

# Insects and fungi on a C<sub>3</sub> sedge and a C<sub>4</sub> grass exposed to elevated atmospheric CO<sub>2</sub> concentrations in open-top chambers in the field

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## ABSTRACT

The effects of elevated atmospheric CO<sub>2</sub> concentration on plant–fungi and plant–insect interactions were studied in an emergent marsh in the Chesapeake Bay. Stands of the C<sub>3</sub> sedge *Scirpus olneyi* Grey. and the C<sub>4</sub> grass *Spartina patens* (Ait.) Muhl. have been exposed to elevated atmospheric CO<sub>2</sub> concentrations during each growing season since 1987. In August 1991 the severities of fungal infections and insect infestations were quantified. Shoot nitrogen concentration ([N]) and water content (WC) were determined. In elevated concentrations of atmospheric CO<sub>2</sub>, 32% fewer *S. olneyi* plants were infested by insects, and there was a 37% reduction in the severity of a pathogenic fungal infection, compared with plants grown in ambient CO<sub>2</sub> concentrations. *S. olneyi* also had reduced [N], which correlated positively with the severities of fungal infections and insect infestations. Conversely, *S. patens* had increased WC but unchanged [N] in elevated concentrations of atmospheric CO<sub>2</sub> and the severity of fungal infection increased. Elevated atmospheric CO<sub>2</sub> concentration increased or decreased the severity of fungal infection depending on at least two interacting factors, [N] and WC; but it did not change the number of plants that were infected with fungi. In contrast, the major results for insects were that the number of plants infected with insects decreased, and that the amount of tissue that each insect ate also decreased.

*Key-words:* C<sub>3</sub>; C<sub>4</sub>; elevated CO<sub>2</sub>; plant/fungi interactions; plant/insect interactions.

## INTRODUCTION

During the past 150 years the concentration of CO<sub>2</sub> has increased by approximately 60 μmol mol<sup>-1</sup>. This increase is expected to continue into the next century, when atmospheric CO<sub>2</sub> concentrations ([CO<sub>2</sub>]<sub>a</sub>) may reach 700 μmol mol<sup>-1</sup> (Watson *et al.* 1990) and are expected to affect C<sub>3</sub> species by (1) increasing the rate of photosynthe-

sis (Long & Drake 1991); (2) increasing the growth and yield of crop species (Kimball 1983); (3) decreasing the nitrogen concentration in the shoots ([N]) of C<sub>3</sub> plants (Conroy 1992); and (4) increasing plant water and nitrogen efficiencies (Schönfeld, Johnson & Ferris 1989; Sionit *et al.* 1981). In C<sub>4</sub> plants, elevated [CO<sub>2</sub>]<sub>a</sub> is expected to increase water use efficiency, but in general C<sub>4</sub> plants are expected to derive smaller benefits in growth and yield than C<sub>3</sub> plants (Wong 1979; Rogers *et al.* 1983).

These CO<sub>2</sub>-induced changes in plant tissues may have profound implications for plant–animal interactions. Reduced [N] lowers the nutritional value of the plants to consumers, and the increased availability of photosynthates could result in more carbon-based defence compounds. Herbivorous insect larvae respond to reduced [N] by increasing tissue consumption to maintain total nitrogen intake (Scriber & Slansky 1981), and/or by reducing growth (Price 1984).

On plants grown in elevated [CO<sub>2</sub>]<sub>a</sub>, lepidopteran larvae increased their consumption of plant tissue (Lincoln, Couvet & Sionit 1986; Lincoln & Couvet 1989; Fajer, Bowers & Bazzaz 1989), showed reduced early instar development rates (Fajer *et al.* 1989; Akey & Kimball 1989), and exhibited increased rates of mortality in high-fertilizer treatments (Akey & Kimball 1989).

The disease severity of two common fungal pathogens, powdery mildews and rusts, increased when their hosts were fertilized with nitrogen (Shaner & Finney 1977; Paul & Ayres 1990). This suggests that such diseases may be less severe on C<sub>3</sub> plants grown in elevated [CO<sub>2</sub>]<sub>a</sub> since these plants tend to have reduced shoot [N]. Conversely, diseases caused by pathogenic fungi become more severe as host water content increases (Woolacott & Ayres 1984; Oerke & Schönbeck 1986), and since elevated [CO<sub>2</sub>]<sub>a</sub> increases water use efficiency (Wong 1979; Arp *et al.* 1993), there may be an increase in fungal disease severity on both C<sub>3</sub> and C<sub>4</sub> hosts. This potential increase in disease severity may be offset by the effects of reduced shoot [N] in the C<sub>3</sub> species, but there may be no such compensatory effect in C<sub>4</sub> plants since their [N] is not generally affected by elevated [CO<sub>2</sub>]<sub>a</sub>. Thompson, Brown & Woodward (1993) found that wheat grown in elevated [CO<sub>2</sub>]<sub>a</sub> had

reduced [N] and reduced disease severity. However, in a drought treatment,  $[\text{CO}_2]_a$  had no effect on wheat [N], but did have a positive effect on water content (WC), and disease severity increased.

To distinguish between the effects of reduced [N], which can reduce both fungal disease severity and insect infestation, and increased WC, which increases fungal disease severity (Thompson *et al.* 1993), we studied fungal infections and an insect infestation on native  $C_3$  and  $C_4$  species growing in near-monoculture. In an emergent marsh in the Chesapeake Bay, near-monocultures of  $C_3$  and  $C_4$  plants have been exposed to elevated  $[\text{CO}_2]_a$  in open-top chambers during each growing season since 1987. Fungi were observed on both types of plant, and insect larvae were observed to feed on the  $C_3$  plants. In this system, [N] was significantly reduced in the  $C_3$  plant but not in the  $C_4$  plant (Curtis, Drake & Whigham 1989), and the water potential increased in both species in the elevated  $[\text{CO}_2]_a$  treatment (Arp *et al.* 1993). In this paper we characterize the response of both insects and fungi to elevated  $[\text{CO}_2]_a$  in a natural environment. The host plants were the  $C_3$  sedge *Scirpus olneyi* Grey. and the  $C_4$  grass *Spartina patens* (Ait.) Muhl.

## MATERIALS AND METHODS

### Site description

The study site was a brackish marsh on the Rhode River, a sub-estuary of the Chesapeake Bay. Brackish marshes present vegetation with a variety of environmental stresses. Flooding, poor drainage, anoxia, high salinity, and toxic sulphur-containing compounds characterize the edaphic environment (Valiela & Teal 1974; Mendelssohn & Seneca 1980). High concentrations of electrolytes can cause low leaf water potentials (Drake 1989) and nitrogen stress (Valiela & Teal 1974). Adjacent monocultures of the  $C_3$  sedge *S. olneyi* and the  $C_4$  grass *S. patens* are found here.

Ten chambers have been placed on the same sites in each community between April and November every year since 1987. Half of the chambers in each community received no additional  $\text{CO}_2$  and half received sufficient extra  $\text{CO}_2$  to raise the concentration to ambient plus  $340 \mu\text{mol mol}^{-1}$ . In each community five unchambered control sites were also monitored. Additional descriptions of the site appear in Drake (1992) and Leadley & Drake (1993). Both *S. olneyi* and *S. patens* are perennials; during the winter the shoots die back completely and only the below-ground parts of the plants survive until spring. The fungus and insect populations in this study therefore developed during the year of the study.

### Plant material

In August 1991, 10 shoots were removed from each chamber, giving a total of 50 shoots from each of the three plant

communities. A wire circle (40 cm diameter) was placed over each site 90 cm above the ground for *S. olneyi* and 30 cm above the ground for *S. patens*. The wire had 10 evenly spaced marks on its perimeter, and plants touching the wire nearest to each mark were selected for removal. Thus only plants of a certain minimum height located in the centre of the chambers were sampled.

The [N] and WC were determined for both species. WC was determined from plants sampled 4 and 5 d after the biotroph sampling for *S. olneyi* and *S. patens*, respectively. Pre-dawn fresh weight was measured, and plants were dried at  $60^\circ\text{C}$  for 72 h and weighed again. WC was calculated as mass of water per unit weight, expressed as  $\text{g kg}^{-1}$ .

Plant [N] was determined by Kjeldahl analysis. *S. olneyi* plants were grouped into four categories per chamber: those with insect damage, those without insect damage, those with fungal damage, and those without fungal damage. Equal amounts of ground plant material from each group were pooled and mixed, and 100 mg of this mixture was analysed for [N]. For the [N] analysis of *S. patens*, plants were grouped by chamber, dried and ground, and 100 mg of this mixture was analysed. All the *S. patens* plants were infected with fungi and none was infested with insects, so these samples were not subdivided.

### The biotrophs

Fungal lesions were visible on both *S. olneyi* and *S. patens* plants. The rust pathogen *Puccinea sparganioides* Ellis & Barth. (Farr *et al.* 1989) was isolated from bright yellow/orange lesions on the *S. olneyi* plants. The fungal lesions on *S. patens* plants were dark brown, and completely encircled 5 to 10 mm length of the stem. Attempts to culture conidia from these lesions were unsuccessful and their identity remains unknown.

The severity of fungal infection, i.e. the area covered by fungal colonies, on each plant was quantified by ranking (Oerke, Steiner & Schönbeck 1989). Ranking involves assessing the leaf area covered by fungus for each plant relative to the area covered on all other plants in the sample. Before ranking, plants were labelled in code by a third party to disguise their treatment origin from the investigators. The ranking process was as follows: plants were placed in line of increasing relative leaf area covered by fungus. The relative surface area infected was judged visually by comparing one plant with the next. This procedure allowed each plant to be assessed in comparison with all other plants sampled. The resulting rank gave the order of increasing relative leaf area infected.

Herbivore damage to *S. olneyi* was caused by the larvae of a nocturnal Lepidopteran leaf mining moth. The larvae emerge from eggs laid in the stem, eat their way up the interior of the stem, burrow a clearly visible exit hole from the plant and pupate (Mosher 1969). Before pupation the larva is restricted to one plant (Mosher 1969) which means that pupation occurs on the exterior of the host plant or a

near neighbour, and the number of larvae emerging to enter pupation is the same as the number of exit holes per plant. The exit holes were counted and stems sectioned longitudinally to determine the length of necrotic tissue left by each larva. There were no insects present on *S. patens* plants, probably due to their high salt content.

### Statistical analysis

In each analysis the chamber was the unit of replication, giving 5 replications per treatment. The 10 plants per chamber were treated as repeated measures. Differences among treatments were tested with the Fisher PLSD multiple comparison test within an analysis of variance (Day & Quin 1989), and significance is reported at either the 90 or the 95 per cent confidence level. Correlations of biotroph behaviour with either [N] or WC were calculated using linear regressions. The rank data were transformed to rankits in order that they satisfy the assumptions of parametric statistics (Iman & Conover 1979). Analysis of the severity of infection by fungi was performed on the rankits.

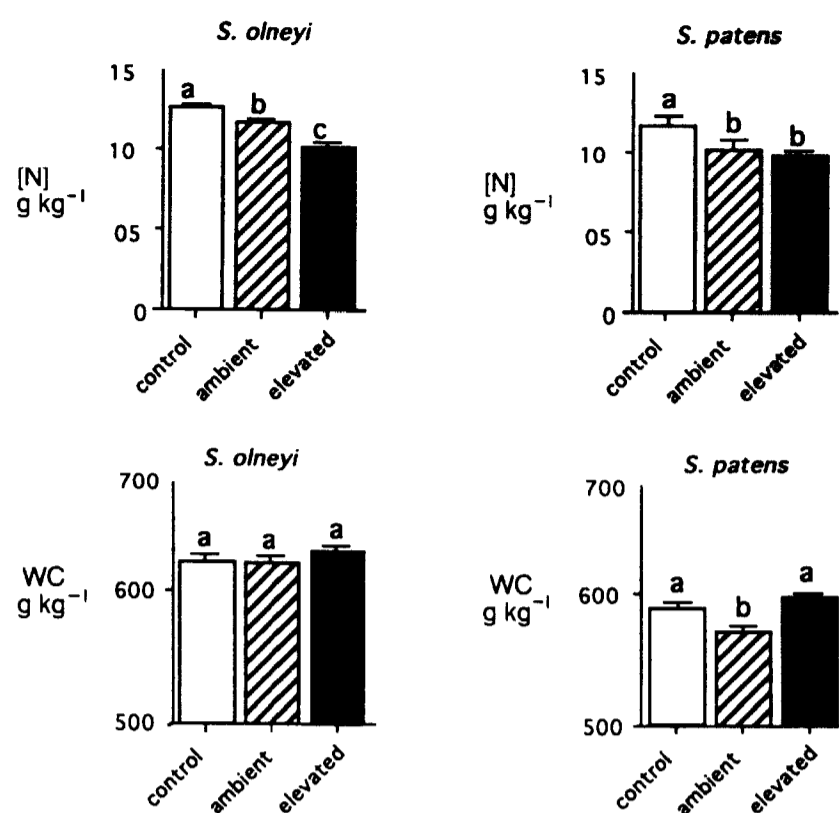
## RESULTS

Tissue nitrogen concentration [N] for *S. olneyi* was 13, 12 and 10 g kg<sup>-1</sup>, for plants from the unchambered control plots, normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and elevated [CO<sub>2</sub>]<sub>a</sub> chambers, respectively (Fig. 1). There were significant differences amongst all three groups ( $p \leq 0.05$ ), but there was no significant effect of elevated [CO<sub>2</sub>]<sub>a</sub> on the WC of *S. olneyi* (Fig. 1).

The mean WC for *S. patens* was 585, 568 and 592 g kg<sup>-1</sup>, for plants from the unchambered control plots, normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and elevated [CO<sub>2</sub>]<sub>a</sub> chambers, respectively (Fig. 1). There was a significant difference between the WC for *S. patens* plants from the normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and elevated [CO<sub>2</sub>]<sub>a</sub> chambers ( $p \leq 0.05$ ), but no significant effect of elevated [CO<sub>2</sub>]<sub>a</sub> on [N] (Fig. 1).

### Insects on *Scirpus olneyi*

The mean number of stems infested per sample was 9.2, 8.2 and 6.0 for plants from the unchambered control plots, normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and elevated [CO<sub>2</sub>]<sub>a</sub> chambers, respectively (Fig. 2a). There was a significant difference between the number of plants infested in the normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and the number infested in the elevated chambers ( $p \leq 0.05$ ). When the uninfested plants were removed from the analysis, there was a 27% reduction in the number of larvae per stem, and the length of necrotic tissue left behind as the larvae ate their way up the stem was also significantly reduced in elevated compared to ambient [CO<sub>2</sub>]<sub>a</sub> ( $p \leq 0.05$ ) (Fig. 2a). The correlation between the mean number of leaf miners per stem and



**Figure 1.** The [N] and WC of the aerial parts of *S. olneyi* and *S. patens*. Bars are standard errors and different letters denote significant differences at  $p \leq 0.05$ . [N] is in g kg<sup>-1</sup> dry weight, and WC is in g kg<sup>-1</sup> fresh weight.

the [N] of the stems was highly significant ( $p = 0.001$ ) (Fig. 2b).

The correlation between insect infestation and [N] extended to comparisons within treatments. The [N] was 11, 7 and 9% higher in the infested plants than in the uninfested plants in the control, normal ambient [CO<sub>2</sub>]<sub>a</sub> and elevated [CO<sub>2</sub>]<sub>a</sub> treatments, respectively. Within each treatment, [N] was significantly higher in the infested than in the uninfested plants ( $p < 0.1$ ) (data not shown).

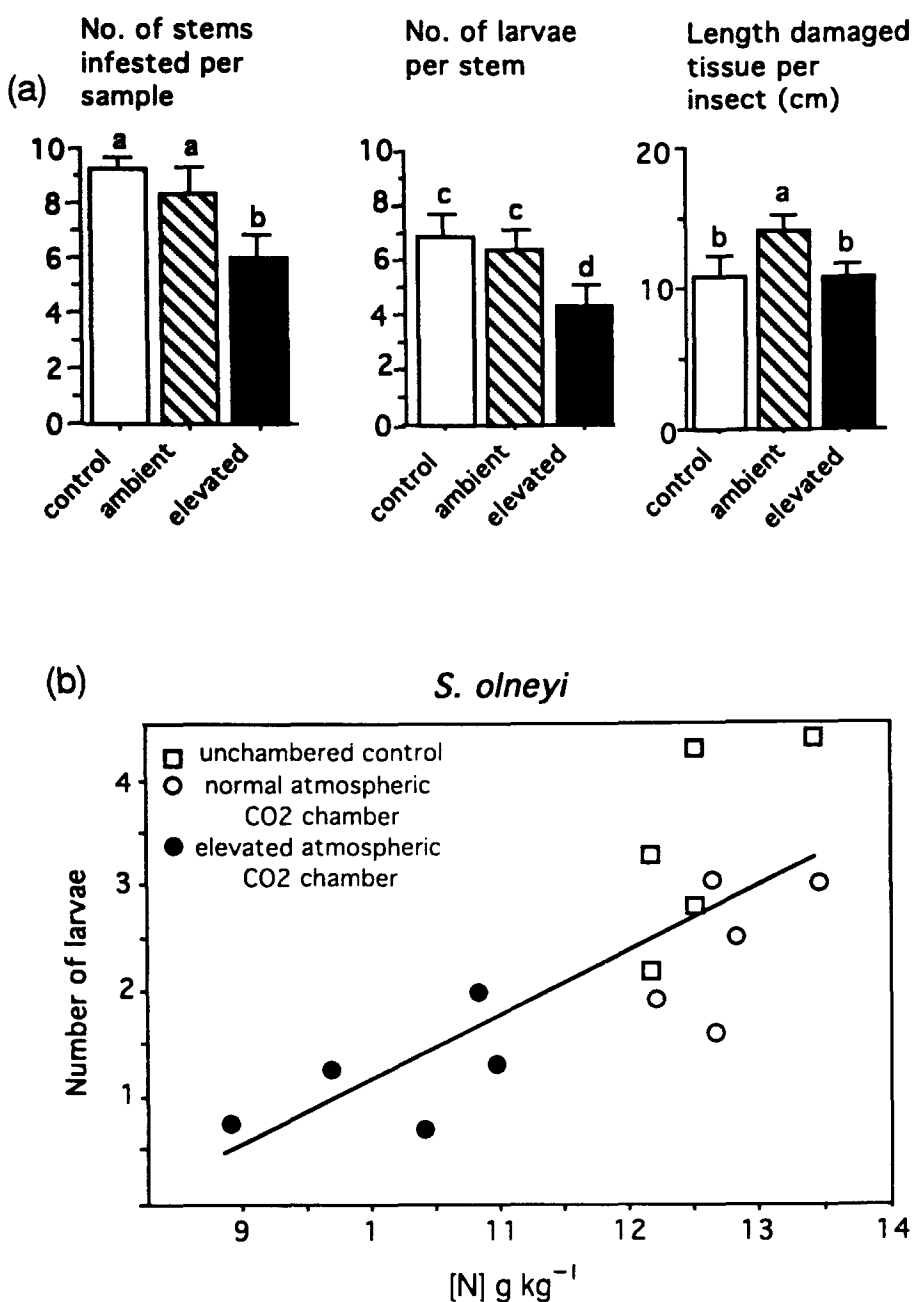
### Fungi on *Scirpus olneyi*

In the C<sub>3</sub> sedge *S. olneyi*, the mean rank for fungal infection per treatment was 75, 58 and 45 for the unchambered control plots, the normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and the elevated [CO<sub>2</sub>]<sub>a</sub> chambers. The transformed ranks were significantly different ( $p \leq 0.05$ ) (Fig. 3a), and the correlation between mean fungal rank and mean [N] was highly significant ( $p < 0.0001$ ) (Fig. 3b).

Exposure to elevated [CO<sub>2</sub>]<sub>a</sub> did not alter the number of *S. olneyi* plants infested with at least one fungal lesion. When the plants within any one CO<sub>2</sub> treatment are considered, [N] for infested plants was not significantly different from [N] for uninfested plants. The same was true for all treatments. Thus, the decrease in [N] did not affect the number of individual hosts infested but it did decrease the severity of the infections.

### Fungi on *Spartina patens*

In the C<sub>4</sub> grass *S. patens* the mean rank of fungal infection per treatment was 45, 42 and 77 for the unchambered con-



**Figure 2.** (a) The mean number of *S. olneyi* stems per sample infested with leaf miners ( $n = 10$ ), the mean number of larvae per stem, and the mean length of tissue damaged per larva. Bars are standard errors, and different letters denote significant differences at  $p \leq 0.05$ , with the exception of the difference between c and d, which is significant at  $p \leq 0.1$ . (b) The number of larvae per plant plotted against [N] for the Lepidopteran leaf miner on *S. olneyi* grown in unchambered control plots (□) and in ambient (○) and elevated (●) [CO<sub>2</sub>]<sub>a</sub>. The regression includes only infested plants ( $r^2 = 0.66$ ,  $p \leq 0.001$ ).

control plots, the normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and the elevated [CO<sub>2</sub>]<sub>a</sub> chambers, respectively (Fig. 3a). The transformed ranks for plants from the normal ambient [CO<sub>2</sub>]<sub>a</sub> chambers and plants from the elevated [CO<sub>2</sub>]<sub>a</sub> chambers were significantly different ( $p \leq 0.05$ ). The correlation between the rank of infection and the WC of the host was significant ( $p = 0.003$ ).

## DISCUSSION

### Insects

In the future, plants will grow in an atmosphere increasingly rich in CO<sub>2</sub>. This will alter tissue composition,

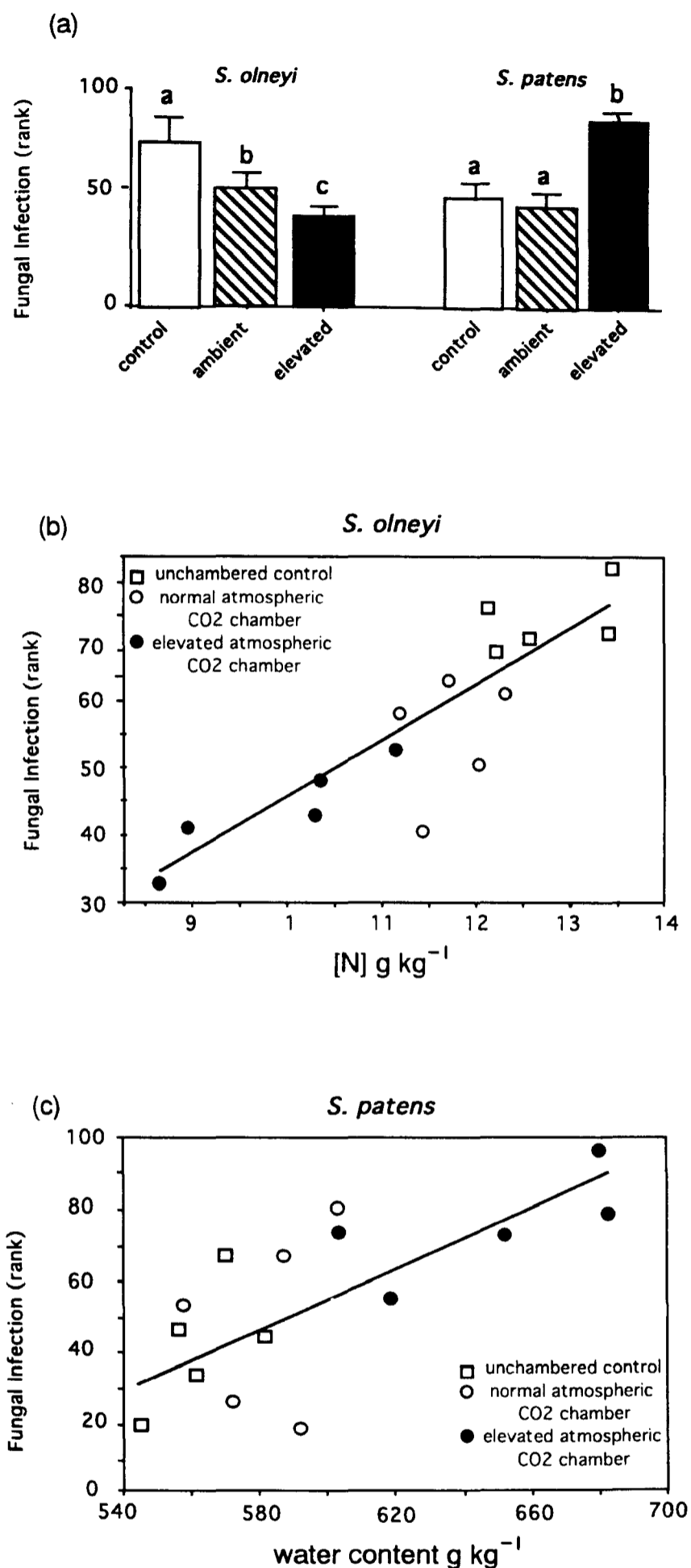
including [N] (Wong 1979; Conroy 1992) and the water content (Schöfeld *et al.* 1989) of the foliage. These are important determinants of the nutritional quality of plants for insects (Lewis 1984) and fungi (Woolacott & Ayres 1984; Shaner & Finney 1977).

Insects were only present in the parts of the plants with the greatest [N]. We observed that the larvae hatched early in the season when plant [N] was highest (Curtis *et al.* 1989), and ate their way up the stems; they never ate downwards. The highest [N] was always within the upper third of the stem throughout the rest of the season (Curtis *et al.* 1989). In this way the insect spent the larval stage of its life-cycle in the most nitrogen-rich part of its host.

The chambers contained from 200 to 450 *S. olneyi* stems, each of which was equally available for oviposition, hatching of eggs, and development of larvae. Nevertheless, there were trails of necrotic tissue in as few as 50% of *S. olneyi* stems within a single sample. Within each CO<sub>2</sub> treatment, plants with trails of necrotic tissue had a greater [N] ( $p \leq 0.1$ ) than those with no evidence of the insect. Stems with no trails of necrotic tissue were checked at 10× magnification for dead larvae and even the smallest necrotic trail. Neither was found, and, since eggs should hatch irrespective of CO<sub>2</sub> treatment, we assume that no eggs were oviposited. The observation that trails of necrotic tissue were more often present in plants with greater [N] extends to the comparison between CO<sub>2</sub> treatments: there were more trails in the plants grown in ambient CO<sub>2</sub> (Figs 1 & 2a), and these plants had significantly more [N] than the plants grown in elevated [CO<sub>2</sub>]<sub>a</sub>.

The major findings were that insect infestation was less severe, and the larvae that were present consumed less tissue in the plants grown in the elevated [CO<sub>2</sub>]<sub>a</sub> treatment (Fig. 2a). The apparent ability of these insects to select for high-[N] plants suggests that the response of insects to rising [CO<sub>2</sub>]<sub>a</sub> may include behavioural changes. Nevertheless, population densities of these insects may be reduced in a future high-CO<sub>2</sub> world, which is also a conclusion of Akey & Kimball (1989), who found increased mortality of beet armyworm (*S. exigua*) reared on plants grown in elevated CO<sub>2</sub> in high-fertilizer treatments. This conclusion is in contrast to the findings of experiments in which captive larvae were fed plant tissue grown in different CO<sub>2</sub> concentrations (Lincoln, Couvet & Sionit 1986; Fajer, Bowers & Bazzaz 1989; Lincoln & Couvet 1989). In these studies, the reduced nutritional value of the plants to insect larvae caused increased tissue consumption, presumably to maintain total nitrogen intake (Scriber & Slansky 1981).

The explanation for the diverging results may be in part that in our study the female moths were not restricted to any one treatment during oviposition. However, after oviposition the larvae were restricted to one plant until pupation. The fact that they ate less tissue therefore implies that either their nitrogen use efficiency increased (Slansky 1974) or their development was restricted (Dixon 1973). Restricted development could be a consequence of increased host defence capabilities, which can vary with the nutritional status of the host (Haukioja & Niemelä



**Figure 3.** (a) The disease severity (rank) of fungal infections of the aerial parts of *S. olneyi* and *S. patens* grown in unchambered control plots and in ambient and elevated [CO<sub>2</sub>]<sub>a</sub>. Bars are standard errors, and different letters denote significant differences at  $p < 0.05$ . (b) The mean rank of infection with *Puccinia sparganioides* per chamber plotted against [N] for *S. olneyi* grown in unchambered control plots (□) and in ambient (○) and elevated (●) [CO<sub>2</sub>]<sub>a</sub>. The regression included only *S. olneyi* that were infected ( $r^2 = 0.76$ ,  $p < 0.0001$ ). (c) The mean rank of fungal infection per chamber plotted against WC for *S. patens* grown in unchambered control plots (□) and in ambient (○) and elevated (●) [CO<sub>2</sub>]<sub>a</sub>. The regression includes all the *S. patens* plants, since all plants were infected ( $r^2 = 0.51$ ;  $p = 0.003$ ).

1976). Another possibility is that different host water status may reduce the availability of free amino acids, an important source of nutrition to insects (White 1974).

### Fungi

The response of plant [N] to elevated [CO<sub>2</sub>]<sub>a</sub> can affect the disease severity of fungal infections. The infection of *Puccinia sparganioides* in the C<sub>3</sub> sedge *S. olneyi* was less severe in elevated [CO<sub>2</sub>]<sub>a</sub>. The mechanism may be diminished nutritive quality accompanying a reduction in [N] (see Fig. 3b). It is also possible that there may have been an increase in the levels of defence compounds. The reduced severity of the fungal infection in the *S. olneyi* plants inside the chambers compared to plants in the control plots may be due to the barrier presented by the chambers, which are 2 m high for this plant community. The chambers in the *S. patens* community are 1 m tall, which may account for the lack of a chamber effect on the severity of infection in this community.

Changes in other aspects of host physiology, such as phenolic concentrations, may also inhibit the growth of fungi, and these changes can correlate with [N] (Király 1964; Matsuyama & Dimond 1973). Nevertheless, the correlation between fungal disease severity and shoot [N] reported in this study suggests a direct effect of the nutritional status of the tissue on the disease. Positive correlations between [N] and disease severity have been reported previously. In agricultural studies in the field, Oerke *et al.* (1989) and Scholze & Röver (1989) reported higher severities of mildew infections on crops fertilized with nitrogen, and Paul & Ayres (1990) found increased infection of black rust in plants fertilized with nitrogen.

In contrast to the reduction in fungal disease severity in *S. olneyi*, plants of the C<sub>4</sub> grass *S. patens* grown in elevated [CO<sub>2</sub>]<sub>a</sub> were more severely infected than plants grown in ambient [CO<sub>2</sub>]<sub>a</sub> (Fig. 3a). The severity of infection was correlated with WC (Fig. 3c). Fungal growth was positively correlated with water content in crops (Oerke & Schönbeck 1986), and the mechanism for the correlation may be that host water deficits reduce the sporulation of fungus (Woolacott & Ayres 1984). Thompson *et al.* (1993) grew wheat under severe water deficit in normal ambient [CO<sub>2</sub>]<sub>a</sub> and elevated [CO<sub>2</sub>]<sub>a</sub>. They found that [N] was the same in each CO<sub>2</sub> treatment, but WC for the plants grown in elevated [CO<sub>2</sub>]<sub>a</sub> was significantly higher. The increased WC correlated with increased disease severity.

Plants grown in elevated [CO<sub>2</sub>]<sub>a</sub> commonly have modified WC and [N]. In this and other (see Conroy 1992) studies, the C<sub>3</sub> plant had reduced [N] and fungal disease severity. While we found no significant increase in WC in the C<sub>3</sub> plant, WC in C<sub>3</sub> plants can increase significantly with increasing [CO<sub>2</sub>]<sub>a</sub> (Fajer *et al.* 1989), and in such cases fungal disease severity may remain unchanged (Thompson *et al.* 1993). These compensatory effects make it difficult to predict the effect of rising [CO<sub>2</sub>]<sub>a</sub> on the fungal infections of C<sub>3</sub> plants. In contrast, the predominant effect of

elevated  $[\text{CO}_2]_a$  on  $C_4$  plants is to increase water status, with a smaller effect on  $[\text{N}]$ , which suggests that the fungal disease severity in  $C_4$  plants will increase as the concentration of atmospheric  $\text{CO}_2$  continues to rise.

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