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Original article

Elevated atmospheric CO_2 alters the arthropod community in a forest understory

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ABSTRACT

The objective of this study was to determine the extent to which overall population sizes and community composition of arthropods in a naturally occurring forest understory are altered by elevated CO_2. The Free Air Concentration Enrichment (FACE) method was used to fumigate large, replicated plots in the Piedmont region of North Carolina, USA to achieve the CO_2 concentration predicted for 2050 ($\sim$580 $\mu l\, l^{-1}$). In addition, the extent to which unrestricted herbivorous arthropods were spatially delimited in their resource acquisition was determined. Stable isotope data for spiders ($\delta^{13}C$ and $\delta^{15}N$) were collected in ambient and elevated CO_2 plots and analyzed to determine whether their prey species moved among plots. Elevated CO_2 had no effect on total arthropod numbers but had a large effect on the composition of the arthropod community. Insects collected in our samples were identified to a level that allowed for an assignment of trophic classification (generally to family). For the groups of insects sensitive to atmospheric gas composition, there was an increase in the numbers of individuals collected in primarily predaceous orders (Araneae and Hymenoptera; from 60% to more than 150%) under elevated CO_2 and a decrease in the numbers in primarily herbivorous orders (Lepidoptera and Coleoptera; from −30 to −45%). Isotopic data gave no indication that the treatment plots represented a "boundary" to the movement of insects or that there were distinct and independent insect populations inside and outside the treatment plots. A simple two-ended mixing model estimates 55% of the carbon and nitrogen in spider biomass originated external to the elevated CO_2 plots. In addition to changes in insect performance, decreases in herbivorous arthropods and increases in predaceous arthropods may also be factors involved in reduced herbivory under elevated CO_2 in this forest.

1. Introduction

Increases in atmospheric CO_2 from anthropogenic inputs have the potential to stimulate plant productivity (Long et al., 2006); however, predicted increases in productivity from enhanced photosynthesis and water use efficiency may be reduced by increased losses to insect herbivory (Aldea et al., 2005; Hamilton et al., 2005). Growth under elevated CO_2 changes myriad chemical and structural properties that affect the suitability of plant material to herbivorous insects (Robinson et al., 2012). Increased herbivory may result from elevated consumption rates on the part of herbivores compensating for reduced availability of growth-limiting foliar nitrogen (Bezemer and Jones, 1998) or impaired defense signaling and reduced defense investments in foliage grown under elevated CO_2 (Zavala et al., 2008).

In contrast with simplified agro-ecosystems, the response of complex plant and animal communities to global change is highly variable (Tylianakis et al., 2008). Recent studies have documented that loss of foliage to arthropod herbivores decreases under elevated CO_2 in woody communities (Hamilton et al., 2004; Knepp et al., 2005; Stiling and Cornelissen, 2007), and that the fitness and in some cases the population size of herbivorous insects may decline in communities exposed to elevated CO_2 (Hillstrom and Lindroth, 2008; Hillstrom et al., 2010). The factors mediating this response are not well understood, although Knepp et al. (2007) demonstrated that elevated CO_2 reduced the nutritional quality of foliage of two species of *Quercus* for *Antheraea polyphemus*, and

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growth under elevated CO_2 often drives a decrease in the carbon:nitrogen ratio of foliage in trees (Lindroth, 2010). General community patterns of foliage loss may reflect overall abundances of herbivores and their predators, in addition to altered feeding and performance of individual herbivores.

Despite their likely importance in predicting community responses to global atmospheric change, effects of elevated CO_2 on naturally occurring arthropod assemblages have not yet been widely characterized. Examining these effects is challenging because sampling the arthropod community at any particular time point may miss important temporal dynamics of immigration and emigration, seasonal emergence of arthropods, or changes in abundance of rare but important species. Furthermore, changes in arthropod feeding preferences (Agrell et al., 2006), altered interspecific competition among insect herbivores (Stacey and Fellows, 2002) and tri-trophic interactions that may include both insects and vertebrates (Holton et al., 2003; Muller et al., 2006) make meaningful predictions difficult.

The objective of this study was to determine, in a naturally occurring forest understory, the extent to which the relative population sizes and composition of the arthropod community were altered by elevated CO_2. We hypothesize that reduced numbers of herbivorous insects or reduced feeding and performance of individual herbivores contribute to reduced foliage loss under elevated CO_2. Arthropods were identified to order or below where possible and their feeding guild noted. Because our experiment used large-scale undisturbed plant and insect assemblages, we also determined the extent to which herbivorous arthropods, allowed unrestricted movement, were spatially delimited in their resource acquisition. Relatively stationary predators, such as web-building spiders, possess an isotopic $\delta^{13}C$ and $\delta^{15}N$ signature that mirrors the dietary intake of their relatively mobile prey (Post, 2002). Thus, stable isotope data for spiders collected in ambient and elevated CO_2 plots were analyzed to determine the extent to which herbivorous prey species (the bulk of prey captured by spiders) move into and out of the elevated CO_2 plots.

2. Methods

2.1. Research site

Arthropods were sampled from the understory of a pine plantation where replicated plots were exposed to ambient or elevated atmospheric CO_2 at the Duke Forest Free Air Concentration Enrichment (FACE) experiment (http://face.env.duke.edu/main.cfm). The experimental forest is located in the Piedmont region of North Carolina (35°97′N 79°09′W), which is characterized by warm summers with average daytime high temperatures of ~32 °C and cool winters, with average daytime high temperatures of 4 °C and higher. The forest overstory is dominated by loblolly pine (*Pinus taeda* L.) with sweetgum (*Liquidambar styraciflua* L.) and yellow tulip-poplar (*Liriodendron tulipifera* L.) as sub-dominants (DeLucia et al., 1999). Forty-eight species of woody plants have established naturally in the understory of this forest (J. Pippen and W. Cook, unpublished data). The soil is a clay-rich Alfisol with low nitrogen and phosphorus availability (Schlesinger and Lichter, 2001). This section of Duke Forest was farmed a century ago, and the current plantation was established in 1983 after a regenerating forest was clear-cut in 1979.

The FACE system increases atmospheric CO_2 concentration in three 30-m diameter plots within an expansive stand of loblolly pine (Hendrey and Kimball, 1994; Lewin et al., 1994; Hendrey et al., 1999). Beginning in 1996, the FACE system was used to maintain the concentration of CO_2 in the forest canopy at 200 $\mu l\,l^{-1}$ above ambient levels (~577 $\mu l\,l^{-1}$ at 1 m and ~586 $\mu l\,l^{-1}$ at 0.25 m height in 1996; G. Hendrey, personal communication). This level was chosen to represent the CO_2 concentration predicted for the year 2050 (Houghton et al., 2001). Three additional fully instrumented control plots received ambient air (CO_2: 386 ± 27 $\mu l\,l^{-1}$). The pine canopy provided complete cover (DeLucia et al., 2002) and saplings in the understory were in shade; the average photon flux density in the understory was 121 $\mu mol\,m^{-2}\,s^{-1}$ between 08:00 and 17:00 h (Singaas et al., 2000). There is no indication that elevated CO_2 induced photosynthetic acclimation in hardwood saplings (DeLucia and Thomas, 2000).

The CO_2 used for fumigation in the elevated CO_2-FACE plots was depleted in ^{13}C relative to the general atmosphere. Thus, a greatly depleted fumigation gas ($\delta^{13}C = -43.1‰$) mixed with ambient air ($\delta^{13}C = -8‰$) produced a $\delta^{13}C$ environment within the plots of −21‰ (Andrews et al., 2000). As part of a different experiment to examine the nitrogen cycle in the FACE, a ^{15}N tracer (75% $^{15}NH_4Cl$ and 25% $K^{15}NO_3$ at a rate of 0.015 g $^{15}N\,m^{-2}$ in 0.25 l $H_2O\,m^{-2}$) was applied to all plots in May 2003 using backpack sprayers. An even application of the stable isotope tracer was achieved, with an average total soil ^{15}N signature of 484 (±29)‰ in the Oi horizon 1 week after tracer application (Lichter et al., 2005).

2.2. Arthropod communities

We sampled arthropods every 2 weeks through June and July 2005 using yellow sticky cards (BioQuip, Rancho Dominguez, CA, USA). The sticky card method provided a precise relative measurement between ambient and elevated CO_2 plots but could not be used to accurately estimate the number of arthropods per unit land area (Pedigo, 1994; Reisig et al., 2010). For each sample, 32 cards were placed in each FACE plot: 16 aerial cards were used to catch flying insects (8 at 1 m from ground; 8 at 2 m from ground) and 16 cards were placed on the ground to catch walking insects (cards on the ground were covered by plastic plates with a 1-cm gap between plate and ground) and left in place for 72 h ($n = 192$/date). All arthropods were identified at least to order and to lower taxonomic levels where possible with the objective of assigning them to feeding guilds. Statistical analyses were conducted on groupings by order (except for Diplopoda (Class), Chilopoda (Class) and Acari (Subclass); Fig. 1).

2.3. Isotopic studies, tissue analysis and spider collection

Spiders were collected from webs in elevated CO_2 plots from late June through mid-August. Spiders were classified by web type and included species in families Araneidae, Tetragnathidae, Theridiidae

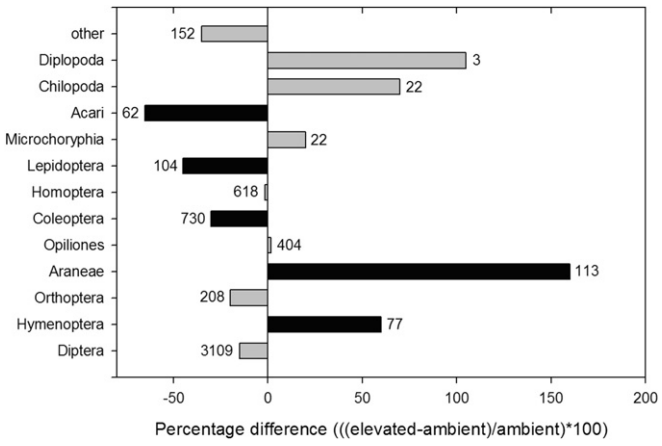

Fig. 1. The difference in arthropod taxa in elevated CO_2 plots relative to ambient CO_2 plots. Significant (black bars) differences ($n = 3$) were recorded for CO_2 effect in two-way ANOVA (no significant date by CO_2 interactions were found) for Acari ($P = 0.023$), Lepidoptera ($P = 0.094$), Coleoptera ($P = 0.099$), Araneae ($P = 0.063$), and Hymenoptera ($P = 0.097$), but not total arthropods ($P = 0.726$). The total number of specimens (both control and treatment) is shown next to each bar.

and Linyphiidae. Spiders were captured along a radial transect (0.3–2 m above ground level) from the center of each plot out to a distance of 45 m; sampling extended 30 m beyond the perimeter of the plot (plot radius is 15 m). At each location where a spider was captured, leaf tissue from naturally established saplings was collected from up to three trees within 0.5 m. Leaf tissue was dried at 65 °C in a drying oven. Spiders were stored in sealed canisters in a freezer and then lyophilized before further analysis. Leaf tissue for carbon and nitrogen analyses was collected from a set of six species of hardwood saplings in replicated subplots within the FACE plots (Knepp et al., 2005; Mohan et al., 2007).

Dried tissue samples (spiders and associated leaves) were weighed with a balance (Model M-2200, Denver Instrument, Denver, CO, USA) and ground to a fine powder with a mortar and pestle; subsamples (2.55–3.15 mg) were weighed with a microbalance (Model 4504MP8; Sartorius Corp., Edgewood, NY, USA). Tissue nitrogen (N) and carbon (C) content were measured with an elemental analyzer (Model 4010; Costech Analytical Technologies, Valencia, CA, USA), and tissue $\delta^{15}N$ and $\delta^{13}C$ were measured with a continuous flow isotope ratio mass spectrometer (Model Delta Plus; Thermo Finnegan, San Jose, CA, USA). Isotope analyses were conducted at the Stable Isotope Laboratory at Cornell University, Ithaca, NY. The proportion of spider carbon or nitrogen derived from inside the plot versus outside the plot was calculated with a simple mixing model as in Dawson et al. (2002).

2.4. Statistical analyses

The arthropod community was analyzed by two-way analysis of variance (ANOVA), with CO_2 treatment and date of collection as main effects and the number of individuals in an order or the total number of arthropods across orders as the dependent variable. Initial analyses determined that trap placement did not affect either the quality or quantity of arthropods collected, so the trap counts were combined, resulting in a single total count or count per order for each plot in the analysis. To avoid pseudoreplication, all data from subsamples within a plot were combined yielding $n = 3$ (three ambient and three elevated CO_2). Given the limitation on sample size inherent in all FACE experiments, we sought to avoid type II errors by setting critical $P < 0.1$ as in previous studies (Hamilton et al., 2004; Dermody et al., 2005).

The ratio of carbon-to-nitrogen in plant tissues was analyzed by two-way ANOVA, following appropriate transformation, with species (*Quercus rubra*, *Q. velutina*, *Q. alba*, *Q. palustris*, *Acer rubra* and *Cercis canadensis*) and CO_2 treatment as main effects. As for the arthropods, a single average value of C/N per plot (three ambient and three elevated) per species was analyzed (466 samples total).

Because each spider collected and the sample of surrounding vegetation were not independent, isotope differences between plants and spiders and between the inside and outside of a plot and were analyzed by repeated measures analysis of variance with plot (inside/outside) as a between-subjects effect and plant and spider values as repeated measures. The plot specification determines whether isotope enrichment (^{15}N) or depletion (^{13}C) inside the plot leads to differences in plants and spiders as a function of their location inside or outside the plot. The repeated measure evaluates whether the signatures of spiders and plants differ, and a significant interaction between location in plot and the repeated measure evaluates whether spider and plant signatures are differentially affected by location and would suggest movement of herbivorous prey beyond the isotopic spatial boundaries of their host plants.

3. Results

3.1. Arthropod community composition

Elevated CO_2 had a large effect on the composition of the arthropod community (Fig. 1), with no detectable effect on the total number of individuals ($F = 0.128$, $P = 0.726$, $df = 2$). There were substantial decreases in Lepidoptera and Coleoptera. Members of the Lepidoptera were exclusively herbivores and came from five taxa (Pyralidae, Notodontidae, Tortricidae, Incurvariidae and "miscellaneous Microlepidoptera not identifiable to family"). Of the 19 families of Coleoptera represented, the largest majority (6) are primarily herbivorous (Anobiidae, Chrysomelidae, Curculionidae, Elateridae, Nitidulidae, Tenebrionidae), with some families containing primarily fungus feeders (Anthribidae, Derodontidae, Erotylidae, Lathridiidae), some mixed feeding guilds (Cantharidae, Dermestidae, Lycidae, Mordellidae, Scarabaeidae), some primarily carnivorous families (Lampyridae, Pyrochroidae, Rhipiphoridae, Staphylinidae) and one family comprising detritivores (Silphidae). Members of the subclass Acari (mites and ticks) also declined under elevated CO_2 (Fig. 1); based on the positioning of the traps, Acari sampled in this study were likely to have been predatory.

In contrast to the primarily herbivorous Lepidoptera and Coleoptera, there was a significant increase in the elevated CO_2 plots in members of the strongly carnivorous orders, Araneae and Hymenoptera. With one exception (Meehan et al., 2009), families in the Araneae are overwhelmingly carnivorous (Agelenidae, Dysderidae, Oonopidae, Pholcidae, Sparassidae, Thomisidae), and 11 of the 17 families (or in one case superfamily) of Hymenoptera were carnivores (Bethylidae, Braconidae, "Chalcidoidea that could not be determined to family", Encyrtidae, Ichneumonidae, Mymaridae, Platygastridae, Proctotrupidae, Pteromalidae, Scelionidae, Torymidae). Five families of Hymenoptera comprise herbivores (Argidae, Cephidae, Cimbicidae, Cynipidae, Tenthredinidae) and one contains mixed feeding guilds (Formicidae). The significant decline in primarily herbivorous members of the Lepidoptera and Coleoptera and increase in Araneae and Hymenoptera suggest a rebalancing of the arthropod community away from herbivores toward carnivores under elevated CO_2.

Total arthropod populations decreased over the course of the season ($F = 27.9$, $P < 0.001$), and the differences between ambient and elevated CO_2 tended to decrease but were not statistically significant (Fig. 2, no time by CO_2 interaction—see Fig. 1 legend).

Differences in the composition of the arthropod community could not be attributed to changes in plant C/N ratio, as there was no detectable CO_2 effect ($F = 0.76$, $P = 0.392$, $df = 2$) or species by CO_2 effect ($F = 0.577$, $P = 0.717$, $df = 2$) and only a significant species effect ($F = 18.608$, $P < 0.001$, $df = 2$) on the ratio.

3.2. Arthropod resource acquisition

Plants growing inside the elevated CO_2 plots could be distinguished by their depletion in ^{13}C and enrichment in ^{15}N compared to plants outside the plots (Fig. 3; Table 1; significant plot effects in Table 2). Average leaf $\delta^{13}C$ was $-41.77‰$ inside the plots compared to $-36.61‰$ outside; $\delta^{15}N$ was $8.27‰$ inside and $-1.51‰$ outside (Table 1). Although spider $\delta^{13}C$ and $\delta^{15}N$ showed the same patterns as plants ($\delta^{13}C = -33.83‰$ inside, $\delta^{13}C = -31.52‰$ outside; $\delta^{15}N = 9.20‰$ inside, $\delta^{15}N = 4.63‰$ outside), their absolute average signatures differed for both isotopes (Fig. 3; significant organism effect in Table 2). For both isotopes, the differences between spiders inside the plots and spiders outside the plots are less than for plants inside and outside the plots (significant plot × organism interactions in Table 2). Trophic enrichment from plants to spiders for $\delta^{13}C$

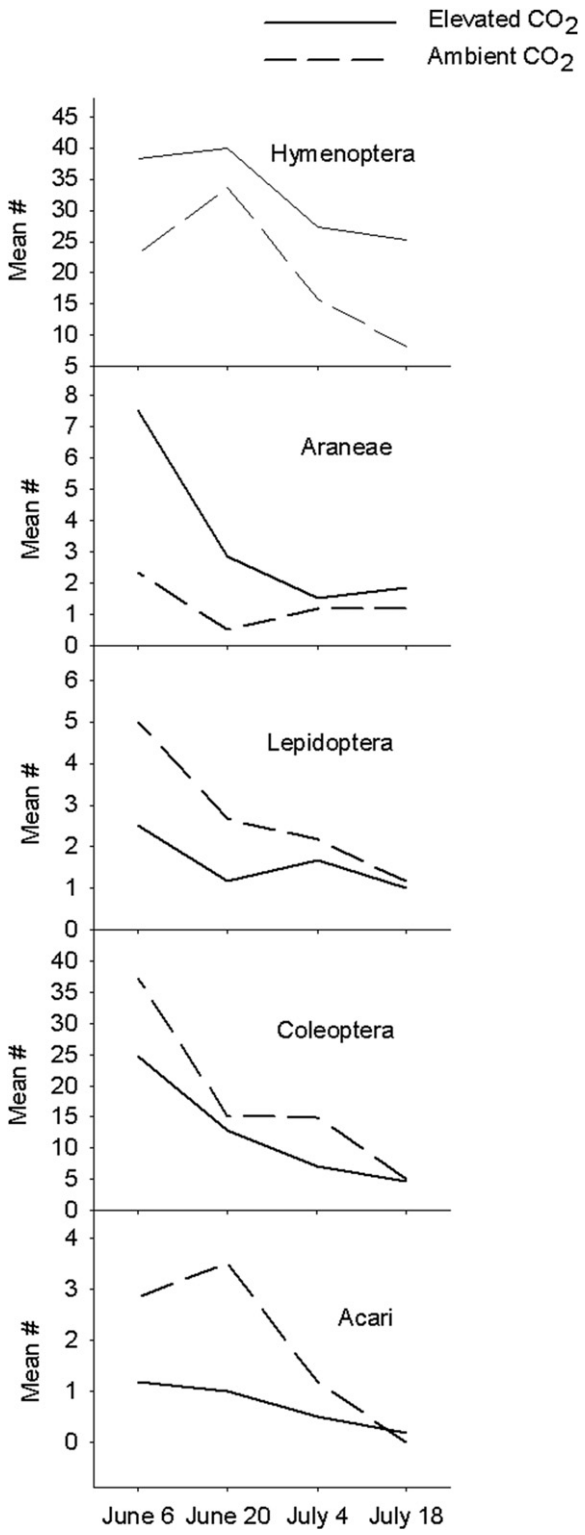

Fig. 2. Temporal declines in arthropod taxa. The declines were significant (date main effect from two-way ANOVA reported in Fig. 1) for the Araneae ($P = 0.088$), Lepidoptera ($P = 0.065$), Coleoptera ($P < 0.001$), and Acari ($P = 0.014$).

under ambient CO_2 conditions was 5.1‰ and 7.9‰ under elevated conditions and for $\delta^{15}N$ the difference was greater, with ambient trophic enrichment of 6.1‰ compared to only 0.93‰ under elevated conditions.

4. Discussion

Exposure of a pine plantation to elevated CO_2 caused substantial changes in the composition of the arthropod community in the forest understory. While insect orders contain a variety of feeding guilds, the Lepidoptera and to a lesser extent Coleoptera that were collected in this study were primarily herbivores and the Araneae and Hymenoptera were primarily predators. Elevated CO_2 plots had more individuals from primarily carnivorous groups compared to ambient plots, whereas ambient CO_2 plots had more individuals from primarily herbivorous groups (Fig. 1). These changes in the composition of the arthropod community support our hypothesis that a reduction in herbivorous insects contributed to reduced foliar damage under elevated CO_2 (Hamilton et al., 2004; Knepp et al., 2007), and are consistent with a meta-analysis documenting decreased herbivore abundance under elevated CO_2 (Stiling and Cornelissen, 2007). Hillstrom and Lindroth (2008) also reported a change in species composition in an aggrading aspen–birch forest exposed to elevated CO_2 but did not resolve significant differences among feeding guilds.

The decline in insect herbivores in this study may have been caused by the increase in insect carnivores. This increase in carnivore numbers might have been indirectly related to effects of elevated CO_2 on plant quality that in turn affected herbivore susceptibility to predators. If elevated CO_2 adversely affected herbivore feeding efficiency and necessitated compensatory feeding, as has been seen in other elevated CO_2 studies (Knepp et al., 2007; Bezemer and Jones, 1998), the increased feeding activity may itself have attracted predators. For example, Bernays (2003) found that feeding activity of lepidopterans itself increased the likelihood of predation.

Despite our attempt to detect changes in leaf C/N, we could not identify a change in plant chemical composition that explained the differences we observed in arthropod community. Past studies suggest that a decrease in nutritional quality or chemical defense may have contributed to poor performance and increased mortality of herbivores under elevated CO_2. Working in this same forest, Knepp et al. (2005) reported that reduced herbivory under elevated CO_2 was associated with a small increase in C/N and specific leaf area and a decrease in the concentration of defensive phenolic compounds. There was, however, considerable variation among species and years. A closer examination of two oak species revealed that lower digestibility of foliage, greater protein precipitation capacity in frass and lower nitrogen concentration in larvae contributed to slower growth and greater mortality of *A. polyphemus* caterpillars (Knepp et al., 2007).

Although FACE experiments offer a realistic simulation of ecological reality, low statistical power and high year-to-year and interspecific variation make it difficult to unravel the proximate mechanisms controlling herbivory. In contrast to the results reported by Knepp et al. (2005, 2007), Hamilton et al. (2004) also failed to identify a specific chemical change in leaf composition that provided a mechanism for observed herbivory patterns, although the general trend of reduced leaf herbivory across 12 understory species suggests a community-wide response to elevated CO_2. Another study at a different forested FACE system also found no effect of CO_2 or species by CO_2 interaction on leaf C/N ratios (Sanders et al., 2004). Reduced herbivory under elevated CO_2 in forest systems may reflect a combination of reduced herbivore performance and increased predation that restricts herbivore population sizes. Also, a direct effect of CO_2 on the animals themselves cannot be ruled out (Guerenstein and Hildebrand, 2008).

There was no indication that the plots represented a "boundary" to the movement of insects or that there were distinct and independent insect populations inside and outside the plots. Both ^{13}C

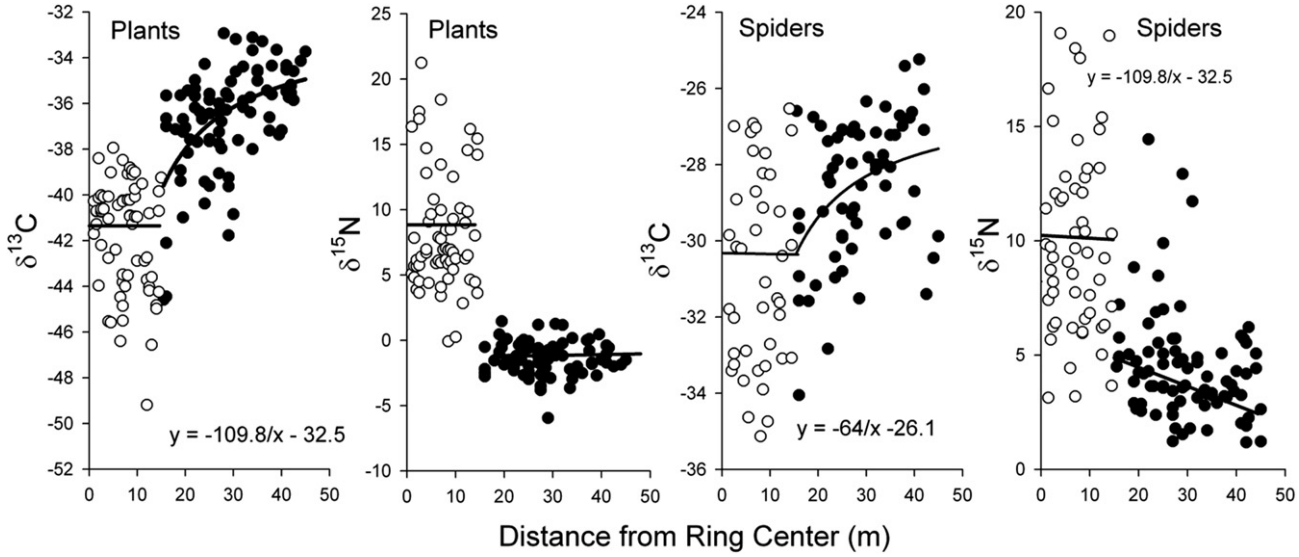

Fig. 3. Stable isotopic signatures (^{13}C and ^{15}N, per mil) of plants and spiders vs. distance from center of elevated CO_2 plots. Open circles are samples from within the plots, closed circles are samples from outside the plots. Solid lines indicate best-fits (equations provided for nonlinear fits) separately for points inside the plot and outside.

and ^{15}N isotope data indicated that insects moved across plot boundaries. The isotopic composition of any pool, in this case the body of a spider, is defined by the isotopic sources and all fractionations that occur during incorporation into the pool. The base carbon resource of the food chain (plants) is clearly differentiated between inside (elevated CO_2) and outside (ambient CO_2; Figs. 2 and 3). As carbon does not undergo significant fractionation during incorporation into animals (~0.39‰; Post, 2002), we used a simple two-ended mixing model (Dawson et al., 2002) to estimate the amount of carbon in spider biomass originating from within the FACE plot versus from without. Using this model, it was estimated that 55% of the carbon in spider biomass in elevated CO_2 plots originated external to the plots. This finding suggests that a large proportion of spider prey items were relatively mobile and traveled into the plot from the exterior.

Consideration of the $\delta^{15}N$ of spiders is more complicated. Significant fractionation occurs with respect to nitrogen when incorporated into animals (3.4‰; Post, 2002). In the present study, spiders from inside the plot were enriched in ^{15}N compared to spiders from outside the plot (Table 2). This enrichment could have originated from two sources: the more enriched baseline within the plot (from the application of ^{15}N to the soil described in Lichter et al., 2005) or from the spiders within the plots feeding at a higher trophic level compared to spiders outside the plots. Distinguishing between these two mechanisms of enrichment is not possible. However, to a first approximation, it can be assumed that spiders inside the plot were feeding at the same trophic level as spiders outside because the likely bulk of spider prey items (e.g. Diptera, Homoptera, and Orthoptera; Wise, 1993; Foelix, 1996) did not show changes with elevated CO_2. Under this assumption, there would be a similar level of fractionation inside and outside the plot, and a two-ended mixing model indicated that 55% of the nitrogen in spiders from inside the plot originated external to the plot. This is the same proportion of prey derived from outside the plot as estimated from differences in ^{13}C discussed above. Although spiders feeding at a higher trophic level could potentially exhibit a similar level of enrichment, this explanation seems less likely than a simple mixing of internal and external sources of nitrogen.

With the growing body of literature on the effects of elevated CO_2 on plant–herbivore interactions, it is becoming possible to draw meaningful generalizations particularly for insect performance indicators such as relative consumption rate, development time and conversion efficiency (Stiling and Cornelissen, 2007). However, there is still little known about the effects of elevated CO_2 on entire naturally occurring arthropod assemblages. In agroecosystems such as soybean, an increase in the abundance of leaf-chewers under elevated CO_2 has been directly linked to increased losses of leaf tissue (Aldea et al., 2005; Hamilton et al.,

Table 1
Carbon 13 ($\delta^{13}C$) and nitrogen 15 ($\delta^{15}N$) isotopic contents (mean ± s.e.) and trophic enrichment for adjacent tree foliage and spiders collected inside or outside of the FACE plots.

	Inside plot	Outside plot
$\delta^{13}C$ (per mil)		
Leaf	−36.61 ± 0.25	−41.77 ± 0.31
Spider	−31.52 ± 0.84	−33.83 ± 1.05
Trophic enrichment	5.1	7.9
$\delta^{15}N$ (per mil)		
Leaf	−1.51 ± 0.40	8.271 ± 0.505
Spider	4.631 ± 0.354	9.204 ± 0.451
Trophic enrichment	6.1	0.93

Table 2
Analysis of Variance (repeated) table displaying the sum of squares, degrees of freedom (d.f.), *F* statistic and probability value for carbon 13 ($\delta^{13}C$) and nitrogen 15 ($\delta^{15}N$) isotopic contents of adjacent spiders and tree foliage collected inside or outside of the FACE plots.

Source	Sums of Squares	d.f.	*F*	*P*
$\delta^{13}C$				
Plot	756	1	25.9	<0.001
Organism	2294	1	95.9	<0.001
Plot × organism	109	1	4.6	0.035
Error(org)	2679	112		
Error(plot)	3260	112		
$\delta^{15}N$				
Plot	2742	1	262	<0.001
Organism	665	1	71.8	<0.001
Plot × organism	360	1	38.9	<0.001
Error(org)	1027	111		
Error(plot)	1161	111		

A repeat-measure ANOVA was employed because adjacent spiders and foliage were not independent samples; Organism (plant and insect signatures) was the repeated measure.

2005; Dermody et al., 2008). In two woody systems, the opposite is true (Hamilton et al., 2004; Knepp et al., 2005; Stiling and Cornelissen, 2007). Results from this study suggest that, in addition to changes in insect performance (Knepp et al., 2007), decreases in herbivorous arthropods and increases in predaceous arthropods may contribute to reduced herbivory under elevated CO_2 in forest systems.

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