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Nitrogen and Carbon Cycling in a Model Longleaf Pine Community as Affected by Elevated Atmospheric CO_2

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ABSTRACT / Increasing global atmospheric CO_2 concentration has led to concerns regarding its potential effects on terrestrial ecosystem and the long-term storage of C and N in soil. This study examined responses to elevated CO_2 in a typical regenerating longleaf pine-wiregrass community. The model community consisted of five plant species: (1) an evergreen conifer (*Pinus palustris*), (2) a bunch grass (*Aristida stricta*), (3) a broadleaf tree (*Quercus margaretta*), (4) a perennial herbaceous legume (*Crotalaria rotundifolia*), and (5) a herbaceous perennial (*Asclepias tuberosa*) grown at two CO_2 concentrations (ambient and twice ambient). The CO_2-enriched plots had greater aboveground biomass than ambient plots, mainly due to increased pine biomass. After 3 years, samples of the soil (Blanton loamy sand: loamy, siliceous, semiactive, thermic Grossarenic Paleudult) were collected from 0- to 5-, 5- to 10-, and 10- to 20-cm depth increments. Microbial respiration, potential C and N mineralization, and C turnover were measured during a 120-day incubation of the soil samples. Elevated CO_2 decreased soil C respiration and C turnover, but increased N mineralization. Results indicate that soil C sequestration is likely for soils in this longleaf pine ecosystem.

The combined impact of population increases, industrial expansion, and deforestation has resulted in changes to the global environment, including an increased atmospheric CO_2 concentration (Holland 1978, Smil 1985, Warneck 1988). The implications for global warming and local climate shifts have been highly debated, but regardless of the eventual outcome of the climate issue, vegetation will be directly impacted by enriched atmospheric CO_2 (Poorter 1993, Strain and Cure 1994, Prior and others 1994, Wittwer 1995, Pritchard and others 1999). 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 CO_2 has prompted recent speculation on the ability of terrestrial ecosystems to sequester C (Gifford and others 1996). 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 the C in these pools.

Soils play a major role in the global C budget, not only because of the large amount of C stored in soil, with estimates ranging from 1395 to 1636 $\times$ 10^{15} g (Ajtay and others 1979, Schlesinger 1984, Post and others 1992), but also because soil's contribution to the annual flux of CO_2 to the atmosphere is 10 times than that contributed by fossil fuel (Post and others 1990). In the contiguous United States, forests are estimated to contain 50,830 Mt of carbon, with 51% of this total contained in the soil (Heath and others 2002).

Forest lands have been estimated to have the carbon sequestration potential of 0.53 t C/ha/yr by the Intergovernmental Panel on Climate Change (Kimble and others 2002). However, the fate of residue derived from

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forest plants grown under elevated CO_2 has not been resolved. Elevated atmospheric CO_2 has been shown to increase biomass production (Strain and Cure 1994, Prior and others 1994, Wittwer 1995, Pritchard and others 1999), which could increase C storage in soil. However, this will depend on the level of C mineralization during residue decomposition. It has been theorized that the commonly observed increase in plant C:N ratio under elevated CO_2 could lead to slower residue decomposition resulting in increased soil C storage. However, slower decomposition of leaf litter due to elevated CO_2 is not supported by the literature on litter quality (Hom 2002). Others have suggested that increased biomass might enhance microbial activity, resulting in a "priming effect" and, thus, no increase in C storage (Lamborg and others 1984). Alternatively, the microbial preference for easily decomposable plant material produced under CO_2-enriched conditions could reduce the turnover of more resistant organic material, thereby increasing soil C (Goudriaan and de Ruiter 1983, Lekkerkerk and others 1990).

Previous research considering the effect of elevated CO_2 on the decomposition of individual plant parts indicates that increased soil C storage could occur (Torbert and others 1995, 1998). However, these past studies did not consider the impact of increased biomass input and the changes in soil brought about by changes in competition between different plant species. The objective of this study was to determine the impact of atmospheric CO_2 enrichment of a typical regenerating longleaf pine-wiregrass community on potential soil C and N mineralization.

Materials and Methods

A model of a regenerating longleaf pine–wiregrass ecosystem was constructed in Spring 1998 at the National Soil Dynamics Laboratory in Auburn, Alabama, USA, on an outdoor soil bin (2 m deep × 6 m wide × 76 m long) containing a Blanton loamy sand (loamy, siliceous, thermic Grossarenic Paleudult). Descriptions of the study site and the model ecosystem have been previously reported (Pritchard and others 2001). Briefly, an assemblage of five early successional forest species representing major functional guilds within a typical longleaf pine–wiregrass community were chosen for study: longleaf pine (*Pinus palustris,* a C_3 evergreen conifer); wiregrass (*Arisida stricta,* a C_4 bunch grass); sand post oak (*Quercus margaretta,* a C_3 broadleaf tree); rattlebox (*Crotalaria rotundifolia,* a C_3 perennial herbaceous legume); and butterfly weed (*Asclepias tuberosa,* a C_3, nonleguminous, herbaceous perennial). These species are common associates throughout the southeastern US. Prior to transplanting into the model community, all plants were grown in 15 cm^3 containers from seed collected from natural sources.

Prior to planting, the soil bin was divided into 0.75 m^2 quadrants each possessing 16 equally spaced planting positions. The community was constructed by randomly assigning individuals of each species (three pines, three wiregrass, two oaks, one rattlebox, and one butterfly weed) into positions within each quadrant; six planting spaces per quadrant were left empty. This regime achieved planting densities reflective of naturally regenerating longleaf pine–wiregrass ecosystems (Haines and others 1999). Plants were regularly irrigated during Summer 1998 to facilitate community establishment using a metered drip irrigation system to deliver exact and consistent watering throughout the bin; thereafter, plants received only ambient rainfall. During the first two months, dead plants were replaced; thereafter, mortality was attributed to causes other than transplanting, and gaps were not refilled.

Open-top chambers, encompassing 7.3 m^2 of ground surface area, were used to deliver target CO_2 concentrations of 365 μmol/mol (ambient) or 720 μmol/mol (elevated) beginning in June 1998. The open-top field chambers, 3-m diameter and 2.4-m high, were described in detail by Rogers and others (1983). The bin was divided into six blocks, and each CO_2 treatment was randomly assigned to one chamber within each block.

Aboveground biomass of each plant species was measured by destructively harvesting in June 2001 after three years of CO_2 exposure. Belowground biomass was also collected by taking eight large cores (25 cm × 60 cm depth) between rootstocks. An additional four soil samples (3.8 cm diameter) were collected from 0-to 5-, 5- to 10-, and 10- to 20-cm depth increments to investigate elevated CO_2 on soil C and N cycling. Subsamples of the soils were dried (55°C), ground to pass a 0.15 mm sieve, and analyzed for total N and C on a LECO CN 2000[1] (LECO Corp., Saint Joseph, Michigan, USA). Soil inorganic N (NO_2-N + NO_3-N and NH_4-N) was extracted with 2 M KCl and measured by standard colorimetric procedures using a Technicon Autoanalyzer 3 (Bran+Luebbe, Buffalo Grove, Illinois, USA).

An incubation study was conducted: sieved (2 mm) soil samples were weighed (25 g dry weight basis) and placed in plastic containers. Deionized water was added

[1]Names are necessary to report factually on available data: however, the USDA neither guarantees nor warrants the standard of the production, the use of the name by USDA implies no approval of the product to the exclusion of others that may be suitable.

Table 1. Effect of atmospheric CO_2 concentration on plant biomass production after three years of growth[a]

	Biomass (g/m^2)	
Species	Ambient	Elevated
Butterfly weed	13 a	5 b
Rattlebox	4 a	2 b
Sand post oak	142 a	201 a
Longleaf pine	2712 a	5237 b
Wiregrass	682 a	470 b
Total	3552 a	5915 b

[a]Values represent means of 6 replications. Means within a row followed by the same letter do not differ significantly ($\alpha = 0.1$).

to adjust soil water content equivalent to −20 kPa at a bulk density of 1.3 Mg/m^3. The containers were placed in sealed glass jars with 10 ml of water for humidity control, and a vial containing 10 ml of 1 M NaOH as a CO_2 trap. The jars were incubated in the dark at 25°C and removed after 30, 60, and 120 days. Carbon dioxide in the NaOH traps was determined by titrating the excess base with 1 M HCl in the presence of $BaCl_2$. Potential C mineralization was the difference between CO_2 -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 was used to calculate C turnover. A ratio of C mineralized to N mineralized during the incubation was also calculated. Statistical analyses were performed using the Mixed procedure of SAS, and means were separated using least significant difference at an a priori 0.10 probability level.

Results and Discussion

Elevated atmospheric CO_2 resulted in an increase in biomass production in the longleaf ecosystem compared to the ambient CO_2 conditions (Table 1). However, examination of the biomass data for each of plant species indicated that only the longleaf pine showed a significant positive response to elevated atmospheric CO_2 treatment. The post oak trees exhibited a positive, but nonsignificant, response to elevated CO_2. The other plant species had a significant negative response to elevated CO_2. These results were most likely due to the dominant response of the tree species (particularly longleaf pine) resulting in increased competition for limited resources in the model ecosystem, thereby decreasing biomass production of the other plant species. Regardless of this negative response for three of the five plant species, the dominant longleaf pine biomass increase due to elevated CO_2 resulted in a significant increase in total biomass production after three years of CO_2 exposure (Table 1). The increase in plant biomass due to elevated CO_2 occurred both above and below the ground. This suggests that longleaf pine ecosystems could sequester more C in a future CO_2-enriched environment.

Regardless of changes in biomass production with elevated CO_2, only small changes were observed for soil total C concentration (Table 2). In fact, while a similar trend was observed for soil C at all soil depths, only the 5- to 10-cm depth resulted in a significant increase in total C with the elevated CO_2 treatment. Total N was not significantly impacted by atmospheric CO_2 concentration, and there was no significant CO_2 effect on soil C:N ratio (Table 2). The small changes observed in soil C with elevated CO_2 treatment, despite the large input of C, are not unexpected for several reasons. First, soil C is a very large pool relative to biomass C inputs, while at the same time, new residue inputs of C and N into the soil system are very dynamic and much of the new C inputs are lost during microbial respiration. Furthermore, much of the input of C into soil is in the form of intact roots, which is not accounted for in these measures of soil C. The result is that measurable changes in soil C occur only after a change has been sustainable for many years. In addition, measurements of soil C and N are inherently variable, which would contribute to the lack of significance observed. Regardless, the significant increase in soil total C at the 5- to 10-cm depth and consistent increase in soil total C observed at the other depths after only 3 years of the longleaf pine system indicates that increased soil C sequestration could occur under elevated CO_2 conditions.

The lack of significant differences in soil total C and N and C:N ratio do not necessarily indicate that substantial changes have not occurred in the cycling of C and N in the soil. The incubation study was conducted to more precisely measure the changes that may occur in cycling of C and N in the soil. A steady level of C mineralization was observed throughout the 120-day incubation of the soil samples (Table 3). At the end of 120 days, a small impact that was correlated to soil depth could be observed, with an increase in C mineralization at the 0- to 5-cm depth compared to the 10- to 20-cm depth. This was likely due to increased biomass inputs from leaf litter at the soil surface during the study (surface residue may be more reactive with soil microorganism compared to root biomass, resulting in higher levels of C mineralization) (Table 3). Even though total soil C and total biomass input were higher with the elevated CO_2 treatment, C mineralization (while not always significant) was consistently reduced during the incubation compared to the ambient CO_2 conditions at all three soil depths (Table 3). A significant

Table 2. Effect of atmospheric CO_2 concentration on soil total C and N concentration and C:N ratio at three soil depths increments after three years of growth[a]

	Total C (g/kg)		Total N (g/kg)		C:N Ratio (g/g)	
Depth (cm)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0–5	3113 a	3222 a	157 a	152 a	19.9 a	22.1 a
5–10	2637 a	2745 b	114 a	114 a	23.4 a	24.8 a
10–20	2645 a	2771 a	107 a	115 a	25.1 a	24.6 a

[a]Values represent means of 6 replications. Means within a row for each sampling date followed by the same letter do not differ significantly ($\alpha = 0.1$).

Table 3. Effect of atmospheric CO_2 concentration on soil C mineralization during a 120-day soil incubation at three soil depths increments after three years of growth[a]

	Mineralization (mg/kg)					
	0–30 days		0–60 days		0–120 days	
Depth (cm)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0–5	46.8 a	49.4 a	106.1 a	86.4 b	254.5 a	222.6 b
5–10	50.0 a	42.8 a	96.0 a	83.6 b	239.7 a	230.0 a
10–20	43.2 a	42.9 a	85.5 a	89.4 a	215.6 a	207.6 a

[a]Values represent means of 6 replications. Means within a row for each sampling date followed by the same letter do not differ significantly ($\alpha = 0.1$).

Table 4. Effect of atmospheric CO_2 concentration on soil C turnover during a 120-day soil incubation at three soil depths increments after three years of growth[a]

	Turnover (mg/kg)					
	0–30 days		0–60 days		0–120 days	
Depth (cm)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0–5	1.50 a	1.54 a	3.46 a	2.69 b	8.24 a	6.92 b
5–10	1.89 a	1.57 b	3.64 a	3.06 b	9.10 a	8.36 a
10–20	1.64 a	1.55 a	3.24 a	3.23 a	8.13 a	7.50 a

[a]Values represent means of 6 replications. Means within a row for each sampling date followed by the same letter do not differ significantly ($\alpha = 0.1$).

reduction in C mineralization was observed at the 0- to 5-cm depth at both the 60- and 120-day sampling dates. Likewise, a significant reduction was observed at the 5- to 10-cm soil depth at the 60-day sampling date (Table 3).

As noted earlier, the rate of C mineralization can be influenced by the amount of organic C present. Soil C turnover is a measure of the rate of C mineralization relative to the amount of total C present in the soil. The level of C turnover observed in the study is shown in Table 4. Unlike C mineralization, there was no observable difference for C turnover between soil depths, further indicating that the reduction in C mineralization with soil depth was a result of increased biomass input at the upper soil depths.

As was seen with the C mineralization, C turnover during the incubation was (while not always significant) consistently lower for the elevated CO_2 treatment compared to the ambient CO_2 treatment (Table 4). A significant reduction in soil C turnover was observed for the 60- and 120-day sampling dates at the 0- to 5-cm soil depth for elevated CO_2. Likewise, a significant reduction was observed for soil C turnover at the 30- and 60-day sampling dates at the 5- to 10-cm depth for elevated CO_2 (Table 4). The results of the C mineralization and C turnover indicate that sequestration of C in soil could occur in longleaf pine ecosystem under elevated CO_2 conditions.

It has been commonly theorized that the increase in plant C:N ratio generally observed with plants grown un-

Table 5. Effect of atmospheric CO_2 concentration on soil N mineralization during a 120-day soil incubation at three soil depths increments after three years of growth[a]

	Mineralization (mg/kg)					
	0–30 days		0–60 days		0–120 days	
Depth (cm)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0–5	1.26 a	1.37 a	2.29 a	2.43 a	2.62 a	3.19 b
5–10	0.54 a	0.59 a	0.89 a	1.08 b	1.03 a	1.14 b
10–20	0.41 a	0.52 a	0.75 a	0.85 a	0.72 a	0.86 a

[a]Values represent means of 6 replications. Means within a row for each sampling date followed by the same letter do not differ significantly ($\alpha = 0.1$).

der elevated CO_2 could lead to slower plant decomposition (Bazzaz 1990). However, investigations of plant decomposition have not generally found a reduction in decomposition rate despite changes in the C:N ratio (Torbert and others 1998, Cotrufo and Ineson 2000). Despite an overall 7% decrease in N and 6% increase in lignin reported, little reduction in residue decomposition has been reported in literature (Hom 2002). In this study, a reduction in soil C mineralization was observed with elevated CO_2 (Table 3). However, this study examined the cumulative impact of an elevated CO_2 treatment on C dynamics in a mixed community of plants, and not just the decomposition of isolated plant materials grown under elevated CO_2 conditions.

The N mineralization during the incubation was very small; the highest N mineralization observed was only 3 mg/kg after 120 days (Table 5); this is consistent with expected levels of N mineralization rates for forested soils. Much higher levels of N mineralization was observed at the 0- to 5-cm depth compared to the 5- to 10- and 10- to 20-cm depth at all three sampling dates. This depth response for N mineralization was consistent with the depth response observed for C mineralization (Table 3). The N mineralization during the incubation was (while not always significant) consistently higher for the elevated CO_2 treatment compared to the ambient CO_2 treatment (Table 5). A significant increase in soil N mineralization was observed for the 60- and 120-day sampling dates at the 0- to 5-cm soil depth for elevated CO_2 (Table 5). Likewise, a significant increase was observed for soil N mineralization at the 30- and 60-day sampling dates at the 5- to 10-cm depth for elevated CO_2 (Table 5). It has been theorized that the reduction in N availability in forested ecosystems could reduce plant response to elevated CO_2 conditions (Strain and Bazzaz 1983). The results from this incubation study indicates that N mineralization was increased and therefore the potential for N limitations to reduce plant response to elevated CO_2 in this forested ecosystem might not be a problem. Further, this could also be a partial explanation as to why the longleaf pine out competed the other plant species. Unlike the other species in the study, the longleaf pine is an evergreen species which will grow all year long and with its more extensive root system, could utilize any available N for growth throughout the year.

These results are different from our findings on agronomic crops on this soil type (Torbert and others 1995, 1998). Our findings in those studies indicated that the effects of elevated CO_2 on plant decomposition would have little affect on C mineralization, but a reduction in N mineralization. Nitrogen cycling within the plant/soil system could likely be altered with elevated CO_2 in the agroecosystems and may be the controlling factor for C storage. In the current study, the C mineralization was reduced, while simultaneously increasing N mineralization.

The ratio between C mineralization and N mineralization is considered to be an index of the level of recalcitrant C in soil being mineralized; an increase in C:N mineralization indicates a decrease in recalcitrant C being mineralized (i.e., more C being released relative to the N being released). A distinct difference was observed in the level of C:N mineralization for soil depth during the incubation (Table 6). As soil depth increased, the level of C:N mineralization increased, indicating that the level of recalcitrant C mineralized was decreased with depth, perhaps related to root inputs. This would be consistent with the smaller amount of total C mineralized and the fact that little difference could be observed for C turnover between soil depths (Tables 3 and 4).

The C:N mineralization ratio was consistently lower (while not always significant) for the soil under elevated CO_2 conditions compared to the soil in the ambient CO_2 treatment (Table 6). A significant decrease in soil C:N mineralization ratio was observed for the 120-day sampling date at the 0- to 5-, and 10- to 20-cm soil depths for elevated CO_2 (Table 6). Likewise, a significant decrease was observed for soil C:N mineralization

Table 6. Effect of atmospheric CO_2 concentration on soil C:N mineralization ratio during a 120-day soil incubation at three soil depths increments after three years of growth[a]

	Mineralization ratio (g/g)					
	0–30 days		0–60 days		0–120 days	
Depth (cm)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0–5	40.8 a	36.6 a	51.1 a	37.7 a	104.1 a	73.2 b
5–10	92.8 a	73.3 b	108.2 a	78.13 b	236.2 a	209.3 a
10–20	124.4 a	88.4 a	125.6 a	108.5 a	315.9 a	252.6 b

[a]Values represent means of 6 replications. Means within a row for each sampling date followed by the same letter do not differ significantly ($\alpha = 0.1$).

ratio at the 30 and 60 day sampling dates at the 5- to 10-cm depth for elevated CO_2 (Table 6). This indicates that, even though there was the same or perhaps more organic C with the elevated CO_2 treatment, organic matter decomposition in the elevated CO_2 treatment was from more recalcitrant C pools compared to the ambient CO_2 treatment.

Other studies have observed shifts in the soil pools of C decomposition when plants are grown under elevated atmospheric CO_2 conditions. For example, Goudriaan and de Ruiter (1983) and Lekkerkerk and others (1990) found with ^{14}C data that microbial preference for easily decomposable plant material produced during growth under CO_2-enriched conditions could reduce the turnover of more resistant organic material. Similarly, studies with soybeans using ^{13}C data indicated that elevated CO_2 conditions resulted in a shift in decomposition preference for new soil C (Torbert and others 1997). Johnson and others (2000) reported that, while they could not find any significant difference in the N dynamics from decomposition in litter bags from trees grown under elevated CO_2 conditions, the natural abundance ^{15}N was significantly greater with elevated CO_2 in both live and senesced needles, indicating a shift in uptake to different soil N pools. In this study, the C:N ratio would indicate that the shift was toward more recalcitrant C sources with the elevated CO_2 treatment. This could have been the result of different C inputs to the soil, with a significant increase in longleaf pine residue and a significant decrease in non-tree species residue under the elevated CO_2 treatment. Because C_4 and C_3 plant species were grown together, isotopic techniques could not be used to differentiate new C inputs. Therefore, it was not possible to distinguish if the C being respired was from old sources of soil C or from new C sources that were more recalcitrant in nature due to elevated CO_2 growing conditions. Nevertheless, a shift in decomposition C pool preference would explain the results in this study where less C was mineralized, but more N was released under elevated CO_2 conditions.

Conclusions

In this study, elevated atmospheric CO_2 resulted in increased biomass production primarily from the longleaf pine species but not the other competing plant species in the ecosystem. While only small changes were observed for soil total C and N pools, distinct changes were observed in the C and N cycling processes, which indicate that long-term changes in total C and N pools may occur. Elevated CO_2 decreased soil C respiration and C turnover. At the same time, increased N mineralization was observed with elevated CO_2. This would indicate that, 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 CO_2 conditions compared to today's conditions. The C:N mineralization ratio was consistently lower for the soil under elevated CO_2 conditions compared to the soil in the ambient CO_2 treatment. This indicates that the primary source of C in the decomposition processes has been shifted to a different (more recalcitrant) C pool. Results from this study indicate that increased C sequestration is likely in soil within a longleaf-wiregrass ecosystem under elevated atmospheric CO_2 conditions.

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