Nonlinear grassland responses to past and future atmospheric CO₂

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Carbon sequestration in soil organic matter may moderate increases in atmospheric CO₂ concentrations (C₄) as C₄ increases to more than 500 μmol mol⁻¹ this century from interglacial levels of less than 200 μmol mol⁻¹ (refs 1-6). However, such carbon storage depends on feedbacks between plant responses to C₄ and nutrient availability. Here we present evidence that soil carbon storage and nitrogen cycling in a grassland ecosystem are much more responsive to increases in past C₄ than to those forecast for the coming century. Along a continuous gradient of 200 to 550 μmol mol⁻¹ (refs 9, 18), increased C₄ promoted higher photosynthetic rates and altered plant tissue chemistry. Soil carbon was lost at subambient C₄, but was unchanged at elevated C₄, where losses of soil carbon offset increases in new carbon. Along the experimental gradient in C₄ there was a nonlinear, threefold decrease in nitrogen availability. The differences in sensitivity of carbon storage to historical and future C₄ and increased nutrient limitation suggest that the passive sequestration of carbon in soils may have been important historically, but the ability of soils to continue as sinks is limited.

The concentration of CO₂ in the atmosphere has increased dramatically since the last Glacial Maximum, most recently owing to fossil fuel burning and land conversion to agriculture. This increase in C₄ has focused attention on the role of terrestrial ecosystems in sequestering anthropogenic CO₂ (refs 2, 5, 7, 11, 12). The long-term consequences of rising C₄ on C sequestration are highly dependent on feedbacks between plant responses to C₄ and nutrient dynamics. Plant growth is often enhanced with increases in C₄ (refs 6, 14), sometimes leading to changes in plant tissue chemistry and organic inputs to soils (refs 15, 16). These and other feedbacks controlled by microbial processes may either increase (refs 17, 18) or decrease (refs 19, 20) nutrient availability, and moderate the long-term ability of ecosystems to sequester C₄ (refs 21, 22). For C sequestration to be important at decadal and century timescales, nutrient availability must not hinder higher plant production and new organic C must be stabilized in soil pools with relatively long turnover times. The partitioning of C among soil organic matter (SOM) pools with different turnover rates is thus a crucial determinant of C sequestration in many systems and is tightly coupled with plant tissue chemistry and nutrient dynamics (refs 23, 24).

A field experiment in an intact C₃-C₄ grassland in central Texas provided a continuous gradient of C₄ from 200 to 550 μmol mol⁻¹ permitting the measurement of critical threshold and nonlinear responses to past, present and future atmospheric CO₂. Plant and ecosystem properties, including water-use efficiency, photosynthesis, respiration rates and primary productivity, often change with rising C₄, but it is not likely that all such responses were or will be linear (refs 25, 26). Physiological thresholds (refs 27, 28), transient or acclimatory responses (refs 29, 30), and the strong coupling of plant and soil responses (refs 31, 32) are examples of mechanisms that may drive nonlinear processes in nature. Nonlinear and threshold responses are the focus of several new international programmes (ref. 33) and may explain some of the apparent contradictory results observed in recent CO₂ studies (refs 17, 18). Furthermore, research on how intact ecosystems respond to both past and future C₄ provides a context that can demonstrate the sensitivity of C dynamic changes to changes that have already occurred as well as those forecast for the coming century. Extrapolation from experiments that impose step changes in C₄ is complicated by the possibility that plants may evolve as C₄ changes more slowly in nature. There is some evidence, however, that perennial plants have not evolved quickly enough to be closely adapted to current C₄ (ref. 24).

Figure 1: Effects of CO₂ treatments on various species. a: Maximum CO₂ assimilation for three species (Brachypodium distachyon, Sorghum bicolor, Bromus japonicus) in 1999, showing a significant positive relationship between maximum CO₂ assimilation and treatment CO₂ in all species (P < 0.01). b: C/N ratio for leaves from the two C₄ species show a positive, linear increase with increasing treatment CO₂. c: C/N ratio for Brachypodium distachyon leaves, crowns and leaves. Roots showed an exponential increase in C/N ratio with increasing CO₂ (P < 0.03), crowns showed a positive, linear increase (P < 0.05). d: Relative change in phenolic concentrations in Brachypodium distachyon roots (expressed relative to ambient values). There was a strong, exponential increase in root phenolic content (P < 0.001), with an apparent threshold at C₄ slightly above ambient levels.
Along the experimental gradient, plants responded to higher $C_4$ by increasing photosynthesis and net primary production (Fig. 1a, Table 1). As treatment $CO_2$ increased, maximum $CO_2$ assimilation rates increased linearly for both $C_3$ and $C_4$ plants $^{19}$ (Fig. 1a; $P < 0.01$). Associated with this increase in $CO_2$ assimilation was a 50% increase in above- and belowground net primary production at elevated $CO_2$ compared to subambient $CO_2$ (Table 1). Tissue chemistry was altered as well, with an increase in tissue C/N with higher $C_4$ and an exponential increase in phenolic concentration (Fig. 1b–d). $C_4$ and species type were highly significant predictors of C/N, with C/N positively correlated with $C_4$ (analysis of covariance (ANCOVA); $P < 0.001$ for $C_4$; $P < 0.001$ for species). The concentration of phenolic compounds in roots of one of the dominant species in the system, the C. Grass B. ischaemum, showed a strong threshold effect, with little variation in plants grown at subambient $C_4$, but an exponential increase above ambient $CO_2$ (Fig. 1d; $P < 0.001$).

Soil C storage and belowground metabolism were greatly altered. Despite a linear increase in photosynthesis along the gradient, soil C storage was much more sensitive to subambient than to elevated $C_4$ (Fig. 2a). At subambient $C_4$, bulk soil C stocks decreased by 11%, or 450 g m$^{-2}$, between 1996 and 2000 (Table 2). However, there was no concomitant increase in soil C storage at elevated $C_4$ (Fig. 2a), with soil C increasing by a modest 3.3% (144 g m$^{-2}$) over the same time period (Table 2). The relationship between treatment $CO_2$ and the change in bulk soil organic C over three years follows an asymptotic function (Fig. 2a; $P < 0.05$), suggesting that the ability of soils to act as sinks for anthropogenic $CO_2$ will slow or reach saturation.

Accompanying altered soil C storage was an important change in soil organic matter chemistry. Total organic matter C/N was linearly associated with treatment $C_4$ (Fig. 2c; $P < 0.01$), in a pattern similar to that observed for plant tissue chemistry. There was also a divergence in patterns of soil respiration at super- versus subambient $C_4$. Soil CO$_2$ flux at peak plant growth was 40% higher at elevated than at subambient $C_4$, suggesting that much of the increase in C fixed with rising $C_4$ is lost to microbial or root respiration (Table 1).

The changes observed in particulate organic matter (POM) demonstrate a shift in the balance between new and old SOM. POM is a relatively labile class of SOM, with a residence time of between 10 and 50 years $^{11,25,26}$. The 14% loss in POM carbon at subambient $C_4$ paralleled the loss in total organic C (Table 2). However, in contrast to total organic C, POM C increased linearly with treatment $CO_2$, even at elevated $C_4$ (Fig. 2b). These findings indicate that at elevated $C_4$, increases in POM C were largely offset by losses in the older, mineral-associated organic matter $^{11,25,26}$ (Table 2). Even within the POM class, there were increases at elevated $C_4$ in the two most labile fractions (free and macroaggregate POM), while there was a decrease in the most recalcitrant fraction (microaggregate POM) $^{11,25,26}$ (Table 2). This represents a change in ecosystem C partitioning to faster cycling organic matter $^{11,25,26}$, which may explain why higher C assimilation and production did not lead to increased C sequestration. Our result is similar to those of other studies that reported that at low nutrient availability and elevated $CO_2$, carbon was lost from the mineral-bound fraction of SOM $^{11,25,26}$.

Similarly, an annual grassland exposed to a doubling of $C_4$ had
higher ecosystem C uptake and belowground allocation but little extra C storage. Much of the increased C was partitioned to rapidly cycling pools that make a negligible contribution to long-term storage because of their small size and relatively high turnover rates.

The feedback between plant responses to C4 and nutrient dynamics is vital in determining C sequestration in ecosystems. Nitrogen mineralization rates decreased dramatically and non-linearly with increasing CO2 (p < 0.01), with the largest changes occurring at subambient concentrations (Fig. 3). Net N mineralization was three times higher at 200–240 μmol mol−1 CO2 than at 530–550 μmol mol−1. Because of the changes in the chemical composition of detritus and increased C supply, microbes at high CO2 may need to mineralize older, mineral-associated SOM to meet their nutritional requirements. As a result, there was a decrease in plant-available N as a consequence of microbial immobilization and a loss in C stored in mineral-associated fractions of organic matter. Some workers have concluded that suppressed N availability under elevated CO2 may increase C storage by suppressing decomposition rates, but we found that there were only modest gains in soil C storage at the lowest N availability. In contrast to other grassland CO2 studies, our results are apparently a consequence of altered plant litter chemistry rather than an indirect effect of altered soil water status, as increases in plant water-use efficiency along the gradient were offset by higher plant biomass (data not shown). Increases in C4 resulted in higher nitrogen-use efficiency by plants, but a threefold decrease in nitrogen availability will probably have a detrimental effect on long-term plant productivity and, ultimately, on ecosystem carbon storage.

Higher net primary productivity, altered plant tissue chemistry, modifications of SOM composition and stocks, and changes in nutrient availability with increases in C4 suggest that both forests and grasslands are sensitive to rising CO2. The capacity of future ecosystems to act as sinks for anthropogenic CO2 will be determined by feedbacks among ecosystem processes and will be sensitive to the location of specific thresholds that influence the magnitude of the change in ecosystem dynamics. In this grassland, soil C stocks and net N mineralization are much more sensitive to subambient than elevated CO2, indicating that we are currently at an important threshold. Soils may have played a role in passively sequestering C since the last interglacial period, but their ability to continue to act as a C sink may be limited by nutrient availability. To assess the impacts of rising CO2 on carbon sequestration patterns and nutrient dynamics requires knowledge of potential threshold responses and the legacy of historical and prehistorical changes.

Methods

Experimental system

Two parallel, elongated chambers (1 m tall × 1 m wide × 60 m long) were constructed on a grassland dominated by the C4 perennial grass Bothriochloa ischaemum (L.) Keng and Ambient air plus the C3 perennial forbs Solanum dimidiatum Raf. and Ratibida columnaris (Sims) D. Don. Pure CO2 was injected into the eastern chamber to initiate the elevated gradient (350–350 μmol mol−1), while ambient air was injected into the western chamber, initiating the subambient CO2 gradient (365–200 μmol mol−1). Gradients have been maintained during the growing season since May 1997 by altering flow rate through the chambers. At night, air flow in the chambers is reversed, maintaining a C4 gradient at 150 μmol mol−1 above daytime concentrations. The chambers are divided into 5-m sections, and air is cooled and dehumidified in each section to maintain air temperature and vapor pressure deficit near ambient conditions. Our results span pre-treatment data (1996–1997) and the three complete growing seasons during which the grassland was exposed to C4 gradient (1998–2000).

Soil analyses

Soil respiration was evaluated monthly using a LI-COR 6200. Total inorganic and organic soil carbon was determined using a two-temperature combustion procedure designed specifically for calcareous Blackland Prairie soils. Four soil cores were collected from each of the 20 sections in stratified, random positions. Total C and N were measured using a CE Instruments NC 2000 elemental analyser (ThermoQuest Italia). We measured POM in two aggregate size classes (macroaggregates (250–53 μm), microaggregates (250–53 μm)) using the method described in ref. 26 to determine POM C. Mineral-associated C was determined by difference between total C and POM C. We determined POM C using four soil samples from each section (n = 88) that were collected in September 1997 and December 2000. We used a month-long, in situ open-core incubation method described in ref. 29 to measure net nitrogen mineralization.
Statistical considerations

The experimental system is constructed to resolve the shape of ecosystem responses to a gradient in CO2. The experimental design uses a regression approach to test for significant CO2 effects based on changes in slope along the gradient. We used regression models to test for significant relationships between C3 and the response variable, using the regression wizard in SigmaPlot 5.0 for Windows (SPSS Inc.). We tested linear, logarithmic, power and hyperbolic functions to fit the data, and selected the model with the highest adjusted R^2 after examining the residual plots for normality and homoscedasticity. When models were nearly the same in their explanatory value (R^2 values within 0.05), we report results for the CO2 model. Because this experimental system is oriented in one direction across the landscape, it is possible that the measured responses may have been influenced by some unidentified factor co-varying with CO2 treatment. However, extensive pretreatment data, including such ecosystem characteristics as soil C stocks, net primary productivity and soil respiration, revealed no such trends before Emission (Table 1 and additional data not shown). Furthermore, the system design ensured that key environmental variables (photosynthetically active radiation, T, relative humidity, and so on) remained similar across the gradient. The absence of strong threshold responses at the transition between the two provides further evidence that neither landscape position nor within the chamber significantly influenced observations. To control for any pre-existing variation in soil organic matter, we evaluate the change in soil C stocks between 1997 and 2000 rather than absolute levels (Table 2).

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Competing interests statement

The authors declare that they have no competing financial interests.

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