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The Secret Lives of Roots

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Notably, the time course of Pak and Sheng's scheme is slow and the spatial pattern of the targeted depletion of SPAR within neurons is global. Hence, the Snk-SPAR signaling pathway may be a homeostatic regulatory process that destabilizes synaptic connections in response to neuronal activity. Combined with local activity-

induced processes that stabilize synaptic connections (9), such a mechanism may help to shape the pattern of neuronal connectivity.

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## ATMOSPHERIC SCIENCE

# The Secret Lives of Roots

Susan E. Trumbore and Julia B. Gaudinski

**R**oots play key roles in vascular plants. They take up water and nutrients from the soil, provide physical stabilization, and store carbon compounds. In some plants, roots maintain symbiotic relationships with fungi, exchanging sugars in return for nutrient scavenging. To maintain these functions, plants transfer a substantial fraction of their carbon below ground.

But just how much carbon gets transferred? And how long does it stay? Answering these questions is increasingly important for predicting how ecosystems will respond to environmental change. On page 1385 of this issue, Matamala *et al.* (1) use a new isotopic technique to study root dynamics, a crucial factor in below-ground carbon storage and transfer.

The transfer of carbon below ground is poorly constrained because roots, the main pump supplying carbon to soils, are difficult to observe and to quantify in situ. Roots are intimately bound to the soil and form highly complex networks, with branches ranging in length and diameter from meters to micrometers. Fine roots (<2 mm in diameter) are considered to be the dynamic part of the root system, responsible for most below-ground carbon and nutrient cycling. Until recently, fine roots were assumed to live for about a year. New observations, including those of Matamala *et al.* (1), challenge this assumption, calling for a reexamination of widely held views on fine root ecology.

Measuring root biomass requires manually picking or washing roots out of a known volume of soil, and then separating living from dead by examining each root individually. This task is challenging and tedious, especially because many samples must be analyzed to account for large spatial variation. Before the 1990s, fine root

production rates were estimated from seasonal changes in living root biomass, measurements of root growth into root-free soil cores, or nutrient budgets (2). Fine root lifetimes were determined by dividing the live root biomass by the annual production rate, typically yielding values of <1 to 3 years (3–5).

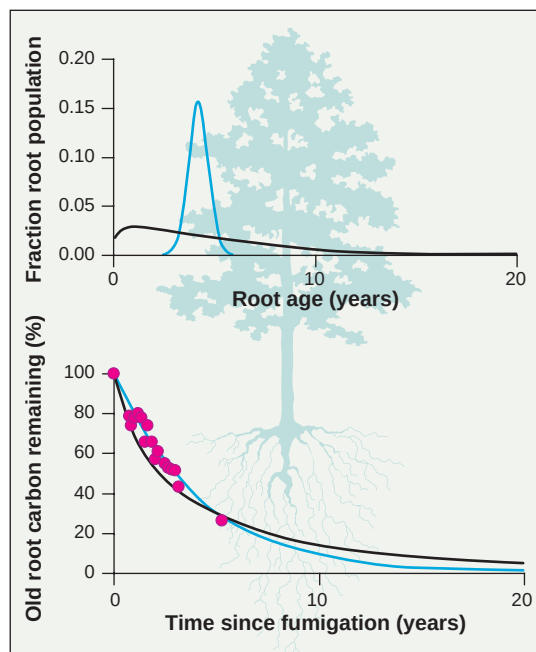
In the past decade, two new methods have been applied to the study of fine roots. In the early 1990s, multiple sequential camera images taken inside clear tubes

(called minirhizotrons) inserted into the soil allowed the first in situ observations of root growth and mortality (6). Minirhizotrons offered a much more dynamic picture of roots than did the traditional coring methods. Roots were found to live for a few months on average, although a few individuals persisted for several years.

A second new method compares the radiocarbon ( $^{14}\text{C}$ ) content of fine roots with the record of  $^{14}\text{C}$  in atmospheric  $\text{CO}_2$  to estimate the time elapsed since the root carbon was fixed from the atmosphere. The mean age of fine root carbon determined with this method ranges from several years to more than a decade in temperate forests (4). Matamala *et al.* (1) use another isotopic method to study root dynamics: They introduce  $^{13}\text{C}$ -enriched  $\text{CO}_2$  into free-air  $\text{CO}_2$  enrichment experiments, and then track the appearance of the  $^{13}\text{C}$  tracer below ground. The tracer was soon apparent in new roots grown after  $\text{CO}_2$  fumigation began, but was only slowly incorporated into the standing pool of live fine roots in the soil. The results are consistent with fine root lifetimes of 4 to 6 years, in accord with  $^{14}\text{C}$ -based estimates.

Whereas minirhizotrons call attention to the ephemeral and dynamic nature of roots, the isotope measurements indicate that most root carbon is at least several years old. How can such disparate observations be reconciled? The answer lies in the assumption that fine root lifetimes are normally distributed about a single mean age. By casting aside this assumption and acknowledging that different kinds of roots have different lifetimes, much of the problem can be solved (5, 7) (see the figure). The two measurement techniques gather information about different ends of the root lifetime continuum. Together, they can help to capture the real shape of root age distribution in soils.

Matamala *et al.* (1) focus on the implications of root longevity



**Root age distribution and carbon dynamics. (Top)** The blue curve assumes that root ages are normally distributed; therefore, mean age equals the mean residence time (MRT; inventory divided by annual production rate). The black curve represents a root population in better agreement with both minirhizotron and isotopic observations. The mean age is 5 years, but because of the large number of ephemeral roots, the MRT is only 1.5 years and below-ground production cannot be predicted solely from inventory and mean age. **(Bottom)** The two populations would respond differently to the tracer introduced by Matamala *et al.* (1). However, their data (circles) do not definitively distinguish between the two models.

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for estimates of root production and the capacity of soils to store carbon. If most root biomass is long-lived, the amount of plant carbon used to grow roots has been overestimated in the past. However, if root populations are skewed significantly, the relationship between the mean age of a plant root system and its annual root production (that is, inventory divided by mean age) no longer holds (see the figure).

The total transfer of plant carbon below ground is constrained by measurements of soil respiration and leaf litterfall (8). This carbon supports all root functions, not just growth. If less carbon is used to grow long-lived roots, then more must go to ephemeral roots, root exudates, fungi, and root respiration. If carbon cycling through these components returns to the atmo-

sphere quickly, below-ground carbon storage potential may indeed have been overestimated. However, we do not really understand the pathways this carbon takes; some may be retained in soils for many years through microbial recycling or sorption mechanisms.

It remains unclear why some roots survive for years while others die quickly. Radiocarbon and minirhizotron data from the same forest in central Sweden show that roots 0.3 mm in diameter can live for 3 months or 8 years (9). Root studies must move beyond sampling based on arbitrary criteria such as diameter. Sampling based on root form and function (10) could perhaps be done by focusing on root branching order, length, and nitrogen content, or by relating root function to root age (11).

Unless we recognize that root behavior is as complex as that of its counterparts above ground, the rules governing transfer of carbon to roots and the role of roots in soil carbon cycling will remain well-kept secrets.

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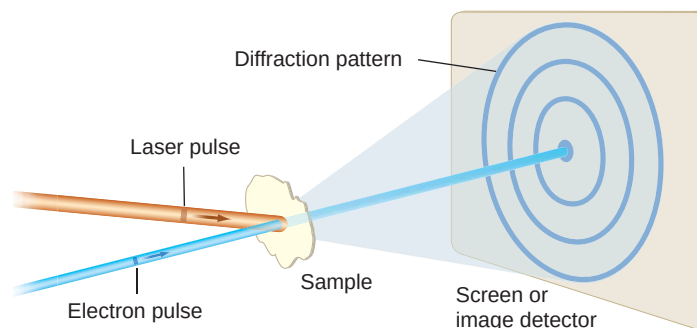
## MATERIALS SCIENCE

# A Picosecond View of Melting

Dietrich von der Linde

Most information on atomic structure at our disposal today comes from diffraction experiments. When a beam of electrons or x-rays hits a material, part of the radiation is scattered, giving rise to a diffraction pattern from which the atomic structure of the material can be retrieved. However, until recently, only static structures could be observed. This meant that, for example, the extremely fast changes in atomic configuration associated with chemical reactions could not be observed. Only the initial state and the outcome of a chemical reaction could be captured.

To directly monitor the changes in atomic configuration underlying the breaking or formation of chemical bonds requires a time resolution of  $10^{-14}$  s (10 femtoseconds) to  $10^{-12}$  s (1 picosecond). On page 1382 of this issue, Siwick *et al.* (1) demonstrate electron diffraction experiments with a time resolution of  $5 \times 10^{-13}$  s. On this fast time scale, they can monitor the changes in atomic configuration that occur when an intense short laser pulse causes aluminum metal to melt within a few picoseconds. The work is a new landmark in time-resolved structural investigations.



**Ultrafast time-resolved electron diffraction.** A short laser pulse excites the sample by depositing energy in the illuminated area. To monitor the structural changes caused by the laser excitation, a pulsed electron beam is directed onto the excited area, and diffraction patterns are recorded for different delay times between laser pulse and electron pulse. The delay time can be controlled with femtosecond precision.

Ultrafast electron diffraction was first demonstrated almost a decade ago by Williamson *et al.* (2), who achieved a time resolution of  $\sim 20$  picoseconds. Zewail and co-workers have pioneered picosecond time-resolved electron diffraction studies of chemical reactions in the gas phase (3). Subpicosecond x-ray pulses have also been generated, enabling researchers to perform ultrafast x-ray diffraction experiments on laser-induced structural transitions in semiconductor crystals. X-ray diffraction from selected lattice planes of the crystals was measured during and after strong excitation by an ultrashort laser pulse. The long-range atomic order typical of the crystalline state was destroyed within a few hundred femtoseconds (4, 5), indicating that the struc-

tural transition from the solid to the liquid state occurred during this very short time.

In a recent extension of time-resolved x-ray diffraction, much more subtle atomic motions that leave the crystalline order intact have been observed. In these experiment, snapshots of the atomic configuration were recorded that revealed a coherent vibrational mode of the crystal atoms set up by a femtosecond laser pulse (6).

However, only selected features of the atomic structure could be measured in these x-ray time-resolved diffraction experiments. To date, it has not been possible to obtain more complete structural records, mainly because the weak pulses from today's laser-driven subpicosecond x-ray sources make it very difficult to gather the data needed for a full evaluation of the atomic structure. This limitation should be overcome in

the future when much more powerful sources such as x-ray free electron lasers become available (7).

Electrons offer a basic advantage over x-rays for the exploration of atomic structure: They are scattered much more efficiently than x-rays. The scattering cross sections (a measure of the strength of the interaction with the atoms) for electron scattering exceed those for x-ray scattering by more than a factor of  $10^5$ . However, it is difficult to squeeze electrons into a short pulse. The reason is that electrons are electrically charged particles, which repel each other. The more electrons in a pulse, the faster the pulse broadens during propagation from its source to the target. This basic difficulty long prevented the generation of sub-

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