiration at a stable basal rate.

INTRODUCTION

Growth models in most crops, but particularly field crops, have largely ignored the factors controlling belowground carbon allocation. Environmental and cultural factors can strongly influence allocation to roots and mycorrhizal fungi. Seedling studies in citrus, for example, indicate that mycorrhizal colonization, soil temperature, plant age and soil moisture and phosphorus limitations all can influence the fraction of total photosynthate used for root growth and maintenance (Eissenstat et al., 1993; Kosola and Eissenstat, 1994; Bryla et al., 2001). Much less work has been done in bearing fruit trees in the field, which will be the focus of this review.

Carbon allocation belowground is influenced by both the demands of the shoot for water and nutrients and the demands of the roots for photosynthate to provide the energy for maintenance of the tissue. Root:shoot communication is not well understood but the manifestations of resource limitations above- or belowground on allocation are widely reported. In modeling belowground allocation, many of the responses are not linear and should be considered in this context. Moreover, most studies on root:shoot allocation have been conducted using young plants in pots. Seedling responses to resource limitations may be quite different from bearing trees. For example, in a perennial root system, the amount of roots available for water and nutrient absorption is a function of both root birth and root death. Root mortality has rarely been studied in the context of resource availability and carbohydrate competition between roots and shoots.

An important first step in developing a predictive model is to have some notion of the patterns of the processes that are being modeled. In the case of root growth, root mortality and root respiration, few observations exist of these processes in relation to crop load, pruning and environmental stresses. Recent research in citrus and grape have provided some important new observations of these processes which should aid in modeling the amount of carbon allocated below ground.

ROOT PRODUCTION

Root production represents the initiation of new roots and the extension and radial growth of existing roots. Root production is a function of both availability of carbohydrates and mineral nutrients to sustain root growth and the presence of the mix of soil environmental conditions favorable for root growth. As soils dry, soil impedance typically greatly increases, which often presents a barrier to root growth, especially of the fine lateral roots. Coarser framework roots may be capable of growth at much lower soil water potentials, as roots of larger diameter often tolerate much higher soil impedance before their growth is deflected (i.e., buckling pressure; Whiteley et al., 1982). The growth of fine lateral roots that initiate from major laterals is often restricted at low soil water content (Fernandez and Caldwell, 1975). For example, in a sandy soil in Florida, citrus trees (*Citrus paradisi/Citrus aurantium*) exhibited reduced root growth near the soil surface and greater root growth deeper in the soil in non-irrigated compared to irrigated trees (Fig. 1). Similar results were observed in dry years in Concord grape (LH Comas et al., unpubl. data). Overall root growth in Concord grape can be restricted in dry years in unirrigated vines (Fig. 2a). Irrigation had little effect on yield and aboveground vegetative growth on the balanced pruned (80-node) vines in years of late-season drought, indicating that carbohydrates were not severely limiting root growth of the non-irrigated Concord grapes.

Evidence that root growth may be limited by carbohydrates is provided by estimates of shoot and crop growth in grape relative to root growth (Fig. 2). In Concord grape, there is initially high demand for shoot carbon in the spring and early summer as the canopy develops and also by the crop in summer up to veraison (Fig. 2b). There is then an approximately two-week period of limited carbon demand by aboveground growth before the crop demand increases again as the grapes turn from green to purple (veraison). The total aboveground crop demand can be compared to modeled total canopy carbon gain from net CO₂ fixation (Fig. 2c). A clear period of reduced carbon demand aboveground around veraison is associated with a large spike of root growth belowground in the irrigated vines. In the non-irrigated vines, however, no such pulse of root growth occurs, presumably because of the unfavorable soil conditions. These data suggest that roots, shoots and crop may compete for carbohydrates during the growing season. There is also a spike of root growth in both irrigated and non-irrigated vines for the first two weeks following bloom. At this time, photosynthesis exceeds aboveground demand and yet reserves are strongly depleted (Goffinet and Lakso, unpubl. data), again consistent with strong carbon demands for root growth.

ROOT LIFESPAN

Root lifespan is controlled by many factors and is often difficult to predict (Eissenstat and Yanai, 1997; 2002). Plants can shed roots to reduce costs of maintaining inefficient roots and extend longevity of roots in more favorable soil locations (Eissenstat and Yanai, 2002). Root lifespan is usually longer in deeper roots than shallower roots as demonstrated in citrus (Kosola et al., 1995), grape (Anderson et al., 2003) and peach (Wells et al., 2002a). For example, in Concord grape, a root at a 40-cm soil depth had a 9-21% lower risk of mortality than a root at a 10-cm depth, depending on the year (Anderson et al., 2003). Causes for extended lifespan of deeper roots are not known definitively. Deeper fine lateral roots often have lower N concentrations than roots near the soil surface (e.g., Pregitzer et al., 1998). The environment of deeper soil may be more benign than near the surface. Soil below 20 cm is typically associated with greater soil moisture availability, less temperature fluctuation, and lower herbivore and pathogen pressure than surface soil layers.

Root diameter and root order can strongly influence root lifespan. The finest diameter roots have much shorter lifespans than the more coarse roots (Wells and Eissenstat, 2001; Wells et al., 2002a; Anderson et al., 2003) and roots of 1st order (no laterals) typically die sooner than those of higher order (Wells and Eissenstat, 2001; Eissenstat et al., 2000; Wells et al., 2002a). The finer roots with no laterals (e.g., order =

1) also typically have higher N concentrations and higher metabolic activity, which is often associated with short lifespan (reviewed by Wells and Eissenstat, 2003).

One way to predict root lifespan is to estimate lifetime costs (root construction and maintenance respiration) and lifetime benefits (nutrient uptake over the root's lifetime) (Yanai et al., 1995; Eissenstat and Yanai, 1997; Bouma et al., 2001; Volder et al., in press). Ideally, data on how the physiology of the roots changes with age is required to accurately estimate root efficiency (benefits/costs). In a comparison of apple and citrus, Bouma et al. (2001) found that the species with short-lived roots (apple), exhibited rapid declines in both phosphate uptake capacity and root respiration with age. The species with the long-lived roots (citrus), in contrast, exhibited respiration and P uptake capacity that remain at a stable low level after the roots were more than a couple of weeks old. Based on root morphology and uptake capacity, a solute transport model was then used to estimate lifetime root efficiency under different soil conditions. Optimal root lifespan was estimated to be the lifespan that maximizes lifetime root efficiency. Despite the difference in morphology, root construction costs and physiology of citrus and apple roots, under similar soil conditions there were not great differences in root efficiency after roots were constructed. This was because changes in phosphate uptake kinetics were tracked by changes in root respiration, so that the daily root efficiency (uptake/cost) was fairly constant. This work showed that soil factors affecting solute transport, root depletion zones and ultimately, nutrient uptake, are more important than uptake kinetics in affecting root efficiency.

The previous work on root efficiency focused on modeling the efficiency of an individual root and did not include possible allocation to root defense for root herbivory or parasitism, which can be appreciable as previously demonstrated in citrus (Kosola et al., 1995) and in peach (Wells et al., 2002b). Another approach to this problem is to model the efficiency of a cohort of roots, which includes parameters to describe root allocation to defense and a probabilistic parameter to express herbivory or pathogen pressure (Yanai and Eissenstat, 2003). This approach is more consistent with what may be expected at the whole plant level, which would be to maximize the efficiency of the root system as a whole and not just the efficiency of individual root elements. It also better reflects minirhizotron data, where similar roots in similar locations in the soil have a range of lifespans. Progress with the cohort approach to modeling optimal median root lifespan of a population of roots awaits more information on how root defense varies among roots in a root system, and how much it changes in relation to herbivore pressure and with root age.

ROOT RESPIRATION

Root respiration represents a large plant expenditure of carbon. Many factors influence the rate at which carbohydrates are consumed during respiration, including differences among species, root age, and nutrient supply (Lambers et al., 1996). Two factors that commonly dominate root respiration in the field, however, are soil temperature and soil moisture. Modelers have often been successful at explaining a significant proportion of the observed variation in CO₂ evolution by using moisture and temperature as the main driving variables (Carlyl and Ba Than, 1988; Alm and Nobel, 1991; Bryla et al., 2001).

Respiration is generally predicted to increase in an exponential fashion with an increase in temperature. Short-term measurements have consistently indicated respiratory responses exhibit a strong temperature response. Most models describing this temperature response typically assume the Q_{10} is about equal to 2 (i.e., respiration doubles with a 10 °C increase in temperature) (Atkin and Tjoelker, 2003). In reality, the Q_{10} can range from 1.3 to more than 3, depending on the growth temperature. Atkin and Tjoelker (2003) show that Q_{10} exhibits a linear decrease with an increase in temperature where the Q_{10} of respiration = $3.0 - 0.045T$ between 5 and 35 °C where T represents the growing temperature in °C. Consequently, tissues in soils of about 5 °C will exhibit a much larger increase in respiration with a 10 °C increase than tissues in soils of 30 °C.

Temperature shifts that occur on a time scale of about 1 h as occurs during a typical day elicit different respiratory responses from temperature changes that have a longer time constant (ie., 2 d or more). For example, Bryla et al. (2001) found a Q_{10} response of about 1.8 in citrus and Huang et al. (unpublished data) found a Q_{10} response of about 1.75 in grape roots exposed to a change in temperature every 1 h when grown at about 20 °C (Fig. 3). When roots are exposed to a constant temperature for three days or more at higher temperatures, respiration no longer exhibits corresponding high respiratory rates, indicating the ability of plants to reduce metabolism at sustained high temperatures and presumably reduce carbohydrate consumption (Fig. 4). In citrus, for example, respiration remains essentially constant at temperatures above 23 °C. Similar results have been observed in Concord grape except sustained temperatures above 30 °C lead to reductions in respiration and eventually, root death (Huang, Lakso and Eissenstat unpubl data). The effect of this acclimation can be modeled using the following equation:

$$R_T = [R_{STD}] \times \left[Q_{10}^{\left(\frac{T - T_a}{10} \right)} \right]$$

where R_T is the predicted respiration at any given temperature, R_{STD} is the theoretically maximum respiration at some standard temperature (e.g., 23 °C) where soil moisture is not limiting, T_a is the average soil temperature (°C) over the acclimation period for temperatures above 23°C and Q_{10} could be treated as a constant as done in Bryla et al., (2001) or could be estimated as a function of growing temperature as described previously.

Many investigators have reported declines in root respiration with reductions in soil moisture (reviewed by Bryla et al., 2001). In citrus, Bryla et al. (2001) examined the interaction of soil temperature and soil moisture (Fig. 5). They found that root respiration declines in a sigmoidal fashion with soil water content. Interestingly, the respiration at low soil water content was very similar to the respiration at low soil temperature, suggesting a basal respiration had been reached which was required to maintain the metabolism necessary for tissues to remain viable. The effects of moisture on respiration were modeled by including both a basal, R_B , and activity, R_A , component to total respiration: $R_{TOTAL} = R_A + R_B$ (Bryla et al., 2001). The effects of soil water content, SWC, on the value of R_A was determined using the following equation:

$$R_{SWC} = R_B + \frac{R_A}{\left[1 + e^{-\left(\frac{SWC - a}{b} \right)} \right]^c}$$

where a, b, and c are fitted constants. As R_B is largely independent of temperature, the effects of temperature only need to be applied to R_A . Thus, we can model the effects of temperature and moisture on root respiration by substituting R_{STD} in the first equation with R_{SWC} in the last equation at temperatures where acclimation occurs (see Bryla et al., 2001). By using this modeling approach, Bryla et al. (2001) were able to account for 87% of the variation in soil respiration in the experiment previously described using red grapefruit trees on sour orange rootstock in sandy soil in central Florida where temperature and moisture were manipulated. If temperature acclimation was not included in the model, predicted respiration was 37% higher than observed and predicted and observed values were not significantly correlated.

CONCLUSIONS

In conclusion, respiration can be effectively modeled, at least in citrus but probably in a range of fruit trees, if the amount of fine root mass is known and the values to parameterize the responses of root respiration to temperature and moisture as outlined here have been determined. We still are not at the stage where we can model root growth effectively, but observations clearly indicate that root growth can be limited at low soil moisture contents. If soil conditions are favorable, root growth appears greatest during

periods when crop and aboveground vegetative carbon demand are relatively low with respect to canopy C gain. Sufficient observations have developed for empirical models of root lifespan. Cost:benefit models show some promise at more mechanistically describing variation in lifespan. Parameterizing models with respect to herbivory and parasite pressure, however, continue to be a challenge.

ACKNOWLEDGEMENTS

This research was supported by grants from the Eastern Viticulture Consortium, the NY Wine and Grape foundation, and NSF, for which the authors are grateful.

Literature Cited

- Alm, D.M. and Nobel, P.S. 1991. Root system water uptake and respiration for *Agave deserti*: observations and predictions using a model based on individual roots. *Ann. Bot.* 67:59-65.
- Anderson, L.J., Comas, L.H., Lakso, A.N. and Eissenstat, D.M. 2003. Multiple risk factors in root survivorship: a 4-year study in Concord grape. *New Phytol.* 158:489-501.
- Atkin, O.K. and Tjoelker, M.G. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plant Sci.* 8:343-351.
- Bouma, T.J., Yanai, R.D., Hartmond, U., Wang, L., Flores, D., Elkin, A.D. and Eissenstat, D.M. 2001. Estimating age-dependent costs and benefits of roots with contrasting lifespan: comparing apples and oranges. *New Phytol.* 150:685-695.
- Bryla, D.R., Bouma, T.J., Hartmond, U. and Eissenstat, D.M. 2001. Influence of temperature and soil drying on respiration of individual roots in citrus: integrating greenhouse observations into a predictive model for the field. *Plant, Cell Environ* 24:781-790
- Carlyle, J.C. and Ba Than, U. 1988. Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus radiata* stand in south-eastern Australia. *J. Ecol.* 76:654-662.
- Eissenstat, D.M., Graham, J.H., Syvertsen, J.P. and Drouillard, D.L. 1993. Carbon economy of sour orange in relation to mycorrhizal colonization and phosphorus status. *Ann. Bot.* 71: 1-10.
- Eissenstat, D.M. and Yanai, R.D. 1997. The ecology of root lifespan. In: Homes, I (ed). *Advances in Ecological Research*. Vol. 27. pp. 1-60. Academic Press, San Diego, CA.
- Eissenstat, D.M., Wells, C.E., Yanai, R.D. and Whitbeck, J.L. 2000. Building roots in a changing environment: implications for root longevity. *New Phytol.* 147:33-42.
- Eissenstat, D.M. and Yanai, R.D. 2002. Root life span, efficiency, and turnover. p. 221-238. In: Y. Waisel, A. Eshel and U. Kafkafi (eds.), *Plant Roots: The Hidden Half*. 3rd edn. Marcel Dekker, Inc., New York.
- Fernandez, O.A. and Caldwell, M.M. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.* 63:703-714.
- Hall, A.J., Conner, D.J. and Whitfield, D.M. 1990. Root respiration during grain filling in sunflower: the effects of water stress. *Plant Soil* 121:57-66.
- Kosola, K.R. and Eissenstat, D.M. 1994. The fate of surface roots of citrus seedlings in dry soil. *J. Exp. Bot.* 45:1639-1645.
- Kosola, K.R., Eissenstat, D.M. and Graham, J.H. 1995. Root demography of mature citrus trees: the influence of *Phytophthora nicotianae*. *Plant Soil* 171:283-288.
- Lambers, H., Atkin, O.K. and Scheurwater, I. 1996. Respiratory patterns in roots in relation to their functioning. p. 323-362. In: Y. Waisel, A. Eshel and U. Kafkafi (eds.), *Plant Roots: The Hidden Half*, 2nd edn. Marcel Dekker, Inc., New York.
- Nicolas, M.E., Lambers, H., Simpson, R.J. and Dalling, M.J. 1985. Effect of drought on metabolism and partitioning of carbon in two varieties of wheat differing in drought tolerance. *Ann. Bot.* 55:727-742.
- Pregitzer K.S., Laskowski, M.J., Burton, A.J., Lessard, V.C. and Zak, D.R. 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiol.* 18:665-670.

- Volder, A., Smart, D.R., Bloom, A.J. and Eissenstat, D.M. (in press). Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *New Phytol.*
- Wells, C.E. and Eissenstat, D.M. 2001. Marked differences in survivorship among apple roots of different diameters. *Ecology* 82:882-892.
- Wells, C.E., Glenn, D.M. and Eissenstat, D.M. 2002a. Changes in the risk of fine root mortality with age: a case study in peach, *Prunus persica*. *Am. J. Bot.* 89:79-87.
- Wells, C.E., Glenn, D.M. and Eissenstat, D.M. 2002b. Soil insects alter fine root demography in peach (*Prunus persica*). *Plant, Cell, Environ.* 25:431-439.
- Wells, C.E. and Eissenstat, D.M. 2003. Beyond the roots of young seedlings: the influence of age and order on fine root physiology. *J. Plant. Growth Regul.* 21:324-334.
- Whiteley, G.M., Hewitt, J.S. and Dexter, A.R. 1982. The buckling of plant roots. *Physiologia Plantarum* 54:333-342.
- Yanai, R.D., Fahey, T.J. and Miller, S.L. 1995. Efficiency of nutrient acquisition by fine roots and mycorrhizae. p. 75-103. In: W.K. Smith and T.M. Hinckley (eds.). *Resource Physiology of Conifers*, Academic Press, New York.
- Yanai, R.D. and Eissenstat, D.M. 2003. Coping with herbivores and pathogens: a model of optimal root turnover. *Funct. Ecol.* 16:865-869.

Figures

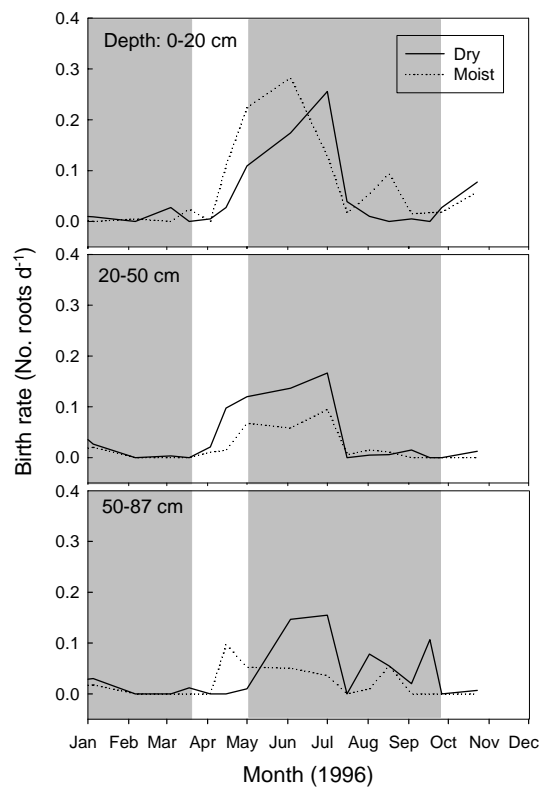


Fig. 1. Effects of soil moisture on root growth at different soil depths.

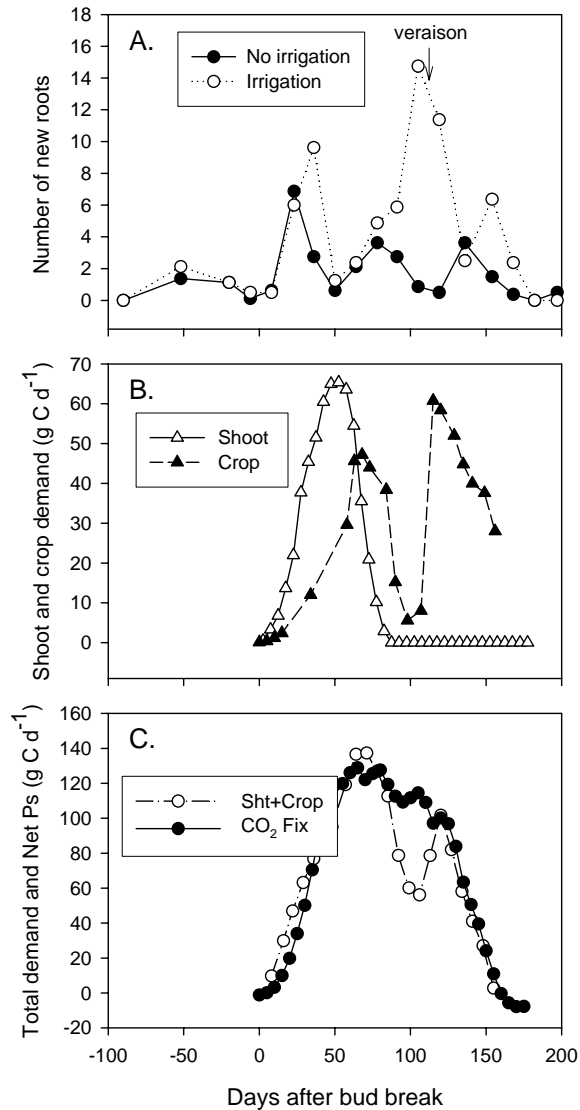


Fig. 2. Relationship of seasonal patterns of root growth with aboveground C demand and total net photosynthesis (Ps). A. Root growth in Concord grape vines in a relatively dry growing season (1998) in Fredonia, NY in irrigated and non-irrigated vines. B. Shoot and crop C demand over the season for 80-node vines. C. Total (shoot + crop) carbon demand and estimated total canopy photosynthesis (CO₂ fixation). Note that in the period around bloom and around veraison (about 100 d after bud break) the spikes of root growth in the irrigated vines corresponded to the period of reduced aboveground C demand relative to canopy CO₂ fixation.

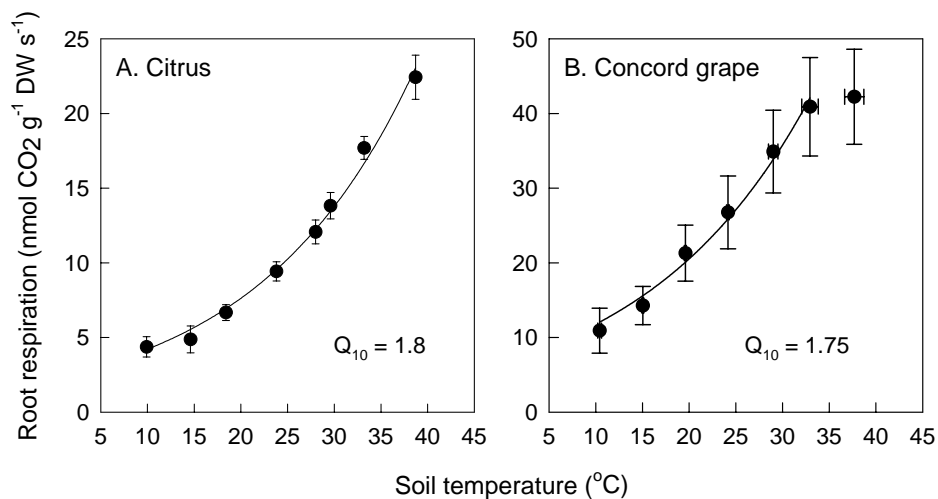


Fig. 3. Unacclimated root respiratory responses to temperature of a single branch of fine roots. A. Respiratory response of 2-year-old sour orange trees in a greenhouse measured at various temperatures for 1 h (after Bryla et al. 2001). B. Respiratory response of 1-year-old Concord grape vines in a greenhouse to 1-h changes in temperature (Huang, Lakso and Eissenstat unpubl. data). In grape, at temperatures above 33°C an increase in temperature caused little change in respiration.

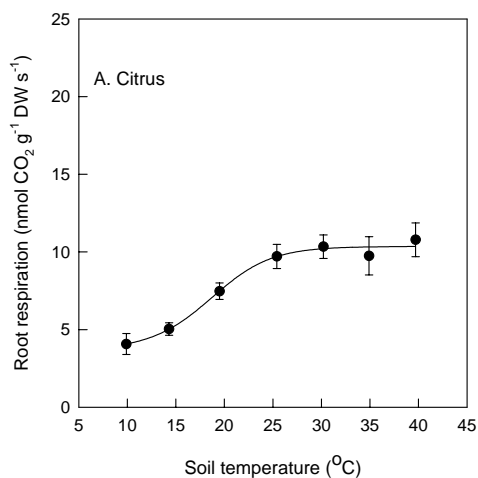


Fig. 4. Acclimated respiratory response of a single branch of citrus fine roots to changes in temperature over 6 d (from Bryla et al. 2001). Below about 23°C, citrus roots exhibited similar temperature response as roots exposed to only 1h at a specific temperature as shown in Fig. 3A. At temperature above 23°C, citrus roots exhibited no further reaction to temperature. Curve fitted by sigmoidal regression analysis.

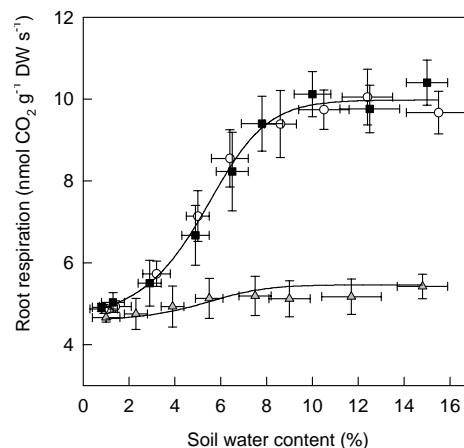


Fig. 5. Effects of soil water content on the respiration of roots at three different temperatures (after Bryla et al., 2001). Each point represents the daily averages of root respiration and soil water content during a 10-d drying period controlled at 15 (triangle shaded gray), 25 (open circle) or 35 (closed box) °C. Error bars indicate one SE (n=3). Lines represent fit of data using a sigmoidal function.