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Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland to elevated atmospheric CO_2 concentration

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Abstract

Acclimation of photosynthesis and respiration in shoots and ecosystem carbon dioxide fluxes to rising atmospheric carbon dioxide concentration (C_a) was studied in a brackish wetland. Open top chambers were used to create test atmospheres of normal ambient and elevated C_a(= normal ambient + 34 Pa CO_2) over mono-specific stands of the C_3 sedge *Scirpus olneyi*, the dominant C_3 species in the wetland ecosystem, throughout each growing season since April of 1987. Acclimation of photosynthesis and respiration were evaluated by measurements of gas exchange in excised shoots. The impact of elevated C_a on the accumulation of carbon in the ecosystem was determined by ecosystem gas exchange measurements made using the open top chamber as a cuvette.

Elevated C_a increased carbohydrate and reduced Rubisco and soluble protein concentrations as well as photosynthetic capacity(A) and dark respiration (R_d; dry weight basis) in excised shoots and canopies (leaf area area basis) of *Scirpus olneyi*. Nevertheless, the rate of photosynthesis was stimulated 53% in shoots and 30% in canopies growing in elevated C_a compared to normal ambient concentration. Elevated C_a inhibited R_d measured in excised shoots (−19 to −40%) and in seasonally integrated ecosystem respiration (R_e; −36 to −57%). Growth of shoots in elevated C_a was stimulated 14-21%, but this effect was not statistically significant at peak standing biomass in midseason. Although the effect of elevated C_a on growth of shoots was relatively small, the combined effect of increased number of shoots and stimulation of photosynthesis produced a 30% stimulation in seasonally integrated gross primary production (GPP). The stimulation of photosynthesis and inhibition of respiration by elevated C_a increased net ecosystem production (NEP = GPP − R_e) 59% in 1993 and 50% in 1994. While this study consistently showed that elevated C_a produced a significant increase in NEP, we have not identified a correspondingly large pool of carbon below ground.

Introduction

The continued rise in atmospheric CO_2 concentration (C_a) is one of the most certain aspects of anthropogenic effects on atmospheric composition and climate. The potential response of terrestrial ecosystems to rising C_a has been the subject of much debate, focusing on the central issue of whether, in the long run, plants can sustain CO_2 stimulation of carbon assimilation and if so, where additional carbon might be stored. Over very long time spans and on the global scale, processes affecting terrestrial ecosystem carbon turnover appear to be more or less in equilibrium since the pools of carbon are believed to have remained stable (Goudriaan, 1995). However, in the medium term of decades to centuries, the rise in C_a is now expected to stimulate some carbon assimilation (Gifford et al., 1996). Ecosystem carbon balance is the difference between two fluxes: carbon assimilation by photosynthesis and carbon loss through respiration of plants and decom-

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position of plant matter by microbes and animal consumers.

Because the rate of photosynthesis in C_3 species is not saturated at current levels of C_a, it is thought that rising atmospheric C_a will stimulate carbon accumulation in terrestrial ecosystems, a small fraction of which will ultimately enter the slowly metabolized soil carbon pool and in this form can be considered stored carbon. Based upon well-know responses of key crops to long-term exposure to elevated C_a, it has been estimated that the 25% increase in atmospheric C_a since the industrial revolution, has stimulated photosynthesis and growth of key crops by about 15% (Allen et al., 1987). To put this in perspective, terrestrial net ecosystem production (NEP) is estimated to be approximately 50 GtC a^{-1} at present (Field et al., 1995; Goudriaan, 1995). A stimulation of NEP of only 12% would be equivalent to total anthropogenic CO_2 production, estimated to be approximately 6 Gt C a^{-1} (Goudriaan, 1995).

Several arguments have been put forward challenging the idea that rising C_a will stimulate NEP and suggesting that the stimulation of terrestrial carbon sequestration by rising C_a may be relatively small. First, acclimation of photosynthetsis to high C_a may obviate any stimulation of production because plants grown in elevated C_a often have a much lower capacity of photosynthesis (Sage, 1994) than their counterparts grown in normal C_a. The most often cited example of this occurred in a study of Arctic vegetation where acclimation in the dominant species, *Eriophurm vaginatum*, was completely homeostatic within three weeks and plants in elevated C_a had a rate of photosynthesis in elevated C_a no higher than the rate for plants grown in normal ambient C_a (Oechel et al., 1994). Second, additional mineral resources, particularly nitrogen and phosphorus, would be required to accompany the addition of more carbon. As plant production in most native ecosystems is thought to be nitrogen limited, the argument has been made that there would be insufficient nutrient available to accomodate much additional carbon.

But this picture of physiological processes in a higher CO_2 world fails to account for the fact that plants grown in higher C_a are more nutrient, light and water use efficient. Studies during the past 5-10 years have required a re-evaluation of possibilities for CO_2 stimulation of ecosystem carbon accumulation. Acclimation has come to be viewed as optimization of resource use maintaining carbon balance in the face of changing availability of CO_2. Typically, the rate of photosynthesis is maintained higher in elevated C_a than in plants grown in normal ambient C_a even in plants acclimated to chronic exposure to the higher levels of C_a (Long and Drake, 1992). Moreover, contrary to the earlier expectation that rising C_a would stimulate dark respiration, thus burning off any additional carbon from the stimulation of photosynthesis, it is now clear that chronic exposure to higher C_a reduces dark respiration (Azcón-Bieto et al., 1994; Curtis, 1996; Gunderson and Wullschleger, 1994). Efficiency of photosynthesis, water and nitrogen use all increase in plants grown in elevated C_a (Bowes, 1993; Long and Drake, 1992) suggesting that some carbon could be added to accommodate the potential increased C:N. Rising C_a and temperature may also stimulate nitrogen mineralization (Gifford, 1996) methane production (Dacey et al., 1994) and N fixation. Thus it is not at all clear that there would be an insignificant effect of rising C_a on NEP in terrestrial ecosystems.

It is essential to conduct field experiments which are sustained long enough to give the general outlines of the responses to be expected as atmospheric C_a rises. Since it will be impossible to study every system, it is necessary to aim at understanding general principals of ecosystem function so that models can be employed to make estimates of carbon storage.

The impact of acclimation of photosynthesis and respiration on ecosystem carbon balance have not been evaluated through field experiments. Reviews indicate that environmental factors, such as low nitrogen, that limit sink strength also result in lower photosynthetic capacity (Curtis, 1996). In this paper we review our published data on the acclimation of photosynthesis and respiration to elevated C_a and relate these data to new data on net ecosystem production (NEP) in monospecific stands of the C_3 sedge, *Scirpus olneyi*, growing in brackish marshes along Chesapeake Bay in Maryland, USA.

Methods

The ecosystem studied was a brackish wetland on the Chesapeake Bay, Maryland. The site and the methods for treating the plants with normal ambient and elevated C_a (= norman lambient + 34 Pa CO_2) are discussed in several publications (Arp, 1991b; Curtis et al., 1989a; Drake, 1992; Drake and Leadley, 1991; Drake et al., 1996; Leadley and Drake, 1993). Nitrogen was available mainly as ammonia and averages about 15 mg N kg^{-1} dw soil (Matamala, unpubl. results).

Table 1. Acclimation of photosynthesis and respiration in *Scirpus olneyi* exposed to elevated C_a in open top chambers in the native environment. Data on photosynthesis are from Jacob et al. (1995) Figure 2, and Table 1, 1994. Data on respiration measured by O_2 consumption and Cytox activity, (μmol O_2 kg dw^{-1} s^{-1}) are from Azcon-Bieto et al. (1994), Table 2, and Figure 1; and data on CO_2 efflux (μmol CO_2 kg dw^{-1} s^{-1}) from Gonzalez-Meler (1995), Figure 2.4. Carboxylation efficiency (CE, mol m^{-2} s^{-1}); Assimilation (A) at growth C_a (μmol m^2 s^{-1}) total soluble protein, Rubisco, sugars and starch (g m^{-2}). All differences significant at $p<0.05$ except in soluble protein and Rubisco ($p<0.07$)

	A	E	(E-A)/A, %
CE	0.14	0.11	−21.4
A_o at growth C_a	18.0	27.5	52.7
A at 350 ppm	18.0	9.7	−46.0
R_d			
CO_2 efflux	5.2	4.2	−19.0
O_2 uptake	2.6	1.5	−46.0
Cytox activity	11.5	5.0	−57.0
Soluble Protein	2.1	1.3	−38.0
Rubisco	0.95	0.55	−42.1
Sugars	19.7	29.8	51.3
Starch	51.3	79.0	54.0

Scirpus olneyi is exposed to full sunlight and high temperatures during the peak of the growing season. Open-top chambers have been in place each growing season since 1987 when the treatments with elevated C_a began.

Methods for determining acclimation of photosynthesis in *Scirpus olneyi* are reported in Jacob et al. (1995). Respiration of shoots of *Scirpus olneyi* was reported by Azcón bieto et al. (1994) and Gonzàlez-Meler (1995). These data are summarized in Table 1. Net ecosysten production was determined from ecosystem gas exchange measurements made periodically throughout the season using the approach outlined in Leadley and Drake (1993). We used two approaches to verify that the measurements we made were accurate. First, we used data on photosynthesis of leaves to estimate ecosystem gas exchange using a model for canopy gas exchange and these estimates were very close to the measured values (Long and Drake, 1991). Second, we surrounded the chambers with a tent large enough to allow the gas space around the chamber to be filled with the exhaust gas from within the chamber and compared the measurements of respiration obtained in this manner with those obtained without this tent. This would show whether the measurements of gas exchange at night were biased by the outside air indicating a leak. We found that the measurements we were making with and without the tent were nearly identical indicating that there were no substantial leaks. The problem of the possibility of gas escaping into the soil was not considered an important source of error since the soils are water logged and very highly compacted. There is a physical barrier projecting 10 cm into the soil around the base of the open top chamber which forms a gas seal with the soil. Data on incident photosynthetically active photon flux (PPF, 400-700 nm) were obtained using a pair of Eppley thermopiles. PPF is the difference between the flux measured by a thermopile fitted with a clear dome passing all wavelengths longer than 400 microns and that of a second thermopile fitted with a dome passing only wavelengths longer than 700 microns.

To obtain net seasonal carbon flux, data for daytime CO_2 flux (grosss primary production, GPP) and nighttime CO_2 flux (ecosystem respiration, R_e) were treated separately. Net ecosystem photosynthesis was determined from periodic measurements of net CO_2 flux and PPF and the seasonal trend of these measurements. GPP was divided by total daily PPF and this ratio plotted against Julian date. Values for this ratio for any day during the growing season (1 May-1 November) were estimated from the seasonal curve and this value was multiplied by total daily PPF to obtain estimated GPP for that day. R_e was determined by periodic measurements of nighttime net ecosystem CO_2 flux. We obtained reliable data during windy periods when the air was well mixed and C_a was constant although few measurements were continuous throughout the night. Consequently, we assumed that the rate of nighttime net CO_2 loss for the whole night was the rate obtained during the part of the night when stable background CO_2 concentration prevailed. These rates were plotted against Julian date and the total nighttime carbon loss for each night of the year was estimated by multiplying the rate for each night by the number of hours of darkness. The total CO_2 lost at night was then summed for the entire season. It was assumed that there was no loss of carbon between Julian days 1 and 100 and between days 300 and 365. Although this assumption is reasonable in that the temperature of the soil is very low during the fall and winter and the loss of carbon is expected to be similarly reduced, this approach will underestimate annual CO_2 loss by ecosystem respiration. But since our estimate of net ecosystem carbon assimilation is also reduced due to reduction of incident light by the chamber walls of approximately 15%

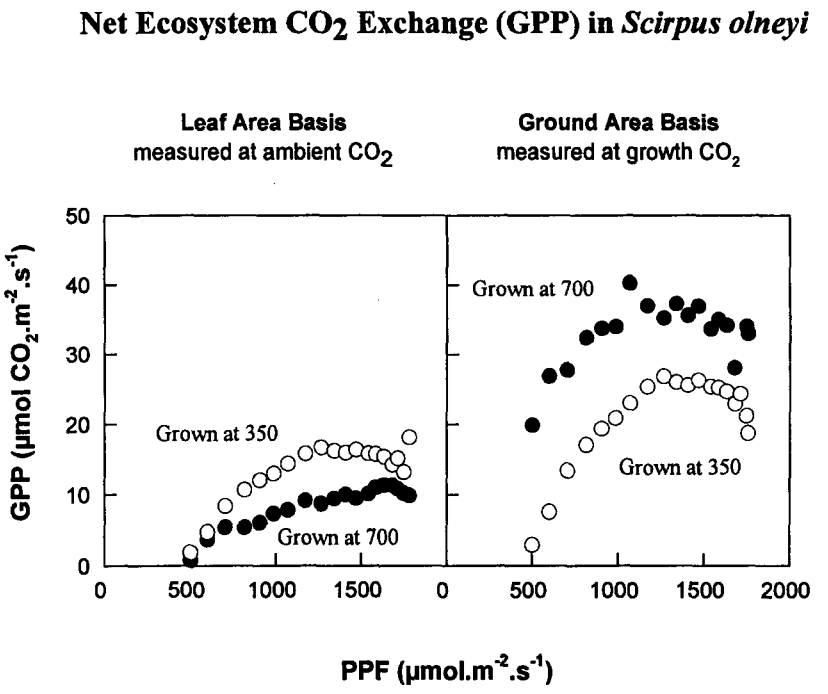

Figure 1. The effect of acclimation of photosynthesis on ecosystem gas exchange determined from light response curves in two plots in the *Scirpus olneyi* community grown in elevated and normal ambient C_a. Data on left: both treatment plots measured at normal ambient C_a results expressed on a leaf area basis to show the effect of acclimation. Data in panel on right: the same treatments as those in the left panel except that measurements were made at the growth concentrations and the results expressed on the basis of ground area to illustrate the combined effects of elevated CO_2 stimulation of numbers of shoots and stimulation of photosynthesis. Data taken 26 and 27 July, 1995.

(Drake and Leadley, 1991) it was felt that these effects would tend to be offsetting. This procedure includes the inaccuracy of these and other simplifications.

Results

The following differences were observed in plants grown at elevated C_a compared with those grown at the present normal ambient concentration (Table 1): reduced carboxylation efficiency (CE) and reduced net photosynthetic capacity when measured at normal ambient C_a or when compared at the same C_i; increased starch and carbohydrate concentrations; reduced Rubisco and soluble protein concentrations. When measured at normal ambient C_a concentration (35 Pa), photosynthetic capacity of plants grown in elevated C_a was reduced −46% compared with plants grown in normal ambient C_a. However, when compared at the operational C_i, there was a 52.7% increase in net photosynthesis of plants in elevated compared with normal ambient C_a (Table 1).

The reduction of carboxylation efficiency (CE) in elevated C_a was due to the reduction of the concentration of Rubisco in the leaf tissues (Table 1) although the ratio of Rubisco to the total soluble protein was unaffected by C_a treatment. There was a linear correlation between the Rubisco concentration in the stems and CE in *Scirpus olneyi* (Jacob et al., 1995). Total soluble sugars increased by 51% and starch by 56% (Table 1). Although some of the decline in soluble protein concentration could be attributed to dilution by an increase in starch in *Scirpus olneyi*, the major factor was a real reduction in protein and Rubisco concentration. There was a significant reduction of about 38% in total soluble protein and about 42% in Rubisco (per unit dry weight). R_d was consistently reduced in plants grown in elevated C_a whether measured by CO_2 loss or by O_2 consumption and whether expressed per unit area of tissue, per unit dry weight, or per unit of nitrogen (Table 1). Ecosystem respiration (R_e) was determined from the rate of respiration for several hours each night (Figure 3A) multiplied by the total number of hours of darkness for each night to give total respiratory loss of CO_2 at night (Figure 3B), data for 1994.

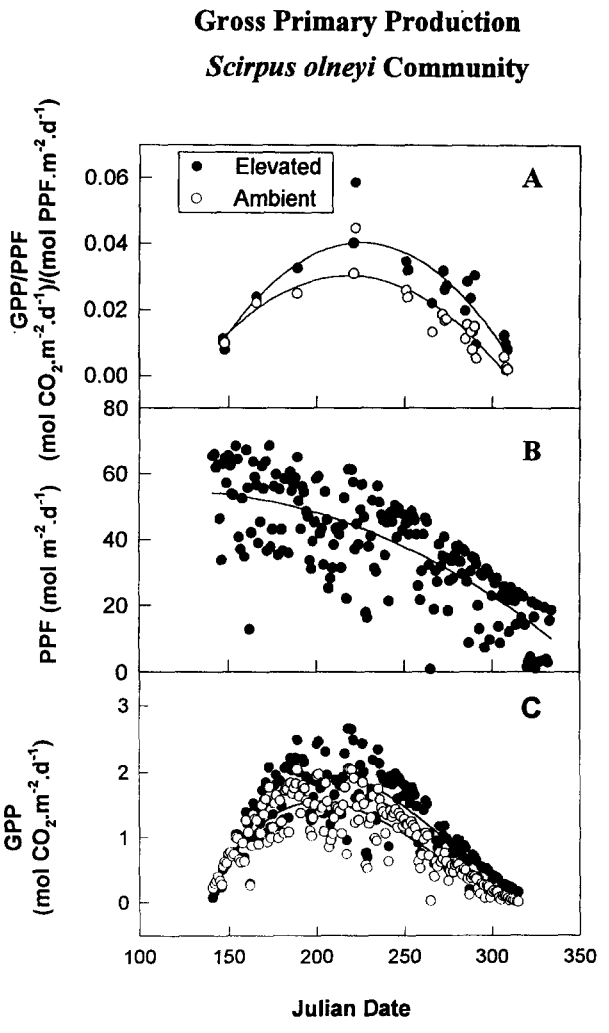

Figure 2. Gross primary production (GPP) determined from measurements of daily net ecosystem C_a assimilation and incident PPF in the *Scirpus olneyi* community, 1994. **A**: the ratio of total daytime GPP to total PPF. **B**: Total daily PPF. **C**: GPP obtained by product of total daily PPF in B by the value of GPP/PPF for that day in panel A above.

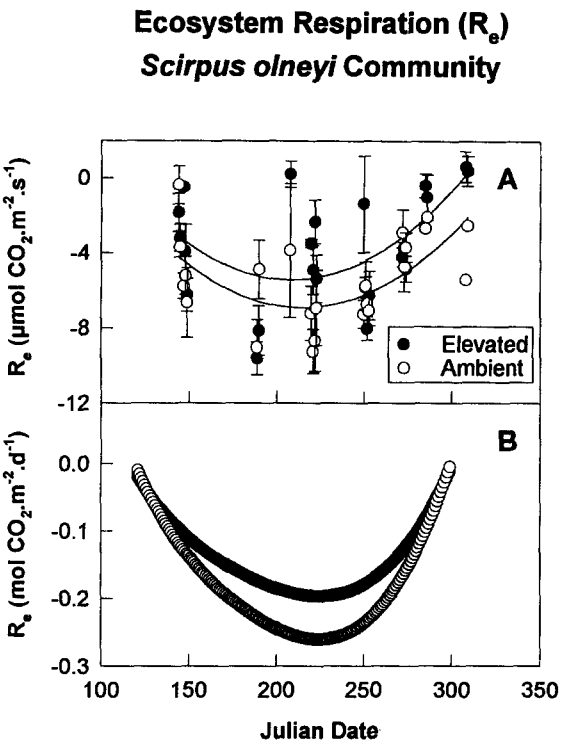

Figure 3. Ecosystem respiration (R_e) determined from nighttime rate of respiration (A, mean of five chambers) and the total number of hours of darkness per night, 1994.

Table 2. Annual carbon fluxes, 1993 and 1994 (Kg C m^{-2}) in the *S. olneyi* community. All treatment differences for values of carbon fluxes (GPP, R_e,NEP) significant at $p<0.05$

C_a	GPP	R_e	NEP
	(kg C m^{-2})		
A	2.08	0.49	1.59
E	2.72	0.21	2.51
$\frac{E-A}{A}$%	31	−57	58
A	1.89	0.44	1.45
E	2.45	0.28	2.17
$\frac{E-A}{A}$%	30	−36	50

There was a significant difference ($p<0.038$) between the rate of respiration in normal ambient and elevated C_a for 1994, Figure 3. Respiration of this ecosystem is largely that of the aerial biomass since soil respiration is anaerobic.

We measured GPP in pure stands of the C_3 sedge, *Scirpus olneyi*, as outlined and reported in Drake and Leadley (1991), Leadley and Drake (1993), and Drake et al. (1996). In Figure 1, we show the effects of acclimation to long term elevated C_a exposure on GPP measured at low and high C_a throughout July 26 and 27, 1995. After gas exchange measurements, we determined the total number of shoots, stem height and width for each stem and from those data we computed total stem area of *Scirpus olneyi* within each chamber used in the gas analysis measurements. Total stem area (one surface only for each of the three surfaces) was equivalent to leaf area index of 0.97 in the elevated chamber and 0.81 in the normal ambient chamber for which data are shown in Figure 1. When compared at

normal ambient C_a, GPP (per unit stem area) in plants grown in elevated C_a was reduced −43% compared with plants grown in normal ambient (Figure 1, left panel). However, when compared at the growth concentration and on a unit ground area basis, GPP was stimulated about 40% (Figure 1, right panel). Elevated C_a inhibited respiration of shoots about the same amount whether measured as CO_2 loss or as O_2 consumed (−19% and −40%, Table 1) and irrespective of the basis for measurement (area, dry weight or nitrogen, Azcón Bieto et al., 1994; Table 2) or as whole ecosystem respiration, R_e (Table 2, −36 and −57% for 1993 and 1994).

Figure 2 illustrates the seasonal behavior of photosynthetic light use efficiency (ratio of total daily GPP to total daily PPF). Assuming 85% absorption, the apparent light use efficiency at the peak of the season, in August, was approximately 2.5% and 3.4% at normal ambient and elevated C_a respectively (Figure 2, panel A). Total seasonal GPP for the years 1993 and 1994 were obtained by summing the product of daily PPF (Figure 2B) by the value of the the ratio GPP/PPF (Figure 2A). Seasonal GPP was taken as the sum of all daily GPP values. Elevated C_a stimulated GPP by 31 and 30% and inhibited R_e in 1993 and 1994 (Table 2). The relative stimulation of net ecosystem production (NEP = GPP - R_e) by elevated C_a was 59 and 50% respectively for 1993 and 1994.

Discussion

Our data on acclimation of photosynthesis in *Scirpus olneyi* clearly shows that although there is a reduction in the capacity for photosynthesis, elevated C_a stimulates carbon uptake per unit of ground area (Table 2, Figure 2). Many studies have shown that the high rate of CO_2 assimilation observed when plants grown at present normal ambient C_a are exposed to elevated C_a may not be maintained in the long term (Arp, 1991b; Bowes, 1993; Cure, 1985; Curtis, 1996; Gunderson and Wullschleger, 1994; Sage, 1994; Stitt, 1991). This response to chronic elevated C_a exposure, in which the photosynthetic capacity is often lower in high C_a grown plants, has been termed acclimation (see Sage 1994; and Gunderson and Wullschleger, 1994 for discussion of definition). Acclimation is rarely completely homeostatic resulting in no increase in net CO_2 assimilation although there a few reports indicate that this does happen in native ecosystems (e.g. Tissue and Oechel, 1987). In some studies, there is virtually no effect on photosynthesis and some measurements even show an increase in photosynthetic capacity (e.g. Arp and Drake, 1991; Curtis, 1996; Long and Drake, 1992). When acclimation was first observed in long-term studies of the effects of elevated C_a on native species (Tissue and Oechel, 1987), it was prematurely concluded that rising atmospheric C_a would have relatively little effect on the capacity of ecosystems to assimilate some fraction of the anthropogenic CO_2 responsible for global climate change.

In most cases, reduction in photosynthetic capacity is not large enough to reduce the rate of photosynthesis when compared with the rate in plants in present normal ambient concentrations (Curtis, 1996; Long and Drake, 1991). Several reviews (Arp, 1991; Bowes, 1993; Cure, 1985; Curtis, 1996; Gunderson and Wullschleger, 1994) have concluded that when compared at the operational values for ambient C_a concentration (i.e. the value of photosynthesis measured at elevated C_a compared with the value measured at present normal ambient C_a) elevated C_a will stimulate photosynthesis (leaf area basis) by about 30–50%.

The CO_2 stimulation of photosynthesis is temperature dependent and increases sharply above 25 °C (Long and Drake, 1992). A relatively large stimulation at high C_a may also reflect the mitigation of water stress. Field measurements reported here were carried out at relatively high temperatures, often in the range 35–45 °C during midday.

It is unclear how acclimation is regulated by such factors as developmental stage of the plant, environmental conditions, resource availability, or internal carbon balance. Acclimation is often accompanied by a decrease in the carboxylation efficiency, the content of Rubisco, the concentration of soluble proteins and tissue N (Bowes, 1993; Long and Drake, 1992; Nie et al., 1995a,b; Sage, 1994; Stitt, 1991). Acclimation to elevated C_a appears to be tightly coupled to a suite of genetic and environmental factors which determine the availability of carbon sinks. Whenever growth is restricted, as it is likely to be in plants at low temperature, in limiting nutrient supply, or in small pots (which limits both sink size and nutrient supply) the capacity to store additional carbon is low and the capacity of the source (photosynthesis) must necessarily decline. When growth is not limited, (as for example in the flush of new leaves in spring or during the filling of fruits in crops) the plant may be able to utilize the full capacity of photosynthesis and reduction of the photosynthetic capacity may not occur. Long (this volume) points out that there was little acclimation throughout the growth

cycle of wheat supplied with abundant N but that in plants given limiting N, acclimation of photosynthesis caused reduction in Rubisco and (presumably) reduction in tissue N. Stitt (1991) proposed a conceptual model to describe the long-term acclimation of photosynthesis to elevated C_a in which increased source activity of leaves leads to accumulation of carbohydrates. Nie et al. (1995a,b) report findings that are consistent with this model: assays for rbsc which encodes for the small subunit of Rubisco in wheat exposed to elevated C_a showed no reduction of the Rubisco and hence no reduction of the photosynthetic capacity. In this case, wheat appears to have had sufficient N to store and process all additional carbon made available by the increased efficiency of photosynthesis in elevated C_a.

Through effects on tissue nitrogen concentration, acclimation has other consequences for plants that indirectly impact ecosystem carbon balance. Plants exposed to elevated C_a often have higher C:N which, in plants exposed to limiting nitrogen content, as native species often are, is a result of reduction in soluble protein and especially of Rubisco. This reduction in tissue N by itself results in higher nitrogen use efficiency but may also lead to slower decomposition and significant effects on plant/insect interaction (Thompson and Drake, 1994).

Studies of whole plants and of plant tissues grown in long-term elevated C_a exposure have shown that plant mitochondrial respiration capacity and activity is often inhibited. Azcón-Bieto et al. (1994) demonstrated a strong relationship between the rate of dark respiration in tissues of *Scirpus olneyi* and the activity of a key respiratory enzyme: Cytochrome c oxidase had lower activity in plants grown in elevated C_a than in those grown in normal ambient C_a. The inhibition of respiration occurred whether expressed on area, dry weight or nitrogen basis. The mechanism for the effects reported by Amthor (1991) is in part related to direct effects of the C_a on the activity of enzymes involved in mitochondrial electron transport (Gonzàlez-Meler et al., 1996), to reductions in the amount of respiratory enzymes (Azcón-Bieto et al., 1994) and to changes in the tissue composition.

Applied to the findings of this long-term field study of the effects of elevated atmospheric C_a on ecosystem processes, the term acclimation as used here fits the definition offered by Sage (1994) to mean "...physiological...responses which improve performance and survival...by enhancing growth, resource use efficiency...stress tolerance and/or the lifespan of an individual in the modified environment."

In a previous paper (Drake et al., 1996), it was shown that the seasonal mean values for the relative stimulation of GPP measured at midday varied from a low of 16% in 1993 to a high of 65% in 1988 with an overall average stimulation of 44% by elevated C_a through eight years of exposure (Drake et al., 1996). The stimulation of GPP was correlated with seasonal mean temperature in the range of 28-35 °C (Drake et al., 1996) suggesting that the effects of elevated C_a on ecosystem photosynthesis integrated through the season are broadly consistent with the response of photosynthesis to temperature at the leaf level. Elevated C_a also stimulated growth of more shoots so that when compared on a ground area basis, elevated C_a stimulated ecosystem photosynthesis by 30% (GPP, Table 2, Figure 2). At the same time, elevated C_a reduced respiration in excised shoots (−36% Table 1) and in the canopy in the field (−36 to −57% Table 2). When the two effects were combined, elevated C_a stimulated NEP 50 and 58% (Table 2).

By our measurements, elevated C_a increased carbon in this ecosystem (Table 2). The additional carbon came as a small increase in aboveground biomass production and a larger increase (35%) in the production of fine roots (Drake et al., 1996). Indirect evidence of higher carbon input to soils in this ecosystem is the higher rates of methane production (Dacey et al., 1994), increased invertebrate activity and increased nitrogen fixation (unpublished results).

Our results show that elevated C_a can substantially increase ecosystem carbon uptake. The challenge now is to find this additional carbon within the soil.

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