

ocean (Ajtay *et al.*, 1979; Falkowski & Raven, 1997; Field *et al.*, 1998).

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Key words: silicon, active transport, diatoms, grasses, rice, silica, silicic acid, weathering.

Woody plants, carbon allocation and fine roots

Sitting on the veranda, the sun reflects off the Mosel and the long rows of *Vitis vinifera* sloping down to the river. It's a lazy autumn afternoon and my mind drifts from the nuances of the Embden-Meyerhof-Parnas pathway to the beautiful, neatly manicured rows of grape vines. The leaves are pale yellow and the physiological processes preceding the advent of the dormant season are unfolding. These vines are highly integrated physiological systems, with water, minerals, amino acids, carbohydrates, growth regulators, and other organic substances moving freely, though often in phases, between roots and shoots. How old are these vines? How deeply rooted are they, perched on this dry, south-facing slope? The ability of woody plants to survive for decades, centuries, sometimes millennia, is due in part to their capacity to withstand environmental stress by shifting their resources from roots, to shoots, to storage reserves. Grapes are no exception – vines can be in production for decades, and they survive the year-to-year vagaries of nature and horticultural manipulations designed to encourage higher berry yields by shifting resource allocation. In this issue of *New Phytologist* (pp. 489–501), Anderson *et al.* report how irrigation, pruning and annual variations in weather influence the survivorship of roots of Concord grape, *Vitis labruscana*. There are two interesting perspectives raised:

- The importance of whole plant source–sink relationships in driving fine root lifespan.
- Fine roots as modular plant organs with different life expectancies depending on various environmental and developmental factors.

Carbon allocation to roots

Interest in the form and function of woody plant root systems has grown tremendously in recent years. The structural ('woody') portion of the root system serves important transport and storage functions and these roots can penetrate several meters vertically into the soil (Nepstad *et al.*, 1994). Experimental removal of woody shrubs from semiarid regions of the world results in an increase in water yield from entire watersheds, and carbon allocation to roots plays a significant role in the global carbon cycle (Jackson *et al.*, 1997, 2000). Some of the most widely applied forest productivity models are now calibrated by allocating carbohydrates to roots first in recognition of the fact that root to shoot relationships fundamentally control productivity at the species level (Landsberg *et al.*, 2003). Whole plant source–sink relationships exhibit strong seasonal rhythms and respond to defoliation, pruning and stress. Prominent among the functions ascribed to roots is their role in the storage of carbohydrate reserves. In fact, the root systems of woody plants typically contain higher concentrations of reserve carbohydrates than the stem system (Loescher *et al.*, 1990).

The seasonal cycle of carbohydrate reserves

There are numerous reports of seasonal variations of carbohydrate reserves in roots, which provide indirect evidence for the role of these substances in woody plant growth. The general pattern is for root reserves to decline, often quite rapidly, just before or with the onset of the growing season, when shoots and roots are rapidly expanding. Then, when shoots are fully refoliated, reserves begin to build back up to preflush levels, reaching a maximum early in the dormant season. Although variation occurs among species, this general pattern has been consistent among diverse taxa (Dickmann & Pregitzer, 1992). Anderson *et al.* (2003) demonstrate that roots produced before bloom in the spring have the shortest lifespan and they speculate that this may be caused by lower carbohydrate reserves.

The strongest direct evidence for the seasonal cycling of root carbohydrate reserves comes from ^{14}C studies. If leaves are exposed to $^{14}\text{CO}_2$ late in the growing season, the tracer is transported to the root system, as well as to sites of branch and stem storage (Kandiah, 1979; Lippu, 1998). The key regulatory event that shifts translocation of carbohydrate on a particular shoot axis basipetally to the root system appears to be bud set (Isebrands & Nelson, 1983). During rapid shoot elongation little carbohydrate build-up occurs in the roots. As a particular shoot axis ceases growth and sets buds, particularly if it is removed from still active vegetative and reproductive sinks (Quinlan, 1969), basipetal translocation to the lower stem and roots predominates. A great deal of

the $^{14}\text{CO}_2$ assimilated in autumn is stored as reserves in the root system (Lippu, 1998). Nguyen *et al.* (1990) reported that starch concentrations in the fine roots of one *Populus* genotype increased an astonishing 75 times between September and November. Thus, in autumn, there is a strong downward pulse of nonstructural carbohydrates, which are stored in the root system during the dormant season. Interestingly, most of these reserves appear to be used primarily for root maintenance respiration during the dormant season and new shoot growth the following spring (Lippu, 1998). Fine root growth in the spring appears to be fuelled primarily by current photosynthate, not dormant season carbohydrate reserves (van den Driessche, 1987; Lippu, 1998). However, the role of seasonal source–sink relationships and the utilization of stored reserves in determining rates of root growth and lifespan are not well understood and we await more definitive studies from mature plants. Much of what we know comes from young fruit trees and nursery-sized conifers. It has never been easy to use $^{14}\text{CO}_2$ in the field on mature woody plants. Thankfully, $^{13}\text{CO}_2$ as a tracer has a bright future (Ehleringer *et al.*, 2000), and it should be very useful in field situations where $^{14}\text{CO}_2$ is always problematic. The implementation of $^{13}\text{CO}_2$ experiments explicitly designed to understand transient physiological processes – such as the seasonal storage and remobilization of carbohydrate reserves in woody plants – should prove fruitful in the future.

Shoot sink strength alters root mortality

Carbon allocation patterns are very complex in perennial plants because of the multiple-age structure of leaves and roots. Farrar & Jones (2000) examined four hypotheses related to carbohydrate allocation and concluded that the 'shared-control' hypothesis was most consistent with empirical data from a number of studies. Anderson *et al.* (2003) report that higher grape yields and pruning increase the risk of fine root mortality. In both cases, there is obvious indirect evidence that the sink strength of the shoot system can directly influence the lifespan of fine roots. Exposure of plants to ozone directly reduces photosynthetic capacity and shifts carbohydrate allocation to the repair of the shoot system. This in turn results in a decrease in carbon allocation to roots and mycorrhizas and increases fine root mortality (Anderson, 2003). In many cases decreased allocation to roots in response to ozone exposure occurs quickly (Gorissen & van Veen, 1988). It seems safe to conclude that the lifespan of fine roots can be very dynamic and depends fundamentally on whole plant patterns of carbon allocation. Increasing shoot sink strength can result in decreased fine root lifespan. The challenge seems rather obvious – we need to understand the whole plant. Isolated studies of shoot and root systems will not be as profitable as integrated studies of whole plants.

Fine roots as plant modules

The fine roots of mature woody plants are ephemeral plant modules (*sensu* Harper, 1977) which arise from adventitious buds. Populations of fine roots can be studied using classical demographic techniques and they have a life cycle with different probabilities of transition from one physiological state to another (Hendrick & Pregitzer, 1992). In recent years we have learned that specific root length, nitrogen concentration, and rate of root respiration increase from the proximal to the distal end of the fine root system (Pregitzer *et al.*, 1997, 2002; Burton *et al.*, 2002). The root tips are metabolic 'hot spots' and of course this is also the primary point of association with mycorrhizas. Wells & Eissenstat (2001), Wells *et al.* (2002), and now Anderson *et al.* (2003) have shown that small diameter roots have a higher risk of mortality (shorter lifespan) than larger diameter roots. In other words, the more you migrate toward the distal end of the lateral fine root system, the more active the root is physiologically and the greater the risk of mortality (the shorter the average lifespan). Pregitzer *et al.* (2002) report putative lateral fine root 'branch scars' along the perennial roots of numerous North American trees. The obvious hypothesis is that fine roots have preprogrammed points of 'abscission', but this idea remains untested. The focus on roots themselves is, however, too 'phyto-centric'. Mycorrhizas are strong sinks for plant carbohydrates and King *et al.* (2002) report that mycorrhizal roots have a significantly lower risk of mortality than nonmycorrhizal roots (Pregitzer, 2002). Lifespans of metabolically active fine roots at the distal end of the branching root system must be all about carbohydrate sink strength (Anderson, 2003).

The take home message

What is the take home message? It seems likely that lateral fine root branches exhibit as much variability in form and function as we see in shoot systems (Reich *et al.*, 1999; Wright & Westoby, 2002). Perhaps fine root form and function are directly related to leaf structure, lifespan and physiology – as Grubb (2002) points out, we need to turn our attention to coordinated studies of leaf and root properties. However, when it comes to fine roots, there are serious points of confusion. First, we do not know how to describe the basic plant module. Should we focus on diameter, position of a root segment on the branching root system, or try to understand how lateral fine root branches are constructed? Clearly, it will be difficult to compare the structure, lifespan and physiology of fine roots among plant taxa if we can't decide how to describe the basic sampling unit. Anderson *et al.* (2003) seem to advocate a focus on diameter, but I believe we need to understand the structure, lifespan and physiology of entire lateral fine root branches from the point where they arise from adventitious buds. Just

what in the world is the 'modular unit' under consideration? Since we often observe only a part of the fine root system, for example in minirhizotrons, we have yet to develop a complete understanding of how fine roots are assembled and how they die. It would be useful if plant anatomists took an interest in this fundamental issue. Second, it is possible that different roots on the same root system have different primary functions, for example, water vs nitrogen uptake (Gebauer & Ehleringer, 2000). If this phenomenon were common, fine root structure, lifespan and physiology might well depend on the essential soil resource being acquired. After all, plants have more than one problem to solve in the soil (e.g. water, nitrogen, phosphorus). Finally, mycorrhizas are yet another interesting wildcard. Do some roots team up with certain mycorrhizas to acquire a specific essential soil resource, altering their branch structure, lifespan and physiology in the process? We still don't understand the structure, lifespan and physiology of lateral fine root branches, but Anderson *et al.* have raised many, very interesting questions.

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Key words: Concord grape (*Vitis labruscana*), fine roots, woody plant physiology, root lifespan, carbon allocation.

Meetings

Healthy soils, healthy people

Rhizosphere, preferential flow and bioavailability: a holistic view of soil-to-plant transfer, Ascona, Switzerland, September 2002.

International workshop on plant–soil interactions, Beijing, P.R. China, October 2002.

Increasing worldwide recognition of the need for ‘healthy soil’ with respect to plant biodiversity and productivity, and hence human wellbeing, is spawning a range of important conferences. Multidisciplinary and – not the same thing