Rising Atmospheric CO_2 Reduces Sequestration of Root-Derived Soil Carbon

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Forests have a key role as carbon sinks, which could potentially mitigate the continuing increase in atmospheric carbon dioxide concentration and associated climate change. We show that carbon dioxide enrichment, although causing short-term growth stimulation in a range of European tree species, also leads to an increase in soil microbial respiration and a marked decline in sequestration of root-derived carbon in the soil. These findings indicate that, should similar processes operate in forest ecosystems, the size of the annual terrestrial carbon sink may be substantially reduced, resulting in a positive feedback on the rate of increase in atmospheric carbon dioxide concentration.

The concentration of CO_2 in the atmosphere has risen from its preindustrial level of ~280 μmol mol^{-1} to 376 μmol mol^{-1} in the year 2003 (*1*) as a result of the combustion of fossil fuels and land-use changes such as deforestation. This continuing increase would be far more rapid were it not for the removal of large amounts of CO_2 from the atmosphere and its storage in ocean and terrestrial ecosystems; the size of the global terrestrial carbon sink during the 1990s was 2.8 ± 0.9 Gt C yr^{-1}, of which approximately one-quarter was absorbed by northern temperate and boreal forests (*2*). Because forest carbon sinks are such an important control on atmospheric CO_2 concentration and associated climate change, it is important to quantify their potential for increased carbon storage as CO_2 concentrations continue to rise, and to understand the mechanisms that determine their magnitude.

The majority of carbon stored in global vegetation is in forests. The growth of trees and the preservation of old forests are therefore of prime importance in regulating the size of the overall terrestrial carbon sink (*3*). In temperate and boreal forests, the amount of carbon stored in the soil is about four times as high as that stored in the vegetation, and 33% higher than total carbon storage in tropical forests (*4*). Thus, there is considerable potential for long-term sequestration of carbon in the soils of temperate/boreal forests where, in biochemically stable or mineral-bound form, it could have a residence time of hundreds to thousands of years (*5*). Many studies have concentrated on the effects of elevated CO_2 on plant productivity, but the belowground exchange of carbon between plants and soil remains poorly understood (*6*), particularly in relation to the transfer of newly fixed carbon to, and storage in, long-term soil carbon pools (*7*). Fine root production and turnover represent a substantial proportion of annual net primary productivity in trees and forests (*8–10*). Our experiment was therefore designed to quantify sequestration of root-derived carbon in soil beneath a range of tree species native to much of Europe, grown at CO_2 concentrations ranging from current ambient to 300 μmol mol^{-1} above ambient.

We used three pairs of tree species of contrasting shade tolerance/successional status (*11*) to represent a wide range of taxonomic, physiological, and ecological types. Trees were grown for 2 years under four CO_2 concentrations (ambient and ambient +100, +200, and +300 μmol mol^{-1}) to obtain response curves over this range and at two levels of soil nutrient availability to enable testing of the extent to which responses to elevated CO_2 are nutrient limited (*12–14*). To overcome the difficulties in directly measuring changes in carbon content of native forest soils (*15*, *16*), soil carbon sequestration was quantified by using stable isotope natural abundance techniques, which enabled accurate measurement of sequestration of plant-derived carbon transferred to the soil over the course of the experiment (*7*, *11*, *17*, *18*). Because leaf litter was removed from the soil (*11*), carbon inputs over the course of the experiment were derived solely from root turnover and exudation. Trees were grown in large, deep mesocosms containing C_4 grassland soil inoculated with microbes (including mycorrhizal fungi) and mesofauna from native UK woodlands and placed in well-ventilated hemispherical greenhouses (*11*).

All tree species responded similarly to elevated CO_2 (tables S1 to S6 and figs. S5 to S11) except for a significant increase in specific leaf area of the first-season needles of *Pinus* at elevated CO_2, which caused a corresponding increase in the leaf area ratio of *Pinus* at the end of the first growing season (table S3) and a significant interaction between species and CO_2 concentration regarding the ratio of fine roots to structural roots (table S3). Therefore, the values shown in Figs. 1 to 3 are means of all six species, expressed as percentages of their low-nutrient, ambient CO_2 controls. In this way, the large absolute differences between species (tables S1 to S6) are excluded to show the overall effect of CO_2 concentration (which was the same across all species) and nutrient supply. In all species, increasing CO_2 concentration caused a decline in stomatal conductance (g_s) (Fig. 1A and table S2) and in maximum (i.e., light and CO_2 saturated) photosynthetic rate (A_{max}) (Fig. 1B and tables S1 and S2) at both soil nutrient levels. There were no changes in the specific leaf area of second-season leaves (table S3) to account for the reductions in A_{max} (which was measured on a leaf area basis). Therefore, the reduction in A_{max} was due directly to physiological adjustments rather than changes in leaf morphology. There was a 15% decrease in leaf nitrogen content from ambient to ambient +300 μmol mol^{-1} CO_2 (table S4), which probably contributed to the decline in A_{max}. Despite reduced g_s and A_{max}, net photosynthetic rate (i.e., actual CO_2 uptake by the trees) was substantially increased under elevated CO_2 at both soil nutrient levels (Fig. 1C and table S2). Increased photosynthesis was associated with an initial stimulation of growth, which was only maintained where nutrients had been added (Fig. 1D and table S3). The growth response to CO_2 concentration was not linear but occurred mainly between ambient and ambient +100 μmol mol^{-1}.

Despite enhanced tree growth, we found a marked decline in sequestration of root-derived carbon in the soil as CO_2 concentration increased, particularly between ambient +100 and +200 μmol mol^{-1} (Fig. 2 and table S5). After 15 months, soil carbon sequestration was reduced by more than 40% at the highest CO_2 concentration, relative to ambient. The addition of nutrients caused a slight increase in the amount of root-derived carbon sequestered in the soil (Fig. 2); however, the response to CO_2

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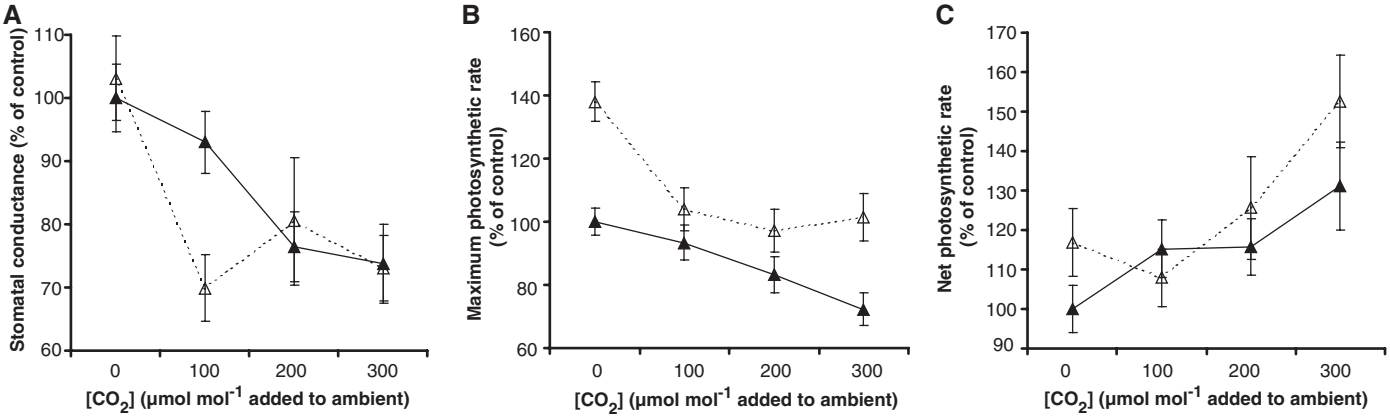
concentration was unaffected, even though plant (*12*) and soil (*19*) nitrogen status are expected to influence the effects of elevated CO_2 on soil organic matter decomposition. The reduced sequestration of root-derived carbon in the soil under elevated CO_2 was associated with an increase in soil microbial respiration as measured at the end of the experiment (*11*); the increase in carbon sequestration with added nutrients was associated with lower respiration rates (Fig. 3 and table S6). Even though irrigation rates were adjusted for a slight excess supply of water (*11*), there was a slight increase in soil moisture content at elevated CO_2 concentrations (fig. S10), which was probably due to the reduction in g_s. However, there was little loss of carbon in drainage water, and the amount was unaffected by CO_2 concentration (fig. S11). Therefore, it seems likely that reduced carbon sequestration in the soil resulted, at least in part, from enhanced turnover of root-derived carbon associated with increased microbial respiration over the course of the experiment. The possibility that respiration of the roots themselves (not measured) increased under elevated CO_2 cannot be discounted, but the existing literature does not point in this direction (*20*).

Differences in the net carbon exchange of European forests tend to be driven by changes in respiration rates at more northerly latitudes (*16*), with ~50% of total ecosystem respiration heterotrophic in nature (*21*). Therefore, any effect of increased atmospheric CO_2 concentration resulting in increased heterotrophic respiration could have important implications for the carbon balance of these forests. Increased soil moisture throughout the year may result in higher rates of respiration (*16*, *21*). However, although there was a small increase in soil moisture at elevated CO_2 concentrations in our experiment (fig. S10), this was not correlated with respiration rates ($P = 0.784$). Therefore, the increase in microbial respiration was probably a result of changes in the quantity (*6*, *15*, *19*, *22*) and quality (*6*, *12*, *19*, *23*) of inputs of root-derived organic matter from the trees.

Carbon flux to the soil may be increased by enhanced fine root production (*9*, *15*), turnover rates (*8*) or increased root exudation (*6*). Root biomass responded to CO_2 concentration and nutrient addition in a similar manner to total biomass (table S3). Within individual species, there were no significant relationships between microbial respiration and fine root biomass ($P > 0.999$). However, although we only measured root biomass at the beginning and end of the growing seasons, elevated CO_2 may have affected patterns of root mortality and regrowth over the course of the winter, resulting in the clear effect on carbon sequestration after 10 months (Fig. 2). Elevated CO_2 has also been shown to cause an increase in midseason fine root production, followed by a corresponding increase in mortality (*9*). Previous studies of trees have shown that increased fine root production and mortality under elevated CO_2 were associated with enhanced microbial activity and loss of CO_2 from soil respiration (*15*, *22*, *23*). These effects were found to be associated with changes in the composition of the microbial community, but as in our experiment (figs. S8 and S9), total microbial biomass was unaffected (*23*). An increase in respiration with no change in microbial biomass may also have been associated with faster rates of microbial turnover, for example, as a consequence of increased grazing by soil fauna (*24*).

Alternatively, the stimulation of microbial respiration may have been associated with changes in the overall or temporal quantity and quality of root exudates. Fine root carbon/nitrogen ratio at the end of the experiment was unaffected by CO_2 concentration (table S4),



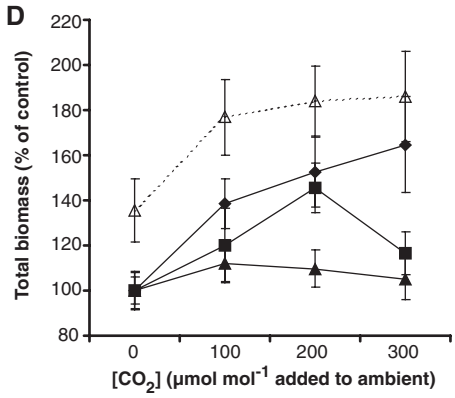


Fig. 1. (**A**) Stomatal conductance of the final harvest plants. Values are means for six species measured on two occasions (July and August of the second growing season) (±1 SE, $n = 18$), expressed as percentage of the ambient CO_2 control with no added nutrients for each species. Measurements were taken using only the second-season needles of the conifers. Solid triangles, no added nutrients; open triangles, added nutrients. Mean photosynthetically active radiation (PAR) = 495 $\mu mol\ m^{-2}\ s^{-1}$; mean leaf temperature = 24.6°C. The effect of CO_2 concentration did not vary over time, and there was no significant $CO_2 \times$ nutrient interaction. The effect of added nutrients was not significant; main CO_2 effect, $P = 0.002$. (**B**) Maximum photosynthetic rate (A_{max}) of the final harvest plants measured during July and August of the second growing season at saturating light and [CO_2] (2000 $\mu mol\ mol^{-1}$). Values are means for six species measured on two occasions (July and August of the second growing season) (±1 SE, $n = 18$), expressed as percentage of the ambient CO_2 control with no added nutrients for each species. Measurements were taken using only the second-season needles of the conifers. Solid triangles, no added nutrients; open triangles, added nutrients. PAR was 1500 $\mu mol\ m^{-2}\ s^{-1}$; mean leaf temperature = 21.2°C; mean leaf internal CO_2 concentration = 1470 $\mu mol\ mol^{-1}$. The effect of CO_2 concentration did not vary over time, and there was no interaction between CO_2 and added nutrients. Main nutrient effect, $P < 0.001$; main CO_2 effect, $P < 0.001$. (**C**) Net photosynthetic rate as measured in (A). Solid triangles, no added nutrients; open triangles, added nutrients. The effect of CO_2 concentration did not vary over time, and there was no significant $CO_2 \times$ nutrient interaction. The effect of added nutrients was not significant; main CO_2 effect, $P = 0.004$. (**D**) Total biomass of plants harvested after 5, 10, and 15 months. Values are means for six species (±1 SE, $n = 18$), expressed as percentage of the ambient CO_2 control with no added nutrients for each species. Diamonds, 5-month; squares, 10-month; and solid triangles, 15-month harvests, no added nutrients; open triangles, 15-month harvest, added nutrients. There was no significant $CO_2 \times$ nutrient interaction, and the $CO_2 \times$ harvest date interaction was not significant ($P = 0.052$). Main nutrient effect, $P < 0.001$; main CO_2 effect, $P = 0.002$.

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and there was no change in soil nitrogen mineralization rate (fig. S7). This suggests that the increase in respiration was associated mainly with enhanced turnover of root-derived sugars from exudation. Plants are able to actively up-regulate the quantity or alter the quality of exudates to, for example, alleviate biotic or abiotic stress or enhance nutrient acquisition (either by altering the soil chemical environment or through mutualistic associations with fungi or bacteria) (*6*). Such responses could have resulted in enhanced microbial respiration and a corresponding decline in the sequestration of root-derived carbon in the soil at elevated CO_2 concentrations.

Elevated CO_2 commonly results in enhanced plant growth and increased carbon inputs to the soil, which stimulates microbial respiration (*25*). However, although elevated CO_2 caused an increase in microbial respiration, which was associated with reduced sequestration of new carbon in mineral-bound form, in soil beneath grassland communities (*26*), no previous studies have shown a similar effect in soils growing trees. In contrast to our experiment, CO_2 enrichment caused an increase in soil carbon sequestration beneath *Betula* seedlings over the course of one growing season (*27*), but the effect on microbial respiration is not known. Free-air CO_2 enrichment (FACE) also caused an increase in the sequestration of new carbon in C_4 soil cores transplanted into former agricultural ground beneath 2- to 3-year-old *Populus* saplings; however, in one species of *Populus*, the opposite effect was observed in the first of two growing seasons (*28*). Given the difficulties associated with directly measuring changes in soil carbon content (*15*, *16*) and in comparing carbon sequestration in native forest soil of ambient and FACE plots (*7*, *29*, *30*), there is insufficient evidence to predict with certainty whether plant responses to elevated CO_2 will result in increased or decreased sequestration of new carbon in the soils of forest ecosystems.

Our data reveal a marked decline in sequestration of root-derived carbon in the soil at elevated CO_2 concentrations in a wide range of tree species. This effect occurred independently of plant and soil nutrient status. Two caveats need to be noted. First, young trees, grown in mesocosms in a semicontrolled environment and protected from major herbivores, may respond differently from mature trees growing in a natural forest. Second, the experiment ran for only two growing seasons and the input of leaf litter to the soil was excluded. Therefore, the possibility that longer term increased inputs of leaf litter under elevated CO_2 could counteract the effect on the sequestration of root-derived carbon cannot be ruled out. Furthermore, although soil microbial respiration increased under elevated CO_2, the effect of this on the decomposition of native soil carbon is not known. Nevertheless, this study clearly demonstrates that a mechanism exists that may drastically affect the potential for sequestration of new carbon in forest soils. Even small shifts in the carbon balance of forests could cause a large feedback on atmospheric CO_2 concentration, given that the annual exchange of CO_2 in the form of terrestrial photosynthesis and respiration is approximately 9 to 10 times as large as annual emissions from the burning of fossil fuels (*3*, *21*). Our results suggest that the incorporation of root-derived carbon into stable, medium- or long-term forest soil carbon pools may be substantially reduced as atmospheric CO_2 concentration exceeds 100 μmol mol^{-1} above current ambient. This would have the potential to trigger a large positive feedback on the rate of increase in global atmospheric CO_2 concentration and associated climate change.

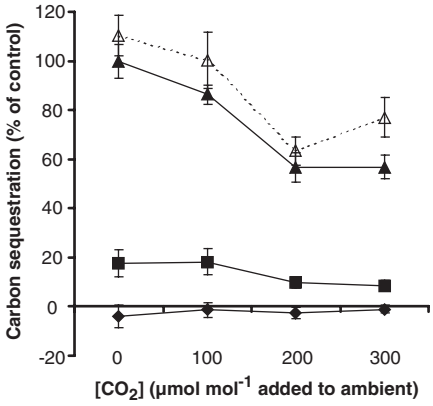

Fig. 2. Carbon sequestration in the soil after 5, 10, and 15 months. Values are means for six species (±1 SE, n = 18), expressed as percentage of the ambient CO_2 control, with no added nutrients for each species at the final harvest. Absolute values of carbon sequestration at the final harvest ranged from 2.4 to 1.4 mg C g^{-1} dry soil (no added nutrients) and from 2.6 to 1.6 mg C g^{-1} dry soil (added nutrients). Diamonds, 5-month; squares, 10-month; and solid triangles, 15-month harvests, no added nutrients; open triangles, 15-month harvest, added nutrients. There was no significant CO_2 × nutrient interaction. Main nutrient effect, P = 0.005; main CO_2 effect, P < 0.001; CO_2 × harvest date interaction, P < 0.001.

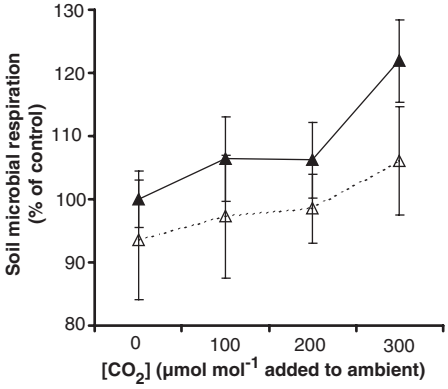

Fig. 3. Soil microbial respiration measured after the final harvest. Values are means for six species (±1 SE, n = 18), expressed as percentage of the ambient CO_2 control with no added nutrients for each species. Solid triangles, no added nutrients; open triangles, added nutrients. There was no significant CO_2 × nutrient interaction. Main nutrient effect, P = 0.024; main CO_2 effect, P = 0.038.

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