that accompany the phase transition. Before the phase transition (~1 ps), we calculated \( N_t \) to be 12.2 ± 0.3, which, within error, is the expected number for an fcc lattice (12). The loss of lattice structure and the subsequent atomic rearrangements reduce \( N_t \) to 10.0 ± 0.3 at 6 ps. There is no observable change on longer time scales, as \( N_t = 10.0 ± 0.3 \) at 50 ps as well.

The new technique of femtosecond electron diffraction has provided an unprecedented atomic-level view of ultrafast solid-liquid phase transition dynamics. In this instance, the picture it provides can be expressed in terms of an average pair correlation function, \( H(r) \), which contains detailed information on nearest-neighbor distances, coordination numbers, and mean square vibrational amplitudes of the non-equilibrium state at each instant during the transition. This is a general technique, however, and can be applied to myriad systems in which photoinduced structural dynamics occur on the femtosecond time scale. Excellent candidates for investigation include condensed-phase processes, surface chemistry, and even time-resolved protein crystallography in cases where electron diffraction is viable. The single most important achievement is that of subpicosecond time resolution with sufficient structural sensitivity to reveal the atomic details of even nonreversible transition state processes that are central to concepts in chemistry and biology.

References and Notes
8. The key advantage of using electron diffraction for such investigations is the 10^7 to 10^10 enhancement in scattering cross-section as compared with x-rays. The result is that the mean free path for elastic scattering of electrons (~25 nm for 30-keV electrons through AI) is nearly perfectly matched with the excitation volume in studies of laser-induced phase transitions, which is inherently limited to several times the optical penetration depth.
12. Materials and methods are available as supporting material on Science Online.
17. The electron pulse duration (at the sample) is strongly dependent on the number of electrons in the pulse and on the beam diameter. Pulses containing 6000 ± 500 electrons, as used in these experiments, have a duration of 600 ± 100 fs at the sample, whereas pulses containing 3000 ± 500 electrons have a duration of only 450 ± 50 fs.
22. The expected lattice temperatures are calculated using the two-temperature model (TTM) described in [21]. The material parameters that enter the TTM are the electron heat capacity coefficient \( \gamma = 125 \text{ J/m}^3\text{K}^2 \) (from which the electron heat capacity \( C_e = \gamma T_e \)) is determined; the lattice heat capacity \( C_l = 2.4 \times 10^8 \text{ J/m}^3\text{K}^2 \) and the electron-phonon coupling constant \( g = 3.1 \times 10^{17} \text{ W/m}^3\text{K}^2 \) (from [21]).
27. To convert the measured (\( f \)) to electron units requires a normalization constant, \( N_0 \), to be determined. We used a standard procedure that makes use of the high-angle fitting criterion to perform an initial determination of \( N_0 \) and then fine-tuned this value by minimizing oscillations near \( r = 0 \) in the calculated \( H(r) \). Further discussion of this procedure, and errors associated with the incorrect determination of \( N_0 \), can be found in [18, 26] and references contained therein.
29. The average density in all cases was taken to be that of solid Al, \( \rho_0 = 0.06021 \text{ atoms/Å}^3 \). Because the phase transition will result in a decrease in \( \rho_0 \) (the density of solid Al is approximately 6% higher than that of liquid Al), the \( N_0 \) values determined at 6 and 50 ps are likely overestimated by a few percent.
30. Supported by the Canada Foundation for Innovation, the Ontario Innovation Trust, the Natural Sciences and Engineering Research Council of Canada, and the Connaught Fund. J.R.D. gratefully acknowledges the support of a Walter C. Summer fellowship.

Supporting Online Material
www.sciencemag.org/cgi/content/full/302/5649/1382/ DC1
Materials and Methods
Figs. S1 and S2

Impacts of Fine Root Turnover on Forest NPP and Soil C Sequestration Potential
Roser Matamala,1*, Miquel A. González-Meler,2 Julie D. Jastrow,1 Richard J. Norby,3 William H. Schlesinger4

Estimates of forest net primary production (NPP) demand accurate estimates of root production and turnover. We assessed root turnover with the use of an isotope tracer in two forest free-air carbon dioxide enrichment experiments. Growth at elevated carbon dioxide did not accelerate root turnover in either the pine or the hardwood forest. Turnover of fine root carbon varied from 1.2 to 9 years, depending on root diameter and dominant tree species. These long turnover times suggest that root production and turnover in forests have been overestimated and that sequestration of anthropogenic atmospheric carbon in forest soils may be lower than currently estimated.

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Roots provide a path for movement of carbon and energy from plant canopies to soils; thus, root production and turnover directly impact the biogeochemical cycle of carbon in terrestrial ecosystems. However, accurate estimates of root life-spans and turnover rates have been elusive, and the impacts of root turnover on belowground processes in terrestrial ecosystems are not well known (1). Uncertainties in estimates of root longevity prevent proper quantification of net primary productivity (NPP) and belowground C allocation in forests. The contribution of root C to the formation of soil organic matter depends on root productivity, turnover rates, exudation, mycorrhizal colonization, and soil characteristics, all of which vary with forest type. Current estimates have indicated that fine root production contributes from 33 to 67% (2–4) of the annual NPP in forest ecosystems. These estimates assumed root turnover rates of about 1 year, despite reported turnover rates ranging from days to several years (7). Estimates of root turnover and longevity have been obtained through conventional biomass assessments (4, 5), nitrogen budgeting (6), direct observation in minirhizotrons (7), pulse-labeling experiments using 14C- (8) or 13N-enriched fertilizers (9), and measurements of bomb-derived radiocarbon in root
We monitored root C turnover in two forest plantations growing under free-air CO2 enrichment (FACE): loblolly pine, *Pinus taeda*, near Durham, North Carolina, planted in 1980 (12), and sweetgum, *Liquidambar styaciflua*, in Oak Ridge, Tennessee, planted in 1988 (12). The two stands were similar in many respects: Trees were about 12 m tall when CO2 treatments commenced and were in a linear growth phase, having fully occupied the site. The continuous CO2 fumigation with FACE technology uses a depleted 13CO2 source, which alters the isotopic composition of CO2 during photosynthesis. Trees in FACE plots incorporated depleted 13CO2 into new biomass, including root tissues. As the experiment continued, the standing crop of fine roots was progressively dominated by roots that reflected the new signature of ambient CO2, which allowed us to estimate root C turnover during a 5-year period while the trees were exposed to added CO2.

Fine roots were obtained from intact soil cores and from root ingrowth cores (12). Roots sampled from intact cores exhibit changes in the 13C of the root population over time, which reflect the mixture of new and old roots (Fig. 1). Roots sampled from ingrowth cores exhibit changes in the 13C of the root population over time, which reflect the mixture of new and old roots (Fig. 1). Roots sampled from ingrowth cores exhibit similar changes, so incorporation of soil CO2 by 192 parts per million (ppm) in pine and 150 ppm in sweetgum with the use of depleted 13CO2 [delta 13C equalled -44 per mil (%e) and -55% relative to the Pee Dee Belemnite standard, respectively], which changed the delta 13C of CO2 in the FACE treatment from -8% (ambient) to -20% and -21% in the pine and sweetgum forests, respectively. This change affected the 13C composition of the vegetation, which is also determined by discrimination against atmospheric 13CO2 during photosynthesis.

Table 1. Isotopic 13C signatures of roots before (ORNL pretreatment, 1997) and after CO2 fumigation started (ACO2 indicates ambient CO2, ECO2 elevated CO2). The delta 13C of roots from the ingrowth cores grew from placement in June 1997 through collection in August 1998 for the pine site and from placement in October 2001 through collection in October 2002 for the sweetgum site. Ingrowth sweetgum roots <2 mm in diameter were pooled together.

<table>
<thead>
<tr>
<th>Root size class</th>
<th>Pretreatment delta 13C (%)</th>
<th>Ingrowth cores delta 13C (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ACO2</td>
<td>ECO2</td>
</tr>
<tr>
<td></td>
<td>Pine roots</td>
<td></td>
</tr>
<tr>
<td>R&lt;1 mm</td>
<td>-27.6 ± 0.2</td>
<td>-39.6 ± 0.1</td>
</tr>
<tr>
<td>1 &lt; R&lt;2 mm</td>
<td>-27.6 ± 0.4</td>
<td>-39.5 ± 0.2</td>
</tr>
<tr>
<td>R&gt;2 mm</td>
<td>-27.7 ± 0.4</td>
<td>-38.5 ± 0.8</td>
</tr>
<tr>
<td></td>
<td>Sweetgum roots</td>
<td></td>
</tr>
<tr>
<td>R&lt;1 mm</td>
<td>-27.0 ± 0.2</td>
<td>-37.5 ± 0.4</td>
</tr>
<tr>
<td>1 &lt; R&lt;2 mm</td>
<td>-26.5 ± 0.2</td>
<td>-37.5 ± 0.4</td>
</tr>
</tbody>
</table>

The difference in delta 13C of the newly grown FACE roots from ingrowth cores as compared to pretreatment- or ambient-CO2 grown roots was 11.4% for pine and 11.2% for sweetgum, averaged across all diameter size classes. The delta 13C of roots from ingrowth cores was similar to the measured delta 13C of new leaves (~39.2 ± 0.83 SE %) produced after CO2 enrichment began (13). Thus, new root tissues with a diameter <5 mm were produced entirely from C fixed after the start of fumigation, and for pine this C was newly fixed and not mobilized from storage (14). New leaf and new root delta 13C signatures were similar, so incorporation of soil CO2...
into roots via phosphoenolpyruvate carboxylase (PEPC) was negligible in these forests (15, 16).

The disappearance of the old C in the root population followed an exponential decay function (Fig. 2) (17). We estimated mean residence time (MRT) of root C as the average number of years that a molecule of C, once it is fixed by photosynthesis and incorporated to new root mass, stays in the root system. This MRT is not sensitive to, but integrates, short-term climatic variability. The MRT of C in fine roots, <1 mm in diameter, was 4.2 years (with an error range of 4.0 to 4.6 years) for the pine forest and 1.25 years (1.1 to 1.4 years) for the sweetgum plantation. Because of the exponential loss of C from any annual cohort of roots, C has a maximum residence (i.e., 95% turnover) in roots <1 mm in diameter of about 12 years for pine and 4 years for sweetgum. The MRT of C in roots with diameters between 1 and 2 mm was 5.7 years (5.1 to 6.6 years), with a calculated maximum residue that can be >18 years for pine (Fig. 2). Sweetgum roots of this diameter had a MRT of 3 years (2.7 to 3.3 years) and a maximum residue of over 9 years. Similarly, the MRT of thicker pine roots, 2 to 5 mm in diameter, was 6.3 years (5.5 to 7.2 years), with a maximum residue greater than 18 years (Fig. 2).

The pine forest showed a very slow replacement of old root C, suggesting that the fine root population is composed mainly of semipermanent roots that survive for many years. In contrast, the rapid turnover of C in roots under sweetgum forest suggests that its fine root system is composed mostly of ephemeral roots that do not survive more than one growing season. The smaller average diameter of sweetgum roots (0.5 mm) as compared to pine roots (0.8 mm) is consistent with their more ephemeral nature (18, 19).

With the use of the conventional method, i.e., the division of the maximum standing crop by annual gross production, we estimated that the MRT of fine roots <1 mm in diameter would be 3 years for pine (20) and 0.6 years for sweetgum (21). The discrepancy between conventional and δ13C-based estimates is substantial. It is possible that our δ13C-based estimates of root C turnover have been influenced by the exposure of the trees to atmospheric CO2 enrichment. However, the long MRT of fine root C in the pine forest was confirmed by 14C dating of root tissues collected under ambient CO2 (roots <1 mm in diameter were dated at 4 to 5 years old by 14C dating). Further, no difference in turnover rates between ambient and elevated plots was found in the sweetgum forest (21). Estimates of MRT by isotopic turnover of carbon includes the time from photosynthesis until its incorporation into the root system.

Although this time is short, it could, in part, explain differences between conventional and isotopic estimates. Our isotopic estimates suggest that pine forests have much slower root C turnover rates than previously reported, which may indicate a conservative use of resources and energy in nutrient-poor soils (22). Assuming a 1-year MRT for fine roots, Jackson et al. (2) estimated that roots account for a third of terrestrial NPP. If the turnover of fine roots is much slower, this will substantially reduce estimates of the contribution of roots to the global annual NPP of terrestrial ecosystems.

The two forests exhibited very different ecosystem dynamics. The NPP of sweetgum increased by 21% under elevated CO2 during the first 3 years of the study. During this period, there was a shift in C allocation from woody biomass to fine roots, increasing the proportion of forest NPP diverted to roots from 12 to 16% under elevated CO2 (19). The pine forest also showed a CO2 treatment effect, increasing NPP by 25% under elevated CO2 (23). Although root production increased moderately, only 5 to 7% of total pine forest NPP was directed to roots (20). Although there are other pathways that deliver C to soils (for example, root exudation, turnover of mycorrhizal fungi, and surface litter), root turnover is a major input to soil organic matter. Thus, ecosystem differences in C allocation to roots and root turnover rates could be important determinants of changes in soil C storage resulting from atmospheric CO2 enrichment.

Schlesinger and Lichter (24) measured C accumulation in the soil of the pine forest after 3 years of CO2 fumigation. They found an increased sink for C in the forest floor, but the C in soil mineral horizons did not differ significantly from that under ambient CO2 conditions. Although root production increased under CO2 fumigation, the slow root C turnover in the pine forest is consistent with minimal effects on soil C, because after 3 years only 45% of the root C was replaced and available for entry into the soil pool. Overall, root production in the sweetgum forest was 45 to 50% greater than that in pine forest. The greater response of root production in sweetgum grown at elevated CO2, coupled with the higher annual turnover of these roots, means that annual C inputs to soil in the sweetgum forest could be two times greater than in the pine forest. Thus, we might expect a greater increase in soil C after a shorter time period in the sweetgum forest than in the pine forest. Preliminary results show a significant increase in C concentration for the surface 5 cm of the mineral soil under the sweetgum plantation after only 3 years of CO2 enrichment (25). Models predicting ecosystem C sequestration in soils must attend the possibility that this potential is strongly affected by root production and the MRT of C in the root system.

References and Notes
12. Information on materials and methods is available on Science Online.
16. Because the δ13C of soil CO2 is enriched (–28‰ to –32‰) as compared to the leaf C signature (~39‰) under elevated CO2, the activity of PEPC in roots would enrich the δ13C of the root system. For example, under ambient CO2 conditions, a 1% change in the isotopic composition of root tissue as a result of PEPC would imply that 35% of the total root C was fixed by PEPC. Under elevated CO2 conditions, because of the different signatures of the root and soil CO2, a 1% change in the isotopic composition of the root would require only 8% of the total root carbon to be fixed by PEPC. The fact that there was no enrichment in the root tissues compared to leaves suggests that PEPC does not incorporate substantial amounts of CO2 into root biomass.
25. J. D. Jastrow, unpublished data.
26. We thank L. Giles and S. Oleynik for advice and measurement of 13C for the samples; J. Gaudinski and S. Trumbore for measurement of 13C in root samples; R. M. Miller for field support and comments; H. Hemric, H. Bortz, S. Jawdy, S. O'Brien, V. Oleynik, J. Pippen, R. Rao, L. Taneva, and T. Vugteveen for their field and laboratory assistance; and all Duke University and Argonne National Laboratory students who helped process root samples. The Duke and Oak Ridge FACE projects are supported by the U.S. Department of Energy (DOE), Office of Science, Office of Biological and Environmental Research, with ancillary research funding for the Duke facility from the Electric Power Research Institute and NSF. The authors were supported primarily by the Terrestrial Carbon Processes Program of DOE’s Climate Change Research Division; M.A.G.-M. was supported by UIC, and R.M. was partially supported by the Spanish fellowship Programa Formacion de Personal Universitario en el Extranjero.

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