Landscape and Watershed Processes

Effects of Elevated Carbon Dioxide on Soils in a Florida Scrub Oak Ecosystem

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ABSTRACT

The results of a 3-yr study on the effects of elevated CO_2 on soil N and P, soil pCO_2, and calculated CO_2 efflux in a fire-regenerated Florida scrub oak ecosystem are summarized. We hypothesized that elevated CO_2 would cause (i) increases in soil pCO_2 and soil respiration and (ii) reduced levels of soil-available N and P. The effects of elevated CO_2 on soil N availability differed according to the method used. Results of resin lysimeter collections and anion exchange membrane tests in the field showed reduced NO_3^- in soils in Years 1 and 3. On the other hand, re-analysis of homogenized, buried soil bags after 1 yr suggested a relative increase in N availability (lower C to N ratio) under elevated CO_2. In the case of P, the buried bags and membranes suggested a negative effect of CO_2 on P during the first year; this faded over time, however, as P availability declined overall, probably in response to P uptake. Elevated CO_2 had no effect on soil pCO_2 or calculated soil respiration at any time, further suggesting that plant rather than microbial uptake was the primary factor responsible for the observed changes in N and P availability with elevated CO_2.

THE long-term effects of elevated CO_2 on plant growth and ecosystem C sequestration may be constrained by the availability of limiting nutrients. While most studies show increased soil respiration under elevated CO_2, suggesting increased allocation of C belowground (Hungate et al., 1997; Johnson et al., 1994; Körner and Arnone, 1992; Vose et al., 1995), the results of experiments examining the effects of elevated CO_2 on soil nutrient availability have been mixed. Some studies have shown, for instance, that elevated CO_2 can cause (i) increased soil N availability (Zak et al., 1993; Körner and Arnone, 1992; Hungate et al., 1997); (ii) decreased N availability, because of N immobilization in high C to N ratio–litter and/or labile organic compounds (Bernston and Bazzaz, 1996; Cotrufo et al., 1994; Diaz et al., 1993); or (iii) either mixed or no effects (O'Neill, 1994; Randlett et al., 1996). The sensitivity of tests for N mineralization and immobilization may be a factor in some cases. For example, Johnson et al. (2000b) found that although elevated CO_2 caused no effect on litter mass loss or N concentration in a field litterbag study, abiotic (sterilized) ^{15}N immobilization in the senesced litter was lower in ponderosa pine (*Pinus ponderosa* Laws.) fumigated with elevated CO_2 in a laboratory study. Johnson et al. (2000b) also noted higher natural ^{15}N abundance in needles and litter from plants grown under elevated CO_2 and hypothesized that this reflected N uptake from a recalcitrant soil N pool.

Studies on the effects of elevated CO_2 on P also have produced conflicting results. Norby et al. (1986) found an increase in soil-extractable P with elevated CO_2 in a greenhouse study with white oak (*Quercus alba*) L. and speculated that elevated CO_2 increased phosphatase activity. On the other hand, Johnson et al. (1995) found reduced soil-extractable P levels under elevated CO_2 in a greenhouse study of ponderosa pine growing in a poor soil, but no effects of elevated CO_2 were found on either plant P uptake or soil-extractable P when the plants were grown on a richer soil. Johnson et al. (1995) concluded from these two studies that the effects of elevated CO_2 on soil P "were inconsistent and no general conclusions can be drawn." In a field study of ponderosa pine, Johnson et al. (1997) found statistically significant effects of elevated CO_2 on extractable P in various treatment combinations and at various times during the 6-yr experiment; however, these effects were inconsistent among treatments and years, and in part reflected pretreatment differences.

In this paper, we summarize the results of three years of investigation into the effects of CO_2 on soils from an open-top chamber study in a Florida scrub oak ecosystem. Previous results from this site have shown that elevated CO_2 caused increased fine root biomass and negative effects on soil C and N availability. In a pilot study that preceded the current study, Day et al. (1996) found that elevated CO_2 caused greater root length densities in a minirhizotron study. Hungate et al. (1999) found that elevated CO_2 had no effect on microbial biomass N, but caused decreased N mineralization, nitrate leaching, and increased specific NH_4^+ immobilization (NH_4^+ immobilized per unit microbial N) in soils during the first 14 mo. The increased specific NH_4^+ immobilization was explained by increased root growth combined with decreased quality of C input to the soil (Hungate et al., 1999). Similarly, Shortemeyer et al. (2000) found no effects of elevated CO_2 on microbial biomass C and N, but lower C accumulation in buried, homogenized soil bags during a 1-yr period. Shortemeyer et al. (2000) found lower soluble C, ninhydrin-reactive N, and microbial activity in rhizosphere soil at one sampling date, however, and hypothesized that this was caused by N limitations, which were in turn caused by increased N uptake by plants.

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Abbreviations: OTC, open-top chamber; PRS, plant root simulator.

Based on the literature cited above and the fact that the soils at this site were very poor in nutrients, we hypothesized that elevated CO_2 would cause (i) increases in soil pCO_2 and soil respiration and (ii) reduced levels of soil-available N and P.

METHODS AND MATERIALS

Site

The study site is located on Merritt Island, a barrier island off the east coast of central Florida and part of the Kennedy Space Center (28°38′ N, 80°42′ W). The substrates are well-drained Pomello (sandy, siliceous, hyperthermic Oxyaquic Alorthod) and Poala (Spodic Quartzipsamments) sands. Both soils are acidic and low in nutrients, and nutrients tend to be concentrated in the standing biomass and in the O and A horizons (Schmaltzer and Hinkle, 1992). The experimental site is representative of a fire-maintained, scrub-oak palmetto community. The shrub layer was comprised of rhizomatous schlerophyllous evergreen oaks, which resprouted from belowground after fire. Three oak species, myrtle oak (*Quercus myrtifolia* Willd), sand live oak (*Q. geminata* Small), and Chapman oak (*Q. chapmanii* Sarg.) typically constitute up to 85% of aboveground biomass in these system (Schmaltzer and Hinkle, 1992). Also present is the saw palmetto [*Serenoa repens* (W. Bartram) Small], which typically contains considerable biomass in its rhizomes (Schmaltzer and Hinkle, 1996). The climate is subtropical, warm and humid, with the 100-yr average annual precipitation total of 1310 mm masking high year-to-year variability. One-hundred-year average mean maximum and minimum temperatures in July, the hottest month, are 33.3°C and 21.8°C, respectively, and in January, the coldest month, are 22.3°C and 9.5°C, respectively (Mailander, 1990).

Experimental Design

The study site was burned in August 1995 with a few remaining areas burned in January 1996 prior to siting of 16 open-top chambers (OTCs). Of the 16 OTCs, 8 were maintained at current ambient CO_2 and 8 at ambient plus 350 $\mu L\ L^{-1}$ (elevated). The OTCs were octagonal in design with the largest diameter 3.66 m and the sides 1.4 m long. Each chamber was 3.3 m high with the frustum at the midpoint providing a chamber volume of 18.9 m^3. Eight unchambered control plots of identical surface area were also established. The plots were blocked according to preburn aboveground biomass, species composition, and proximity. Each block consisted of one of each of the eight ambient OTCs, eight elevated OTCs, and eight unchambered control plots.

Soil Leaching Measurements

Two methods to measure soil nutrient leaching were employed during the experiment, but only one proved viable. Initially (January 1996), we installed ceramic cup lysimeters to collect soil solution. However, we found that damage due to intensive solar radiation and animals precluded the reliable operation of these lysimeters, and after approximatley 4 mo without complete collections, they were abandoned. Beginning in February 1997, resin lysimeters were used to collect cumulative soil N and P leaching. Resin lysimeters have decided advantages over traditional soil solution collection lysimeters in terms of cost and maintenance, especially under harsh field conditions such as those encountered in this study. Questions have been raised as to the effects of collection efficiency, effects on soil water flow, and microbial transformations on resin flux estimates (Kjønass, 1999; Schnabel, 1983; Schnabel et al., 1993; Susfalk, 2000; Torbert and Elkins, 1992). Nontheless, resin lysimeters have been used successfully to obtain indices of leaching in several previous studies, and microbial transformations have generally been found to be minimal (Kjønass, 1999; Schnabel et al., 1993; Susfalk, 2000). The resin lysimeters used in this study consisted of a 5.5-cm-long, 4-cm-i.d. PVC pipe within which a resin bag was sandwiched between layers of washed silica sand. Ten grams of oven-dried Rexyn I-300 (H-OH) resin (Fisher Scientific, Fair Lawn, NJ) were placed in a section of nylon pantyhose, using cable ties to secure each end. This resin bag was placed on a 20-g layer of moist, washed silica sand at the bottom of the tube and covered with another 20-g layer of silica sand. In order to keep the sand in the tube until installation, the bottom of each PVC tube was covered with cheesecloth held in place with a rubber band. The lysimeters were installed by excavating a small hole and tunneling beneath the A horizons at approximately 15 cm depth. The resin lysimeters were installed in February 1997, and removed and replaced in December 1997, December 1998, and December 1999. After collection, resins were removed from the lysimeters, placed into 250-mL Erlenmeyer flasks, and extracted with 100 mL of 1.0 *M* KCl with shaking for 1 h. The extract was filtered (Whatman No. 1) and stored at 4°C until analysis. The extracts were analyzed for NH_4^+, NO_3^-, and ortho-P by automated colorimetric analysis at the Desert Research Institute (Reno, NV). Three 10-g replicates of untreated resins were extracted in the same way and served as blanks. Fluxes were calculated from the amount of NH_4^+, NO_3^-, and ortho-P extracted from the resins (minus blanks) divided by the surface area of the lysimeters (12.6 cm^2). The flux for Year 1 was annualized by assuming that fluxes for the month of January 1997 were equal to one-twelfth those for the entire year (i.e., measured flux was multiplied by 1.091). The data for 1997 were reported previously (Hungate et al., 1999); here we update the data set with data from 1998 and 1999.

Measurement of Soil Nutrient Availability

To avoid the unacceptable effects of destructive soil sampling, less intrusive methods were used. In 1997, soil-available P was measured using anion exchange membranes (Cooperband and Logan, 1994). A 39-cm^2 square of anion exchange membrane (BDH [Darmstadt, Germany] Product no. 55164) was converted into the bicarbonate form, which is known to adsorb more orthophosphate than the chloride form (Sibbesen, 1978). This was accomplished by four 1-h sequential rinses of 200 mL 0.5 *M* $NaHCO_3$ (pH adjusted to 8.5) with intermittent stirring in a 250-mL flask. The membrane was placed into a slit in the surface soils (two replicates per chamber) in February 1997. A length of fishing line was sewn through each membrane and tied to guy wires in the chambers to facilitate relocation. The membranes were retrieved in December 1997 and extracted with 30 mL of 0.5 *M* NaCl by shaking for 1 h. The NaCl solution was then decanted, and replaced with a fresh 30 mL of 0.5 *M* NaCl and shaken for another hour. After this extraction process, the NaCl solutions were combined and analyzed for orthophosphate on an Alpkem RFA 300 colorimeter (OI Corp., College Station, TX) using EPA600/479020, a molybdate and ascorbic acid method (Fishmann and Friedman, 1985). Because of the loss of some membrane material during removal from the soil, the extractable P values were expressed as milligrams P per gram of membrane material. Due to the considerable difficulties encountered in installing and relocating membranes as well as the loss of membrane

material during retrieval, the use of membranes was discontinued after this collection.

In July 1999, soil N and P availability were measured using plant root simulator (PRS) probes (Western Ag Innovations, Saskatoon, SK, Canada), which consist of either anion- or cation-exchange membranes conveniently imbedded in plastic stakes for easy installation and recovery. In this case, the probes were installed for a period of 2 wk before recovery. Upon recovery, the probes were extracted with 40 mL of 1 *M* KCl by shaking for 1 h. Extractant from the cation exchange probe was analyzed for NH_4^+, and the extractant from the anion exchange probe was extracted for NO_3^- and ortho-P using automated colorimetric analysis.

Homogenized soil bags (David et al., 1990; Johnson et al., 2000a) were buried in the chambers to assess changes in soil C, N, and P with greater precision and less disturbance than would be possible with conventional soil sampling. Homogenized samples from the C horizon were placed in 1-mm mesh bags, labeled, and inserted in the A horizons of each chamber (three per chamber) in February 1997. One bag from each chamber was retrieved in December 1997, and the rest were left for later recovery. Soils from the bags were analyzed for C and N on a Perkin–Elmer (Norwalk, CT) CHN Analyzer for C and N and for extractable P with 0.5 *M* HCl plus 1 *M* NH_4F (Olsen and Sommers, 1982). The homogenized bags were not intended to provide estimates of actual rates of soil change (because the disturbance of homogenizing soils precludes this), but rather to provide a means of measuring relative treatment effects on soil chemical properties. David et al. (1990) used this technique to detect very small changes in soil chemical properties in response to acidification treatments to a Spodosol in Maine.

Measurement of Soil pCO_2 and Calculation of Soil Carbon Dioxide Efflux

The measurement of soil pCO_2 and calculation of soil CO_2 efflux were performed according to the methods outlined by Johnson et al. (2000a). Between April 1997 and January 2000, soil pCO_2 concentrations were monitored approximately monthly from gas wells established at 15 cm depth in each chamber (in triplicate). There was a sampling gap between November 1998 and June 1999 due to personnel changes and various logistical considerations. The gas wells consisted of 4-mm Tygon tubing inserted to the proper depth in the soil and fitted at the surface with a stoppered, female end of a plastic union. The three tubes all exited the OTC at 20 cm above the soil surface through an acrylic panel, removing any need to open or enter the OTCs during sampling. Samples for CO_2 analyses were obtained with Hamilton gas syringes (50 mL; Wilmad Corp., Buena, NJ) from the section of tubing between the large syringe and the union. During gas collections, stoppers were removed and 15 mL of soil gas were withdrawn from each well, completely evacuating the tubing. A second 50-mL sample was then removed for analysis. Carbon dioxide concentrations were measured on a LiCOR (Lincoln, NE) 6262 infrared gas analyzer using peak heights compared with a CO_2 standard gas (Boggs Gases, Titusville, FL). These measurements were made between three and five 5-mL volumes from each 50-mL sample. For each sampling period, soil temperature was recorded at 1-, 10-, and 50-cm depths in one OTC and one unchambered control plot. Soil moisture was recorded between 0 and 15 cm in each OTC and control plot.

Soil moisture was measured by time domain reflectometry in each plot using Campbell (Logan, UT) CS615 soil moisture reflectometers. Probes were calibrated individually by measuring probe output at four known soil moisture contents ranging from field capacity to residual water content. We placed A horizon soil in four 30-cm-diam. × 60-cm-deep PVC cylinders, adjusted water content in each (residual, 25%, 75%, and 100% of field capacity), and then measured the output of each probe when placed in each cylinder. We then developed a third-degree polynomial to describe the relationship between probe output and volumetric water content. Probes were connected to a multiplexer–datalogger array programmed to record volumetric water content every 11 min. For calculating soil CO_2 flux, we used the average water content for the days in which soil pCO_2 was measured, as described below. Cumulative soil respiration was estimated using the profile method (De Jong and Schappert, 1972; De Jong et al., 1974; Johnson et al., 1994, 2000a; Mattson, 1995). For the diffusion coefficient, we used the Moldrup et al. (1996) formulation, which depends upon commonly measured soil properties (total soil porosity, moisture content, percent clay, and percent fine sand). Cumulative CO_2 flux was calculated by trapezoidal integration of respiration values (Cotrufo et al., 1994; Johnson et al., 2000a) for the periods April 1997 through November 1998 and June 1999 through January 2000.

Statistical Analyses

Statistical analyses were performed using Microsoft Excel (Microsoft, 1998) for Student's *t*-tests and DataDesk (DataDesk, 1997) software for repeated measures ANOVA. For treatment effects on soil bags, membranes, PRS probes, and pCO_2, Student's *t*-tests were used. For the resin lysimeter leaching data, repeated measures analysis of variance (ANOVA) was used.

RESULTS

Soil Leaching

The soil leaching rates for NH_4^+, NO_3^-, and ortho-P for the three sampled years are summarized in Fig. 1. We found no statistically significant differences in the leaching rates of NH_4^+, $NO_3^- + NH_4^+$, or ortho-P in any year or overall; however, there was a trend toward lower ortho-P leaching in 1997 and 1998 under elevated CO_2. Nitrate leaching was significantly lower under elevated CO_2 in 1997, as noted previously (Hungate et al., 1999). This pattern did not continue, however, and there were no significant differences in NO_3^- leaching in 1998 or 1999. We found significant effects of year for NH_4^+, NO_3^-, $NO_3^- + NH_4^+$, and ortho-P but no significant interactions between treatment and year for any measured ion. In the case of NH_4^+, we found a substantial decrease in leaching in 1998 and an increase in 1999. The same pattern also occurred for NO_3^-, but the changes were not as large. In the case of ortho-P, we found a steady decrease in fluxes during the 3-yr sampling period.

Soil Nutrient Availability

The anion membrane test in 1997 indicated significantly lower available P in the elevated CO_2 treatment (Table 1). Similarly, the results of the buried bag study showed significantly lower extractable P in 1997 (Fig. 2). The PRS probe tests in 1999 showed no significant treatment effect on ortho-P or NH_4^+ but significantly lower available NO_3^- and mineral N ($NO_3^- + NH_4^+$)

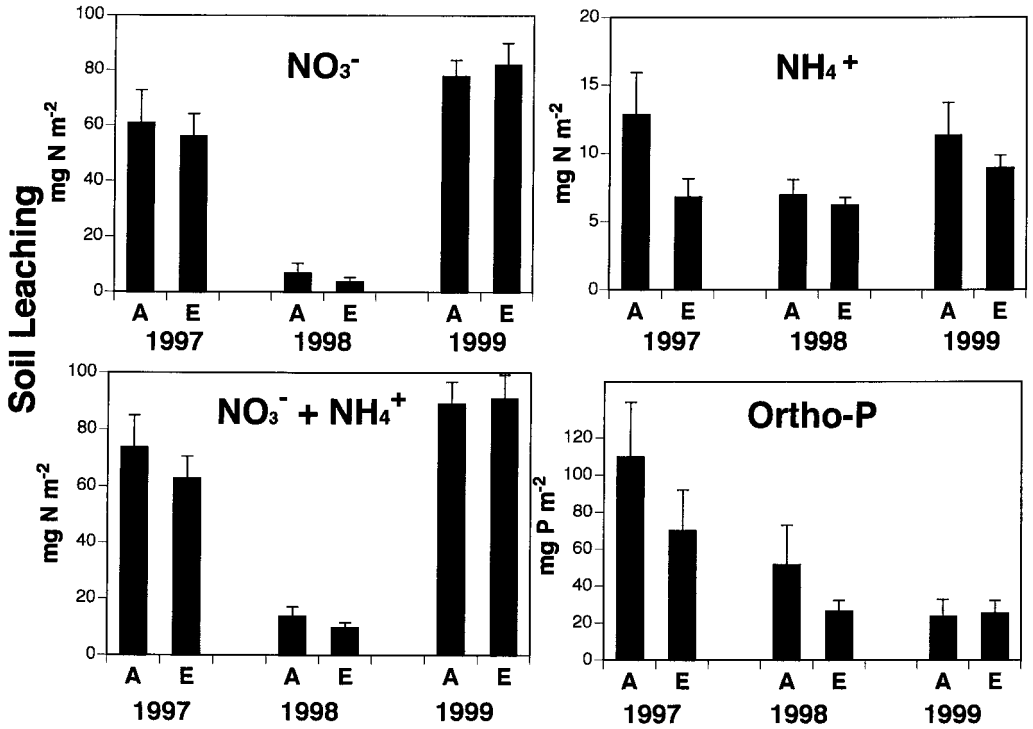

Fig. 1. Leaching rates of NH_4^+, NO_3^-, $NH_4^+ + NO_3^-$, and orthophosphate in 1997, 1998, and 1999 as measured by resin lysimeters. (A = ambient CO_2, E = elevated CO_2).

under elevated CO_2 (Table 1). As noted previously (Shortemeyer et al., 2000), the buried bag tests also showed a reduction in total C in both treatments compared with initial values, but the reduction in the elevated CO_2 treatment was significantly greater than in the ambient CO_2 treatment (Fig. 2). Total N also decreased substantially in the buried bags, but we found no statistically significant differences due to treatment. As a result of this, the C to N ratio was significantly lower in the elevated CO_2 treatment than in the ambient CO_2 treatment.

Soil pCO_2 and Calculated Carbon Dioxide Efflux

Figure 3 summarizes pCO_2 measurements between April 1997 and January 2000. In this figure, the values for pCO_2 under elevated CO_2 are shown as measured and with the additional CO_2 treatment (+350 $\mu L\ L^{-1}$) subtracted from the values. This comparison was made so that the effects of treatment on soil respiration-driven pCO_2 (as opposed to the direct effects of chamber pCO_2) could be more easily assessed. We found considerable variation in pCO_2 between seasons and years, as would be expected, but at no time during the course of these measurements were there statistically significant differences in pCO_2 between the ambient and elevated CO_2 treatments. Similarly, the calculated cumulative CO_2 efflux values (not shown) were virtually identical, indicating no treatment effects on soil respiration. Independent measures of soil respiration at the soil surface also show no treatment effect on soil respiration (G. Hymus, unpublished data, 2000).

Table 1. Results of membrane analyses for soil-available P in 1997 and for soil-available P, NH_4^+, NO_3^-, and $NH_4^+ + NO_3^-$ in 1999.

Nutrient	Ambient	Elevated
	$\mu g\ 10\ cm^{-2}\ d^{-1}$	
1997 (Anion membrane)		
Ortho-P	1.13 ± 0.31	5.17 ± 0.84***
1999 (PRS probes)		
Ortho-P	0.37 ± 0.10	0.48 ± 0.13
NH_4^+–N	0.28 ± 0.03	0.22 ± 0.02*
NO_3^-–N	0.18 ± 0.03	0.09 ± 0.02**
($NH_4^+ + NO_3^-$)–N	0.46 ± 0.05	0.32 ± 0.02**

* Significant at the 0.10 probability level for Student's *t*-test.
** Significant at the 0.05 probability level for Student's *t*-test.
*** Significant at the 0.01 probability level for Student's *t*-test.

DISCUSSION

The resin membrane and buried soil bag data suggest that elevated CO_2 caused reduced soil P availability in the early stages of treatment. The reduced P leaching suggested by the resin lysimeter data, while not statistically significant, corresponds well with the significantly lower P in the resin membranes of the buried soil bags during this initial period. In the case of the resin lysimeters, the differences in P leaching could have been due to both differences in P availability and soil water flux. Soil water flux was probably greater in the elevated CO_2 treatment because of an observed 20% reduction in evapotranspiration (B. Hungate et al., unpublished data, 2000). This would cause the opposite effect on P leaching from that observed, and may have muted the response in P leaching.

Treatments could have caused reduced P availability in soils initially as a result of (i) increased P immobilization by microbes, (ii) increased P adsorption to soils, (iii) increased P uptake by vegetation, or (iv) any combi-

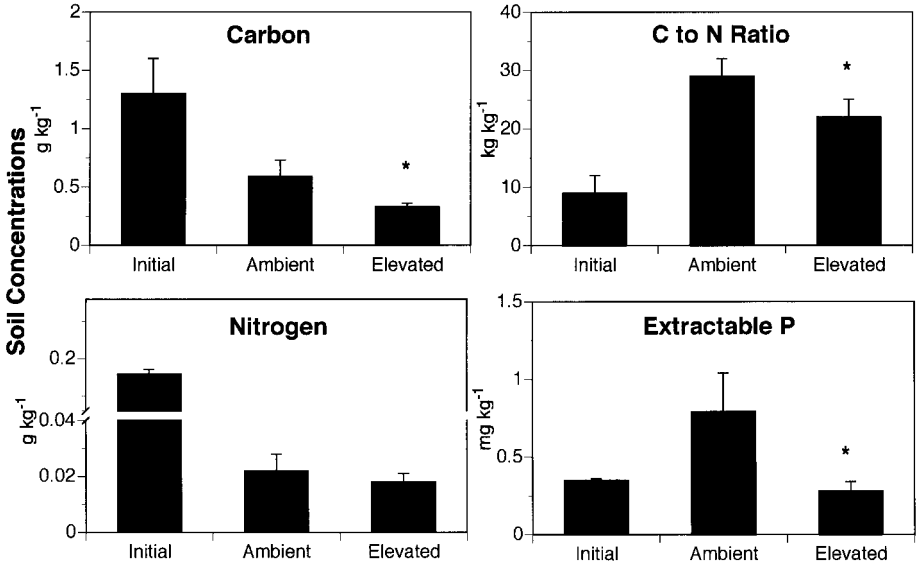

Fig. 2. Total C, total N, C to N ratio, and extractable P in homogenized buried bags retrieved after 1 yr (in 1997). *, **, and * indicate significance at the 0.10, 0.05, and 0.01 probability levels for single factor analysis of variance (ANOVA), respectively.**

nation of the above. We do not believe that microbial immobilization was a factor, given the results of Hungate et al. (1999) and Shortemeyer et al. (2000). They collectively found that there is either no effect or a reduction in microbial activity and soluble organic C with elevated CO_2. As suggested by Shortemeyer et al. (2000), increased plant uptake of N under elevated CO_2 may have reduced the supply of N to microbes, thereby reducing microbial activity due to N limitation. Microbial P uptake would, therefore, be expected to be lower under elevated CO_2 as well. Certainly, the pCO_2 and soil respiration data gave no indication of higher microbial activity under elevated CO_2. Adsorption of P to soils could have changed if pH decreased under elevated CO_2; unfortunately, we have no data to test this hypothesis but consider it unlikely. We do not as yet have data on P uptake by the biomass, but have made preliminary calculations based on biomass estimates thus far and weighted-average P concentrations from Schmaltzer and Hinkle (1996) for the same vegetation type. These calculations suggest that P accumulation in aboveground vegetation at the end of the 1999 growing season was approximately 7 kg ha^{-1} in the elevated CO_2 treatment and approximately 4 kg ha^{-1} in the ambient CO_2

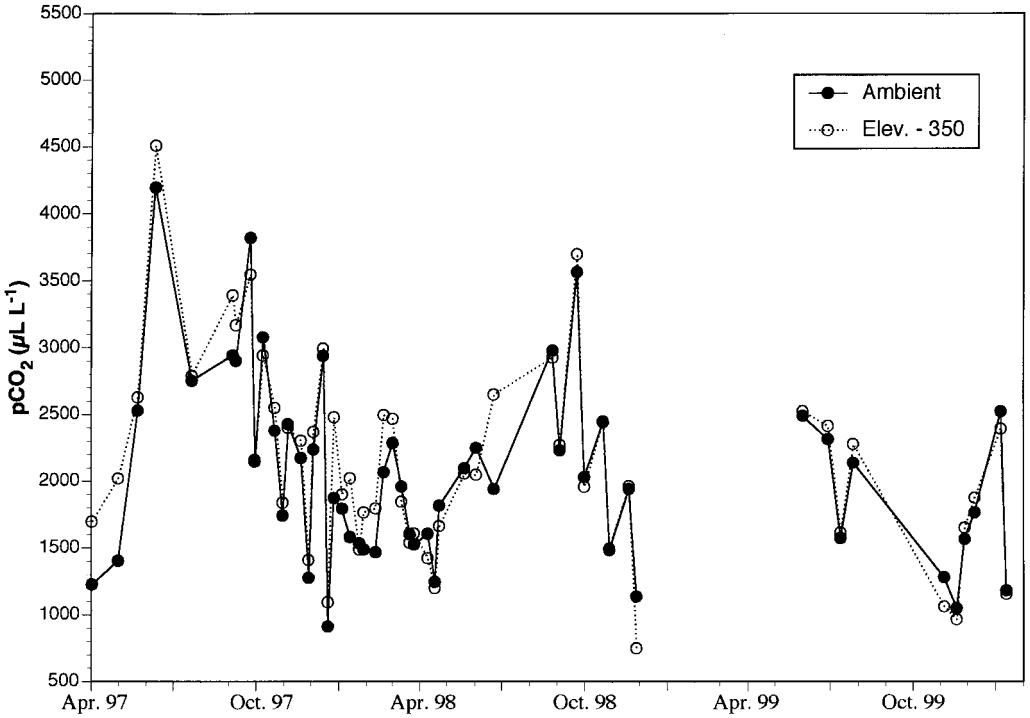

Fig. 3. Soil pCO_2 analyses from gas wells between April 1997 and January 2000.

treatment. Initial values for soil-extractable P (to a depth of 60 cm) combined with bulk density values from Schmaltzer and Hinkle (1996) yield values of 7 to 8 kg ha^{-1} (B. Hungate, unpublished data, 2000). Some of the P accumulated in aboveground biomass could have been mobilized from surviving roots; on the other hand, roots themselves may have accumulated P from soil sources. Thus, these values suggest that plant uptake could have caused a substantial decline in soil-available P levels over this period. Belowground P uptake would add very substantially: Schmaltzer and Hinkle (1996) estimated that saw palmetto rhizomes contained approximately twice as much biomass, N, and P as aboveground biomass in 2- to 4-yr-old scrub oak stands similar to the one studied here. Although plant P uptake during the first year of growth would have been very low (on the order of 1 and 2 kg ha^{-1} in the ambient and elevated treatments, respectively), it still could have contributed to the observed treatment effects on soil-available P pools when belowground uptake is included. Thus, we hypothesize that plant uptake was the primary factor accounting for the initial treatment effects on soil-available P and for the observed overall declines in P leaching in all treatments.

The results reported in this and previous papers from this site suggest that soil-available N under elevated CO_2 is either equal to or (more often) lower than under ambient CO_2. Hungate et al. (1999) reported that soil exchangeable NH_4^+ was lower under elevated CO_2 in March 1997. Shortemeyer et al. (2000) reported lower N availability under elevated CO_2 in the summer of 1998, and the PRS probe data reported here clearly indicate lower N availability in 1999. As discussed earlier, N leaching is a function of both N availability and water flux, the latter of which may have been greater with elevated CO_2 because of reduced evapotranspiration (B. Hungate, personal communication, 2000). Lower NO_3^- leaching under the elevated CO_2 treatment in 1997 was probably due to lower soil-available N, and the lack of differences in N leaching in other cases may have been due to the offsetting effects of N availability and soil water flux. The greatly reduced NH_4^+ leaching in 1998 (compared with 1997 and 1999) may have been due to the drought that year: total precipitation in 1998 was 839 mm compared with 1380 mm in 1997 and 1403 mm in 1999. No reductions in the leaching of NO_3^- or ortho-P during 1998 were noted, however.

The results for N and P leaching in this study contrast to those obtained by Körner and Arnone (1992) for artificial tropical ecosystems. These authors found increased N and P leaching with elevated CO_2 and attributed this to stimulated microbial activity, causing nutrient release in excess of plant demand. On the other hand, Torbert et al. (1996) found reduced NO_3^- leaching with elevated CO_2 in agroecosystems, and attributed it to reduced N release from crop residues and increased N retention in soil organic matter. In this study, we hypothesize that differences in N uptake (which would have amounted to approximately 10 kg ha^{-1} during the first season and accumulated to a difference of approximately 90 kg ha^{-1} by the end of the third growing season) were the major factor causing the reduction in N leaching (which amounted to less than 0.01 kg ha^{-1}) and availability.

The lack of response in soil pCO_2 or calculated respiration at any time during this study is unusual for elevated CO_2 experiments (Allen et al., 2000; Canadell et al., 1996; Edwards and Norby, 1999; Hungate et al., 1999; Johnson et al., 1994; Körner and Arnone, 1992; Verburg et al., 1998; Vose et al., 1995), and difficult to explain in view of the probable increase in root biomass (Day et al., 1996). Part of the reason for the lack of response in soil pCO_2 and respiration may have been the presence of a substantial amount of live root biomass that survived the fire and remained basically intact as the experiment began (especially saw palmetto rhizomes), masking any current treatment effects on fine root biomass or microbial activity. These surviving root systems may not yet have been affected by elevated CO_2, and respiration from them could still reflect prefire biomoass. On the other hand, the results of Hungate et al. (1999) and Shortemeyer et al. (2000) for this site suggest that treatment effects on microbial activity were either negligible or negative, and thus an increase in soil respiration from microbial sources does not seem likely. Further investigation is needed to reconcile the lack of soil pCO_2 and respiration response with other findings in this study.

SUMMARY AND CONCLUSIONS

Hypothesis 1 (elevated CO_2 would cause increased soil pCO_2 and soil respiration) was not supported by the results of this study: there were no treatment effects on soil pCO_2 or calculated soil respiration at any time. This may have been due to the presence of roots and detritus in the soil from before the fire that immediately preceded the initiation of treatment. Hypothesis 2 (elevated CO_2 would cause reduced levels of soil-available N and P) was only partially supported by the results of this study. Resin lysimeter data and membrane analyses suggested reduced NO_3^- in soils; however, the results of the buried bag analyses suggested the opposite (lower C to N ratios in bags buried under elevated CO_2). In the case of P, both the buried bags and the membranes suggested that CO_2 had a negative effect of CO_2 on P during the first year but that this faded over time. Correspondingly, P leaching measured by resin lysimeters declined substantially over time, probably in response to increased P uptake over time in both treatments.

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