Elevated atmospheric CO$_2$ lowers herbivore abundance, but increases leaf abscission rates

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Abstract

Increased levels of atmospheric carbon dioxide (CO$_2$) are likely to affect the trophic relationships that exist between plants, their herbivores and the herbivores' natural enemies. This study takes advantage of an open-top CO$_2$ fertilization experiment in a Florida scrub oak community at Kennedy Space Center, Florida, consisting of eight chambers supplied with ambient CO$_2$ (360 ppm) and eight chambers supplied with elevated CO$_2$ (710 ppm). We examined the effects of elevated CO$_2$ on herbivore densities and levels of leaf consumption, rates of herbivore attack by natural enemies and effects on leaf abscission. Cumulative levels of herbivores and herbivore damage were significantly lower in elevated CO$_2$ than in ambient CO$_2$. This may be because leaf nitrogen levels are lower in elevated CO$_2$. More herbivores die of host plant-induced death in elevated CO$_2$ than in ambient CO$_2$. Attack rates of herbivores by parasitoids are also higher in elevated CO$_2$, possibly because herbivores need to feed for a longer time in order to accrue sufficient nitrogen (N), thus exposing themselves longer to natural enemies. Insect herbivores cause an increase in abscission rates of leaves throughout the year. Because of the lower insect density in elevated CO$_2$, we thought, abscission rates would be lower in these chambers. However, abscission rates were significantly higher in elevated CO$_2$. Thus, the direct effects of elevated CO$_2$ on abscission are greater than the indirect effects on abscission mediated via lower insect densities. A consequence of increased leaf abscission in elevated CO$_2$ is that nutrient deposition rates to the soil surface are accelerated.

Keywords: elevated CO$_2$, insect herbivory, Kennedy Space Center, leaf abscission, *Quercus myrtifolia*

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Introduction

Atmospheric carbon dioxide (CO$_2$) concentrations have risen by about 20% since the industrial revolution and are expected to double by the end of the next century (280 ppm preindustrial vs. 560 ppm, Houghton *et al.*, 1995). Much of the work on the effects of elevated CO$_2$ on natural communities has focused on direct effects on plants (e.g. Potvin & Vasseur, 1997). For example, it is known that elevated CO$_2$ increases photosynthetic rates

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(Drake *et al.*, 1997; Norby *et al.*, 1999) and biomass (Curtis & Wang, 1998; Leadley *et al.*, 1999; Owensby *et al.*, 1999). As plants grow, soil nitrogen (N) must be distributed throughout more plant tissue. This results in lower N levels, thereby increasing C–N ratios (Ceulemans & Mousseau, 1994; Wilsey, 1996; Hughes & Bazzaz, 1997). Changes in C–N ratios can, in turn, affect the production of secondary metabolites (Bryant *et al.*, 1983) promoting the manufacture of carbon (C)-based secondary metabolites (e.g. phenolics) over N-based ones. Increased secondary metabolite production in elevated CO$_2$ can influence herbivore performance and change rates of herbivory (Lindroth *et al.*, 1993, 1995, 2001; Agrell *et al.*, 2000, but

see Fajer *et al.*, 1991; Williams *et al.*, 1997; Hartley *et al.*, 2000). Because changes in CO_2 concentration can have these profound effects on plants, there is a high likelihood that elevated CO_2 could, in turn, drastically affect the herbivores.

Most of the work concerning elevated CO_2 on plant herbivory has been done using insects in controlled greenhouse conditions where plants usually receive plentiful nutrient supplies, where herbivores can not choose where to feed and where natural enemies of herbivores are absent (Lincoln *et al.*, 1993; Arnone *et al.*, 1995; Bezemer & Jones, 1998). Very little information is available on the effects of enhanced CO_2 on plants and rates of herbivory in natural systems, even though such research is critical to prepare us for the changes that may lay ahead (Coviella & Trumble, 1999). What is needed are long-term field studies where both plant and insect are reared in elevated CO_2 spanning multiple generations of insects (Brooks & Whittaker, 1998). The advantage of the present study is that it uses a field-based CO_2 enrichment experiment in order to examine the effects of elevated CO_2 on plant–insect herbivores. Here, we investigate the effects of elevated CO_2 on (i) leaf-miner densities and death rates caused by host plants and natural enemies, (ii) damage to leaves caused by leaf miners and leaf chewers and (iii) insect-mediated leaf abscission.

Field sites and study species

In the south-east U.S., an important forest type is scrub forest, which consists primarily of evergreen, or nearly evergreen, oaks such as *Quercus geminata*, *Quercus myrtifolia*, *Quercus inopina* and *Quercus chapmanii* and, sometimes, Florida rosemary, *Ceratiola ericoides*. An important feature of scrub forest is its low stature. Being fire-maintained, the forest rarely grows above 3–5 m in height, so it is relatively easy to install chambers over the mature canopy in order to elevate CO_2. This would be very difficult to do for other types of mature forests, which grow to much greater heights.

At Kennedy Space Center, we installed 16 open-top chambers (3.6 m diameter and 3 m high) over forest that was burned in January 1996 (Li *et al.*, 2000). The chambers were installed in May 1996 and since then eight chambers have been continuously exposed to elevated CO_2 (710 μL/L) and eight have been exposed to ambient CO_2 (350–360 μL/L) (Li *et al.*, 2000). Our field work focused on herbivory by leaf-mining insects and leaf chewers which feed on the two dominant oaks—*Q. myrtifolia* and *Q. geminata*. These two oak species together account for 95% of the preburn above-ground plant biomass inside the chambers. Leaf miners (Lepidoptera: Gracillaridae) are by far the most common herbivorous insects at our study sites and we recognize six common

genera: *Stigmella*, *Cameraria*, *Buccalatrix*, *Stilbosis*, *Tischeria* and *Acerocercops*. Because the chambers are open-topped, the insect herbivores and their natural enemies—mainly parasitoids—can gain access to vegetation in all cages.

Methods

In May 1998, 2–3 weeks after bud burst, we marked 500 leaves of the most common plant in the community, myrtle oak, *Q. myrtifolia* inside each individual elevated CO_2 and ambient CO_2 chamber for a total of 8000 leaves. Each leaf was numbered individually with a black indelible Sharpie[t] pen. In each chamber, 100 leaves on each of five separate trees were marked for the total of 500. On each tree, 5–l0 consecutive twigs had all the leaves marked, from the first leaves next to the apical meristem to the last leaves closest to the main stem to which the twig connected. Therefore, each twig had 10–20 leaves, all of which were marked. At the time of marking, each leaf was scored as to whether it was damaged by an insect herbivore. Herbivores were assigned to two main groups: (i) herbivores which chewed the leaves—such as limacodid moth larvae (slug moths), hesperid leaf tiers and grasshoppers—and (ii) leaf miners—either *Stigmella*, *Cameraria*, *Tischeria*, *Stilbosis* or *Buccalatrix*.

Subsequent censuses were made monthly for the next two years until June 2000, when every marked leaf had abscised. At each monthly census, all leaves were inspected in order to determine (i) whether they were still attached to the tree, (ii) whether they had new chewing damage or (iii) whether they had new leaf miner damage. A one-way repeated measures of ANOVA (analysis of variance) with CO_2 as the treatment, chamber as the replicate and month as the time interval were used in order to test for differences between the cumulative abscission rates of mined vs. nondamaged leaves, chewed vs. nondamaged leaves and leaves in elevated CO_2 vs. ambient CO_2. In these analyses, only the data from June 1998 to January 1999 were used because after January 1999 most leaves had abscised and nonabscised leaves were too few in number to be statistically relevant. In order to test for differences in leaf miner damage and chewing damage between elevated CO_2 and ambient CO_2, the total percentage of mined and chewed leaves was summed over the 2 years for each chamber. A *t*-test was then performed with CO_2 level as the treatment and chamber as the replicate.

In addition, 10 randomly selected mined and nonmined leaves were removed from each chamber in June 1998. The nonmined leaves were dried at 65 °C, milled to a fine powder and used in order to determine C and N levels using duplicate samples on an elemental analyser (CE instruments). Student's *t*-tests were used for statistical determination of CO_2 effects on elemental composition.

The mined leaves contained *Stigmella* miners and the areas of the mines were traced and measured using a CID-201 leaf area meter (CID, Inc., Vancouver, Washington, USA). The average area of these 10 mines was used as a chamber mean in a *t*-test with CO_2 level as the treatment and chamber as the replicate. For mine area comparisons, one elevated CO_2 chamber and one ambient CO_2 chamber were omitted owing to low levels of miners.

Fates of leaf miners were examined on a subset of 5–15 mined leaves taken from each chamber in each of August, September and October 1998. Fates of each censused miner were assigned to various mortalities based on the condition of the mine as observed under a microscope at $6\times$ magnification. Successfully developed miners leave a crescent-shaped exit hole at the end of the mine where the larvae cut their way out of the leaf in order to drop to the ground to pupate. Parasitized mines exhibit a series of small holes in the upper mine surface from which parasitoid wasps emerge, or parasitoid larvae or pupae can be found within the mine. Mines attacked by predators such as ants are ripped open. The bodies of miners that died within the mine as a result of plant nutritional inadequacy could be found embedded within the mine. Leaf-miner mortality differences between the ambient and elevated CO_2 treatments in each mortality category were compared using a chi-squared test on total miner numbers ($n = 221$ for elevated CO_2 and $n = 229$ for ambient CO_2).

We also compared litter fall between ambient and elevated CO_2 by using three litter fall traps per chamber. These aluminium trays, measuring 5.25 cm wide $\times$ 76 cm long $\times$ 4 cm high were installed at ground level in three areas of each chamber, south-east, south-west and due south. Every other month from May 1998 to May 2000, these trays were emptied and the numbers of mined, chewed and nondamaged myrtle oak leaves were counted and weighed. Differences in rate of leaf fall were compared by converting the data to leaf fall per m^2 and using a one-way repeated measures ANOVA with CO_2 level as the treatment and every other month as the time interval. In March, May and July 1999, five nondamaged leaves from the trays were removed and analyzed for C and N. The average percent of C and N from these three time periods was used in a *t*-test with CO_2 level as the treatment.

Results

By far the greatest level of herbivore damage to the May 1998 cohort of leaves occurred in May 1998, immediately following bud burst (Fig. 1). At this time, when the leaves appeared relatively soft, 3.8% of the leaves were mined and 6.3% were damaged by external feeders, mainly lepidopteran larvae such as hesperid leaf tiers

and grasshoppers. New miners and new chewing damage appeared nearly every month until February 1999, illustrating the multivoltine nature of both leaf miners and leaf chewers. In total, over the 2-year duration of the experiment, 7.3% of the leaves were mined and 15.9% were chewed in May 2000. Added together, this means that nearly a quarter of the myrtle oak leaves, 23.2% were either chewed or mined. Over the 2 years of the study, damage by both chewers and leaf miners was significantly lower in elevated CO_2 than in ambient CO_2 (Fig. 2) ($t_{l4} = 2.591$, $P = 0.021$ for chewers; $t_{l4} = 2.473$, $P = 0.027$ for miners). Together, the level of damage to leaves in elevated CO_2 was only 19% (6% mining + 13% chewing), compared to 30.8% (10.6% mining + 20.2% chewing) for ambient CO_2.

There are several reasons why insect herbivores may be more abundant on foliage in ambient CO_2 chambers than on foliage in elevated CO_2 chambers. First, foliage quality is lower in elevated CO_2. The N percent in elevated CO_2 was only 1.07 compared to 1.21 in ambient CO_2 ($t_{14} = 2.591$, $P = 0.011$). Nitrogen content is often limiting for herbivores (Scriber & Slansky, 1981). Area of mine for *Stigmella*, the most common leaf miner in the community, was significantly greater in elevated CO_2 ($\bar{x} = 0.47$, s.d. $= 0.064$) than in ambient CO_2 ($\bar{x} = 0.347$, s.d. $= 0.08$)($t_{12} = 3.179$, $P = 0.008$). This suggests that foliage quality is reduced in elevated CO_2 and miners must compensate by eating more leaf material. Second, altered C–N ratios may affect the ability of the plant to synthesize defensive compounds (Lincoln & Couvet, 1989; Lindroth et al., 1993; Roth & Lindroth, 1995; Roth et al., 1998). The primary defensive compounds in oaks are tannins and these carbon-rich compounds may increase in the carbon-rich environment of the elevated CO_2 chambers. However, we have preliminary data (Rossi unpublished) that while tannin levels are lower in elevated CO_2 they are not significantly different from tannin levels in ambient CO_2, as is often noted by others (e.g. Bezemer & Jones, 1998; Hartley et al., 2000). For leaf miners, death in the mine was almost 50% greater in elevated CO_2 (Fig. 3) further supporting the idea that foliage quality is impaired in elevated CO_2. Thirdly, attack rates of herbivores by natural enemies may be different between ambient and elevated CO_2 treatments. Death by parasitoids was increased by over 80% in elevated CO_2, compared to ambient CO_2, from 3.9 to 7.2%. This may be because increased mine area attracts more searching parasites. In summary, there was a marginally significant change in leaf miner survivorship between ambient and elevated CO_2 ($x_1^2 = 3.763$, $P = 0.052$).

The presence of leaf miners or chewers increased abscission rates. This is illustrated by following the cohort of leaves that were mined or chewed in May 1998 and comparing them against the cohort of leaves that were
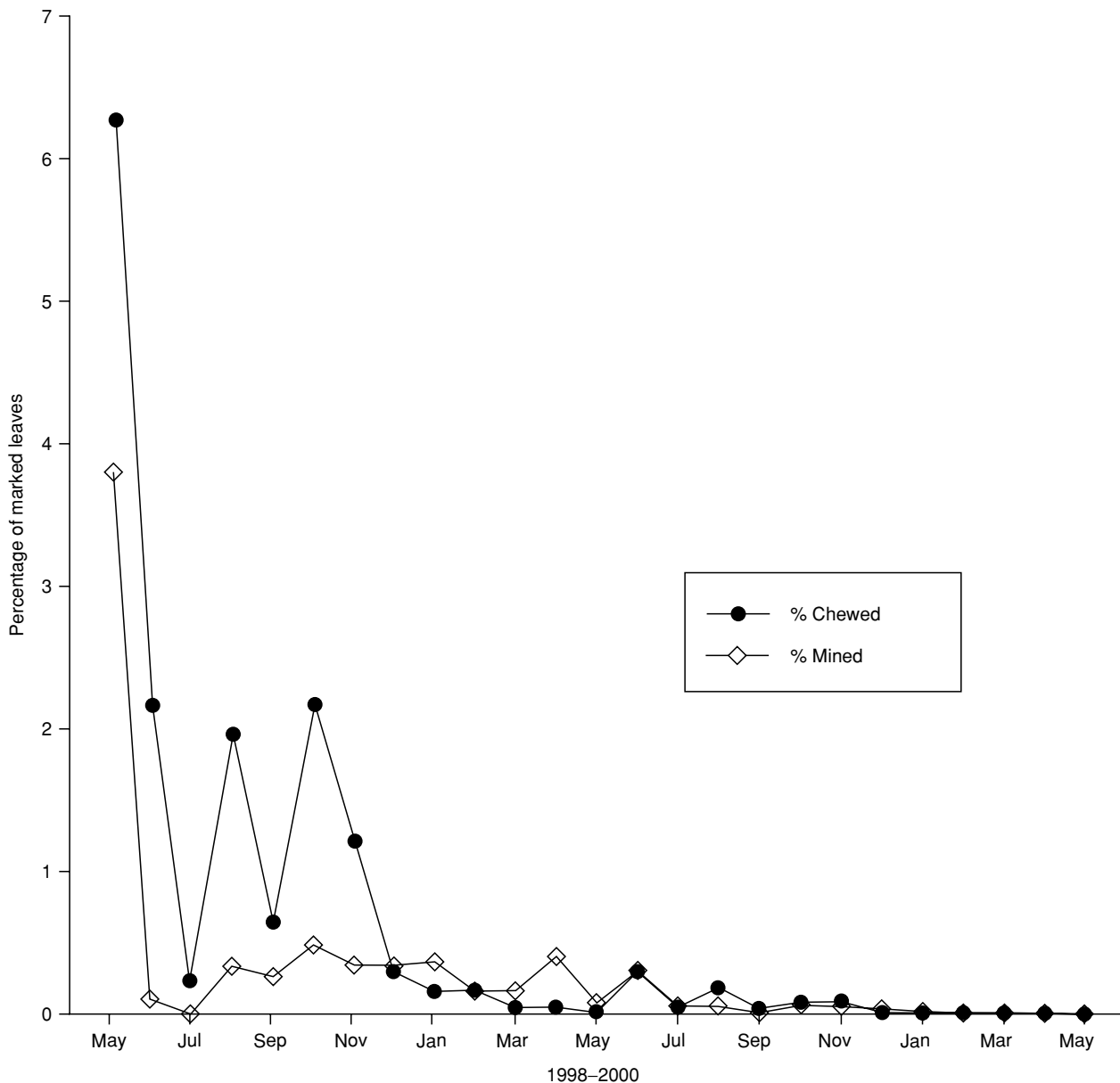
Fig. 1 Percentage of *Quercus myrtifolia* leaves, marked in May 1998, soon after bud burst that suffered new damage or leaf miners in each subsequent month. At the end of June 2000 all leaves had abscised.

never damaged (Fig. 4). While we could have made similar comparisons using leaves that were mined or chewed in any other month and performed similar calculations, we used the May 1998 cohort because this was when most miners and chewers fed and it produced the largest cohort for analysis. There was a significant increase in the abscission rate of mined leaves over nondamaged leaves ($F_{1,30} = 30.454$, $P < 0.001$), and a marginally significant increase in the abscission rate of chewed leaves over nondamaged ones ($F_{1,30} = 3.067$, $P = 0.09$) (Fig. 4). Most likely this is a wound response on the part of the tree

which sheds damaged leaves in order to avoid secondary infection by pathogens (Stiling & Simberloff, 1989). Because miners and chewers increase leaf abscission and because there are fewer mined and chewed leaves in elevated CO_2 chambers, we thought, abscission rates of leaves would be reduced in elevated CO_2 compared to abscission rates of leaves in ambient CO_2. However, the exact opposite was true (Fig. 5). Leaf abscission was significantly earlier in elevated CO_2 than in ambient CO_2 ($F_{1,14} = 4.66$, $P = 0.049$). This means that there is a direct effect of elevated CO_2 which increases leaf abscission.
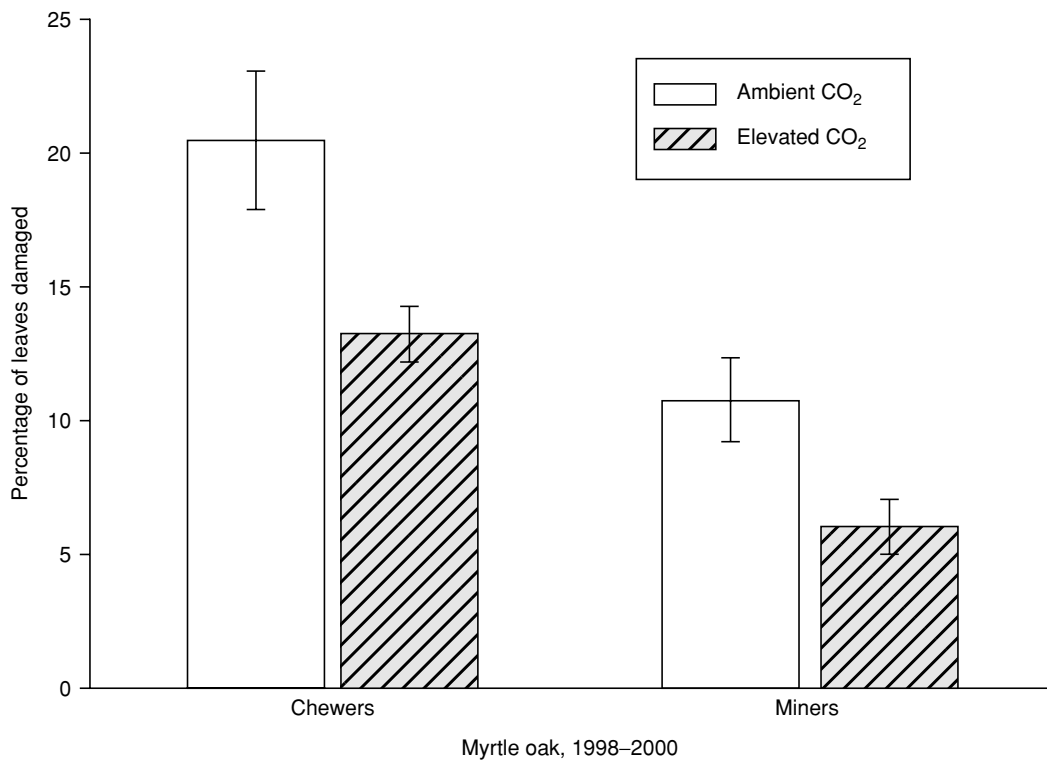
Fig. 2 Cumulative damage to myrtle oak leaves by chewers and miners in elevated and ambient CO_2. Means and standard errors shown.
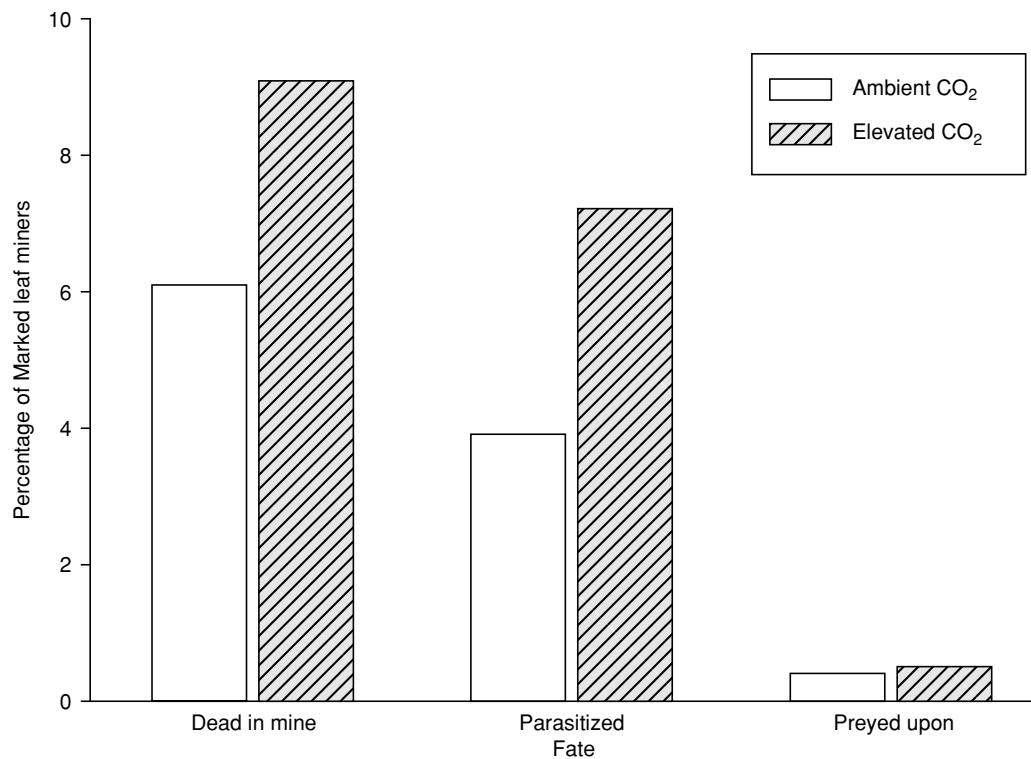

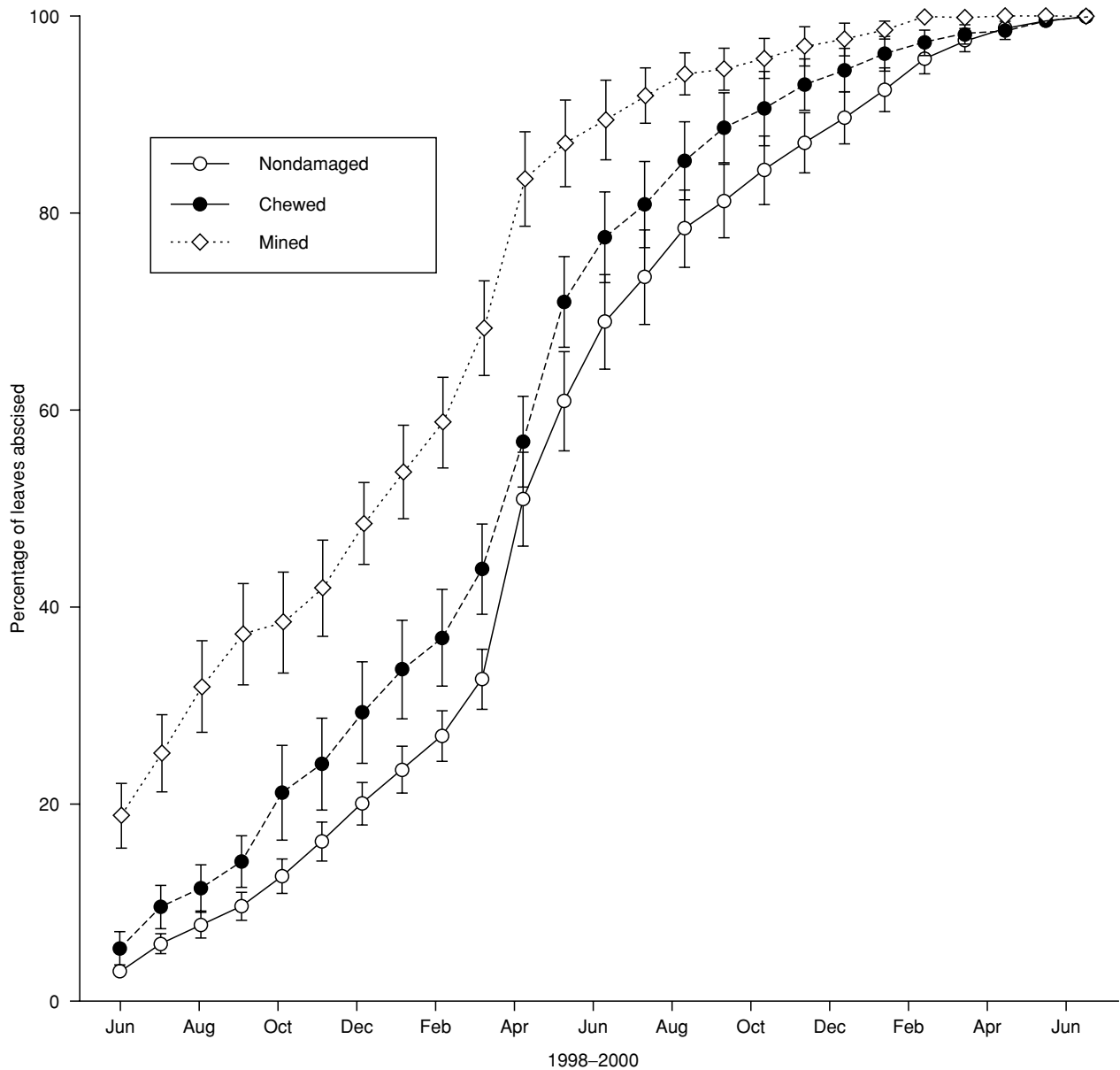**Fig. 3** Fates of leaf miners on *Quercus myrtifolia* during the summer of 1998.

Fig. 4 Rates of abscission of mined, chewed (damaged) and nondamaged myrtle oak leaves, following bud burst in May 1998. Data from ambient and elevated CO$_2$ combined. Means and standard errors shown.

This is in contrast to the indirect effect of elevated CO$_2$ on leaf abscission via insect herbivores, which tends to decrease abscission rates.

In the litter trays, total litter fall was greater in elevated CO$_2$ than in ambient CO$_2$, though the difference in litter fall between ambient and elevated CO$_2$ was only marginally significant (Fig. 6) ($F_{1,16}$ = 3.397, P = 0.087). However, this difference could be lowered because of the confounding effects of chewed and mined leaves, which tend to fall faster and of which there are more in the ambient chambers. When we repeated the analysis using only nondamaged leaves, the difference in abscission between leaves in ambient and elevated CO$_2$ was close to significant ($F_{1,14}$ = 4.329, P = 0.056). There was no difference in abscission of damaged leaves in elevated CO$_2$ compared to damaged leaves in ambient CO$_2$ ($F_{1,14}$ = 0.012, P = 0.754).

There was no significant difference in carbon concentration between litter of ambient CO$_2$ and elevated CO$_2$ (mean = 49.9% ambient, 47.9% elevated, t_{14} = 0.935, P = 0.366). There was also no significant difference in N concentration between litter of ambient CO$_2$ and elevated
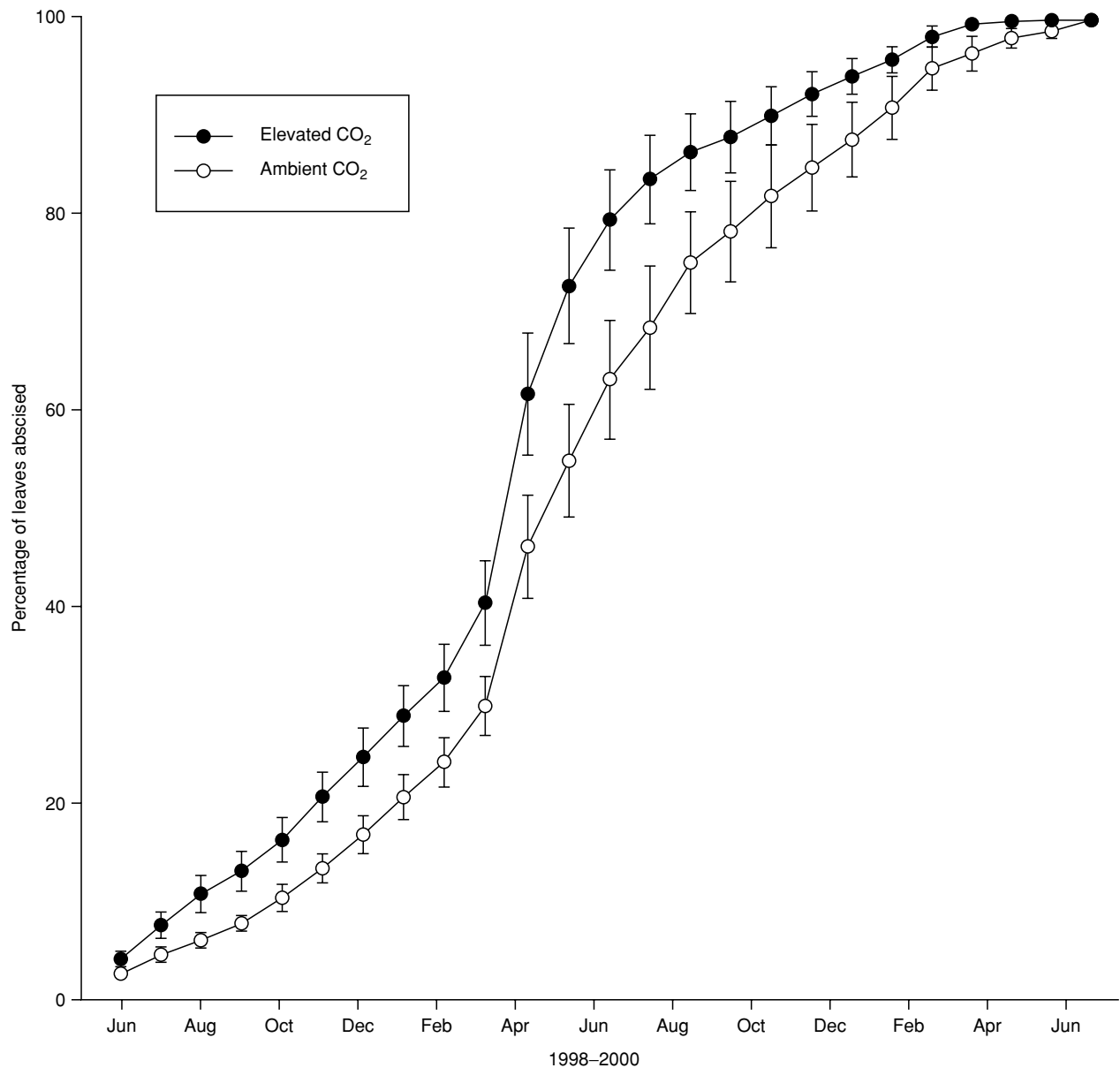
Fig. 5 Abscission rates of all leaves, mined, damaged and nondamaged combined, in ambient and elevated CO_2. Means and standard errors shown. Leaves first appeared and were marked in May 1998 and all had fallen in June 2000.

CO_2 (mean = 0.78% ambient, 0.71% elevated, t_{14} = 0.648, P = 0.536).

Discussion

In the present study, attack rates of leaves by insect herbivores were significantly lower in elevated CO_2. Lower herbivory in elevated CO_2 could be as a result of lower leaf N levels which affect feeding and, ultimately, insect survival. We know that per capita herbivory by *Stigmella* miners increased in elevated CO_2. This

suggests reduced foliage quality which necessitates increased feeding by individual leaf miners. Other cases of compensatory feeding by other insects on elevated CO_2 grown plants in laboratories abound (Fajer *et al.*, 1989; Lincoln *et al.*, 1993; Lindroth *et al.*, 1993, 1995; Salt *et al.*, 1995; Docherty *et al.*, 1996; Kinney *et al.*, 1997; Williams *et al.*, 1997). Brooks & Whittaker (1999) found a 20% reduction in survival of *Neophilaenus* nymphs, which are sap suckers of *Juncus* plants, when both were grown in elevated CO_2 (ambient + 250 ppm), and they attributed this decrease to lower N levels. Furthermore, if herbivores
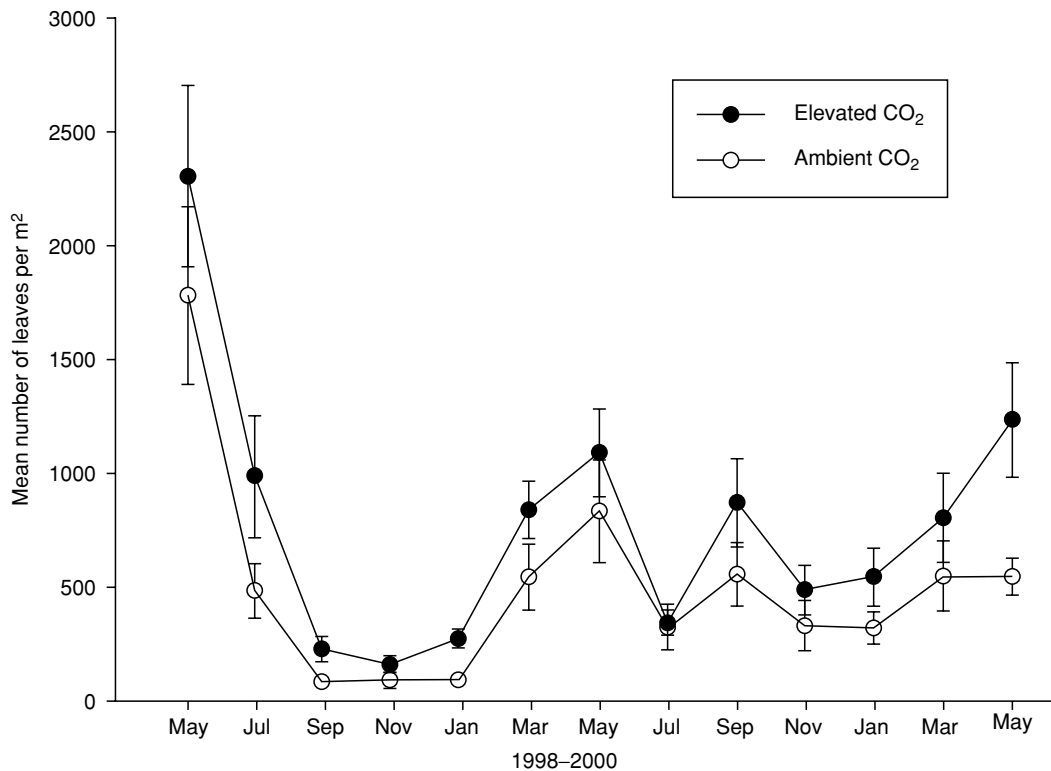
Fig. 6 Bulk litter fall of *Quercus myrtifolia* leaves into litter trays, in ambient and elevated CO$_2$, 1999–2000, with means and standard errors.

have to feed more on foliage in elevated CO$_2$ they may also have to feed for longer (Fajer *et al.*, 1989; Lindroth *et al.*, 1995; Smith & Jones, 1998), exposing themselves for a longer period of time to natural enemies. Our results show higher attack rates of leaf miners by parasitoids when the plants are grown in elevated CO$_2$. In our system, reduced foliage quality and increased rate of attack by parasitoids provide mechanisms which could cause lower densities of insect herbivores in the elevated CO$_2$ chambers.

In this system, insect herbivores accelerate leaf abscis-sion. Leaf mining significantly increases leaf abscission, and chewing marginally increases leaf abscission. This supports earlier studies, which showed that leaf miners increase leaf abscission (Faeth *et al.*, 1981; Stiling & Simberloff, 1989; Stiling *et al.*, 1991). However, overall, abscission rates were greatest in elevated CO$_2$. What is the mechanism by which elevated CO$_2$ increases leaf abscission? Miller *et al.* (1997) suggest that the photosyn-thetic pattern of tobacco plants grown in high CO$_2$ is shifted temporally to an earlier maximum and subse-quent decline. Thus, there appears to be an ontogenetic shift to an earlier onset of natural decline in photosyn-thetic rates associated with senescence. The results of most other studies on leaf ontogeny in elevated CO$_2$ are consistent with this idea and research has shown

elevated rates of senescence for leaves or whole plants grown in elevated CO$_2$ in winter wheat (Sicher & Bunce, 1997), montane grass (Baxter *et al.*, 1994) and ponderosa pine (Houpis *et al.*, 1988), and many herbaceous species (Paez *et al.*, 1983; St. Omer & Horvath, 1983; Curtis *et al.*, 1989). However, the limited results for hardwood trees have been variable more with some species showing increased or decreased senescence but with most species showing no change (Gunderson *et al.*, 1993; McConnaughay *et al.*, 1996).

Changes in herbivory and leaf abscission can both affect the amount of leaf area available for photosynthesis and we can calculate the percentage increase of nonda-maged leaf area that will be available for photosynthesis under elevated CO$_2$. We know that elevated CO$_2$ in-creases plant biomass and leaf area index (L.A.I.) in this system as it does in other systems. Data from May 1999 to June 2000, indicate that, on average, L.A.I. increases by 33% (Hymus *et al.* unpublished). So, for every 100 leaves in ambient CO$_2$ there are 133 leaves in elevated CO$_2$. From the present study, we know that for an average month, an extra 8% of leaves were abscised in elevated CO$_2$. So, of our 133 leaves in elevated CO$_2$, 8% more abscise prematurely than in ambient CO$_2$ leaving 122. We also know that, on average, only 19% of the leaves

were damaged by insect herbivores in elevated CO_2 compared to 30% in ambient CO_2. So, for every 100 leaves in ambient CO_2, 30% are damaged leaving 70 nondamaged. In elevated CO_2 only 19% of our 122 leaves are damaged leaving 99 nondamaged. The average increase in nondamaged leaf area at elevated CO_2 is thus $29/70 \times 100 = 41\%$, much greater than the 33% estimated increase of L.A.I. Hughes & Bazzaz (1997) have commented that the net outcome of elevated CO_2 on plants is higher when insect herbivory is taken into account. In their laboratory study of milkweeds, leaf area was increased 1.6 times in elevated CO_2, but densities of a herbivorous thrips insect were also decreased, so that the increase in nondamaged leaf area was 3.6 times greater in elevated CO_2 than in ambient CO_2. Together, these two studies suggest the need for more studies to include the effect of herbivores when discussing the effect of elevated CO_2 on plants.

Finally, our data also relate to the question of nutrient deposition rates to the soil surface in elevated CO_2. If the increase in L.A.I. in elevated CO_2 is 33% and the increase in abscission rate in an average month is 8%, then the increase in the average amount of leaf fall is $33 \times 1.08 = 35\%$. The amount of N in litter from elevated CO_2 is a little lower than in ambient CO_2 (0.78% ambient, 0.71% elevated). This is in agreement with most other studies, which have also shown little change in N levels in litter produced under elevated vs. ambient CO_2 (Norby & Cotrufo, 1998). The reduction of N per unit of leaf litter in elevated $CO_2 = 0.71/0.78 \times 100 = 9\%$. So for 1000, one-tenth gram leaves in ambient CO_2, 7.8 g of N would be deposited on the soil via abscised leaves. For the corresponding 1350 leaves in elevated CO_2, 9.6 g of N would be deposited. Therefore, a doubling of elevated atmospheric CO_2 could result in about a 23% change in N deposition. By similar calculations a doubling of elevated atmospheric CO_2 could result, for an average month, in a 30% increase in C input to soil by the litter fall pathway. Further work on leaf decomposition in this system is needed in order to measure actual assimilation of N into the soil and N turnover rates (O'Neill & Norby, 1996; Gahrooee, 1998).

In summary, elevated CO_2 can have a multitude of direct effects on plants and indirect effects mediated via herbivores. First, elevated CO_2 lowers herbivore densities and increases herbivore mortality. Second, it increases leaf abscission rates and so changes the nondamaged leaf area available to the plant. Finally, elevated CO_2 could change nutrient deposition rates to the forest floor.

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