
Fine Roots of Trees: A New Perspective

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Commentary

Fine roots of trees – a new perspective

The fine roots of perennial plants are a royal pain to study. They seem to be everywhere in the soil, penetrating the rotting leaf litter, wedged between stones and proliferating in worm casts. Millions of lateral branches serve as the carbon depot for mycorrhizal hyphae that ramify away from the root tip to forage widely for essential nutrients. For the sake of convenience, and to promote sanity, this complex network has often been sampled in ways that fail to relate the structure of the intact system to resource acquisition – position and form of the individual root on the branching fine root system have typically been ignored. The traditional view is therefore that all the fine roots of trees can be treated as a coherent mass. But this view now seems deeply flawed. On pages 000–000, King *et al.* (2002) report on findings in loblolly pine that not only consolidate this view, but also demand a new perspective.

‘One of the most remarkable gaps in our knowledge is that we still do not know which fine roots on the branching root system die and what controls the mortality of individual roots’

What are fine roots?

The woody roots of mature trees are widely distributed, with horizontal roots exploring the soil for distances greater than 20 m from the tree trunk and woody tap roots reaching soil depths that exceed 10 m. These woody roots serve anchorage, transport and storage functions and they are the perennial outposts in a vast volume of soil that enable the tree to solve a key ecological challenge: the rapid acquisition of growth limiting water and nutrients. The acquisition of essential resources from the highly heterogeneous soil volume is performed by small absorbing roots (‘fine roots’) and their mycorrhizal associates. Lateral fine roots of trees

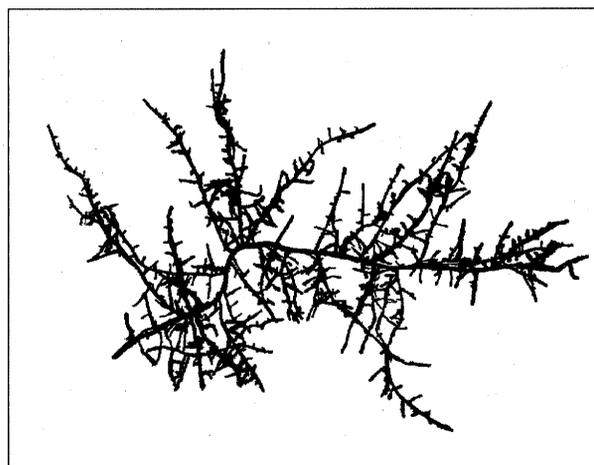


Fig. 1 Image of a very small portion of the fine root system of black spruce (*Picea mariana*). These intact roots were carefully excavated from the forest litter layer in Alaska (Bonanza Creek Long-term Ecological Research Site, 64°40′-N, 148°15′-W), cleaned of organic matter, and a composite digital image created in Adobe Photoshop (Version 5.5, San Jose, CA, USA) using a Zeiss stereomicroscope (Semi 2000-C, Carl Zeiss, Thornwood, New York, USA). All the roots in this image are < 1.0 mm in diameter. 80% of the individual roots in this image are < 0.3 mm in diameter and < 3–4 mm in length.

arise at variable distances from the apical meristem in the pericycle of the parent root, grow through the cortex, and form complex lateral branches. These lateral fine root branches are both morphologically and physiologically responsive to changes in water and nutrient availability (Eissenstat & Caldwell, 1988; Pregitzer *et al.*, 1993; Bilbrough & Caldwell, 1997), and the distal root tips are the primary infection point for mycorrhizas.

From the pick and weigh legacy to a new perspective

The branching fine root system can be highly complex (Fig. 1), and it is this complexity that has driven traditional sampling procedures. In order to determine biomass, for example, the roots are often sampled destructively, sorted into arbitrary size classes (e.g. roots 0–1 or 0–2 mm in diameter), dried and then weighed. Other studies of root growth and function have used line intersection methods to quantify root response, traced root growth along glass plates, utilized minirhizotrons, or extracted roots from the soil, cleansed them of rhizosphere complexity and determined their length using image analysis. In other words, every

segment of the root system in Fig. 1 has often been assumed to have the same form and the same function.

There is now a growing body of evidence that suggests the form of the branching fine root system of trees is directly related to its function. First, smaller diameter loblolly pine roots had shorter life spans than larger roots, a finding also recently reported for the roots of apple (Wells & Eissenstat, 2001). This implies that the life expectancy of an individual root is related to its position on the branching root system, because average root diameter continuously decreases from the proximal to the distal end of any branching structure in a wide variety of trees (Pregitzer *et al.*, 2002). King *et al.* also report that experimental nitrogen additions increased root growth and mortality. Interestingly, very small (diameter 0.2–0.6 mm) loblolly pine roots visibly infected by EM mycorrhizas lived much longer than uninfected roots. Bidartondo *et al.* (2001) recently demonstrated that experimental additions of N increased the sink strength of individual EM mycelium infecting the roots of *Pinus muricata*. It seems plausible that EM fungi increased the sink strength and prolonged the average life expectancy of EM infected loblolly pine roots. So, we cannot expect all of the small diameter roots on a branching root system, such as the one depicted in Fig. 1, to exhibit the same life history.

Further evidence that a root is not necessarily a root

An implied if not explicit assumption has been that all the roots of a given size class function in the same way (e.g. they have the same construction and maintenance respiration costs, and the same rates of nutrient uptake). However, recent studies suggest that this is not the case. Yanai *et al.* (1995) and Eissenstat & Yanai (1997) demonstrated through theoretical analysis that the most efficient roots to maintain would be thin (high specific root length (SRL) : m g^{-1}). Pregitzer *et al.* (1998, 2002) then demonstrated that SRL, tissue N concentration and root respiration rate varied systematically according to the position of an individual root on the branching root system. Roots at the distal end of the root system (first order roots; Fitter, 1982) have high SRL, high N concentrations, and high rates of respiration (Pregitzer *et al.*, 1998, 2002). The implication is that these roots are more active in nutrient acquisition, although this has yet to be proven. Taken together with the results of King *et al.* it appears that individual root physiology and life span may vary according to soil nutrient status, degree of mycorrhizal infection, and the position of a root on the branching root system.

We do not understand how the form of the branching root system is related to its function. How plastic is the form of a lateral fine root branch, and if lateral branch structure is plastic, how is this plasticity related to resource acquisition? In addition to having a poor understanding of plasticity

within a taxon, there is significant variation in fine root diameter, SRL, N concentration, and branch structure among taxa (Pregitzer *et al.*, 2002). It seems very naïve to assume that all fine roots are the same across a wide range of tree species and that cross-species comparisons can be made according to arbitrary size classes all-the-while ignoring variability in fine root form and function among taxa and between environments. Improving our understanding of the branching fine root system should advance rapidly if we turn to the systematic study of the form and physiology of individual roots on the branching root system; such an approach has proven invaluable in developing a better understanding of relationships among the form and function of shoot systems (Field & Mooney, 1983; Reich *et al.*, 1997).

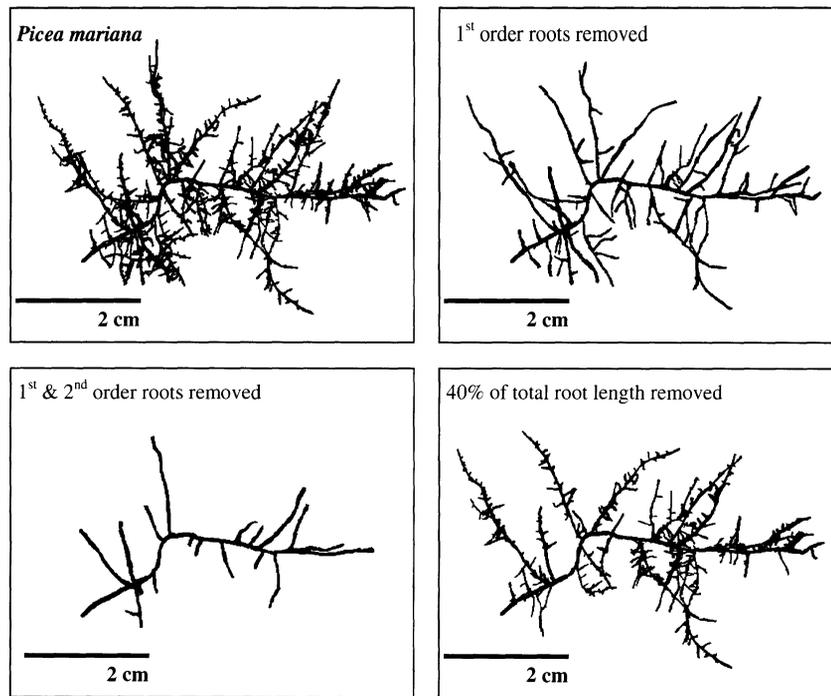
Which fine roots really die?

One of the most remarkable gaps in our knowledge is that we still do not know which fine roots on the branching root system die and what controls the mortality of individual roots. Virtually all of the research designed to understand root growth and mortality in trees has ignored basic lateral branch ontogeny. Lyford (1975) states: 'that a high proportion of small-diameter laterals on tree roots disappear is indisputable because there are many bare spaces or stumps of former laterals along the woody roots in places where laterals must have been numerous just after they developed.' Pregitzer *et al.* (2002) report observing lateral fine root branch scars in a wide variety of North American trees. However, we do not understand the relationship between the form of the root system and the growth and death of new lateral fine roots. Figure 2 illustrates this gap in our understanding of fine root mortality. The image of the intact segment of a *Picea mariana* root system was altered by removing all the first order roots, all the first and second order roots and 40% of the total root length by removing lateral branches at random. How does root mortality really occur in nature? Are there preprogrammed points of abscission? What controls fine root growth and mortality? The results of King *et al.* clearly suggest both nutrient availability and mycorrhizas control rates of root growth and mortality, but we have yet to develop a clear understanding of how this actually influences the structure of the lateral fine root branch through time.

Issues of mass balance

From a forest ecosystem perspective, fine roots account for a significant portion of total net primary productivity and root mortality plays a key role in biogeochemical cycling (Fahey & Arthur, 1994; Jackson *et al.*, 1997). Despite the widespread recognition that fine roots play key roles in ecosystem function, it is still unclear which roots die and decay in response to altered resource availability and the

Fig. 2 Conceptual exercise to illustrate how poorly we understand fine root growth and mortality. The panels show: an intact portion of the fine root system of black spruce as shown in Fig. 1; all first order roots removed; all first and second order roots removed; and 40% of the total root length removed by randomly erasing entire lateral branches. How does fine root mortality actually occur? Is the point of ‘abscission’ fixed or plastic? King *et al.* demonstrate that growth and mortality are influenced by root diameter (position on the branching system), soil nitrogen availability, and mycorrhizal infection, but we do not yet understand the mechanisms regulating plasticity in growth and mortality, although clearly EM sink strength is now implicated (see Bidartondo *et al.*, 2001). Root ordering scheme explained in detail by Pregitzer *et al.* (2002).



arbitrary size class approach to quantifying fine root standing crop sheds little new light on how essential soil resources alter fine root biomass through time. In other words, we have always assumed that arbitrary fine root size classes represent the dynamic portion of the root system important in mass balance calculations. This assumption is correct only if all root size classes are sampled at all times at the same proportion of their biomass in the living root system.

One of the reasons the dynamic mass balance of the fine root system is murky is due to the fact that we do not adequately understand the lifespan and decomposition rate of the various cells and individual root segments that comprise a complicated lateral fine root branch. We may not recover different root segments from soil cores in an unbiased way. As mentioned, smaller diameter roots toward the distal end of the branching root system have much higher SRL and a shorter lifespan. If the chemical composition of roots with a short life span promotes more rapid decay (Zak *et al.*, 2000), then traditional sampling of root biomass could be biased towards longer-lived, recalcitrant tissues.

A relevant analogy is our understanding of above-ground living biomass. If you walk into a forest, you see a wall of live biomass, most of which is represented by standing tree boles. However, most of this living biomass is actually dead xylem tissue, interned in the living bole from years of xylem production. Annual leaf production represents only a small fraction of above-ground standing crop. However, on an annual basis, trees allocate most of their above-ground carbon and nutrients to leaf production, which cycles as

detritus much more rapidly through the soil food web than the various woody tissues. Many of the ‘living’ cells sampled using traditional fine root size classes extracted from soil cores may have been dead for some period of time – dead cells ‘alive’ in the fine roots in the same sense that dead vessel elements reside in living tree boles.

This simple analogy is not meant to imply that fine roots always produce wood and secondary growth, rather to illustrate how poorly we understand the time steps involved in the production, maintenance and mortality of the sometimes complicated lateral fine root branch (Fig. 1). Gaudinski *et al.* (2001) point out that mass balance approaches may be confounded by the traditional application of ‘pick and weigh’ calculations that ignore the fact that some roots in a given size class may live longer and decompose more slowly than others. King *et al.* very clearly demonstrate that very small EM infected roots live, on the average, a much longer period of time than uninfected roots and this clearly demonstrates that we should revisit simple assumptions about the life expectancy of all roots on a complex branch like the one depicted in Fig. 1. We must develop a more comprehensive understanding of the anatomy, physiology, and life history of complex lateral fine root branches before we can better understand the role of fine roots in biogeochemical cycles.

Summary

King *et al.* have demonstrated that the lifespan of the fine roots of loblolly pine is shorter for smaller roots compared

to larger roots, and that EM fungi greatly increase the life expectancy of very small roots. Nitrogen additions also increased the rate of fine root growth and mortality. These results combined with other evidence suggest the position of an individual root on the branching fine root system is directly related to its lifespan and physiological function. The traditional approach of studying fine roots across divergent plant taxa according to arbitrary size classes has serious limitations. Diversity in fine root form and physiological activity between species and environments, and in relationship to symbiotic fungi, may be directly related to the acquisition of essential, growth-limiting soil resources. We will continue to improve our understanding of how the fine roots of trees function if we now turn to the systematic study of the form and physiology of individual roots on the branching root system. We may eventually learn that variability in fine root branch structure and function is just as anatomically, physiologically, and ecologically important as is variability in shoot system structure and function. After all, plants must acquire growth limiting water and nutrients in a highly heterogeneous volume of soil where they host a variety of symbiotic fungi and compete directly with other plants and a biologically complex soil food web. Surely, millions of years of organic evolution must have resulted in multiple 'fine root' solutions to this complex ecological challenge.

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