Seeing the forest for the trees: long-term exposure to elevated CO_2 increases some herbivore densities

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Abstract

The effects of elevated CO_2 on plant growth and insect herbivory have been frequently investigated over the past 20 years. Most studies have shown an increase in plant growth, a decrease in plant nitrogen concentration, an increase in plant secondary metabolites and a decrease in herbivory. However, such studies have generally overlooked the fact that increases in plant production could cause increases of herbivores per unit area of habitat. Our study investigated leaf production, herbivory levels and herbivore abundance per unit area of leaf litter in a scrub-oak system at Kennedy Space Center, Florida, under conditions of ambient and elevated CO_2, over an 11-year period, from 1996 to 2007. In every year, herbivory, that is leafminer and leaftier abundance per 200 leaves, was lower under elevated CO_2 than ambient CO_2 for each of three species of oaks, *Quercus myrtifolia*, *Quercus chapmanii* and *Quercus geminata*. However, leaf litter production per $0.1143\,m^2$ was greater under elevated CO_2 than ambient CO_2 for *Q. myrtifolia* and *Q. chapmanii*, and this difference increased over the 11 years of the study. Leaf production of *Q. geminata* under elevated CO_2 did not increase. Leafminer densities per $0.1143\,m^2$ of litterfall for *Q. myrtifolia* and *Q. chapmanii* were initially lower under elevated CO_2. However, shortly after canopy closure in 2001, leafminer densities per $0.1143\,m^2$ of litter fall became higher under elevated CO_2 and remained higher for the remainder of the experiment. Leaftier densities per $0.1143\,m^2$ were also higher under elevated CO_2 for *Q. myrtifolia* and *Q. chapmanii* over the last 6 years of the experiment. There were no differences in leafminer or leaftier densities per $0.1143\,m^2$ of litter for *Q. geminata*. These results show three phenomena. First, they show that elevated CO_2 decreases herbivory on all oak species in the Florida scrub-oak system. Second, despite lower numbers of herbivores per 200 leaves in elevated CO_2, increased leaf production resulted in higher herbivore densities per unit area of leaf litter for two oak species. Third, they corroborate other studies which suggest that the effects of elevated CO_2 on herbivores are species specific, meaning they depend on the particular plant species involved. Two oak species showed increases in leaf production and herbivore densities per $0.1143\,m^2$ in elevated CO_2 over time while another oak species did not. Our results point to a future world of elevated CO_2 where, despite lower plant herbivory, some insect herbivores may become more common.

Keywords: elevated CO_2, insect densities, insect herbivory, Kennedy Space Center, leaf production, long-term effects, oak trees, species-specific responses

Introduction

There is virtual unanimity that future increases of atmospheric CO_2 will cause substantial changes to

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natural systems (IPCC, 2007). Many studies have shown an increase in plant growth in elevated CO_2 compared with ambient CO_2 (Curtis & Wang, 1998; Norby *et al.*, 1999; Long *et al.*, 2004; Ainsworth & Long, 2005). Elevated CO_2 often also reduces plant nitrogen concentrations and increases secondary metabolites (Lincoln *et al.*, 1993; Poorter *et al.*, 1997; Curtis & Wang, 1998).

Decreased plant quality has been shown to decrease herbivore performance and levels of herbivory in many communities (Stiling & Cornelissen, 2007). On the other hand, increased biomass and leaf production provide increased resources for herbivores, potentially leading to population increases per m^3 of canopy, as reflected in numbers per m^2 of leaf litter. No studies have examined the effects of increased plant production on insect herbivore densities in natural communities over long periods of time. The expense of building chambers or supplying elevated CO_2 to FACE experiments has lead to relatively few investigations of this nature. As a result, the strength of the potentially conflicting pressures of decreased plant quality but increased quantity in a future world of higher CO_2 has not been compared. Most studies investigating the effects of elevated CO_2 on herbivores have used short-term experiments where insect herbivores are fed foliage grown in elevated or ambient CO_2 and digestibility and performance are compared (e.g. Barbehenn *et al.*, 2004; Sudderth *et al.*, 2005; Agrell *et al.*, 2006). Fewer studies have elevated CO_2 levels in the field and measured changes in herbivory over many generations despite the greater validity of this technique to natural conditions (Newman, 2003). In these relatively few studies, herbivory levels are often determined using counts or damage levels on a given number of leaves or branches (Percy *et al.*, 2002; Hamilton *et al.*, 2004; Stiling & Cornelissen, 2007). There have been no attempts to count total numbers of leaves and associated insect herbivores in natural systems under sustained elevated CO_2 levels where both shoot biomass, leaf area and insect densities can change over long periods of time.

The current study investigates the effects of elevated CO_2 on insect herbivory and insect herbivore densities in a Florida scrub-oak forest over 11 years of continuously elevated CO_2. This scrub-oak forest is composed mainly of three oak species whose most common herbivores are leaf-mining and leaf-tying insects. Our results are noteworthy because they show elevated CO_2 (1) decreases insect herbivory per 200 leaves in all years for all oak species, (2) increases leaf production for some oak species and (3) increases total herbivore density per unit area of leaf litter for some oak species.

Methods

This study was conducted at Merritt Island National Wildlife Refuge, within NASA's Kennedy Space Center, in a scrub-oak, palmetto ecosystem (Schmalzer & Hinkle, 1992). The particular area chosen for the study was dominated by three species of oaks, myrtle oak, *Quercus myrtifolia* Willd; sand-live oak, *Quercus geminata* Small and Chapman oak, *Quercus chapmanii* Sargenti; which together accounted for 85–90% of the biomass (Seiler *et al.*, 2009). Of the three species of oaks, *Q. myrtifolia* was the most common, accounting for about 77% of the oak biomass, while *Q. geminata* accounted for approximately 17% and *Q. chapmanii* 6% (Dijkstra *et al.*, 2002). A total of 27 other plant species were identified in the area with Elliott's milk pea, *Galactia elliottii* Nuthall, a nitrogen-fixing legume, the most common.

In January 1996, a two acre area of scrub-oak forest was burned. During the following spring, 16 open top chambers (OTC), each 2.5 m high with octagonal sides of 1.4 m wide, were erected in the study area. Each side consisted of a 4 in. PVC pipe frame covered with Mylar (Melinex 071, Courtaulds Performance Films, Martinsville, VA, USA). The total area covered by each cage was 9.42 m^2. Panels were easily removable to facilitate entry into the chambers. Eight OTCs were maintained at elevated CO_2 (ambient $+ 350$ ppm^{-1} CO_2) and eight at ambient CO_2 (~ 350 ppm in 1996 to ~ 380 ppm in 2007). Studies on the effects of elevated CO_2 on plant–herbivore interactions commonly elevate CO_2 levels by ~ 350 ppm (Sudderth *et al.*, 2005; Agrell *et al.*, 2006). Ambient or CO_2-enriched air was blown into each chamber via four 20.5 cm diameter ducts at a rate of $24–30$ m^3 min^{-1}. Blower speed was reduced at night to 1/3 of the daytime values. These CO_2 concentrations were continuously maintained inside the chambers from mid-May 1996 through mid-June 2007 (except for small periods in 1999 and 2005 when chambers were damaged by hurricanes). During August/September, from 1996 through 2006, we counted the numbers of leaf mines per 200 haphazardly selected leaves on *Q. myrtifolia* and *Q. geminata*. Most mined leaves contained only one species of leafminer. Among the most common leaf-mining genera were *Cameraria*, *Stigmella* and *Buccalatrix*. We also counted the number of leaf-tying lepidopterans per 200 leaves. Again, leaftiers belonged to numerous species. Counts of both leafminers and leaftiers on *Q. chapmanii* were made from 2001 onward, when this species became common enough in the chambers to census.

Leaves were collected every year for nitrogen analysis for each of the three species, except for *Q. geminata* and *Q. chapmanii* in 2005 and 2006. Leaves of each of the three oak species were collected haphazardly throughout the chamber and were oven dried at 70 °C, then ground and analyzed for %N by Dumas Combustion (NC 2100; CE Elantech, Lakewood, NJ, USA) at the Colorado Plateau Stable Isotope Laboratory (http://www.isotope.nau.edu).

Leaf litter was collected in elongate troughs (measuring 0.762 m long by 0.05 m wide, providing 0.0381 m^2 in area) with three troughs per chamber. Troughs were placed in similar positions in all chambers for the

duration of this study. Litter was removed monthly from January 1998 through August 2003 and quarterly from November 2003 until May 2006. Senesced (dead) leaves were sorted by tree species and species of leaf-miner they supported, if any. Litter from *Q. myrtifolia* and *Q. chapmanii* remained pooled until 2001 when *Q. chapmanii* leaves became common enough to census in the trays. Litter from earlier samples had, by then, been chemically analyzed so we could not re-visit those samples and re-sort *Q. myrtifolia* and *Q. chapmanii*. Because we were interested in relative differences in leaf production and leafminer densities between ambient and elevated CO_2 chambers, we calculated the percentage change in senesced leaves for each oak species in elevated over ambient CO_2 for each year. Because all these oaks are evergreen, they drop the majority of their leaves in March–April and bud burst occurs immediately thereafter in April–May. Year is therefore taken to mean growing season from April to March. The number of leafminers and leaftiers per $0.1143\,m^2$ of litter was calculated from the three litter trays for each elevated and ambient CO_2 OTC for each year. Leaf production per year for *Q. myrtifolia* and *Q. chapmanii* combined and for *Q. geminata* alone, was correlated against number of years of CO_2 fumigation.

Statistical analyses of the effects of CO_2 treatment on leafminer and leaftier densities per 200 leaves were performed for each oak species using repeated measures analysis of variance (ANOVA) with CO_2 as the factor and year as the time interval ($n = 11$ years for *Q. myrtifolia* and *Q. geminata* and $n = 6$ years for *Q. chapmanii*). Leaf nitrogen was analyzed with repeated measures ANOVAs with CO_2 treatment as the factor and year as the time interval. Species were analyzed separately because of the missing samples from 2005 and 2006 for *Q. chapmanii* and *Q. geminata*. Leafminer and leaftier numbers per $0.1143\,m^2$ of leaf litter were ln transformed then analyzed using a repeated measures ANOVA for *Q. myrtifolia* and *Q. chapmanii* combined and a separate repeated measures ANOVA for *Q. geminata*.

Results

Numbers of leafminers and leaftiers per 200 leaves in elevated CO_2 decreased significantly from numbers in ambient CO_2 for all oak species, except for leafminers and leaftiers on *Q. chapmanii*, but these also exhibited the same pattern of decrease (Figs 1 and 2, Table 1). There were significant effects of time on all herbivore species but no significant treatment × time interactions for any herbivore species on any of the oak species (analyses not shown in Table 1). Foliar nitrogen also decreased significantly in elevated CO_2 (Table 2, Fig. 3), consistently over time for *Q. geminata*, whereas initial
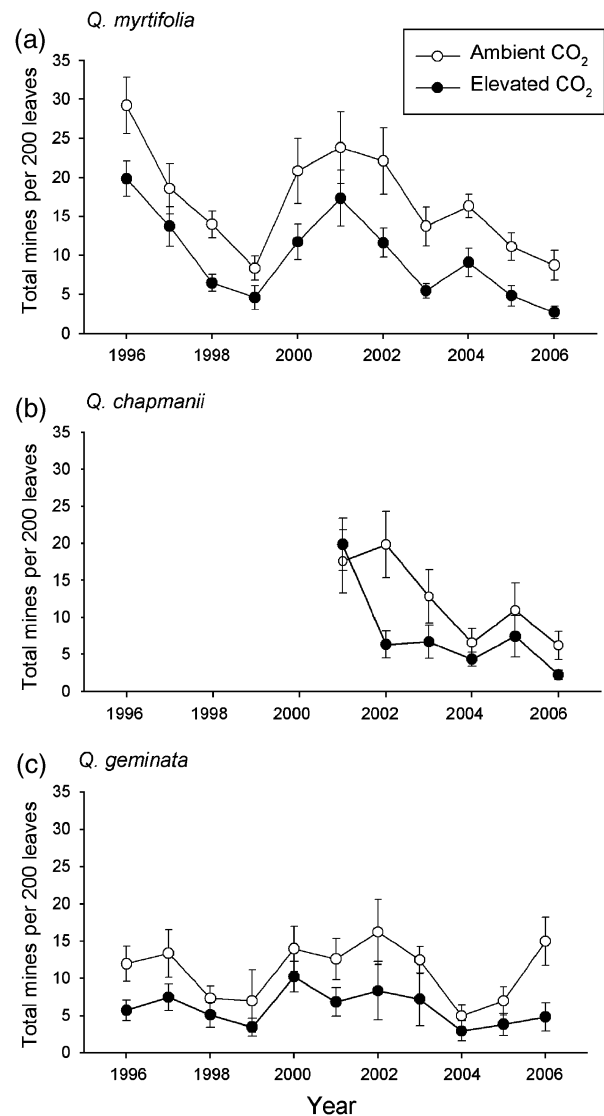

Fig. 1 Density of leaf mines per 200 leaves ± SE, under ambient and elevated CO_2 at Kennedy Space Center, Florida for (a) *Quercus myrtifolia*, (b) *Quercus chapmanii* and (c) *Quercus geminata*.

responses of *Q. chapmanii* and *Q. myrtifolia* varied from year to year (significant or marginally significant CO_2 × time interactions for these two species, Table 2). Averaged across years, elevated CO_2 reduced foliar %N by 7.4% for *Q. chapmanii*, by 9.6% for *Q. geminata* and by 7.5% for *Q. myrtifolia*.

The number of *Q. myrtifolia* and *Q. chapmanii* leaves dropped in litter increased significantly through time ($r = 0.705$, $P = 0.034$), indicating both these species grew more in elevated CO_2 and produced more leaf litter. In contrast, there was a significant decrease in leaf litter of *Q. geminata* leaves over time in elevated CO_2 ($r = -0.754$, $P = 0.019$). This indicates *Q. geminata* grows less well in elevated CO_2 or is outcompeted by the more actively
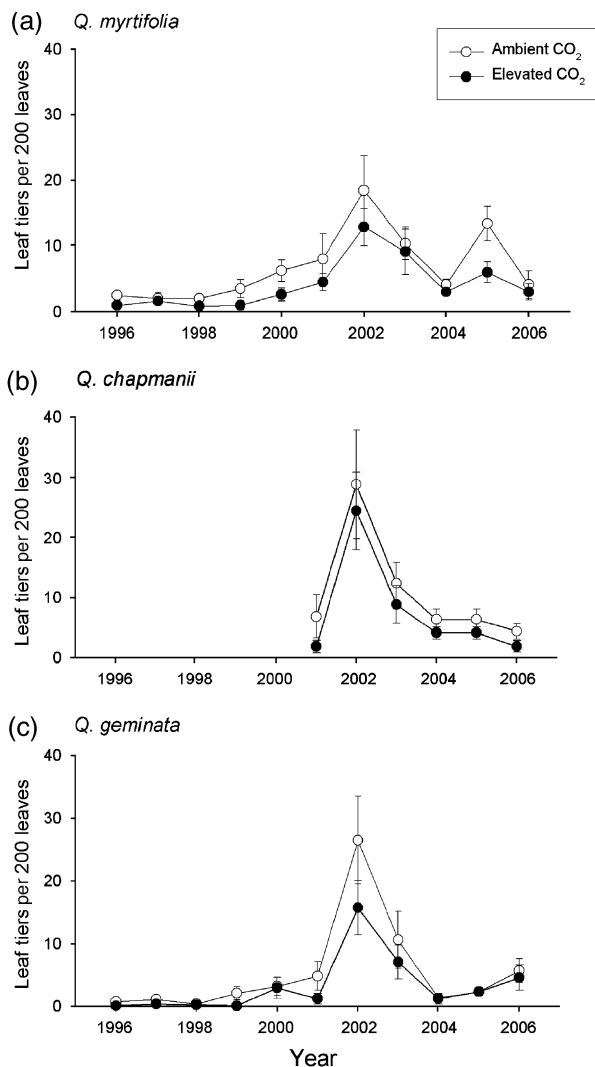
Fig. 2 Density of leaftiers per 200 leaves ± SE, under ambient and elevated CO_2 at Kennedy Space Center, Florida for (a) *Quercus myrtifolia*, (b) *Quercus chapmanii* and (c) *Quercus geminata*.

Table 1 Summary statistics for the effects of elevated CO_2 ($df_{1,14}$) and time ($df_{10,140}$ or $df_{5,70}$) on leafminer and leaftier densities at Kennedy space Center, 1996–2007

Taxa	Host species	CO_2		Time	
		F	P	F	P
Leafminers					
	Q. myrtifolia	29.563	<0.001	11.739	<0.001
	Q. chapmanii	4.316	0.057	7.573	<0.001
	Q. geminata	9.961	0.007	2.856	0.003
Leaftiers					
	Q. myrtifolia	4.841	0.045	10.423	<0.001
	Q. chapmanii	1.511	0.239	12.356	<0.001
	Q. geminata	3.524	0.081	14.469	<0.001

Table 2 Summary statistics for the effects of elevated CO_2 ($df_{1,14}$) and year (time $df_{11,154}$ for *Quercus myrtifolia* and $_{9126}$ for *Quercus chapmanii* and *Quercus geminata*) on nitrogen concentration of green leaves

Plant species	CO_2		Time		$CO_2 \times$ time	
	F	P	F	P	F	P
Q. myrtifolia	22.831	<0.001	15.605	<0.001	1.627	0.096
Q. chapmanii	11.611	0.004	32.279	<0.001	2.642	0.008
Q. geminata	21.817	<0.001	11.708	<0.001	0.618	0.780

growing *Q. myrtifolia* and *Q. chapmanii*. Seiler *et al.* (2008) showed how the relative biomass of *Q. myrtifolia* is stimulated by elevated CO_2 by 120% at the end of the experiment, whereas the biomass of *Q. geminata* was not increased. They also showed that the degree of stimulation was affected by annual rainfall.

There was no significant effect of CO_2 treatment on leafminer density per $0.1143 \, m^2$ of litter for both *Q. myrtifolia* and *Q. chapmanii*, or for *Q. geminata* (Fig. 4a and b, Table 3). However, there was a significant $CO_2 \times$ time effect for *Q. myrtifolia* and *Q. chapmanii*. Initially, leafminer density per $0.1143 \, m^2$ of litter was lower in elevated CO_2 but by the 2001–2002 growing season this pattern reversed and remained reversed until the end of the experiment. There was no effect of CO_2 on leafminer density per $0.1143 \, m^2$ of leaf litter for *Q. geminata* nor an interaction between CO_2 and time. There were no significant effects of CO_2 level on the densities of leaftiers per $0.1143 \, m^2$ of leaf litter for *Q. myrtifolia* or *Q. chapmanii*, though there was a clear trend of higher numbers in elevated CO_2 in all years except 2001–2002 (Fig. 5a and b, Table 3). No significant effects of CO_2 were apparent for leaftiers in *Q. geminata* litter (Fig. 5c).

Discussion

Elevated CO_2 reduced the densities of leafminers per 200 leaves on all species of scrub oaks at Kennedy Space Center for all 11 years of the study. These reductions were maintained regardless of temporal variations in miner densities which may have been caused by changes in abiotic conditions such as rainfall (Seiler *et al.*, 2009). Many other studies have found similar reductions in insect herbivory under elevated CO_2 (reviewed in Lincoln *et al.*, 1993; Watt *et al.*, 1995; Bezemer & Jones, 1998; Hunter, 2001; Whitaker, 2001). More recently, Stiling & Cornelissen (2007) provided a meta-analysis of the effects of elevated CO_2 on plant growth, primary and secondary metabolites and herbivore abundance, survival and reproduction. Their review showed insect abundance in elevated CO_2 was
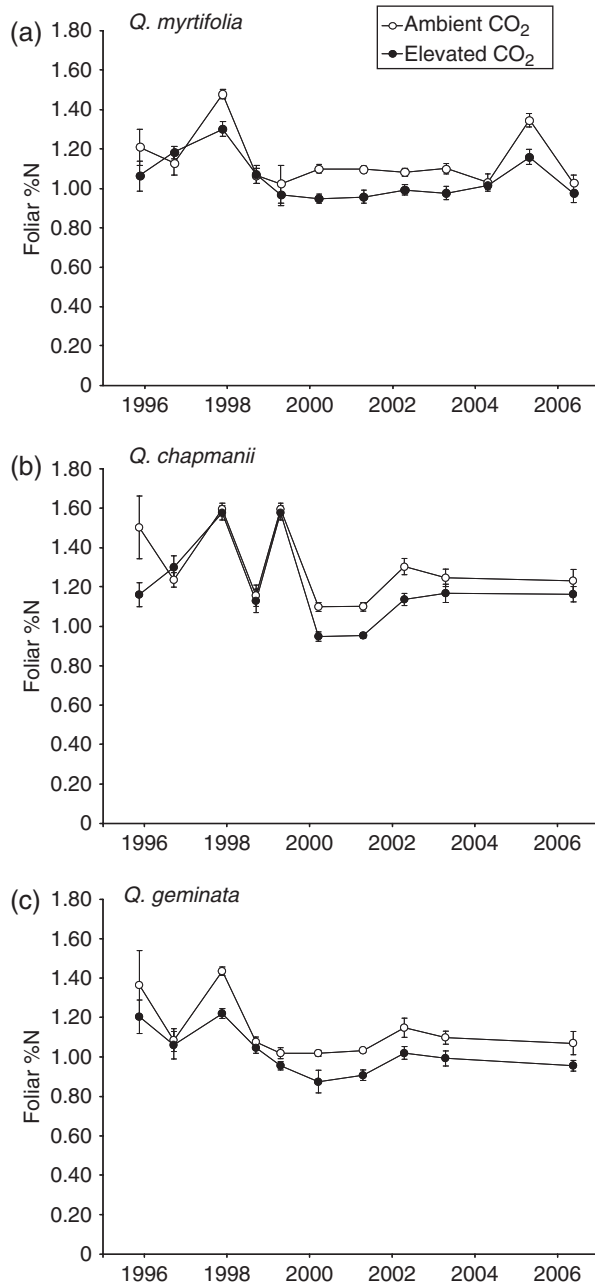
Fig. 3 Foliar nitrogen concentration (%N) $\pm$ SE, over time for each of the three oak species (a) *Quercus myrtifolia*, (b) *Quercus chapmanii* and (c) *Quercus geminata*.

Fig. 4 Density of leaf mines per $0.1143\,m^2 \pm$ SE, of litterfall under ambient and elevated CO_2 at Kennedy Space Center, Florida for (a) *Quercus myrtifolia* and *Quercus chapmanii* and (b) *Quercus geminata*.

reduced by over 20% compared with abundance in ambient CO_2. At least three mechanisms are responsible for this decline. First, because plants grow more in elevated CO_2, but soil nitrogen concentrations remain unchanged, there is a reduction in tissue nitrogen concentration which results in lowered plant nitrogen and decreased nutritive value to herbivores (McGuire *et al.*, 1995). The reduction in tissue nitrogen concentration causes reduced insect herbivore survival and reproduc-
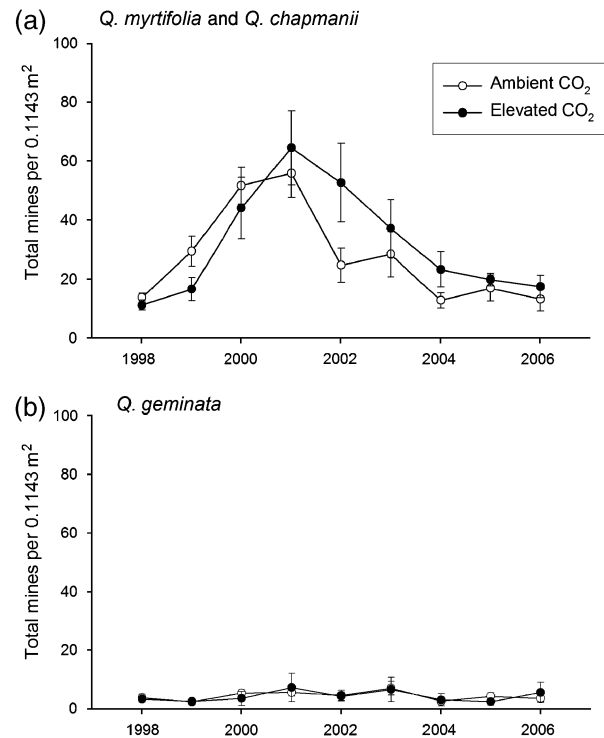
tion. Bezemer & Jones (1998) reviewed evidence from 38 studies and showed foliar nitrogen concentrations decreased by about 15% under elevated CO_2. Stiling & Cornelissen's (2007) review showed a 16.4% decrease in foliar nitrogen concentration. Our data showed a 7.4–9.6% annual reduction in %N for our three oak species in elevated CO_2. Second, elevated CO_2 can cause increases in allocations to C-based secondary metabolites such as condensed and hydrolysable tannins (Peñuelas & Estiarte, 1998). Stiling & Cornelissen (2007) showed significant increases in all secondary compounds under elevated CO_2 in the literature they reviewed, except for terpenes and other C-based compounds. In their review, tannin concentrations increased by almost 30% under elevated CO_2. Earlier studies in our system showed a nonsignificant increase in total phenolics, condensed and hydrolysable tannins (Rossi *et al.*, 2004; Hall *et al.*, 2005). Third, elevated CO_2 can change attack rates of herbivores by natural enemies. Reduced leaf quality under elevated CO_2 often delays insect development (Stiling & Cornelissen, 2007) and in our system this exposes herbivores longer to natural enemies, increasing herbivore death rates (Stiling *et al.*, 1999). Changes in leaf chemistry and natural enemy performance under elevated CO_2 have also been noted in other systems (Holton *et al.*, 2003).

Table 3 Summary statistics for the effects of elevated CO_2 ($df_{1,14}$) and time ($df_{9,126}$) on leafminer and leaftier densities per 0.1143 m^2 of leaflitter at Kennedy space Center, 1998–2007

Taxa	Host species	CO_2		Time		$CO_2 \times$ time	
		F	P	F	P	F	P
Leafminers							
	Q. myrtifolia and *Q. chapmanii*	0.113	0.741	15.120	<0.001	2.447	0.013
	Q. geminata	0.824	0.379	5.790	<0.001	0.683	0.763
Leaftiers							
	Q. myrtifolia and *Q. chapmanii*	1.942	0.185	15.286	<0.001	0.132	0.985
	Q. geminata	0.088	0.771	9.806	<0.001	1.602	0.717
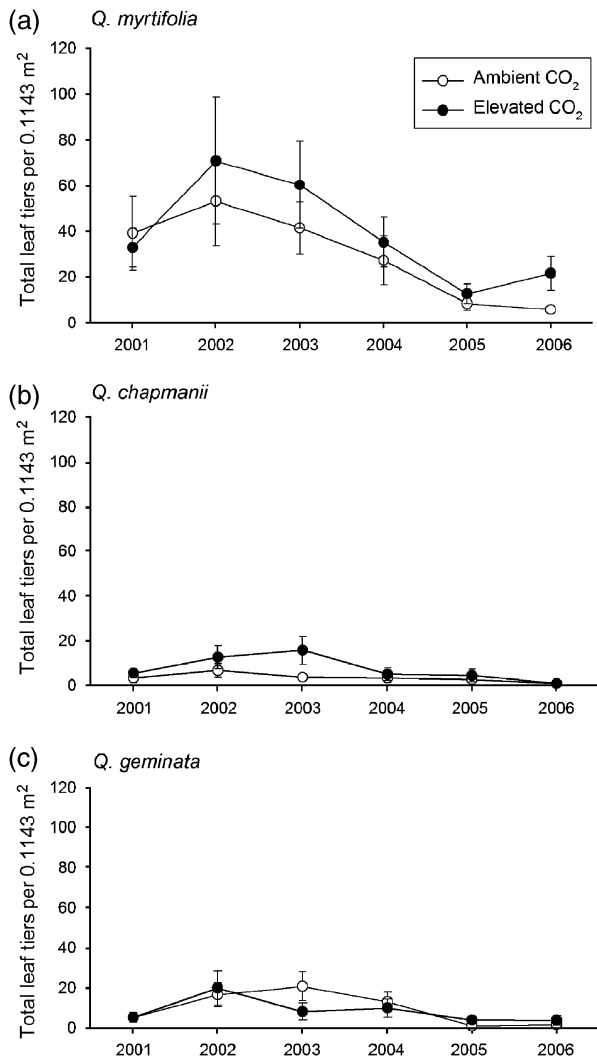
Fig. 5 Density of leaftiers per 0.1143 m^2 ± SE, of litterfall under ambient and elevated CO_2 at Kennedy Space Center, Florida for (a) *Quercus myrtifolia*, (b) *Quercus chapmanii* and (c) *Quercus geminata*.

Our results are similar to other studies on oaks which have all shown elevated CO_2 reduces insect performance (*Quercus petraea*, Hättenschwiler & Schafellner, 2004; *Quercus alba*, Williams *et al.*, 1998 and Knepp *et al.*, 2007; *Quercus velutina*, Knepp *et al.*, 2007). However, other authors have shown that herbivore responses to plants grown in elevated CO_2 vary according to host species or conditions. For example, some legume-feeding herbivores are buffered against CO_2-induced reductions in plant quality because of the plants ability to fix nitrogen (Karowe, 2007). Other authors have shown reductions in herbivore performance on C_3 plants in elevated CO_2 but not on C_4 plants (Sudderth *et al.*, 2005). Some herbivore responses to elevated CO_2 depend on nutrient availability to host plants (Williams *et al.*, 1997; Hättenschwiler & Schafellner, 1999). For example, Goverde *et al.* (2004) demonstrated that the response of a lycaenid caterpillar to elevated CO_2 depended on phosphorous availability. Similarly, performance of the generalist herbivore *Spodoptera littoralis* in elevated CO_2 depended on nitrogen availability and species of host plant. Even with added nitrogen, herbivore growth rates under elevated CO_2 remained low if plants were able to produce nitrogen containing secondary compounds (Schädler *et al.*, 2007).

Elevated CO_2 also increased the total aboveground biomass of our scrub oaks throughout the 11 years of the study, even after canopy closure in 2001 (Seiler *et al.*, 2009). At the end of the study, in June 2007, total aboveground biomass had increased by 67% (Seiler *et al.*, 2009). However, biomass response to elevated CO_2 was species specific. The dominant oak, *Q. myrtifolia*, showed large growth responses to elevated CO_2 as did *Q. chapmanii*. *Q. geminata* showed no significant growth response in elevated CO_2. These trends paralleled photosynthetic responses whereby *Q. myrtifolia* and *Q. chapmanii* showed no acclimation to CO_2 over the course of the study whereas *Q. geminata* did (Seiler *et al.*, 2009). Mean rate of net photosynthesis in *Q. myrtifolia* was increased by 63% in elevated CO_2, nearly twice the 35% stimulation in *Q. geminata* (Ainsworth *et al.*, 2002; Li *et al.*, 2007).

Initially, leafminer densities per 0.1143 m^2 of leaf litter on *Q. myrtifolia* and *Q. chapmanii* declined in elevated

CO$_2$. There were no obvious trends in leafminer density over the same period for *Q. geminata*. When we first reported the effects of elevated CO$_2$ on leafminer density per unit area of leaf litter, for the years 2000–2001, our data showed a significant decrease of leafminers for all oaks (Stiling *et al.*, 2003). The next year, 2001–2002, total leafminer density per unit area of leaf litter under elevated CO$_2$ was greater under elevated CO$_2$ compared with ambient CO$_2$. This difference increased in subsequent years. The increase in leafminers per unit area of leaf litter in elevated CO$_2$ only occurred for *Q. myrtifolia* and *Q. chapmanii*, the two oaks which showed a growth increase under elevated CO$_2$. At the same time, leaftier densities per 0.1143 m^2 for these two oak species were also greater under elevated CO$_2$. Because we only started collecting leaftier data in 2001–2002, the switch to an increased density under elevated CO$_2$ appears relatively quickly. There were no differences in leaftier densities per 0.1143 m^2 for *Q. geminata*.

In conclusion, numbers of both leafminers and leaftiers per 200 leaves on all three species of oaks was reduced every year for 11 years in elevated CO$_2$. However, after canopy closure, leafminer and leaftier densities per 0.1143 m^2 of leaf litter were increased because of increases in leaf production. Such increases were species specific and only occurred on oak species whose growth was increased in elevated CO$_2$. Several other long-term studies have also reported sustained plant biomass stimulation under long-term exposure to elevated CO$_2$ (Rasse *et al.*, 2005; Wittig *et al.*, 2005; Kimball *et al.*, 2007) which suggests increased herbivore and natural enemy densities might occur in other systems, though such data have not been collected. Thus, in a future world of increased CO$_2$ some insect herbivores may increase in density. The degree of increase is likely to be species specific. Where host plant biomass increases and herbivore densities per unit biomass are not changed, as for herbivores on nitrogen-fixing plants, this increase is likely to be greatest. Where host biomass is increased but insect densities per unit biomass are decreased, the increases may be smaller, as for *Q. myrtifolia*. Where host biomass is not increased under elevated CO$_2$ and insect densities per unit biomass are decreased, insect densities may be unchanged or decreased, as for *Q. geminata*. Thus, in a globally changed world, insect herbivore communities, and perhaps those of their natural enemies, are likely to change.

Acknowledgements

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