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Research Article

Temporal Effects of Elevated Carbon Dioxide and Ozone on Soil Carbon and Nitrogen Stoichiometry in a No-till Soybean-Wheat Agro-ecosystem

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Abstract

The effects of elevated CO_2 and O_3 on plants have been studied widely, but their possible effects on carbon: nitrogen stoichiometry of soil organic matter (SOM) has received much less attention. We conducted a five-year field experiment to address such effects on SOM. We used open-top chambers to expose a no-till (NT) soybean-wheat system to a factorial combinations of two CO_2 (360 & 500 μmol mol^{-1}) and two O_3 (25 & 70 nmol mol^{-1}) treatments daily from April to October under ambient light and temperature conditions. Geo-referenced composite soil samples were collected annually and analyzed for soil total organic C (TOC), N (TN), hydrogen (H) concentrations, and bulk density. TOC increased through time under both CO_2 levels, but the increase was significantly greater under elevated CO_2 (585-kg ha^{-1} y^{-1}) compared with the ambient CO_2 (18-kg ha^{-1} y^{-1}). TN decreased over time under both levels of the CO_2 and O_3 treatments. The rate of decrease in TN was greater under elevated CO_2 (216-kg N ha^{-1} y^{-1}) compared to ambient CO_2 (152-kg N ha^{-1} y^{-1}), but it was smaller under elevated O_3 (172-kg N ha^{-1} y^{-1}) as compared to low O_3 (197-kg N ha^{-1} y^{-1}). The C:N was increased significantly over time under both levels of CO_2 or O_3 treatments. Results suggest that increased TOC sequestration at elevated CO_2 could elicit a progressive soil N deficiency. In contrast, the impact of elevated O_3 (+O_3 and O_3+CO_2) may cause a small accumulation of recalcitrant C, which in the long-term could affect SOM labiality. Increased soil N under elevated O_3 may enhance N leaching from soil.

INTRODUCTION

Tropospheric CO_2 and O_3 concentrations have been increasing and will continue to increase in response to human activities [1-4]. At least in the short term, elevated CO_2 can increase plant photosynthesis, water- and nutrient-use efficiencies, net primary production, root production, rhizosphere deposition, and mycorrhizal associations [5], but alter plant biomass composition by increasing C:N stoichiometry with higher proportions of nonstructural carbohydrates, lignin and phenolic compounds [6]. However, it has been suggested that accumulation of lignin and phenolic compounds in plant biomass may be due to nutrient limitations rather than the direct effect of elevated CO_2 [7].

Near-surface O_3 concentration is the product of photochemical reactions of carbon monoxide, methane and other hydrocarbons in the presence of nitrogen oxides [1]. O_3 is a phytotoxic pollutant that affects the integrity and permeability of plant-cell membranes and decreases metabolic efficiency [1,8,9]. Elevated O_3 may decrease crop yield and reduce below-ground carbon allocation [10]. However, plants may acclimate to, or resist, the effects of elevated O_3 through formation of antioxidants [11] and/or changing structural and cellular composition of plant biomass [12]. The latter can result in plant litters that are relatively recalcitrant for soil microorganisms [13,14].

Plant biomass is the main source of SOM formation [15,16]. Effects of elevated CO_2 and/or O_3 on plant biomass may have immediate and variable effects on soil food webs, microbial decomposition of organic matter and biological efficiency, and consequently on the soil's ability as a sink or source of C and other

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nutrients by influencing SOM labiality in response to agricultural management practices [17-19].

No-till (NT) is an agricultural practice that allows surface accumulation of crop residues. Reduced contact between soil microorganisms and crop residues under NT favors dominance of fungal food webs to utilize N poor un-fragmented crop residues [20-22]. Extensive fungal hyphae-plant root associations may aid in the protection of C especially particulate organic matter (POM) in soil macro-aggregates [22]. Furthermore, microbial preference for easily decomposable C-H-O enriched root exudates under elevated CO_2 may slow-down and/or reduce decomposition of high C:N crop residues and subsequent accumulation of C and other nutrients in SOM [22-24]. However, biological processes associated with crop residue decomposition are often influenced by N availability [25]. Decomposition of high C:N crop residue may increase microbial demand for N and, in turn, increase mineralization of low C:N native SOM [26]. Therefore, we hypothesized that no-till surface accumulation of high C:N crop residue produced under elevated CO_2 would be converted to C-H enriched but N-deficient SOM.

Soil functional processes that are mediated by microbes are often C-limited. Therefore, reduced crop biomass with greater recalcitrant composition at elevated O_3 could lead to an intense competition among the heterotrophic microbes for labial C metabolism [27,28]. An intense competition for labile C may favor the dominance of energy inefficient and generalist microbial feeders (e.g. bacteria) under labile C-limited ecosystems [16,21]. As a result, microbes may be forced to mineralize native SOM or autolyse their cells to fulfill increasing demand for labile C [27]. Therefore, we hypothesized that soils with growing crops under elevated O_3 will lose labile C faster but accumulate a small amount of recalcitrant C over time.

Soil organic matter is a major reservoir of nutrients, especially C and N that are stoichiometrically linked. This link is often influenced by H contents to maintain quality, stability and biogeochemistry of SOM [28,29]. A greater availability of high C:N crop residue or a lack of easily decomposable C-H enriched substrates for metabolism under elevated CO_2 or O_3 may be a key factor for C and N sequestration or depletion [30]. Knowledge of how SOM formation and lability will respond to long-term effects of elevated CO_2 or O_3 on plants is important to understand C and N dynamics.

Several studies have evaluated long-term effects of elevated CO_2 and O_3 on below ground responses and soil C dynamics for different plants [4,6,17-19,30]. Soil ability to serve as a sink for C under elevated CO_2 may be limited [6]. Significant variable $CO_2 \times O_3 \times$ time interactions on below ground processes, residue decomposition, and soil C dynamics have been reported [6,19,29-32]. However, there is no long-term research conducted to date examining $CO_2 \times O_3 \times$ time interaction on soil C and N dynamics under continuous NT soybean-wheat agro ecosystems. Therefore, the objective of our study was to address temporal effects of elevated CO_2 and O_3, individually and in combination, on TOC, TN and H contents of SOM under NT soybean (*Glycine max,* L.) - wheat (*Triticumaestivum*, L.) rotation. More specifically, we used analysis of covariance and repeated-measures analysis of variance to address: (1) the temporal change in the responses (i.e., test of the equality of the slope of the temporal trends to zero); (2) the interactive effects of CO_2 and O_3 on the responses studied; and (3) the interactive effects of temporal change and air quality treatments (i.e., test of interaction between time and the main or simple effects of CO_2 and O_3).

MATERIALS AND METHODS

The study was conducted at the USDA-ARS Climate Stress Laboratory field research facility at Beltsville, MD, USA. The soil is a moderately well drained Codorus silt loam (fine sand, acid, mesic, Fluvaquentic Dystrochrept), which is formed from recently deposited alluvium washed from soils developed from acid crystalline rocks of the Piedmont [33]. Initial studies on the soil properties and climatic conditions have been described elsewhere [34].

Experimental treatments and cultural practices

Air quality treatments consisted of a 2^2 factorial combinations of two CO_2 (ambient at 365±5 vs. elevated at 500±5 $\mu mol\ mol^{-1}$) and two O_3 (charcoal filtered air at 25±5 vs. elevated at 70±10 $nmol\ mol^{-1}$) levels. Each treatment combination was replicated twice, using eight open-top chambers (OTC). The OTC's (3-m diameter) were placed on 4-m × 4-m plots in which wheat and soybeans were grown in rotation from seed to maturity under continuous no-till. The CO_2 treatment was supplied daily from a bulk tank for 18-hr (0300 – 2100-hr EST). The O_3 was produced from cylinder O_2 using a Griffin O_3 generator (Lodi, NJ) and supplied daily for 7 h (0900 – 1600-hr EST). All OTC's were equipped with sprinkler irrigation system to maintain near field moisture capacity (16 to 18%, dry weight) of soil [35,36].

Wheat was planted in the fall with split applications of standard N-P-K fertilization in both fall and spring. Wheat was harvested by the 3rd week of June. Short-day soybean seedlings were transplanted to the plots in rows 60-cm apart between plants and 10-cm apart within the rows immediately following wheat harvest. Weeding was performed manually by hand. To control insects, Diazinon 4E (Ciba, Greensboro, NC) @ 1-mL L^{-1} solution was applied. The plots were also sprayed for powdery mildew control on wheat one or more times each spring using Benomyl (Dupont Agricultural Products, Wilmington, DE) at the rate of 0.3-kg ha^{-1}. Following wheat harvest, grasses and weeds in the plots within OTC's were killed with Glyphsophate (Monsanto Chemical, St. Louis, MO) using a 1.5% solution as foliar spray. The treatments were terminated in late October prior to harvesting soybean.

Soil collection, processing and analysis

Soil sampling and analysis started two years after the establishment of plots and 18 months after the initiation of gaseous treatments and continued for four years. Fourteen soil cores (1.9-cm dia.) from 15-cm depth were randomly collected between the rows of plants after fall harvest in late October or early November. Soil samples were then gently sieved through a 2-mm sieve, oven-dried at 105±2°C for 24-h to determine antecedent moisture content for correction of weight when calculating bulk density. A sub-sample of the oven-dried soil was ground with a ceramic mortar and pestle to pass through a 200-μm sieve before analysis.

A 150 to 200-mg sample of air-dried ground soil was used to analyze for TOC, TN and H contents using the LECO® dry combustion method. The thermal oxidation of SOM by LECO dry combustion not only produces CO_2 and N_2 but also H_2O, as a measure of H [28], according to the equation: $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$. Therefore, all H is derived from thermal oxidation of SOM [32]. The stocks of C, N, and H were determined by multiplying with the concurrently measured soil bulk density (ρb). The ρb was calculated using the oven-dried weight of a known volume of soil as: $\rho b\ (g\ cm^{-3}) = (\pi r^{2} * l * n)\ w^{-1}$. Where r is the internal radius of the soil core sampler, l is the length of the soil core, n is the number of soil cores, and w is the total weight (g) of oven-dried soil.

Statistical analysis

Analysis of covariance (ANCOVA) was performed in which the response variables were TOC, TN, H, C:N, and H:N, and explanatory variables were CO_2 and O_3 as class variables, and time (year after the initiation of the CO_2 and O_3 treatments) as a continuous covariate. ANCOVA allowed to detect whether or not: (1) there was a significant temporal change in the response variable being studied (test of the equality of the slopes of the temporal changes to zero), (2) the rate of the temporal changes depended on the treatments (test of interaction between time and class factors—CO_2 or O_3), and (3) there was an interaction between the effects of CO_2 and O_3. The *MIXED* procedure of the *SAS System* was used for statistical analysis. This routine has appropriate options (*RANDOM* and/or *REPEATED*) to allow for appropriate calculation of errors, *F* and *P* values for the factors involved (CO_2, O_3, time), and their interactions. Temporal trends were compared for the main-effects of CO_2 and O_3 when there was no significant interaction between CO_2 and O_3. In case of a significant CO_2-by-O_3 interaction ($CO_3 \times O_3$), the temporal trends were compared for the four simple effects (four combinations of two CO_2-by-two O_3 levels).

RESULTS AND DISCUSSION

The main effects of CO_2 or O_3 on TOC and TN contents, and the C:N and H:N are reported and discussed because the related CO_2-by-O_3 interactions were insignificant. The $CO_2 \times O_3$ effect was significant for H content ($P<0.01$) and for the C:H ($P<0.01$), and thus, the simple effects are reported and discussed for these variables.

Intercepts of the temporal trend for the main- or simple-effects of CO_2 or O_3 for TOC, TN and H contents and their ratios did not differ significantly (Figures 1–9). Since the experiment was established on a single type of soil, we assumed that there was no significant difference in soil properties before the initiation of the CO_2 and O_3 treatments, and that any temporal difference in TOC, TN and H contents should be in response to applied treatments over time. A lack of significant differences among the intercepts of the temporal trends supports these assumptions.

A significant CO_2 × time effect on TOC content ($P<0.05$) shows a clear difference between the slopes of the temporal trends for elevated and ambient CO_2 levels (Figure 1).

While TOC content increased (585-kg C ha^{-1} y^{-1}) under elevated CO_2, it increased marginally (18-kg C ha^{-1} y^{-1}) under ambient CO_2 concentrations. Increased soil C sequestration under elevated CO_2 was anticipated as a result of greater inputs of high C:N crop residues [6,37], slower decomposition [23], fungi dominated microbial processes [15], and greater bio-physical and/or biochemical protection [22,38,39]. Since decreased soil N may limit microbial utilization of C, greater availability of N-poor substrates under elevated CO_2 might reduce decomposition of crop residues. A slower decomposition implies a longer retention of crop residue and eventually greater accumulation of TOC. In addition to slower and higher C assimilation, mycorrhizal associations might contribute in retaining C as particulate organic matter (POM) by enhancing macro-aggregation through bio-physical enmeshing of micro-aggregates [20,22,40,41] or releasing polysaccharides to cement primary particles, POM, and micro-aggregates together to form or stabilize macro-aggregates [21,38,41,42]. A deposition of soybean and wheat roots and mycorrhizal hyphae within pore-spaces [38] and comminuted litter detritus, as POM, may also have incorporated in soil casts and macro-aggregates by the feeding and casting activities of earthworm and other faunas [21].

Soil acidification by legumes (e.g. soybeans) has promoted micro-aggregate formation through complex physico-chemical interactions of plant and microbial derived C compounds with di- and polyvalent metal ions and clays [29,38,39,43]. Since aggregate formation is directly influenced by plant root growth and exudations and indirectly by microbes-faunal activities [42], the increased accumulation and protection of C as POM within macro- and micro-aggregates, are the most important mechanisms enabling greater sequestration of TOC under elevated CO_2 concentrations.

Our results supports most of previous findings [6,31,32,43,44]. It has been reported that soil C sequestration asymptotically increased by 3.3% over a 3- year period [6]. A meta-analysis has shown that mineral soil acts as a sink of C in response to elevated CO_2 [32]. Under elevated CO_2, prairie soil sequestered 336±96 kg C ha^{-1} yr^{-1} at 0 to 15-cm depth [33], which is slightly lower than our results, perhaps due to continuous NT soybean-wheat rotation we used. Since C and N are stoichiometrically linked in SOM, a higher input of biomass N from soybeans might contribute to higher soil C sequestration in our study.

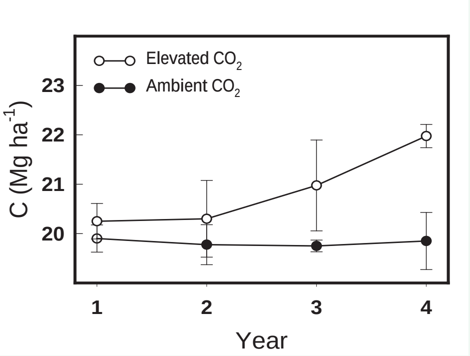

Figure 1 Carbon dioxide and time effects on total soil organic carbon (TOC) content.

Regardless of the mechanism of the effects, an important finding of our study is the elevated CO_2 impact on TOC under continuous NT cropping systems because an incomplete and slow decomposition of high C:N crop residue by fungal food webs may accelerate dissolved organic matter (DOM) production. Such an increase could be important in fueling soil denitrification processes.

Through time, soil TOC remained unchanged under reduced O_3, but it showed an increasing trend that did not reach statistical significance (i.e., slope of temporal increase was not significant) (Figure 2). Moreover, the interaction (test of the difference between the two slopes) was not significant. However, averaged over time, soil TOC was significantly higher under elevated O_3 compared with reduced O_3.

This could be due to greater fine root production and reduced decomposition of partially recalcitrant crop residue as influenced by O_3 fumigation under continuous NT [14,21,22]. Four year exposure of soybean-wheat to elevated O_3 might have increased plant O_3-tolerance of the crops [46]. A less O_3-responsive plants may causes a higher allocation of C to roots, leading to increased plant root biomass and soil TOC under elevated O_3[19]. This is contrary to findings that elevated O_3 reduced soil C [2,46].

Although the effects of $CO_2 \times O_3 \times$ time interaction on TOC were not significant, TOC was higher under the combination of elevated CO_2 and O_3 compared with their reduced levels. This could be due to the combined effects of high C:N litter inputs produced by CO_2 fertilization and partially recalcitrant leaf litters, increased fine root production under O_3 exposures, and slower decomposition of crop residues plus increased biophysical protection of POM under continuous NT over the years [6,13-15,22-24,38,39].

The temporal trends for soil TN differed for elevated CO_2 and O_3 when compared to ambient CO_2 and low O_3 treatments, respectively (Figures 3 and 4). These are indicated by the significance of CO_2 × time and O_3 × time interactions ($P<0.01$). Soil TN decreased over time under both CO_2 levels but the rate of decrease was significantly greater under elevated CO_2 (-216 kg N ha^{-1} y^{-1}) than under ambient CO_2 (-152 kg N ha^{-1} y^{-1}) treatment (Figure 3).

This implies that CO_2 fertilization reduced soil TN content @ 64 kg ha^{-1} y^{-1} as compared to ambient CO_2. Soil TN decreased over time perhaps due to continuous harvest of N-enriched grain/seed or feed, which exceeds the amount of TN returned to soil through fertilization, recycling of plant residues and atmospheric inputs. Results from several previous studies indicate that CO_2 might enhance root growth and facilitate greater soil exploration, thereby increasing N and other nutrients uptake to maintain the CO_2 fertilization effects on plants [39,47]. Although soil N uptake may increase to fulfill a greater overall plant growth, foliar N may decrease in response to greater flux of C-H enriched compounds, leading to a decreased N in litters [29,37,48]. The C:N of plant residues produced at elevated CO_2 is higher than that of native SOM, and an additional amount of N is required to sustain the process of residue decomposition, especially under a net positive C balance in soil [22]. In response to progressive N deficiency, and to fulfill the increasing demand for N and other nutrients, soil microbes often forced to mineralize relatively low C:N native SOM instead of decomposing high C:N plant residue[6,25,26]. The mineralization of native SOM would eventually release soil N available to plants through microbial biomass turnover and a temporary positive feedback on plant growth, which would increase N uptake even further. Therefore, enhanced plant uptake of N and its removal from the site by harvest in combination with mineralization of native SOM for increased microbial N demand in response to greater amount of high C:N litters produced under elevated CO_2 may likely resulted in C-H enriched but N-deficient SOM over time through alterations in the stoichiometry of C, N and H. The effects of progressive decreases in N availability will have a detrimental effect on plant growth, and consequently on soil C storage [6].

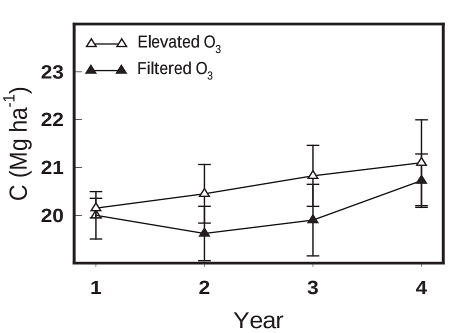

Figure 2 Ozone and time effects on total soil organic carbon (TOC) content.

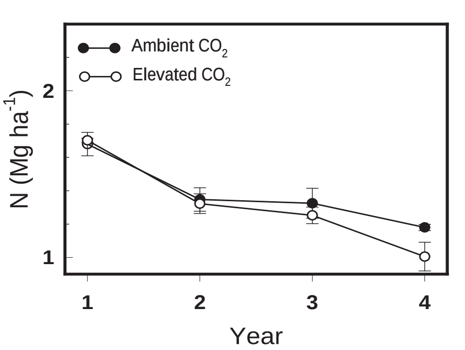

Figure 3 Carbon dioxide and time effects on soil total nitrogen (TN) content.

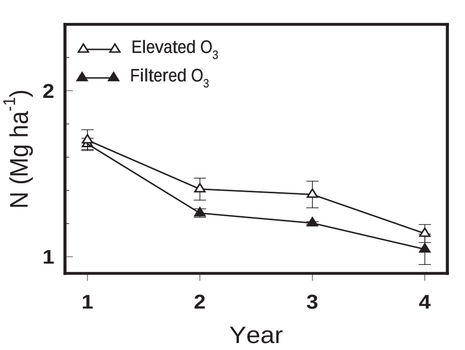

Figure 4 Ozone and time effects on total soil nitrogen (TN) content.

In contrast, the temporal N depletion rate was smaller under elevated O_3 (-172 kg N ha^{-1} y^{-1}) compared to low O_3 (-97 kg N ha^{-1} y^{-1}) treatment (Figure 4).

The elevated O_3 treatment resulted in an excess of 25kg of N ha^{-1} y^{-1} remaining in the soil as compared to low O_3 treatment. Again, reduced N over time by both O_3 treatments might be due to increased N uptake by plants and continuous harvest of N-enriched grain/seed. Using SOM enriched in ^{15}N, it has been reported that soybeans grown under elevated O_3 obtained more N from soil than plants grown under low O_3 due to reduction in N-fixation caused by decreased photosynthetic translocation of ^{13}C to nodules [49,50]. However, reduced temporal N depletionunder elevated O_3 compared with low O_3 in the current study is perhaps due to replenishment of N from incomplete breakdown of the litter fractions. Elevated O_3 can cause plant foliage to age prematurely with proportionally more N to be bound strongly with recalcitrant lignin and phenolic compounds, and decrease N reabsorption before senescence and/or abscission of leaves. This is supported by the findings that prematurely abscised litters produced at elevated O_3 had a higher N content [13]. Despite having a relatively higher N content, such plant litters can be more recalcitrant to microbial decomposition [14]. The recycling of N-enriched prematurely abscised plant litters in soil, may in turn, favor an accumulation of recalcitrant SOM, while increasing mineralization of native SOM due to progressive lacking of labile C to perform soil biological processes.

For the H content, all slopes of the temporal trends under the four combinations of two CO_2-by-two O_3 levels were significantly ($P<0.01$) different from zero (Figure 5).

The H content increased over time under elevated CO_2 irrespective of the O_3 levels, which differed significantly from each other (316 vs. 91 kg H ha^{-1} y^{-1}, respectively). By contrast, the H content decreased under ambient CO_2 irrespective of the O_3 regimes, which also differed significantly from each other (-195 vs. –57 kg H ha^{-1} y^{-1}, respectively). Greater translocation of C-H-O enriched compounds belowground through fine root productions, exudations, sloughed cells, and lysate turnover [23,24,50], accounts for much of the increase in H content (316 kg H ha^{-1} y^{-1}) under elevated CO_2 + low O_3 treatment than under elevated CO_2+elevated O_3 (91 kg H ha^{-1} y^{-1}) treatment. Higher proportion of lignin and other structural carbohydrates in litters as reported elsewhere [13] may be the most important factor in explaining relatively higher depletion of H in native SOM under ambient CO_2+elevated O_3 (-195 kg H ha^{-1} y^{-1}) than ambient CO_2 + low O_3 (-57 kg H ha^{-1} y^{-1}) treatment.

As indicated by the significant CO_2 × time and O_3 × time effects ($P<0.01$) on the C:N, the temporal increase in C:N was greater under elevated CO_2 compared to ambient CO_2 (Figure 6) and under low O_3 compared to elevated O_3 (Figure 7).

Similar patterns were observed for the H:N, but the slope differences were even greater (Figures 8 and 9).

Greater flux of C-H enriched compounds with simultaneous dilution of N in plant litters, mineralization of native SOM and subsequent harvest of large amounts of N in grain/seed, may have translated into the resulting high C:N and H:N under elevated CO_2 (Figures 6-8, respectively). Relatively smaller temporal increase in the C:N and H:N under elevated O_3 (Figures 7-9, respectively) may be due to recycling of phenolic-N enriched prematurely abscised plant litters recalcitrant to incomplete microbial decomposition.

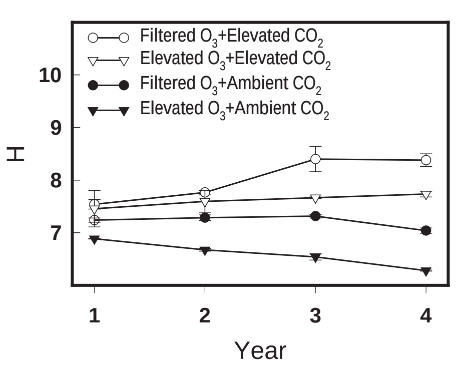

Figure 5 Carbon dioxide, ozone and time effects on total soil hydrogen (H) content.

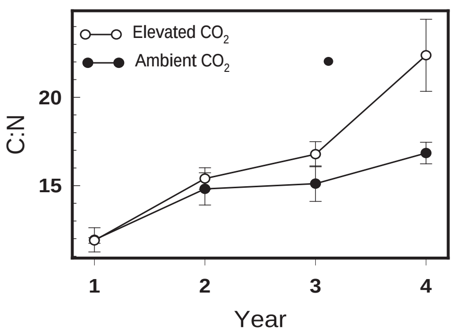

Figure 6 Carbon dioxide and time effects on soil carbon: nitrogen (C:N).

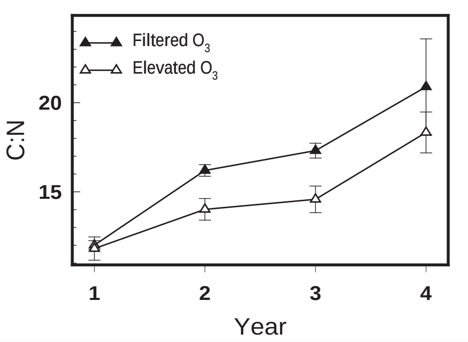

Figure 7 Ozone and time effects on soil carbon: nitrogen (C:N).

A significant CO_2 × O_3 effect ($P<0.01$) was detected for the C:H, but multiple mean comparisons showed no significant difference among the temporal changes in the C:H under the four simple effects (data not shown). The long-term exposure of plants to elevated CO_2 and O_3 concentrations may have produced neutralizing effect on C:H due to protective roles of elevated CO_2 against O_3 induced damage on plants and conversely, reducing the

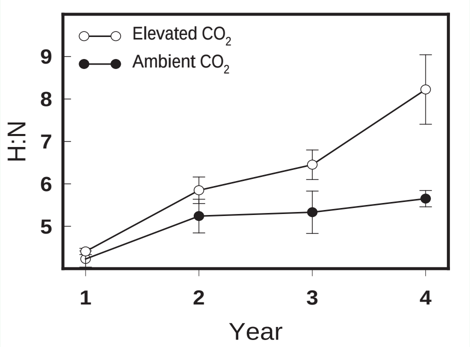

Figure 8 Carbon dioxide and time effects on soil hydrogen: nitrogen (H:N).

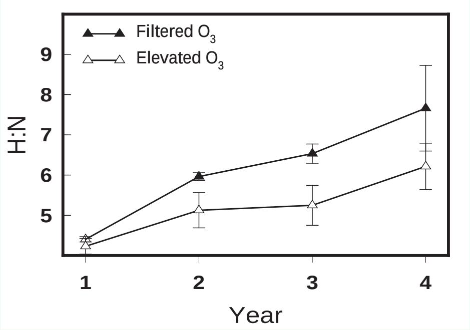

Figure 9 Ozone and time effects on soil hydrogen: nitrogen (H:N).

beneficial effects of CO_2 on plant growth and biomass production by elevated O_3 treatment [35,36].

CONCLUSION

After five years of elevated CO_2 and O_3 exposure treatments on no-till soybean-wheat rotation in the open top field chambers, the results showed that C, N and H dynamics of SOM have been partially altered. Soils with crops under long-term exposure to elevated CO_2 alone acted as temporary and/or transient sinks of C. Results suggest that soils with increases in C-H sequestration eventually become N-limited due to stoichiometric changes in C, N and H contents of the young and/or newly formed soil organic matter. In contrast, long-term effects of elevated O_3 (+O_3 and O_3+CO_2) on plants have caused a small accumulation of recalcitrant C in soil, which, in turn, would reduce the lability of C necessary to perform ecosystem services. Increasing concerns are raised whether more labile C-H with N deficient or recalcitrant C accumulation in new soil organic matter under elevated CO_2 or O_3 will cause negative agro ecosystem-level feedbacks and constrain plant productivity. Increased C sequestration, in particular, under elevated CO_2 could elicit a greater formation and leaching of dissolved organic matter and consequently fueling soil denitrification processes.

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