Multitrophic Effects of Elevated Atmospheric CO_2 on Understory Plant and Arthropod Communities

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ABSTRACT Rising levels of atmospheric [CO_2] will directly affect the responses and community composition of plants. However, few studies have examined how these changes to plant communities will alter insect communities that rely on them. Here, we report on a study that examined the community-level responses of plants, herbivores, detritivores, predators, parasitoids, and omnivores to increased [CO_2] at a Free Air Carbon Enrichment (FACE) facility at Oak Ridge National Laboratory. We found that aboveground net primary productivity for the five dominant plant species in the understory community, C:N ratios of leaf tissue for four of the five dominant understory taxa, amounts of herbivory, and arthropod abundance and richness across all trophic groups did not differ between ambient and elevated CO_2 plots. Abundance and richness of particular trophic groups were higher in ambient than in elevated CO_2 plots. There were also strong temporal effects on community composition, but no distinct treatment effects. These results, although preliminary, suggest that community-level responses to future atmospheric [CO_2] are likely to be species- and trophic-group specific.

KEY WORDS insect communities, plant communities, global change, invasive species, CO_2 enrichment

CONCENTRATIONS OF ATMOSPHERIC carbon dioxide ([CO_2]) have risen by ≈33% since the industrial revolution and are expected to approximately double within the next 100 yr (Houghton et al. 2001). A large body of research shows that rising [CO_2] will have important consequences for plant individuals, populations, and communities (Koch and Mooney 1996, Körner and Bazzaz 1996, Owensby et al. 1999, Niklaus et al. 2001, Poorter and Navas 2003, Weltzin et al. 2003). Under elevated [CO_2], plants tend to have higher rates of photosynthesis and accumulation of photosynthate (Drake et al. 1997, Saxe et al. 1998, Norby et al. 1999, Owensby et al. 1999). Elevated [CO_2] can also influence plant carbon and biomass allocation patterns (Bazzaz 1990, Huxman et al. 2000), water-use efficiency (Eamus 1991), and nutrient uptake rates (Jackson and Reynolds 1996). Changes in photosynthesis rates under elevated [CO_2] can also lead to changes in N concentration and higher C:N ratios in leaf tissue (Bezemer and Jones 1998) because the same amount of N is dispersed over a greater amount of leaf tissue. These responses vary among plant species (Stockle et al. 1992) and may depend on whether species are grown alone or as part of a diverse community (Körner 2000). Elevated [CO_2] may alter species composition and diversity within communities by favoring individual species or functional groups, or by changing the availability of resources such as soil water content or N (Reynolds 1996, Owensby et al. 1999, Dukes 2002).

Because insect communities are often tightly linked to plant communities (e.g., Siemann 1998), as individual plants and their communities respond to increasing [CO_2], interactions between plants and their herbivores may also change. Most of what ecologists know about the effects of elevated [CO_2] on plant–arthropod interactions comes from controlled experiments that focus on the responses of one or a few herbivore species to one plant species (e.g., Bezemer and Jones 1998, Coviella and Trumble 1999, but see Stacey and Fellowes 2002, Stiling et al. 2002, 2003). Despite the accumulating body of work, predicting how rising [CO_2] will alter assemblages of arthropods in natural systems is difficult because the responses of individual taxa are often idiosyncratic, and they are embedded in complex communities that may be structured by myriad indirect interactions and feedbacks (Moon and Stiling 2000, Bailey and Whitham 2002, 2003). Because of this, the results from studies of individually grown plants, or plants grown in monoculture with only a single herbivore species attacking them, often do not scale up to the results of studies involving multiple plant and arthropod species (Körner and Bazzaz 1996, Díaz et al. 1998).

Here we report on a study designed to determine the effects of elevated [CO_2] across multiple trophic levels: plants, their arthropod consumers (detritivores and herbivores), and the natural enemies of those consumers (predators and parasitoids). Specifically,

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we assessed plant and arthropod communities within an in situ understory plant community at the Free Air Carbon dioxide Enrichment (FACE) facility at Oak Ridge National Environmental Research Park, TN, three times during the growing season in 2001. Based on previous studies in other systems, we made several predictions about how plant and arthropod communities would respond to elevated [CO_2]: (1) elevated [CO_2] would alter plant composition, dominance, and annual aboveground net production in the understory plant community; (2) C:N ratio of individual plants would be higher in elevated [CO_2] plots than in ambient [CO_2] plots; (3) these increases in C:N ratios would increase amounts of herbivory because herbivores compensate for the reduction in N concentration through increased consumption; (4) the changes in plant community composition and C:N ratios would be reflected in the relative abundance of both herbivores and detritivores; and (5) changes in richness and abundance of herbivores would lead to changes in the richness and abundance of the parasitoids and predators that attack them.

Materials and Methods

Site Description. We did this research at the FACE facility, Oak Ridge National Environmental Research Park in Oak Ridge, TN (35°54′ N; 84°20′ W). The research site is a planted sweetgum (*Liquidambar styraciflua* L.) monoculture established in 1988 on an old terrace of the Clinch River (elevation, 230 m). In 2001, the sweetgum trees were ≈17 m tall, with a closed canopy, which reduces the light available to the understory between 70 and 95% during the growing season (Belote et al. 2004). The soil, classified as an Aquic Hapludult, has a silty clay loam texture, is moderately well drained, and slightly acidic (water pH ≈ 5.5–6.0). Precipitation is generally evenly distributed throughout the year, with an annual mean of 1,322 mm. The mean annual temperature at the site is 13.9°C. Additional details about the physical and biological characteristics of the site are in Norby et al. (1999, 2002).

Plant cover in the understory is continuous and co-dominated by two non-native invasive plant species, Japanese or Nepal grass [*Microstegium vimineum* (Trin.) A. Camus] and Japanese honeysuckle (*Lonicera japonica* Thunb.) (Belote et al. 2004). *M. vimineum*, a C_4 annual grass, was first reported in Tennessee in the early 1900s, and since its arrival, has spread throughout most of the eastern United States (Fairbrothers and Gray 1972). *L. japonica*, a C_3 perennial woody vine, was introduced into the United States in 1806 and is now naturalized throughout the southeastern United States (Leatherman 1955, Sasek and Strain 1991). The other most common understory taxa at the FACE site are blackberry (*Rubus* spp.), goldenrod (*Solidago canadensis* L.), and seedlings of box elder (*Acer negundo* L.). Additional details about the understory plant community are in Belote et al. (2004).

Experimental Design. FACE technology applies elevated [CO_2] to open, natural systems with minimal effects on abiotic (e.g., light, temperature, precipitation) and biotic (e.g., seed dispersal, animal movement) factors important to natural ecosystems and their plant and animal communities (Hendrey et al. 1999). In 1997, five 25-m diameter plots were established in the sweetgum stand, and in 1998, CO_2 treatments were initiated (Norby et al. 2002). Four plots are surrounded by 24 vertical vent pipes spaced 3.3 m apart. Two of the plots receive elevated [CO_2] (≈548 ppm) delivered to the vent piper by radial blowers. Two control plots receive ambient [CO_2] (≈370 ppm), and one ambient [CO_2] plot has no towers or other infrastructure (Norby et al. 2002). There are no meaningful differences between the ambient plot and the control plots (e.g., Norby et al. 2004). The [CO_2] treatment is maintained each year from April to November. Nighttime fumigation was discontinued in 2001 because it interfered with measurements of soil respiration.

The understory communities did not differ in either soil moisture (estimated as soil volumetric water content) or available light (amount of photosynthetically active radiation) in the understory (Belote et al. 2004).

Plant Sampling. In March 2001, we established four 0.5-m^2 subplots at random locations (away from other structures and walkways) within each of the five plots. We used these subplots to sample both plant and arthropod communities. Within each of the 0.5-m^2 subplots, we determined aboveground net primary productivity (ANPP; $g/m^2/yr$) for all plant species (Belote et al. 2004). In early September, we destructively harvested the subplots by clipping all individuals of each species at ground level. ANPP of woody perennials was determined by marking new shoots in early spring after shoot initiation; this new production was clipped and separated during the destructive harvest. End of season biomass was considered equivalent to ANPP for herbaceous plants. All plant tissue samples were oven dried at 65°C to constant mass. Because only five plant species (*L. japonica*, *M. vimineum*, *Rubus* spp., *S. canadensis*, and *A. negundo*) comprised >90% of the biomass and ANPP in the understory community (Belote et al. 2004), we focused our investigation on those five species.

Leaf Tissue Quality. For each of the five dominant plant species mentioned above, we collected four to five recently emerged but fully expanded leaves from several individuals of each species within or adjacent to the subplots on 15 July 2001. Tissue samples were dried at 50°C for 3 d. We ground the samples to a fine powder in a Wiley mill before analysis of total percent carbon and percent nitrogen on a Carlo Erba C-N analyzer at Oak Ridge National Laboratory.

Amounts of Herbivory. We randomly chose individuals of each the five dominant species in each subplot on 11 July and 17 August 2001. For each individual, we chose eight fully expanded leaves, working from the top of the plant down. For each leaf, we estimated herbivory by classifying it into one of six categories based on the percentage of the leaf tissue

that appeared to be removed by herbivores: 0, 1–20, 21–40, 41–60, 61–80, and 81–100%. We estimated the mean amount of herbivory for each individual by calculating the average midpoint of the range for each of the leaves. We then estimated mean amounts of herbivory for each species by taking the averages of these individual averages. We did not estimate amounts of galling or mining.

Arthropod Sampling. Within each of the subplots, we sampled for insects, mites, and spiders in May, June, and August 2001 using a combination of pitfall traps and sweepnet sampling. Pitfall traps were plastic vials (42.5-mm diameter) buried flush with the ground and partially filled with soapy water and left out for 72 h. We placed one pitfall trap at each end of each subplot. We used a 37.5-cm-diameter sweep net, swung 10 times in each of the subplots during midday when the vegetation was dry. We then transferred the arthropods caught in the sweepnet to a 4-liter plastic bag and froze the contents. Both the pitfall and sweepnet samples were sorted in the laboratory using an Olympia SZX12 microscope (Olympus, Tokyo, Japan). All individuals were identified to morphospecies using only external characters and separated into morphospecies groups based on morphological characters that were easily observable (Oliver and Beattie 1996). These morphospecies were counted and classified into one of five trophic classifications (herbivore, detritivore, omnivore, predator, and parasitoid) based on field observations and published sources. Other studies similar to ours, the use of morphospecies has yielded results both qualitatively and quantitatively similar to those if all taxa were identified to species by specialists (e.g., Oliver and Beattie 1996). In total, we classified 3069 individuals into 158 morphospecies. The most abundant groups were the ants, beetles, and spiders. All specimens are deposited in the collection at the University of Tennessee.

Statistical Analysis. The experimental design was an unbalanced completely randomized design with sampling, wherein subplots are treated as samples within plots (Filion et al. 2000). We tested the effects of $[CO_2]$ treatment on plant and arthropod data (for the specific contrasts described below) with a mixed model analysis of variance (ANOVA; procedure MIXED; SAS Institute 1999), using the model

$$y_{ijk} = \mu + CO_2\,\text{treatment}_i + \text{Rep}(CO_2)_{ij} + \text{subplot}[\text{Rep}(CO_2)]_{ijk}$$

where μ is the overall mean, $[CO_2]$ treatment (i) is a fixed effect, plot replicate (j) is the random effect, and subplots (k) contribute to residual error (yijk) (Filion et al. 2000). All P values, unless noted otherwise, were generated from this model. Because of the limitations of the study design (two elevated rings and three ambient rings), we have very low statistical power (Belote et al. 2004). Thus, we set $\alpha = 0.10$ and urge caution in interpreting; some of our results show that the effects of treatments seem to be strong but lack statistical significance. We tested for normality and homogeneity of variance with the Shapiro-Wilk W-Statistic and Levene's test, respectively, and log-transformed the data as appropriate. We first submitted the data to general ANOVA model to examine the effect of species identification, treatment, and their interaction on NPP, herbivory, C, N, and C:N ratio. We followed a similar procedure to examine the effect of trophic group, treatment, and their interaction on abundance and richness of arthropods between treatments. We then followed these analyses with by examining specific contrasts for each grouping to examine more thoroughly how particular species or trophic groups responded to the CO_2 treatments. Specific contrasts included (1) ANPP for each dominant plant species, (2) [C], [N], and C:N ratio of leaf tissue for each plant species, (3) herbivory of leaf tissue for each plant species on each date, (4) total abundance of arthropods by trophic group across sample dates and by sample date, and (5) richness of arthropods within trophic groups across sample dates and by sample date.

We used detrended correspondence analysis (DCA) and principal components analysis (PCA) to analyze abundance and richness of arthropods within trophic groups for each sample date, and for all dates combined, using PC-ORD (v. 4.0; MJM Software). For each analysis, we removed trophic groups present in <5% of the plots before ordination (Gauch 1982), and excluded outliers as appropriate. We examined relationships between DCA ordination (sample) scores and ANPP of each the five dominant species using joint plots for each ordination (McCune and Grace 2002). In addition, we used DCA and PCA to analyze patterns of abundance of the 75 most dominant morphospecies (present in >75% of the subplots on all dates) for each sample date and for all dates combined.

Table 1. Aboveground net primary production (mean ± SE; g/m²/yr) for five dominant plant species in 2001 in subplots that received ambient $[CO_2]$ and elevated $[CO_2]$

Species	P	Ambient	Elevated
A. negundo	0.87	4 ± 2	2 ± 3
L. japonica	0.003	11 ± 8	45 ± 10
M. vimineum	<0.0001	120 ± 12	64 ± 14
Rubus spp.	0.66	1 ± 1	5 ± 1
S. canadensis	0.04	1 ± 3	22 ± 4

Results and Discussion

Prediction 1: Elevated $[CO_2]$ Would Alter Plant Composition, Dominance, and Annual Aboveground Net Production in the Understory Plant Community. Total plant community ANPP did not differ between $[CO_2]$ treatments (ambient = 136 ± 8 g/m²/yr, elevated = 138 ± 10 g/m²/yr; $P = 0.91$). This result was explained by the differential, and even opposing, response of the different plant species within the community. In particular, production of *L. japonica* in elevated $[CO_2]$ plots was four times greater than in ambient $[CO_2]$ plots (Table 1). The two dominant

Table 2. Mean ± SE C (%), N (%), and C:N ratio of leaf tissue for five dominant plant species in subplots under elevated and ambient [CO_2]

Species	*P*	Ambient	Elevated
A. negundo			
C	0.49	44.8 ± 0.4	44.3 ± 0.5
N	0.72	1.95 ± 0.12	1.87 ± 0.15
C:N ratio	0.57	23.3 ± 1.2	24.6 ± 1.5
L. japonica			
C	0.67	45.3 ± 0.4	44.9 ± 0.5
N	0.11	1.76 ± 0.06	1.57 ± 0.07
C:N ratio	0.10	26.0 ± 0.9	29.0 ± 1.0
M. vimineum			
C	0.37	44.7 ± 0.6	45.6 ± 0.6
N	0.69	2.42 ± 0.21	2.56 ± 0.24
C:N ratio	0.72	18.5 ± 1.5	18.0 ± 1.8
Rubus spp.			
C	0.45	45.6 ± 0.3	45.2 ± 0.4
N	0.76	2.19 ± 0.09	2.15 ± 0.11
C:N ratio	0.84	21.0 ± 0.7	21.2 ± 0.9
S. canadensis			
C	0.83	43.2 ± 0.5	43.3 ± 0.6
N	0.87	2.22 ± 0.09	2.23 ± 0.11
C:N ratio	0.84	19.6 ± 0.7	19.5 ± 0.8

native species, *Rubus* spp. and *Solidago canadensis*, also had higher production in elevated [CO_2] plots than in ambient [CO_2] plots (Table 1). In contrast, production of *M. vimineum* was nearly two times greater in ambient [CO_2] plots than in elevated [CO_2] plots (Table 1). The positive responses of *L. japonica*, *Rubus* spp., and *S. canadensis*, all of which use the C_3 photosynthetic pathway, were not surprising, because they mirror the well-documented "fertilization effect" seen in many other studies (Drake et al. 1997, Saxe et al. 1998, Poorter and Navas 2003). However, the decline in production by *M. vimineum*, a C_4 grass, was surprising, and it may have been a result of interspecific interactions with *L. japonica* or the other taxa (Belote et al. 2004). In summary, elevated [CO_2] affected the composition of the plant community and the dominance of several individual plant species, although it did not affect total production.

Prediction 2: C:N Ratio of Individual Plants Would Be Greater in Elevated [CO_2] than Ambient [CO_2] Plots. The overall ANOVA indicated a strong effect of species on C:N ratios ($P < 0.0001$), indicating that C:N ratios differed among species. However, there were no overall treatment ($P = 0.29$) or species × treatment effects ($P = 0.45$). The independent contrasts analysis revealed that, contrary to our predictions based on other studies, C:N ratios for four of the five dominant plant taxa did not differ between ambient and elevated [CO_2] (Table 2). If we examined C:N ratios early in the growing season to examine how elevated [CO_2] affected young foliage, we may have detected stronger differences between treatments. However, for *L. japonica*, the C:N ratio of leaf tissue was 12% greater in elevated [CO_2] than in ambient [CO_2] plots (Table 2). While many studies have found that elevated [CO_2] reduces N concentration in leaves (Bezemer and Jones 1998, Coviella and Trumble 1999), others have found no effect of CO_2 on leaf C:N ratios (e.g., Awmack et al. 1996, Docherty et al. 1997). For example, Díaz et al. (1998) found that N concentration in leaves of only 2 of the 10 species in their study were affected by changes in [CO_2]. Thus, even though *L. japonica* production is higher under elevated [CO_2], it is a low-quality resource.

Table 3. Herbivory (% of tissue removed; mean ± SE) for five dominant plant species in July and Aug. 2001 in subplots under elevated and ambient [CO_2]

Species	July			Aug.		
	P	Ambient	Elevated	*P*	Ambient	Elevated
A. negundo	0.51	24 ± 2	20 ± 3	0.23	41 ± 5	29 ± 6
L. japonica	0.50	5 ± 3	2 ± 3	0.17	8 ± 1	4 ± 1
M. vimineum	0.31	0.4 ± 0.3	0.5 ± 0.4	0.89	2.5 ± 1.2	2.3 ± 1.5
Rubus spp.	0.39	24 ± 5	17 ± 6	0.47	32 ± 5	27 ± 6
S. canadensis	0.33	27 ± 6	17 ± 7	0.52	46 ± 8	38 ± 10

P values are for arcsin (square root) data transformation.

Prediction 3: Changes in C:N Ratios Would Increase Amounts of Herbivory Because Herbivores Compensate for the Reduction in N Concentration Through Increased Consumption. Overall, amounts of herbivory differed between ambient plots and elevated plots in both July ($P = 0.06$) and August ($P = 0.07$), and there were strong species-specific effects ($P < 0.0001$ for both July and August). For example, amounts of herbivory on *L. japonica* were four to five times lower than the amounts for the three dominant native taxa (Table 3). This is not surprising because *L. japonica* is a non-native plant lacking close relatives from which herbivores could switch (e.g., Connor et al. 1980) and because of its relatively high C:N ratio (Table 2). However, there was no overall species × treatment effects for either July ($P = 0.91$) or August ($P = 0.66$).

There are two general predictions from previous studies as to the effects of elevated [CO_2] on amounts of herbivory. First, Stiling et al. (2002, 2003) found that damage by herbivores on oaks was lower under elevated [CO_2] than ambient [CO_2] because leaf N concentrations were lower under elevated [CO_2]. In contrast, other studies have found that herbivores compensate for the reduction in leaf [N] by increasing their consumption of leaf tissue, thereby increasing damage under elevated [CO_2] (e.g., Williams et al. 1997). Both of these predictions hinge on C:N ratios increasing under elevated [CO_2]. In our study, we found no effect of elevated [CO_2] on herbivory; this may be explained by the lack of differences in C:N ratios in four of the five dominant understory plants. However, even for the one species (*L. japonica*) that showed an effect of [CO_2] on C:N ratio, herbivores did not compensate by foraging more. One interesting avenue for future research in this system could focus on potential changes in plant defensive compounds in these species in response to elevated [CO_2]. It may be that some species, growing in high [CO_2] environments, devote more resources to plant defense, but we did not test this hypothesis in this study.

Table 4. Mean ± SE total abundance of arthropods by functional group in subplots under elevated and ambient [CO_2] across three sampling dates in 2001

Trophic Abundance	*P*	Ambient	Elevated
Detritivore	0.19	73 ± 11	44 ± 13
Herbivore	0.72	19 ± 3	17 ± 4
Omnivore	0.56	28 ± 5	33 ± 6
Parasitoid	0.41	15 ± 1	13 ± 1
Predator	0.05	30 ± 1	25 ± 1

Predictions 4 and 5: Changes in Plant Community Composition and C:N Ratios Would Be Reflected in the Relative Abundance of Both Herbivores and Detritivores. Changes in Richness and Abundance of Herbivores Would Lead to Changes in the Richness and Abundance of Parasitoids and Predators that Attack Them. Total arthropod abundance, the sum of the sweep and pitfall trap samples, did not differ between ambient and elevated [CO_2] plots across the three sampling dates (Total abundance in ambient plots = 165 ± 15, elevated plots = 133 ± 18, $P = 0.26$; Table 4), or on any of the sampling dates (Fig. 1a). Previous studies have found that herbivore abundance is lower under elevated [CO_2] conditions (Stiling et al. 2002, 2003). We found no such difference in this study (Table 4). We also found that the abundances of detritivores, omnivores, or parasitoids did not differ between ambient and elevated [CO_2] (Table 4). Surprisingly, predators were 25% more abundant in ambient than in elevated [CO_2] plots (Table 4), even though their prey were not more abundant. This pattern is driven largely by the greater spider abundances in ambient plots (Fig. 2). To our knowledge, this is the first demonstration that elevated [CO_2] influences spider abundance. Because spiders are dominant and important predators in most terrestrial ecosystems (e.g., Wise 1995, Schmitz and Suttle 2001), future studies on the effects of elevated [CO_2] on multiple trophic levels should consider spiders and how interactions with their prey are altered.

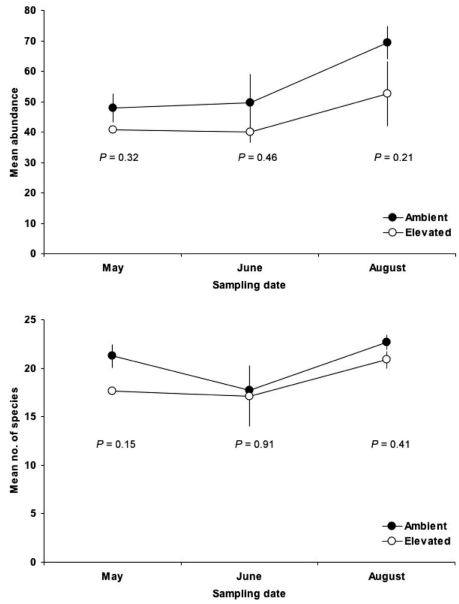

Fig. 1. The effects of season and elevated CO_2 on mean ± SE arthropod abundance (a) and richness (b) across seasons. See Materials and Methods for explanation of *P* values.

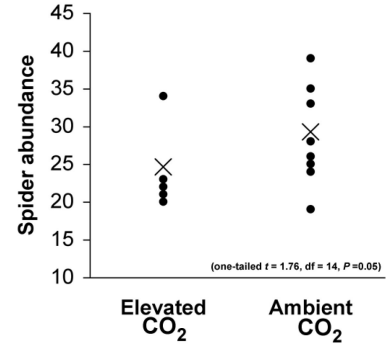

Fig. 2. The effects of elevated CO_2 on the abundance of spiders. Each filled symbol is the total abundance of spiders over the three sampling periods. The crossed symbol is the mean of those values.

Total arthropod richness did not differ across sampling dates ($P = 0.31$) or at each sampling date (Fig. 1b). Similarly, richness within trophic groups did not differ between ambient and elevated [CO_2] plots across sampling dates ($P = 0.31$). However, detritivore richness in May was 40% greater in ambient than elevated [CO_2], and predator richness in August was 19% greater in ambient than elevated [CO_2] (Table 5). It is unclear whether the detritivores are responding, either directly or indirectly, to [CO_2]-caused differences in the quality of leaf litter. At the Duke Forest FACE site, soil microarthropod species richness was reduced in elevated [CO_2], even though litter quality did not differ between plots (Hansen et al. 2001). Furthermore, a recent review by Norby et al. (2001) found that N concentration was lower under elevated [CO_2] than under ambient [CO_2], but that conclusion was discounted for several reasons. However, the sweetgum litter in elevated [CO_2] plots at the Oak Ridge FACE site has consistently had lower N concentration (11–16% lower, except for year 1) than litter in ambient [CO_2] plots (D. W. Johnson et al., unpublished data). Future studies using reciprocal transplants of litter between elevated and ambient [CO_2] plots could help determine if detritivores are affected indirectly or directly by elevated [CO_2]. We attribute the increase in predator richness in August to an increase in spider species richness.

PCA and DCA based on total arthropod abundance and richness, and abundance of the dominant morphospecies, indicated that there were no distinct treatment effects on arthropod community composition (Fig. 3). There were no apparent relationships between the structure of the arthropod communities, based on either trophic group richness or abundance, and the productivity of the dominant plant species (joint plot analysis), although other studies have

Table 5. Mean ± SE trophic group richness in May, June, and Aug. 2001 in subplots under elevated and ambient [CO_2]

Trophic group	May			June			Aug.		
	P	Ambient	Elevated	*P*	Ambient	Elevated	*P*	Ambient	Elevated
Detritivore	0.10	4.6 ± 0.4	3.3 ± 0.4	0.77	3.9 ± 0.4	4.1 ± 0.5	0.82	6.6 ± 0.5	6.4 ± 0.6
Herbivore	0.55	4.5 ± 0.7	3.8 ± 0.9	0.82	4.1 ± 0.9	3.8 ± 1.0	0.50	4.5 ± 0.6	3.8 ± 0.7
Omnivore	0.52	2.1 ± 0.5	2.6 ± 0.4	0.84	2.7 ± 0.6	2.9 ± 0.7	0.14	2.9 ± 0.3	4.0 ± 0.4
Parasitoid	0.60	3.3 ± 0.4	3.8 ± 0.5	0.90	2.3 ± 0.4	2.4 ± 0.5	0.90	2.8 ± 0.4	2.8 ± 0.5
Predator	0.30	5.2 ± 0.4	4.4 ± 0.5	0.50	3.7 ± 0.4	3.1 ± 0.5	0.11	5.3 ± 0.3	4.1 ± 0.4

found such relationships (e.g., Siemann 1998). Instead, there were strong temporal effects such that samples, regardless of treatment, clustered according to the month in which they were sampled (Fig. 3). This suggests, at least for this study, that abiotic conditions associated with time of sampling (e.g., temperature, relative humidity, precipitation) or the phenology of particular arthropod species outweighed the effects of elevated [CO_2] on arthropod community composition. This is not surprising given that insect communities can show tremendous temporal variation in composition, especially when communities are defined broadly to include multiple trophic levels or guilds (e.g., Root and Cappuccino 1992, Boyer et al., 2003). The lack of a CO_2 effect might also be because, especially mobile species (e.g., beetles, grasshoppers), simply disperse among our sample plots, thereby swamping any effect caused by the treatment. Also, note that the sampling design limits our statistical power to pick up especially small effects of [CO_2] on particular groups. However, another study (Belote et al. 2004) used the same sampling approach that we did to examine the details of the effects of the treatments on plant community responses and did detect several significant effects. Thus, we argue that the lack of an effect we detect is caused by a biological rather than a statistical effect.

In summary, elevated [CO_2] had mixed effects on the plant community and its associated arthropods at this FACE site. However, changes in plant community composition did not translate into differences in arthropod communities. Instead, arthropod community composition was more idiosyncratic than plant community composition, and it seemed to be more strongly influenced by intra-annual variation in environmental conditions than by differences in [CO_2]. Perhaps this is not surprising because communities are dynamic and, by definition, contain multiple species that respond differently to elevated [CO_2] (Bezemer et al. 1999). Furthermore, elevated [CO_2] may alter interactions among species, although the community-level ramifications of this are not well known (Stacey and Fellowes 2002, Stiling et al. 2002, 2003). These idiosyncratic, species-specific responses to elevated [CO_2] may buffer one another: the abundances of some species increase while others decrease. To understand the potential effects of global climate change on the complexity of multitrophic interactions that structure most communities, field experiments on entire communities are necessary (Lawton 2000, Hunter 2001, Körner 2001). It will also be necessary to couple experiments on entire communities with mechanistic experiments that focus on the details of particular interactions among species. For example, our results suggest that spiders, which in many terrestrial ecosystems are dominant predators (Schmitz and Suttle 2001, Wise 1995), were strongly affected by elevated [CO_2]. An experiment that manipulates the presence or abundance of spiders under ambient and elevated [CO_2], in natural or controlled environments, could uncover how keystone species or trophic interactions (e.g., predator/prey relationships; see Power et al. 1996), might interact with increases in [CO_2] or changes in other environmental conditions to determine community structure.

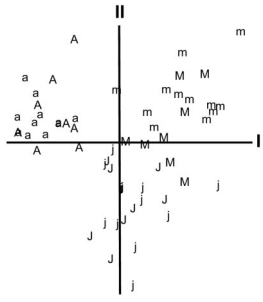

Fig. 3. PCA ordination of arthropod abundance for 75 morphospecies in May (M or m), June (J or j), and August (A or a) for subplots exposed to elevated [CO_2] (capital letters) and ambient [CO_2] (lowercase letters).

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References Cited

Awmack, C., R. Harrington, S. Leather, and J. Lawton. 1996. The impacts of elevated CO_2 on aphid-plant interactions. Asp. Appl. Biol. 45: 317–322.

Bailey, J. K., and T. G. Whitham. 2002. Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. Ecology. 83: 1701–1712.

Bailey, J. K., and T. G. Whitham. 2003. Interactions among elk, aspen, galling sawflies and insectivorous birds alter arthropod diversity. Oikos. 101: 127–134.

Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Annu. Rev. Ecol. Syst. 21: 167–196.

Belote, R. T., J. F. Weltzin, and R. J. Norby. 2004. Response of an understory plant community to elevated CO_2 depends on differential responses of dominant invasive species and is mediated by soil water availability. New Phyt. 161: 827–835.

Bezemer, T. M., and T. H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. Oikos. 82: 212–222.

Bezemer, T. M., K. J. Knight, J. E. Newington, and T. H. Jones. 1999. How general are aphid responses to elevated atmospheric CO_2? Ann. Entomol. Soc. 92: 724–730.

Boyer, A. G., R. E. Swearingen, M. A. Blaha, C. T. Fortson, S. K. Gremillion, K. A. Osborn, and M. D. Moran. 2003. Seasonal variation in top-down and bottom-up processes in a grassland arthropod community. Oecologia (Berl.). 136: 309–316.

Connor, E. F., S. H. Faeth, D. Simberloff, and P. A. Opler. 1980. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. Ecol. Entomol. 5: 205–211.

Coviella, C. E., and J. T. Trumble. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. Cons. Biol. 13: 700–712.

Díaz, S., L. H. Fraser, J. P. Grime, and V. Falczuk. 1998. The impact of elevated CO_2 on plant-herbivore interactions: experimental evidence of moderating effects at the community level. Oecologia (Berl.). 117: 177–186.

Docherty, M., F. Wade, D. Hurst, J. Whittaker, and P. Lea. 1997. Responses of tree sap-feeding herbivores to elevated CO_2. Glob. Chan. Biol. 3: 51–59.

Drake, B., M. Gonzalez-Meler, and S. P. Long. 1997. More efficient plants: a consequence of rising atmospheric CO_2. Annu. Rev. Plant. Phys. Plant Mol. Biol. 48: 607–637.

Dukes, J. S. 2002. Comparison of the effect of elevated CO_2 on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. Plant Ecol. 160: 225–234.

Eamus, D. 1991. The interaction of rising CO_2 and temperatures with water use efficiency. Plant Cell Environ. 14: 843–852.

Fairbrothers, D. E., and J. R. Gray. 1972. *Microstegium vimineum* (Trin.) A. Camus (Gramineae) in the United States. Bull. Torr. Bot. Club. 99: 97–100.

Filion, M., P. Dutilleu, and C. Potvin. 2000. Optimum experimental design for the free-air carbon dioxide enrichment (FACE) studies. Glob. Change Biol. 6: 843–854.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge.

Hansen, R. A., R. S. Williams, D. C. Degenhardt, and D. E. Lincoln. 2001. Non-litter effects of elevated CO_2 on forest floor microarthropod abundances. Plant Soil. 236: 139–144.

Hendrey, G. R., D. Ellsworth, K. Lewin, and J. Nagy. 1999. Free-air CO_2 Enrichment (FACE) system for exposing tall forest vegetation to elevated atmospheric CO_2. Glob. Change Biol. 5: 293–310.

Houghton, J., Y. Ding, D. Griggs, M. Noquer, P. van der Linden, and D. Xiaosu (eds.). 2001. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge.

Hunter, M. D. 2001. Effects of elevated atmospheric carbon dioxide on insect–plant interactions. Ag. For. Entomol. 3: 153–159.

Huxman, T. E., E. P. Hamerlynck, and S. D. Smith. 2000. Reproductive allocation and seed production in *Bromus madritensis ssp. rubens* at elevated CO_2. Fun. Ecol. 13: 769–777.

Jackson, R. B., and H. L. Reynolds. 1996. Nitrate and ammonium uptake for single and mixed-species communities grown at elevated CO_2. Oecologia (Berl.). 105: 74–80.

Koch, G. W., and H. A. Mooney (eds.). 1996. Carbon dioxide and terrestrial ecosystems. Academic, London.

Körner, C. 2000. Biosphere responses to CO_2 enrichment. Ecological Applications 10: 1590–1619.

Körner, C., and F. A. Bazzaz. 1996. Carbon dioxide, populations, and communities. Academic, San Diego, CA.

Lawton, J. H. 2000. Community ecology in a changing world. Ecology Institute, Oldendorf/Luhe, Germany.

Leatherman, A. D. 1955. Ecological life-history of *Lonicera japonica* Thunb. University of Tennessee, Knoxville, TN.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, OR.

Moon, D. C., and P. Stiling. 2000. Abiotically induced direct and indirect effects in a coastal salt marsh: assessing relative importance. Ecology. 81: 470–481.

Niklaus, P., P. Leadley, B. Schmid, and C. Körner. 2001. A long-term field study on biodiversity × elevated CO_2 interactions in grassland. Ecol. Monogr. 71: 341–356.

Norby, R. J., S. D. Wullschleger, C. A. Gunderson, D. W. Johnson, and R. Ceulemans. 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell Environ. 22: 683–714.

Norby, R. J., M. F. Cotrufo, P. Ineson, E. G. O'Neill, and J. G. Canadell. 2001. Elevated CO_2, litter chemistry, and decomposition: A synthesis. Oecologia 127: 153–165.

Norby, R. J., P. J. Hanson, E. G. O'Neill, T. J. Tschaplinski, J. F. Weltzin, R. T. Hansen, W. Chen, S. D. Wullschleger, C. A. Gunderson, N. T. Edwards, and D. W. Johnson. 2002. Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. Ecol. Appl. 12: 1261–1266.

Norby, R. J., J. Ledford, C. D. Reilly, N. E. Miller, and E. G. O'Neill. 2004. Fine-root production dominates response of deciduous forest to atmospheric CO_2 enrichment. Proc. Nat. Acad. Sci. U.S.A. 101: 9689–9683.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. Conserv. Biol. 10: 99–109.

Owensby, C. E., J. M. Ham, A. K. Knapp, and L. M. Allen. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. Glob. Change Biol. 5: 497–506.

Poorter, H., and M.-L. Navas. 2003. Plant growth and competition at elevated CO_2: on winners, losers, and functional groups. New Phyt. 157: 175–198.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. C. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. Bioscience. 46: 609–620.

Reynolds, H. L. 1996. Effects of elevated CO_2 on plants grown in competition, pp. 273–286. *In* C. Körner and F. A. Bazzaz (eds.), Carbon dioxide, populations, and communities. Academic, San Diego, CA.

Root, R. L., and N. Cappuccino. 1992. Patterns in population change and the organization of the insect community associated with goldenrod. Ecol. Monogr. 62: 393–420.

Sasek, T. W., and B. R. Strain. 1991. Effect of CO_2 enrichment on the growth and morphology of a native and an introduced honeysuckle vine. Amer. Journ. of Botany. 78: 68–75.

SAS Institute. 1999. SAS/STAT user's guide. SAS Institute, Cary, NC.

Saxe, H., D. S. Ellsworth, and J. Heath. 1998. Tree and forest functioning in an enriched CO_2 atmosphere. New Phyt. 139: 395–436.

Schmitz, O. J., and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. Ecology. 82: 2072–2081.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology. 79: 2057–2070.

Stacey, D. A., and M.D.E. Fellowes. 2002. Influence of elevated CO_2 on interspecific interactions at higher trophic levels. Glob. Change Biol. 8: 668–675.

Stiling, P., M. Cattell, D. C. Moon, A. M. Rossi, B. A. Hungate, G. J. Hymus, and B. G. Drake. 2002. Elevated atmospheric CO_2 lowers herbivore abundance, but increases leaf absission rates. Glob. Change Biol. 8: 658–667.

Stiling, P., D. C. Moon, M. D. Hunter, J. Colson, A. M. Rossi, G. J. Hymus, and B. G. Drake. 2003. Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. Oecologia (Berl.). 134: 82–87.

Stockle, C. O., P. T. Dyke, J. R. Williams, C. A. Jones, and N. J. Rosenberg. 1992. A method for estimating the direct and climatic effects of rising atmospheric carbon dioxide on growth and yield of crops, part 2. Sensitivity analysis at 3 sites in the midwestern USA. Ag. Syst. 38: 239–256.

Weltzin, J. F., R. T. Belote, and N. J. Sanders. 2003. Biological invaders in a greenhouse world: will elevated carbon dioxide fuel plant invasions? Front. Ecol. Env. 1: 146–153.

Williams, R. S., D. E. Lincoln, and R. B. Thomas. 1997. Effects of elevated CO_2-grown loblolly pine needles on the growth, consumption, development, and pupal weight of red-headed pine sawfly larvae reared within open-topped chambers. Glob. Change Biol. 3: 501–511.

Wise, D. H. 1995. Spiders in ecological webs. Cambridge University Press, Cambridge.

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