Research Article

Nitrogen and Carbon Cycling in a Grassland Community Ecosystem as Affected by Elevated Atmospheric CO₂

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Increasing global atmospheric carbon dioxide (CO₂) concentration has led to concerns regarding its potential effects on terrestrial ecosystems and the long-term storage of carbon (C) and nitrogen (N) in soil. This study examined responses to elevated CO₂ in a grass ecosystem invaded with a leguminous shrub Acacia farnesiana (L.) Willd (Huisache). Seedlings of Acacia along with grass species were grown for 13 months at CO₂ concentrations of 385 (ambient), 690, and 980 μmol mol⁻¹. Elevated CO₂ increased both C and N inputs from plant growth which would result in higher soil C from litter fall, root turnover, and excretions. Results from the incubation indicated an initial (20 days) decrease in N mineralization which resulted in no change in C mineralization. However, after 40 and 60 days, an increase in both C and N mineralization was observed. These increases would indicate that increases in soil C storage may not occur in grass ecosystems that are invaded with Acacia over the long term.

1. Introduction

The rise of CO₂ in the atmosphere is well documented [1]; what has not been documented are the sinks for this C, with an estimated unknown sink of 1.4 × 10¹⁵ gC yr⁻¹ arising from the global C balance [2]. Carbon dioxide is a prime chemical input to the metabolism of higher plants and has a major role in governing plant-water relations and water use efficiency. The increased growth of most plants under higher levels of CO₂ [3–6] has prompted recent speculation on the ability of terrestrial ecosystems to sequester C [7]. However, the fate of C within ecosystems is affected by a biological chain of events which includes competition between plants. The ability of terrestrial ecosystems to sequester C will depend on the cycling of C among the various biomass and soil C pools and on the residence time of C in these pools.

The rate of C mineralization during decomposition of residue derived from plants grown under elevated CO₂ has not been resolved. It has been theorized that the commonly observed increase in plant C : N ratio under elevated CO₂ could lead to slower residue decomposition resulting in increased soil C storage and reduction in available N for plant production [8]. However, slower decomposition of leaf litter due to elevated CO₂ is not supported by the literature on litter quality [9]. Others have suggested that increased biomass might enhance microbial activity, resulting in a “priming effect” thereby leading to no increase in C storage [10]. Alternatively, microbial preference for easily decomposable plant material produced under CO₂-enriched conditions could reduce the turnover of more resistant organic material, thereby increasing soil C [11, 12]. Observations from field and laboratory studies indicate that with elevated atmospheric CO₂, N may limit the rate of plant residue decomposition and slow the release of N from decomposing plant material [13]. This indicates that understanding N cycling as affected by elevated CO₂ is fundamental to understanding the potential for soil C storage on a global scale.

It has also been speculated that changes in elevated CO₂ could impact the competitiveness between plant species, especially between native and invasive plant species. A study by Runion et al. [14] indicated that elevated atmospheric CO₂ increased biomass production in a longleaf ecosystem compared to ambient CO₂ conditions. However, close examination of biomass data for each species in this plant
community indicated that only longleaf pine showed a significant positive response to elevated atmospheric CO2 treatment. In grasslands, invasion by woody legumes such as *Acacia* can alter hydrology, nutrient accumulation and cycling, and C sequestration. The rate and magnitude of these changes are likely to be sensitive to the effects of atmospheric CO2 enrichment on growth and water and N dynamics of leguminous shrubs. Polley et al. [15] indicated that, at the highest CO2 concentration studied, biomass production of grass-tree communities increased more than 2.5-fold as a result of increased leaf photosynthetic rates, leaf area, and N2 fixation.

Previous research, considering the effects of elevated CO2 on the decomposition of individual plant parts and monoculture plant systems has indicated that increased soil C storage could occur [16, 17]. However, these past studies did not consider the impact of increased biomass input and the changes in soil brought about by differing responses of plant species. The objective of this study was to determine the impact of atmospheric CO2 enrichment on potential soil C and N mineralization in a grassland community.

2. Materials and Methods

A study on the effects of elevated CO2 concentrations on the productivity, water use, and N dynamics of the grassland invader *Acacia farnesiana* (L.) Willd (Huisache) was conducted by Polley et al. [15]. To study the impact of atmospheric CO2 enrichment on potential soil C and N mineralization within a grassland community, an incubation study was conducted on soil collected from this study. Descriptions of the study site and the model ecosystem have been previously reported [15]. Briefly, seeds of *Acacia* were planted in fine sandy loam soil (Udic Paleustalfs [18], in wheeled, 380-liter containers (0.9 m deep and 0.65 m on each side)). Three *Acacia* plants were established in each container.

Three individuals each of the C3 grass *Stipa leucotricha* Trin. and Rupe. (Texas winter grass) and the C4 grass *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) were also established from tillers in each container to provide a competitive environment for *Acacia* growth. Three 380-liter containers of the species mix were maintained for 13 months at average CO2 concentrations of 385 (ambient), 690, or 980 μmol mol−1 in air-conditioned greenhouse bays.

Carbon dioxide gas was injected into the greenhouse bays as necessary to maintain the desired concentrations. The CO2 concentration and dewpoint temperature of air in each bay were measured at 4 min intervals with an infrared gas analyzer (Model 6262, Li-Cor, Inc., Lincoln, NE). The CO2 readings were corrected for atmospheric pressure using a pressure indicator (Model DPI 260, Druck Inc., New Fairfield, CT). The CO2 concentration of air averaged 385, 690, and 980 μmol mol−1 for the three CO2 treatments. Air temperature was measured with 25 mm diameter thermocouples, and bay temperature was changed seasonally to approximate outdoor temperature by manually adjusting thermostatic controls.

At the conclusion of the study (13 months), soil samples were collected from 0–20, 20–50, and 50–80 cm depth increments for use in the incubation study. Soil subsamples were dried (55°C) and ground to pass a 0.15 mm sieve. Soil inorganic N (NO2−-N + NO3−-N and NH4-N) was extracted with 2 M KCl and measured by standard colorimetric procedures using a Technicon Autoanalyzer 3 (Bran + Luebbe, Buffalo Grove, IL). Soil subsamples were weighed (25 g dry weight basis) and placed in plastic containers. Deionized water was added to adjust soil water content to an equivalent of −20 kPa at a bulk density of 1.3 mg m−3. The containers were placed in sealed glass mason jars with 10 mL of water for humidity control; each jar also had a vial containing 10 mL of 1 M NaOH which functioned as a CO2 trap. The jars were incubated in the dark at 25°C and removed after 20 and 60 days for inorganic N determination. Carbon dioxide in the NaOH traps was determined by titrating the excess base with 1 M HCl in the presence of BaCl2 after 20, 40, and 60 days. Potential C mineralization was the difference between CO2-C captured in sample traps and in blanks. Potential N mineralization was the difference between final and initial inorganic N contents. The C mineralization divided by total C (initial soil C concentration) was used to calculate C turnover. Statistical analyses were performed using the mixed procedure of SAS [19], and means were separated using least significant difference at an a priori 0.10 probability level.

3. Results and Discussion

Increasing atmospheric CO2 concentration to 980 μmol mol−1 increased biomass production of the woody legume *Acacia* more than 2.5-fold during the initial year of growth due to increased leaf photosynthetic rates, leaf area, and N2 fixation [15]. The increase in biomass at elevated CO2 required no more water than was consumed by the shrubs grown near ambient CO2 concentration. As a result, apparent water use efficiency and biomass production increased by similar relative amounts. Elevated CO2 greatly increased N2 fixation by *Acacia*, with the total N fixed per plant at the highest CO2 concentration being 1.5 times greater compared to ambient CO2 conditions. This positive effect of CO2 on N2 fixation by *Acacia* during its initial year of growth is generally consistent with that reported for woody legumes [20, 21]. Nitrogen fixation promoted by elevated CO2 would be expected to provide additional N to a grassland ecosystem due to the N addition to the soil following litter fall, root turnover, and exudation. These are important factors by which increasing atmospheric CO2 concentration can modify the impact of woody legumes on grasslands. Studies have shown that plant matter grown under elevated CO2 can greatly impact N mineralization [16, 17]. This incubation study was conducted to determine the impact of the elevated CO2 concentration on soil N mineralization in a grassland system.

After 20 days of incubation of the 0–20 cm depth soil, N mineralization was significantly reduced by elevated CO2, with N mineralization being 95% higher at ambient CO2 compared to the 980 μmol mol−1 treatment level (Table 1). During this same measuring period, soil C mineralization and C turnover were not significantly impacted. This indicated that changes under elevated CO2 initially reduced N
mineralization rates. While greater plant inputs were entering the system, with greater total N from the N2 fixation, the quality of the plant residues were such that N mineralization was being limited. This reduction in inorganic N in soil solution in turn limited C mineralization, resulting in no difference in C respiration or C turnover at the 20-day sampling period (Tables 2 and 3). This is consistent with studies by Torbert et al. [17] which indicated that the impact of elevated atmospheric CO2 concentration on plant residue quality may be more important than the impact on plant residue quantity in determining C cycling in soil. They observed that the potential effect of elevated atmospheric CO2 concentration on C storage in agroecosystems will be dependent on the crop species grown, where N cycling within the plant/soil system would likely be the controlling factor for C storage in these systems. Likewise, these results agree with work from a free-air CO2 enrichment (FACE) study utilizing cotton (Gossypium hirsutum L.) [22] and wheat (Triticum aestivum L.) [23], which provided evidence for increased soil C storage even though differences between the two species (cotton and wheat) were noted.

However, unlike the agroecosystem studies, limitations to N mineralization did not persist in this grass ecosystem with *Acacia*. At the 40-day sampling period, a significant increase was observed with C mineralization as atmospheric CO2 was increased (Table 2). Likewise, an increase in the level of C turnover was observed with increasing atmospheric CO2 levels. At the 60-day measurement period, C mineralization was also significantly increased at the 980 μmol mol−1 compared to the ambient level as was C turnover (Tables 2 and 3). The C mineralization for the 980 μmol mol−1 treatment was 98% higher than for the ambient treatment. At this sampling period, unlike the 20-day period, a significant increase in N mineralization was also observed (Table 1). This indicated that after 60 days, N was no longer limiting microbial decomposition of plant material. Since increased biomass inputs into the soil system were observed in this study [15] and the limitations due to N were no longer impacting the decomposition processes, C mineralization also increased.

No significant differences were observed for N mineralization or C mineralization at the 20–50 cm depth or the 50–80 cm depth (Tables 1 and 3). This indicated that most changes in the soil system can be expected to occur in the top 20 cm of the soil profile. This is the portion of the soil that would be most impacted from litter fall and could result in movement of N to grass species from N2 fixation by the *Acacia*. While this study included a deep rooted species in the grass ecosystem, the greatest changes in C and N cycling occurred in the top of the soil profile where most plant rooting occurs.

It has been theorized that a reduction in N availability in ecosystems could reduce plant response to elevated CO2 conditions [24–26]. The results from this incubation study indicate that N mineralization was increased and therefore the potential for N limitations to reduce plant response to elevated CO2 in this grass ecosystem might not occur. This would indicate that over the long term in a grass ecosystem invaded with woody legumes such as *Acacia*, N resources should not be limiting for either microbial decomposition of residues or plant growth in future elevated atmospheric CO2 conditions compared to today’s conditions.

In a study to examine responses to elevated CO2 in a typical regenerating longleaf pine-wiregrass community, Torbert et al. [27] reported, as in this study with mixed plant species, an increase in N mineralization with elevated CO2. At least over the short term in a regenerating longleaf pine system, N resources should not be limiting for either microbial decomposition of residues or plant growth in future elevated atmospheric CO2 conditions compared to today’s conditions. However, elevated CO2 decreased soil C respiration and C turnover in the regenerating longleaf pine-wiregrass community, indicating long-term C sequestration would be likely. In the current study with grass species, an actual increase in soil C mineralization was observed with elevated CO2. This was likely due to the large input of N due to increase in N2 fixation by the *Acacia* into the plant/soil system. Polley et al. [15] reported total N accretion by *Acacia* increased with each increase in CO2 concentration: 55% from 385 to 690 μmol mol−1 CO2, and another 29% from 690 to 980 μmol mol−1 CO2. The increased C mineralization indicated that soil C levels in the elevated CO2 are being reduced compared to the ambient treatments.

These findings are in contrast to other research which reported that C sequestration is likely with increasing atmospheric CO2. Low-N availability of soil frequently limits production on grasslands [23, 24] and may also limit the response of net primary production to changes in CO2 concentration. However, with the *Acacia* included in the grass ecosystem, CO2 enrichment caused large N inputs into the soil system and large increases in biomass (a 2.5-fold increase during the initial year of growth, [15]). Although C inputs to soil increased, C mineralization also increased.

### Table 1: Effect of atmospheric CO2 concentration on soil N mineralization during a 60-day soil incubation at three soil depth increments.

<table>
<thead>
<tr>
<th>CO2 level (μmol mol−1)</th>
<th>0–20 cm</th>
<th>20–50 cm</th>
<th>50–80 cm</th>
<th>0–20 cm</th>
<th>20–50 cm</th>
<th>50–80 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>385</td>
<td>6.86 a</td>
<td>1.91 a</td>
<td>1.37 a</td>
<td>7.51 a</td>
<td>4.01 a</td>
<td>4.54 a</td>
</tr>
<tr>
<td>690</td>
<td>2.91 b</td>
<td>0.59 a</td>
<td>0.69 a</td>
<td>7.85 b</td>
<td>3.86 a</td>
<td>4.89 a</td>
</tr>
<tr>
<td>980</td>
<td>3.52 c</td>
<td>2.91 a</td>
<td>0.46 a</td>
<td>10.04 c</td>
<td>3.30 a</td>
<td>3.89 a</td>
</tr>
</tbody>
</table>

*Values represent means of three replications. Means within a column for each sampling date followed by the same letter do not differ significantly (a = 0.1).*
The results from this short-term study indicate that CO₂ may not increase soil C storage in this grassland ecosystem. Thus, long-term studies with elevated CO₂ will be necessary to clearly determine the impact of *Acacia* invasion in this grassland ecosystem on soil C storage.

References


