Quantifying Ecosystem-Atmosphere Carbon Exchange with a $^{14}$C Label

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The role of terrestrial ecosystems as sources or sinks for carbon to the atmosphere and their contribution to interannual variations in atmospheric CO$_2$ remain hotly-debated topics. Carbon enters terrestrial ecosystems through a single process, photosynthesis, but it is returned to the atmosphere by the combined metabolic activity of plants, animals, and microbes (Figure 1). The largest uncertainties in our understanding of terrestrial carbon cycling are in these return processes, especially how CO$_2$ losses from ecosystems are divided among respiration by living plants—termed autotrophic respiration—versus microbial and faunal decomposition of plant residues—termed heterotrophic respiration (Figure 1); and how seasonal and climatic factors that change plant physiological status and soil conditions influence that partitioning.

In order to study ecosystem-atmosphere carbon exchange in a temperate forest, we studied a large release of radiocarbon ($^{14}$C) that occurred near the Oak Ridge Reservation (ORR), Oak Ridge National Laboratory, Tennessee, in July and August of 1999. This regional $^{14}$C release was incorporated into plants as photosynthetic products, and the fate of these $^{14}$C-labeled materials is being traced over time. Initial results demonstrate the utility of the $^{14}$C label for increasing our understanding of how plants allocate carbon among metabolic respiration, growth, and storage, and what fraction of CO$_2$ respired from soils comes from autotrophic and heterotrophic sources.

**Radiocarbon as a Tracer for the Carbon Cycle**

Radiocarbon ($^{14}$C) is a useful tool for studying the dynamics of carbon exchange between ecosystems and the atmosphere on several time scales. Radiocarbon is naturally produced by the interaction of high-energy cosmic particles with the upper atmosphere. The $^{14}$C that is formed quickly oxidizes to CO$_2$ and enters the Earth's carbon cycle. The residence time of carbon in reservoirs that exchange with the atmosphere on century-to-millennial time scales is determined from the degree to which its $^{14}$C has been decreased below atmospheric $^{12}$C, CO$_2$ values by radioactive decay (half-life = 5730 years).

Radiocarbon can also be used to estimate carbon exchange rates on decadal time scales. Atmospheric thermonuclear weapons testing in the 1950s and 1960s roughly doubled the amount of $^{14}$C in atmospheric CO$_2$ in the Northern Hemisphere prior to the implementation of the Limited Test Ban Treaty in 1963. The rate of incorporation of this “bomb” $^{14}$C provides a measure of the rate of carbon exchange among atmosphere, ocean, and terrestrial carbon reservoirs on time scales of years to centuries.

While bomb $^{14}$C has been used successfully to study carbon cycling on decadal and longer time scales in ecosystems [Trumbore, 2000], it is of limited use on shorter time scales critical to understanding plant allocation and respiration processes. Radiocarbon in atmospheric CO$_2$, peaked at about +900$\%$ in the Northern Hemisphere in 1963, and it has decreased since then due to exchange with ocean and terrestrial carbon reservoirs (Figure 2). During the 1960s, when rates of atmospheric change were most rapid, only a few laboratories were measuring radiocarbon routinely, and observations relevant to short-term carbon cycling in ecosystems were sparse. By the year 2000, atmospheric $\Delta^{14}$C values had fallen to about +80$\%$, and they continue to decline at rates of 4–8$\%$/year [Levin and Hessheimer, 2000]. Measurement precision for radiocarbon in our laboratory is ±5$\%$ for samples with bomb $^{14}$C. Hence, present investigations of short-term carbon cycling are limited to studying carbon exchange on time scales greater than ~2 years.

Much of our understanding of short-term carbon dynamics in plants and soils comes from deliberate additions of $^{14}$C tracers [e.g., Coleman and Fry, 1981]. However, environmental regulations on the release of radioactivity and logistical considerations have, for the most part, limited these studies to small-stature vegetation in plots or enclosures. The release of radiocarbon at the ORR provides a unique opportunity to study shorter-term carbon cycling at the scale of a whole ecosystem by...
Fig. 2. (top) Radiocarbon in the background atmosphere and cellulose is shown isolated from tree rings in the western Oak Ridge Reservation (black star in Figure 4). (bottom) Radiocarbon in soil air (depth is the y-axis) and surface soil respiration is shown from one site in the central Oak Ridge Reservation (white star in Figure 4). Radiocarbon data are expressed as $^{14}$C/$^{12}$C, the deviation in parts per thousand of $^{14}$C/$^{12}$C ratio in the sample from that of the primary oxalic acid (0) standard, with the standard corrected for radioactive decay of $^{14}$C since 1950. All sample $^{14}$C/$^{12}$C ratios are corrected to a common $^{14}$C/$^{12}$C ratio equivalent of 20%o.

Fig. 3. Samples of radiocarbon in leaves, leaf buds, and parasitic plants taken at the central ORR site (white star on Figure 4) from 1996–2001 are shown. The rapid drop in $^{14}$C values in the spring of 2000 occurs when buds grow into full leaves. The carbon in the buds comes from overwinter stores, while the leaves start to produce their own carbon through photosynthesis.

**Fig. 3.** Samples of radiocarbon in leaves, leaf buds, and parasitic plants taken at the central ORR site (white star on Figure 4) from 1996–2001 are shown. The rapid drop in $^{14}$C values in the spring of 2000 occurs when buds grow into full leaves. The carbon in the buds comes from overwinter stores, while the leaves start to produce their own carbon through photosynthesis.

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**Determining Sources of Soil CO$_2$ Emissions**

We took advantage of the large differences in $^{14}$C between carbon fixed in late summer 1999 and in subsequent years to test an isotopic mass balance approach for quantifying the contribution of autotrophic versus heterotrophic components of CO$_2$ emitted from the soil surface. Using a chamber to isolate air in contact with the soil surface, we measured the radiocarbon content of CO$_2$ emitted from soils ($^{14}$CO$_2$; Gaudinski et al. [2000]). We determined the radiocarbon signature of root-metabolized carbon (root respiration; $^{14}$C$_{root}$) by isolating freshly sampled roots in a container and sampling the CO$_2$ evolved in the hour after their removal from the soil. The $^{14}$C content of CO$_2$ derived from decomposition ($^{14}$CO$_2$) was determined by incubating soil and litter samples in jars for 1 week.

**Allocation of the Label**

Previous studies with deliberate $^{14}$C labeling [Harrison et al., 2000] have shown that >90% of the added $^{14}$C may be respired within a few days, with <1% allocated to long-lived carbon pools such as leaves, roots, and wood. The incorporation of the 1999 $^{14}$C release provides a measure of carbon allocation and storage times in these plant compartments. High values of $^{14}$C measured in 1999 tree ring cellulose (Figure 2, top) and in roots known to have grown between April and August 1999 (not shown) mean that carbon fixed immediately after the release was allocated directly to production of these tissues. In contrast, whole-leaf $^{14}$C values increased to a lesser degree over the same period (Figure 3). Leaf buds that grew in early spring 2000 had higher levels of $^{14}$C (Figure 3), indicating that the label was incorporated into non-structural carbohydrate pools of carbon that were stored over the winter of 1999 and then used to grow leaves in 2000. As buds grew into full leaves, the $^{14}$C values dropped as fresh photosynthetic product. The $^{14}$C label was allocated to growth.

Sampling of leaves in the summer of 2000 showed that the amount of label incorporated was highest in the western portion of the ORR, closer to the presumed source (Figure 4). Differences were seen between leaves of oak (Q: Quercus spp.) and maple (A: Acer spp.), with oak leaves having consistently higher $^{14}$C values than maple.

The rate of dilution of the $^{14}$C label can be used to estimate the residence time of carbon in tree storage pools used to fuel new leaf growth. Assuming the drop in the amount of $^{14}$C label from 2000 to 2001 was due to dilution with unlabeled photosynthetic products and assuming storage pools are homogeneous, we estimate the residence time ($\tau$) of carbon by solving the relation $N_{t+\Delta t} = N_{t}e^{-\lambda \tau}$, where $N_{t+\Delta t}$ and $N_{t}$ are the amounts of label in leaf buds (Figure 3) in the buds in years 2000 and 2001. We estimate $\tau$ to be ~6 yr (5.4–6.8 yr) for maple, and 4 yr (3.5–5.2 yr) for oak. Using the drop in $^{14}$C from 2000 to 2001 in squaw root (Canopholis Americana), a parasitic plant thought to derive its carbon directly from oak roots, a residence time is similarly obtained for non-structural carbohydrate pools in oak of ~5 years (Figure 3).

Few measurements of the residence time of carbon in non-structural carbon pools exist for comparison with our estimates.

**Future Studies**

Our results to date demonstrate the utility of the radiocarbon label for tracing short-term
carbon cycling in ecosystems. With new funding from the U.S. Department of Energy, we plan to manipulate the inputs of \(^{14}C\) to further study the dynamics of carbon cycling in the ORR. Over 2.5 hectares of leaf litter that fell in the autumn of 2000 were collected at sites in the western and central portion of the ORR. At four sites on the ORR, including two soil types and two levels of \(^{14}C\) exposure in soil types and two levels of \(^{14}C\), we plan to manipulate the inputs of \(^{14}C\) and further study the sources of carbon cycling. Using the mass balance method described above, we will track the changes in the sources of soil CO\(_2\), emissions over several seasons and years in the manipulated plots. The tracking of \(^{14}C\) respired from the different manipulations will further allow us to separate contributions of leaf litter and root litter decomposition to heterotrophic respiration.

As part of annual sampling of these plots, the radiocarbon label through fine roots and leaf litter will be traced to study the dynamics and fate of carbon—how fast they decompose, and what fraction of their carbon is respired as CO\(_2\), versus that incorporated in microbial biomass or soil organic matter. Measurements of \(^{14}C\) in soil solution will elucidate the role of leaf and root litter as sources of dissolved organic carbon and its role in vertical transport of organic matter in soil profiles.

Discovery of the radiocarbon label in the ORR was serendipitous and unlikely to be repeated in other environments. However, its overall utility leads us to reconsider the use of radiocarbon labeling in natural environments. The use of accelerator mass spectrometry (AMS) increases the sensitivity for detection of \(^{14}C\) by a factor of nearly 10,000 over the decay counting methods used in past pulse labeling experiments. Local labeling experiments may now be feasible for studying the response of plants and microbes in their environment without the addition of a large amount of radioactive tracer to the environment.

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