Final Report
***Rising CO$_2$ and Long-term Carbon Storage in Terrestrial Ecosystems: An Empirical Carbon Budget Validation* (Grant DE-FG02-97ER62458)**

I. Summary

The primary goal of this report is to report the results of Grant DE-FG02-97ER62458, which began in 1997 as Grant DOE-98-59-MP-4 funded through the TECO program. However, this project has a longer history because DOE also funded this study from its inception in 1985 through 1997. The original grant was focused on plant responses to elevated CO$_2$ in an intact ecosystem, while the latter grant was focused on belowground responses. Here we summarize the major findings across the 25 years this study has operated, and note that the experiment will continue to run through 2020 with NSF support. The major conclusions of the study to date are:

- Elevated CO$_2$ stimulated plant productivity in the C3 plant community by ~30% during the 25 year study. The magnitude of the increase in productivity varied interannually and was sometime absent altogether. There is some evidence of down-regulation at the ecosystem level across the 25 year record that may be due to interactions with other factors such as sea-level rise or long-term changes in N supply.
- Elevated CO$_2$ stimulated C$_4$ productivity by <10%, perhaps due to more efficient water use, but C$_3$ plants at elevated CO$_2$ did not displace C$_4$ plants as predicted.
- Increased primary production caused a general stimulation of microbial processes, but there were both increases and decreases in activity depending on the specific organisms considered. An increase in methanogenesis and methane emissions implies elevated CO$_2$ may amplify radiative forcing in the case of wetland ecosystems.
- Elevated CO$_2$ stimulated soil carbon sequestration in the form of an increase in elevation. The increase in elevation is 50-100% of the increase in net ecosystem production caused by elevated CO$_2$ (still under analysis). The increase in soil elevation suggests the elevated CO$_2$ may have a positive outcome for the ability of coastal wetlands to persist despite accelerated sea level rise.
- Crossing elevated CO$_2$ with elevated N causes the elevated CO$_2$ effect to diminish, with consequences for change in soil elevation.

I. Rationale

The possibility that terrestrial ecosystems may be able to slow the rate of CO$_2$ rise is both intriguing and important to pursue as the world struggles to address the challenges of climatic change. When this work began in 1986, the pressing question was whether rising CO$_2$ would stimulate CO$_2$ assimilation and carbon sequestration in terrestrial ecosystems through direct effects on photosynthesis. Later we tackled the far more difficult question of whether this increase in CO$_2$ assimilation would ripple through the ecosystem carbon cycle to cause a long-term increase in carbon sequestration. As the DOE funding of this project ends, there are now thousands of studies that have demonstrated that elevated CO$_2$ elicits a sustained increase in photosynthesis (Ainsworth and Long, 2005), and we have evidence that a substantial portion of this carbon is sequestered as soil organic matter in our tidal wetland ecosystem.

There are myriad feedbacks on carbon cycling that involve plant and microbial physiology, biogeochemistry and other physical and ecological interactions. As a result, increases in photosynthesis can either increase or decrease soil carbon pools (Jastrow et al.

2005), although a small increase in soil carbon is more common. Elevated CO_2 generally enhances plant growth, but growth responses are also highly variable (Lloyd and Farquhar 1996; Owensby et al. 1999; Oren et al. 2001; Nowak et al. 2004). Many of these feedbacks are mediated by microbial communities and microbial-plant interactions.

Nitrogen and water availability are key regulators of plant and microbial responses to elevated CO_2 in upland ecosystems (Curtis and Wang 1998; Geiger et al. 1999; Owensby et al. 1999; Henry et al. 2005) and our analysis of long term data suggests that this generalization applies to a tidal marsh ecosystem exposed to elevated CO_2 for two decades. However, the precise mechanisms at work in this wetland ecosystem can sometimes be quite different from other terrestrial ecosystems. A primary objective of work has been to unravel how elevated CO_2, rainfall, salinity, nitrogen, sea level, and soil elevation interact to regulate carbon assimilation by plants and carbon mineralization by microbes in this ecosystem.

Tidal wetlands sequester soil carbon 10-times faster on an area basis (i.e. per m^2) than any other type of wetland or upland ecosystem (Bridgham, Megonigal and others, in review). This is due to the combined affects of soil saturation, high sedimentation rates, and constant burial due to sea level rise. Despite their relatively small area, soil carbon sequestration in tidal wetlands has been conservatively estimated at 43 Tg C yr^{-1} globally (Chmura et al. 2003). The rate of carbon sequestration in coastal wetlands has increased in the past century, possibly in response to elevated CO_2 and nitrogen deposition (Choi and Wang 2004). If so, soil carbon sequestration in tidal wetlands is upwards of 2% of the annual rate of atmospheric CO_2 rise. This rate of sequestration may double by the end of the 21st century provided that coastal ecosystems can keep pace with accelerating sea level rise. A second objective of our work was to test the interesting possibility that elevated CO_2 will favor the persistence of tidal wetlands by increasing soil elevation. In fact, this was the central hypothesis of a major expansion of the Smithsonian Climate Change Research Facility that took place in 2005.

If coastal wetland area can be maintained as sea level rise accelerates, these ecosystems will serve as increasingly significant sinks of atmospheric CO_2. They will also continue to improve water quality in adjacent estuaries, provide nursery habitat for commercially important fish and shellfish populations, and protect coastal communities against storm surges. In order to understand the extent to which these systems will continue to sequester carbon, we need to understand how they will respond to multiple interacting factors that feedback to control surface elevation (Fig. 1). Our research was focused on two particularly important global change factors, rising atmospheric CO_2 and N eutrophication, which were installed in two phases.

II. Experimental Design
A. Phase I: Long-Term Ecosystem Response to Elevated CO_2

Since May of 1987, we have operated 30 open top chambers in a brackish marsh on the Rhode River, a sub-estuary on the western shore of the Chesapeake Bay. The study site is in the high marsh zone and is representative of brackish high marshes of Mid-Atlantic North America (Jordan and Correll 1991). Dominant plant species in the high marsh are *Scirpus olneyi* and *Spartina patens*. Open top chambers have been used to expose vegetation to elevated CO_2 in a *S. olneyi*-dominated site, a *S. patens*-dominated site, and a mixed site with both *S. olneyi* and *S. patens* (Drake et al., 1989). *S. olneyi* is a perennial C_3 sedge that is less salt tolerant than co-occurring C_4 grasses. *S. patens* is a C_4 perennial grass with relatively high salt tolerance. We secured funding from NSF to continue this long-term elevated CO_2 study as the backbone of the Global Change Research Wetland.

Within each community, we established fifteen 0.47 m^2 circular plots in a randomized block design with three treatments per block (Curtis *et al*., 1989). One chambered plot per block is ventilated with ambient air and another with ambient air + 340 ppm CO_2. The last plot in each block has no chamber but is otherwise treated like the chambered plots. Since 1987, CO_2 exposure began each year when as plants emerged in the spring and continued 24 hours per day through autumn senescence. There were no significant initial differences in the biomass of the three treatments in each community (Arp *et al*. 1993).

The soils at this site are organic (80% organic matter) to a depth of 5 m. The great depth of the organic horizon suggests that the soil surface elevation of this wetland has kept pace with sea level rise for about 5,000 yr. The

Fig. 1. Conceptual model of the multiple interacting factors that impact the key variable soil surface elevation. This model is guiding a large research program funded by the USGS Climate Change Program (see supporting letters), that includes the marsh elevated CO_2 site. More detail is in the section on scaling (**D6**).

high marsh zone where the study is located is 40-60 cm above mean low water level and is inundated ~2% of the time. Salinity averages 10 ppt and varies widely with precipitation. Local sea level rising is 3-4 cm per decade (Najjar et al. 2000).
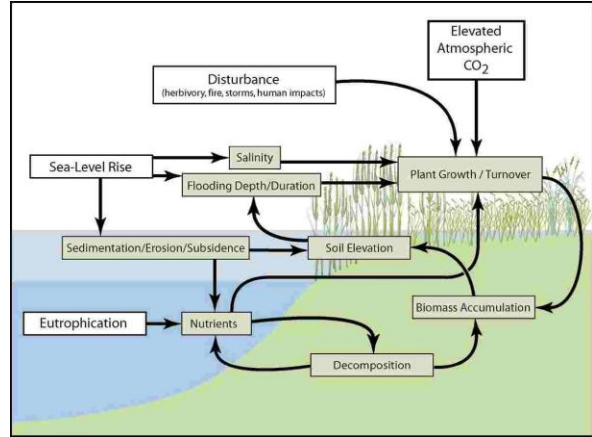
B. Phase II: Soil Elevation Response to Elevated CO_2 and Nitrogen

We completed the construction of a major expansion of the Smithsonian Climate Change Facility that adds 20 open top chambers to the C_3-dominated plant community. This new phase of the experiment is supported by DOE and USGS, and is designed specifically for detailed belowground studies. The experiment is a full cross between two levels of CO_2 and two levels of nitrogen. The nitrogen treatment allows us to test hypotheses to explain dramatic inter-annual variations in C:N ratios, down regulation, and elevated CO_2 effect on photosynthesis and primary production.

III. Major Results
A. Plant Responses
A1. *Leaf and Ecosystem Gas Exchange*

The primary target of CO_2 is photosynthesis and in most C_3 plants (and some C_4 plants) this process is stimulated in leaves exposed to elevated CO_2. Early observations noted that after some time in elevated CO_2, the rate of photosynthesis declined, a phenomenon called acclimation. We have shown that acclimation occurs in the dominant C_3 sedge, but that it does not eliminate a strong increase in leaf level photosynthesis at 2-times ambient [CO_2] (Jacob and Drake, 1994). Acclimation caused a 50% reduction in total protein concentration and in Rubisco.

Table 1. The effect of elevated atmospheric CO_2 on net ecosystem gas exchange (NEE) and two parameters related to acclimation (V_{cmax} and J_{max}). Stimulation is [(E-A)/A] * 100. Negative values mean that the value in elevated CO_2 is smaller that the value in normal ambient CO_2.

		Stimulation (%)		
Year	Rainfall (cm)	NEE	V_{cmax}[1]	J_{max}[2]
2001	138	30	-35	-24
2003	219	55	-18	-16

[1]maximum carboxylation rate
[2]estimated light harvesting capacity

There appears to be large inter-annual variation in acclimation that can be related to variation in rainfall and soil water salinity. During droughts acclimation tends to be more intense (i.e., the CO_2 effect on V_{cmax} is greater) and this may have resulted in a greatly reduced CO_2 stimulation of photosynthesis and NEE compared to wet years (Table 1).

A2. Ecosystem Gas Exchange

Using the open top chamber as a cuvette, we measure the effect of elevated CO_2 on net ecosystem gas exchange (Fig. 2). Annual NEP data were consistent with our limited photosynthetic acclimation data (see Table 1) in that we expected to see little stimulation of NEP in those years of particularly low rainfall when acclimation was more intense (e.g. 1995, 1999). What is somewhat surprising, however, is that these data are inconsistent with a greater relative

Fig. 2: Annual net ecosystem exchange of CO_2 (NEE) and peak shoot biomass of *S. olneyi* (C_3) under ambient (open circles) and elevated CO_2 (filled circles). Dotted red lines represent years of relatively low precipitation (From Rasse et al. 2005).

stimulation of shoot biomass (described below) at our site and that reported by others during years of relatively low precipitation (Owensby et al. 1999). This suggests that drought does not interact with the effects of elevated CO_2 on photosynthesis in the same way it interacts with CO_2 effects on shoot density and biomass accumulation.

A3. Primary Production

The effects of elevated CO_2 and precipitation on biomass production of *S. olneyi* in the *Scirpus*-dominated community at our field site are presented in Fig. 3, which illustrates several salient points. First, as with NEE and acclimation, we found substantial variability in shoot production, ranging over 3-fold during 18 years of data collection. Even one year to the next the range was as much as 2-fold. Second, elevated CO_2 stimulated biomass in every year, averaging about 35% throughout the study. Finally, shoot biomass production declined in years of relatively low rainfall (red dotted lines; seasonal average precipitation 40 cm) compared to wet years (seasonal average precipitation 71 cm) when biomass production was relatively high. Because of the high salt-tolerance of *S.*
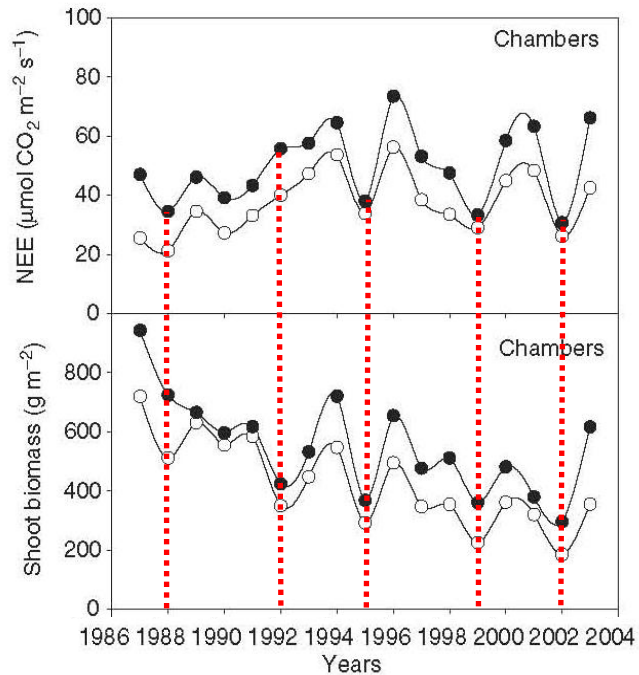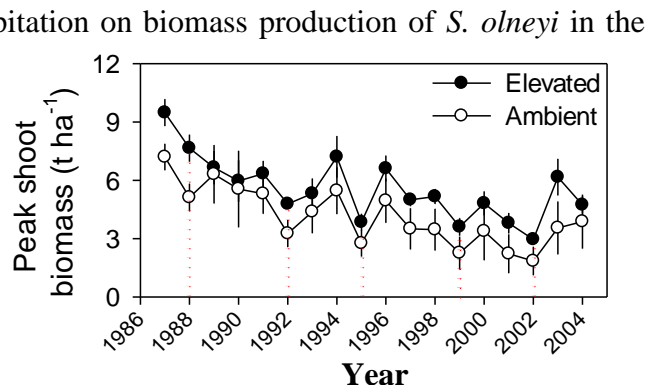

Fig. 3: Annual peak shoot biomass of *S. olneyi* (C_3) under ambient (open circles) and elevated CO_2 (filled circles). Dotted red lines represent years of relatively low precipitation.

patens, the influence of precipitation on biomass was not as pronounced as for *S. olneyi.* Nevertheless, *S. patens* biomass tended to be less in years of relatively low precipitation.

Due to greater declines in C_3 biomass production in response to reduced precipitation, we found a substantial shift in the fraction of C_3 biomass relative to C_4 biomass in the community where both species coexisted (Fig. 4). Elevated CO_2 favored C_3 shoot production during both wet and dry years, but this effect was strongly mediated by precipitation. The combination of elevated CO_2 and high precipitation favored C_3 dominance, while ambient CO_2 and low precipitation favored C_4 dominance. While these data are intriguing and suggest that climate change (i.e. increased precipitation and increased CO_2 as predicted for the northeastern US; IPCC, 2001) may lead to a shift in ecosystem diversity, we cannot predict such an outcome with much certainty until we have a mechanistic understanding of the observed results. In any case, precipitation clearly interacts with elevated CO_2 in this ecosystem.
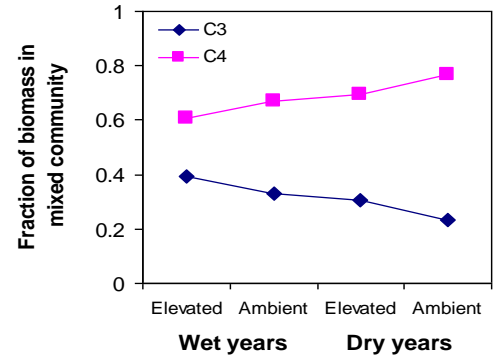

Fig. 4: Fraction of annual shoot biomass as C_3 or C_4 under ambient and elevated CO_2 averaged across wet and dry years.

A4. Precipitation, Salinity and Primary Producton

The manner in which precipitation affects biomass production in this ecosystem is not entirely clear. Because the system is a tidally-influenced wetland, the soil is always saturated to within a few cm of the soil surface and water availability *per se* is not limited. Thus, the influence of precipitation is likely to act indirectly through its effects on salinity in the nearby tidal creek and soil porewater.

Unlike some coastal wetland plant communities that are directly influenced by sea water and have little fresh water inflow (e.g., Morris et al. 1990), the Chesapeake Bay has 150 tributaries that drain over 16 million ha, covering much of the northeastern United States (White 1989). This precipitation-driven freshwater inflow has dramatic effects on the salinity environment of marsh plants. In fact, average salinity of the Rhode River (<1 km from our site) is strongly and negatively related to precipitation received during the growing season (Fig. 5). Salinity declines approximately 1 ppt for each 10 cm increase in precipitation. Thus, changes in precipitation in the northeastern United States will influence salinity in wetlands of the Chesapeake Bay, affecting plant production and causing shifts in species composition and abundance. Given the strong correlation between precipitation and salinity, and the likelihood that the effects of precipitation on plant function are mediated through salinity, we will refer to salinity throughout the rest of the report, recognizing that precipitation is the dominant driver of salinity in this system.
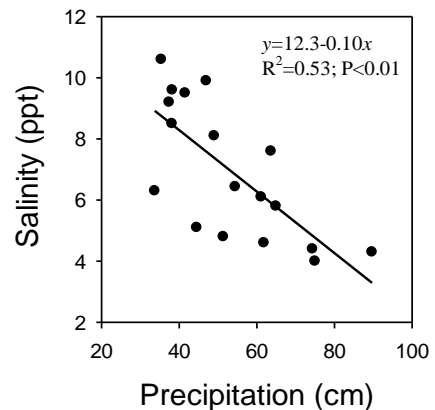
Reduced soil moisture and increased salinity often lead to similar physiological 'drought response' adjustments in plants due to water stress (Munns 2002; Merchant and Adams 2002). For this reason, the relationship between productivity and rainfall observed here has also been reported in

Fig. 5: Relationship between mean tidal creek salinity and total precipitation at the site during the growing season.

other upland terrestrial ecosystems such as grasslands (Tolley and Strian 1984; Owensby et al. 1993, 1999). However, the mechanisms that control these responses are likely to be quite different in the two systems. In tidal wetlands, salinity may be causing ions to build up in plant tissues, which can injure cells and disrupt metabolic processes (Munns 2005). Salt-tolerant plants, such as those in this marsh, have mechanisms for coping with relatively high levels of salt (Flowers and Yeo 1986, Husain et al. 2004). Such mechanisms can regulate growth in saline environments and they affect plant abundance in tidal wetlands (Rozema and Van Diggelen 1991; Pennings et al. 2005). Still, growth is best at relatively low salinities even in halophytes (Rasse et al. 2005). For example, Broome et al. (1995) found nearly a 75% decline in aboveground biomass of *S. olneyi* across a salinity gradient from 0 to 20 ppt. Effects of elevated CO_2 on plant growth depend on the extent to which elevated CO_2 can ameliorate these salt-induced effects on plant function (Rozema et al. 1991; Ball et al. 1997).

A5. Interactions Between Elevated CO_2 and Salinity

Differences in the elevated CO_2 growth response during years of high versus low salinity (Fig. 6) has led to our recent interest in gaining a better understanding of how multiple climate factors affect physiological processes, plant growth and ecosystem function. We found complex interactions between salinity and elevated CO_2 for plant growth. Specifically, the effects of elevated CO_2 on C_3 shoot biomass were greater during high salinity versus low salinity years (Fig. 6). Although CO_2 stimulation of C_3 shoot biomass was greater at high salinity, stimulation of annual root growth was lower. In addition, a significantly greater disparity in C_3 tissue [N] was seen in low salinity years. The C_4 species showed no CO_2 effect during low salinity years and a negative effect during high salinity years. Reasons for a relative decline in shoot

Fig. 6: Elevated CO_2 effects on biomass production and tissue nitrogen concentration in a C_3 plant (right) and a C_4 plant (left) during years of low salinity (open bars) and years of high *salinity (filled bars).*

growth of the C_4 grass at elevated CO_2 and high salinity are unclear, but Rozema et al. (1991) report a similar reduction in growth of *S. patens* under elevated CO_2. In any case, elevated CO_2 appeared to be of no benefit, and perhaps a detriment, for *S. patens* growth during years of high stress (Housman et al., in press).
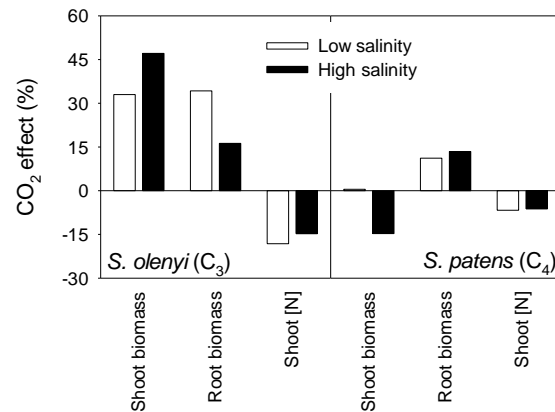
A6. Interactions with Rising Sea Level

Sea level has risen over 10 cm at our site since the onset of the study, allowing us to observe in real time the interaction of elevated CO_2, sea level, biomass production and species composition (Fig. 7). *S. olneyi* shoot biomass increased in proportion to mean sea level, while the biomass of C_4 grasses decreased in proportion to mean sea level. This corresponds to changes in the relative biomass of C_3 and C_4 species with precipitation reported in Fig. 4.

Interactions between mean sea level and elevated CO_2 affected primarily *S. olneyi* shoot production. In the mixed community, elevated CO_2 stimulated *S. olneyi* shoot biomass at low mean sea level (Fig. 7). In contrast, the effects of elevated CO_2 were greatest during high water level years in the *Scirpus*-dominated community (data not shown). This seemingly contradictory response of *S. olneyi* shoot biomass to elevated CO_2 and sea level may reflect the influence of elevation. Because the *Scirpus*-dominated community already occupies low areas in the marsh, an increase in flooding may cause flooding stress. The mixed community occupies higher elevations in the marsh that support *S. patens*, which is more sensitive to flooding than *S. olneyi*. Thus, an increase in flooding in the mixed community may release *S. olneyi* from competition with *S. patens* (Saunders et al. 2006). Interestingly, the relative effects of elevated CO_2 on *S. olneyi* growth were greatest when biomass production was smallest, reflecting a general pattern of greater CO_2 effects on C_3 growth under stressful conditions (Luo and Mooney 1999).
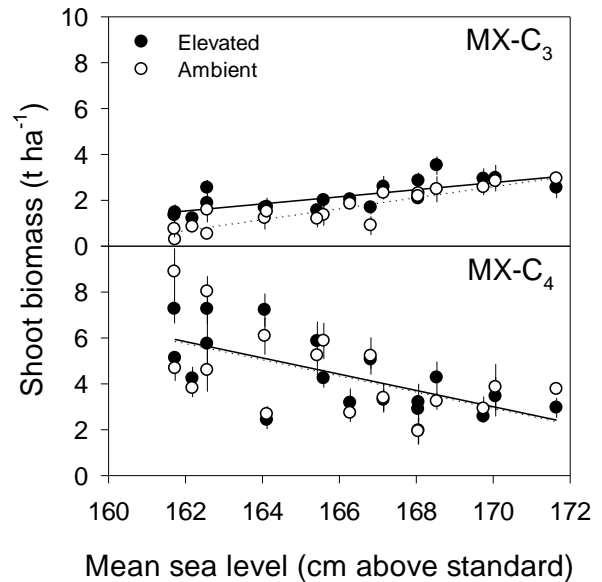

Fig. 7 Shoot biomass production as a function of seasonal mean sea level (MSL) in the mixed-species community. A significant CO_2*MSL interaction ($P<0.05$) was found for the C_3 species.

A7. *Interactions of Precipitation, Salinity and Tissue Nitrogen Content*

Elevated CO_2 significantly reduced shoot [N] over 18 years (Fig. 8). As with biomass, this affect varied with salinity (Fig. 6). For example, during the relatively low salinity years of 1989, 1996 and 2000 (salinity ~4.7 ppt), *S. olneyi* shoot [N] averaged 8 mg g^{-1} across all plots, but averaged 12 mg g^{-1} during the high salinity years of 1988, 1995 and 1999 (~9.8 ppt). Thus, we generally found low shoot [N] in years where biomass production was high and salinity was low (and vice versa).

Relative effects of elevated CO_2 on *S. olneyi* shoot [N] were variable (Fig. 8, lower panel), and this variability was also related to salinity. For instance, the largest relative effects of elevated CO_2 occurred during years of high growth and low salinity (e.g., 1989, 1996, 2000), while relatively small CO_2 effects on shoot [N] were found in low growth, high salinity years (e.g., 1988, 1995, 1999). Thus, years of high plant growth were also years when the CO_2 stimulation of shoot biomass was low, CO_2 depression of tissue [N] was large and soil [NH_4] was low (Matamala and Drake 1999), all of which indicates possible constraints by soil N availability. Still, the implications of variability in
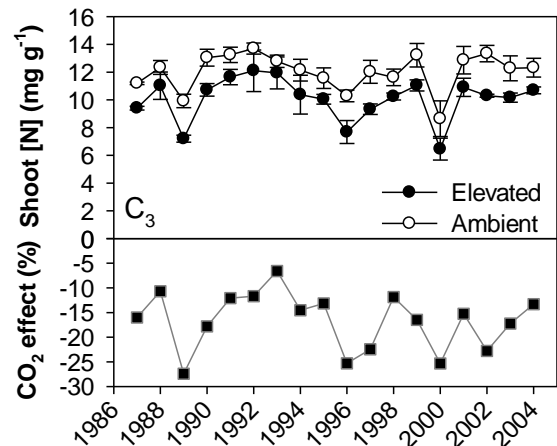

Fig. 8. Variation in the effect of elevated CO_2 on shoot [N]. Years with high shoot [N] correspond to years of low growth and high salinity. The bottom panel shows that absolute [N] was lowest in years that N dilution due to elevated CO_2 was greatest. Data are from the *Scirpus*-dominated site.

tissue N concentration and CO_2 depression of tissue N for ecosystem carbon assimilation, plant growth and decomposition remain unclear. Addressing these interactions is a primary objective of our proposed research.

A8. Elevated CO_2 Effects in Eutrophic Estuarine Environments

Through fossil fuel combustion and agricultural activities, humans have increased the rate of N cycling in the biosphere (Vitousek et al. 1998). All ecosystems experience some amount of anthropogenic N inputs, and regional increases can be enormous. In addition to experiencing direct atmospheric N deposition, estuarine systems may also be subject to increased N loading by drainage or tidal influx, originating from agricultural and wastewater runoff (Morris 1991). Inputs from the latter sources can far eclipse even high atmospheric deposition rates rendering intertidal marshes like ours inordinately susceptible to vast human-induced changes in N loading (Jordan et al. 1983). Nitrogen additions typically increase growth of salt marsh plants (Tyler et al 2003), yet the influence of N-fertilization on net carbon sequestration in marshes has not been examined explicitly to our knowledge.

Although N fertilization and elevated CO_2 both stimulate plant productivity, each perturbation has unique effects on plant physiology that may lead to distinctive influences on ecosystem carbon sequestration and could reveal mechanisms underlying carbon accumulation. Fertilization has been shown to increase soil accretion in a low marsh by stimulating plant growth which thereby increases sediment trapping (Morris 2002). However, the high marsh at our site has an organic soil with very low mineral sediment deposition rates. In this system, the dominant mechanisms that affect ecosystem carbon storage will originate from internal processes, namely the balance of productivity and decomposition. N additions should increase plant production but the potential influence of N additions on decomposition is currently unclear. Recent studies have suggested that N fertilization tends to slow decomposition more recalcitrant carbon pools by suppressing microbial enzyme activity (Waldrop et al. 2004, Knorr et al. 2005).

B. Soil Pools and Decomposition

B1. State of the Carbon Budget

A primary goal of our work during the past several years has been to track the fate of the 'extra' carbon assimilated by the elevated CO_2 treatment in this long-term study. We hypothesized that the carbon could be found sequestered as: (1) perennial root biomass, (2) soil organic matter or (3) the surface litter layer. We also considered the possibility that carbon was exported from the system in several flux streams: (1) winter respiration (which we do not normally measure), (2) dissolved inorganic or organic carbon export, or (3) CH_4 emissions.

Elevated chambers had a larger root biomass pool and supported more winter respiration (Marsh et al. 2005), but there is still a large imbalance that cannot be explained (Table 2). One possibility that we can now dismiss is dissolved carbon export from the chambers in groundwater (Marsh et al., 2005). Horizontal groundwater flux is negligible at our site. To address changes in the soil carbon pool, we extracted two 1 m-deep piston cores from each chamber and found there was no treatment difference

Table 2. Estimates of the excess carbon source and sinks for the period 1988 to 1999.

Excess C Budget Term	Kg C
Source	4.6
Sinks Measured	
Shoot Biomass	0.0
Soil Organic Matter	0.0
Root Biomass	0.5
Winter Respiration	0.4
Methane Emissions	<0.01
Hydrologic Export	0.0
Vertical Accretion	*2.3-4.6*
Total Sinks	0.9
Remaining Missing Sink	3.7

in carbon concentration. However, we did not account for the possibility that the soil surface has risen due to higher shoot and root productivity. In the course of this work, we realized that the last possible sink to be investigated was an increase in the soil organic matter content that manifests as a rise in the soil surface elevation. We began a new field experiment to quantifying this response and found that elevated CO2 does indeed cause an increase in soil elevation that can explain 50-100% of the missing carbon uptake (Table 2). See further discussion of the elevation data in section B4.

B2. Porewater H_2S

There is no appreciable groundwater dilution of porewater solutes such as H_2S at our site. In addition, the soil lacks iron minerals to remove H_2S from marsh porewater. Given that H_2S is toxic to plants and can interfere with nitrogen uptake, we measure $[H_2S]$ in monthly porewater collections (data not shown). $[H_2S]$ tends to be higher in the elevated CO_2 treatment, but the differences are small. Perhaps more importantly, $[H_2S]$ are lower in low rainfall years (e.g. 2002) than high rainfall years (e.g. 2003). These data suggest that changes in $[H_2S]$ do not explain the interannual variation in plant growth we observed (Fig. 3).

B3. Priming Effects on Soil Organic Matter Decomposition

We have a variety of evidence that a portion of the excess carbon produced in response to elevated CO_2 is supporting heterotrophic processes such as nitrogen fixation (Dakora and Drake, 2000), CH_4 emissions (Dacey and Drake, 1994), sulfate reduction (Keller et al., in prep; Wolf et al., in prep) and microbial respiration (Ball, 1996). By extension this means some of the excess carbon is in belowground pools where it supports microbial respiration and decomposition.

Carbon flow into fast-cycling pools can affect slow-cycling soil carbon pools via the so-called priming effect. A *priming effect* is defined as a short-term change in the soil organic matter decay rate caused by a perturbation of the supply of nutrients, organic carbon, or other chemical and biological factors (Kuzyakov et al 2000, Kuzyakov 2002). In the case of elevated CO_2 responses, priming effects occur when the CO_2 treatments change the rate of pre-treatment or 'old' soil organic matter decomposition. The literature on elevated CO_2 priming effects is growing, and it promises to reveal unique and important insights on microbial responses to elevated CO_2. These responses will certainly feedback on soil carbon sequestration.

Interestingly, the literature on priming effects suggests that rising CO_2 may both increase and decrease decomposition of 'old' soil organic matter. For example, elevated CO_2 retarded decomposition of the slow-cycling soil organic carbon pool in a California grassland (Cardon et al., 2001), a response that would enhance the soil carbon sequestration. However, a stimulation of organic matter decay is a more common response to increased plant growth (Cheng and Kuzyakov, 2005) and is likely under CO_2 in many ecosystems.
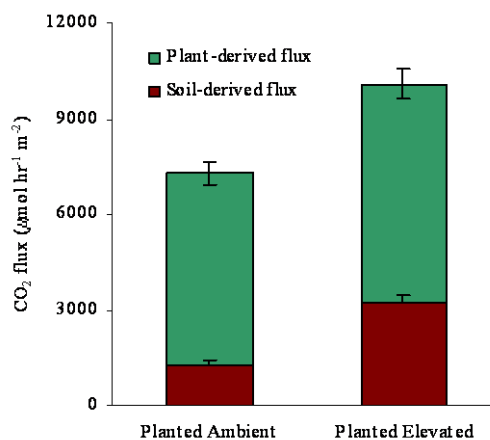

Fig. 9. Stable isotopes were used to separate CO_2 derived from 'new' plant matter versus 'old' soil organic matter. Elevated CO_2 increased in soil organic matter mineralization by 157% and plant respiration by 12% (Wolf et al., in preparation).

In a greenhouse study, we found that exposing *S. olneyi* (the dominant C_3 plant) to elevated CO_2 increased soil organic matter mineralization by 7-fold compared to ambient CO_2 (Fig. 9). Similar results have been observed in uplands. In a poplar plantation, elevated CO_2 simultaneously increased inputs of 'new' soil carbon and losses of 'old' carbon (Hoosbeck et al., 2004). Such an effect is one explanation for why elevated CO_2 has achieved only modest increases in soil carbon (about 15% overall; meta-analysis by Jastrow et al. 2005) and even small net losses (Dijkstra et al. 2005, Pendall et al., 2004). This raises an intriguing question: *will increased carbon inputs due to enhanced plant growth be offset by more rapid carbon processing by microorganisms?* Given the fact that the 'old', existing soil carbon pool is about twice the size of the atmospheric carbon pool, it is important to understanding the mechanisms through which priming occurs. This question is particularly compelling for tidal wetland systems where the soil organic pool contributes to the accretion of new soil that allows the system to keep pace with rising sea level.

Although an increase in soil organic matter decomposition has been observed in upland systems, it is likely that the mechanism for this response at our site has features that are unique to wetland ecosystems. For example, we observed a positive relationship between soil redox potential and root biomass in a greenhouse experiment with S. *olneyi* grown under elevated CO_2 (Fig. 10). This result suggests that the increase in soil organic matter decomposition may have been caused by a shift in microbial community activity. Specifically, the larger root systems of the elevated CO_2 plants may have increased O_2 transport from the atmosphere to the soil via specialized vessels called aerynchyma. This would explain the increase in redox potential. The increased supply of O_2 would have supported greater aerobic decomposition, which is inherently more efficient than anaerobic decomposition (Megonigal et al. 2004). An alternative possibility is that the increased O_2 supply helped activate phenol oxidase enzymes, which have been shown to exert latch-key control over decomposition in peatlands (Freeman et al. 2001).
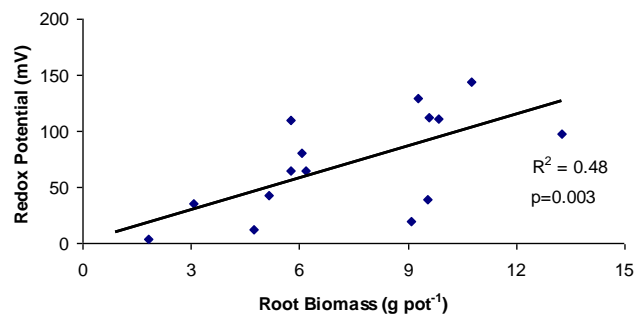

Fig. 10. The relationship between redox potential and root biomass in an elevated CO_2 experiment with *Scirpus olneyi*. Elevated CO_2 plants tended to have larger root biomass and redox potentials, indicating more oxidized conditions than at ambient CO_2.

B4. Elevation Change. In 2005 we completed a major expansion of the Smithsonian Climate Change Research Facility. There are 20 new open-top chambers added to the site, bringing the total to 50. All of the new chambers are in the C_3-dominated plant community. The experimental design is a full cross of two levels of CO_2 (ambient, ambient+360 ppm) and two levels of nitrogen deposition (ambient, ambient+25 g N m^{-2}). The nitrogen treatment will test hypotheses that explain certain puzzling interactions we observed between precipitation, elevated CO_2 and plant tissue nitrogen content (Fig. 8). In addition, it will simulate nitrogen eutrophication, a common disturbance in coastal estuaries (Fig. 1).

The new chambers are 2.0 m-diameter (3.1 m^2 area) and nearly four times larger than the existing chambers. They will accommodate more destructive belowground sampling than the existing chambers and allow detailed measurements of changes in soil surface elevation, a

keystone response variable.

One-half of the plot area were set aside for soil elevation measurements using Soil Elevation Tables (SETs). SETs consist of a stainless steel USGS benchmark rod driven to the point of rejection (7 m at this site), on top of which is mounted an aluminum measurement arm that extends horizontally across the marsh surface (Fig. 11). The arm can be precisely oriented and leveled each time it is deployed, and therefore serves as a stable reference for measuring the elevation of the soil surface. Surface elevation will be measured by lowering 100 fiberglass pins to the soil surface and measuring the distance they fall. Half of the pins are outside the chamber in a no-chamber control plot. Each plot (chamber & control) will have three 'shallow SET pipes' that permit us to isolate treatment effects occurring in the root zone from the remainder of the soil profile. Our SET design is modified from of design that is widely used in tidal wetlands (Cahoon et al. 2002). In addition to the SET measurements, the plots allow routine monitoring of soil water chemistry, shoot biomass, root growth and net ecosystem exchange using the same protocols as for the Phase I plots (Fig. 11).

Our previous work successfully eliminated several potential C sinks that could explain the large imbalance in the C_3 elevated CO_2 carbon budget. We quanitifed shoot and root biomass, soil organic carbon density (i.e. carbon content x bulk density), hydrologic export and several other potential carbon sinks (Table 2). The last remaining sink to quantify was an increase in soil elevation. We found that elevated CO_2 increased soil carbon sequestration (Langley et al. 2009), which appeared as an increase in soil elevation (Figure 12). The increase in soil elevation was sufficient to explain about half of the 'extra' carbon that we sought (Table 2).
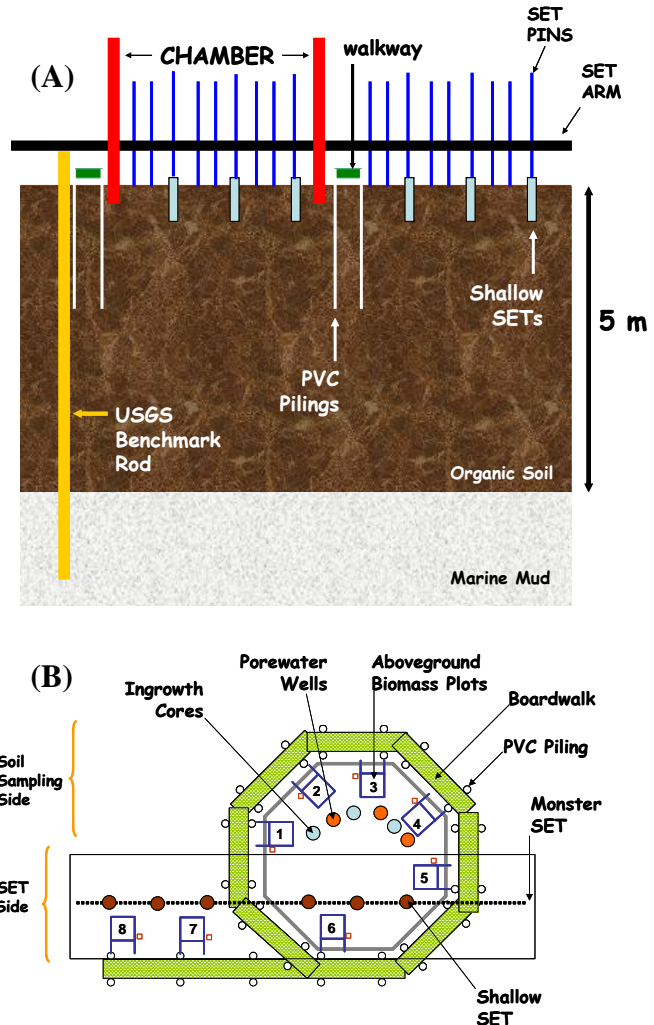
Fig. 11. Side view (panel A) and top view (panel B) of new 2 m-diameter plots for measuring changes in soil surface elevation in response to elevated CO_2 and nitrogen. The treatments will start in spring 2006. The SET has 100 pins. Half the plot is dedicated to SETs.

C. Summary

Coastal wetlands have the potential to sequester soil carbon faster than any other terrestrial ecosystem because of rising sea level (Chmura et al. 2003), and currently account for perhaps 2% of the estimated terrestrial sink for anthropogenic CO_2 emissions (Schlesinger 1997).
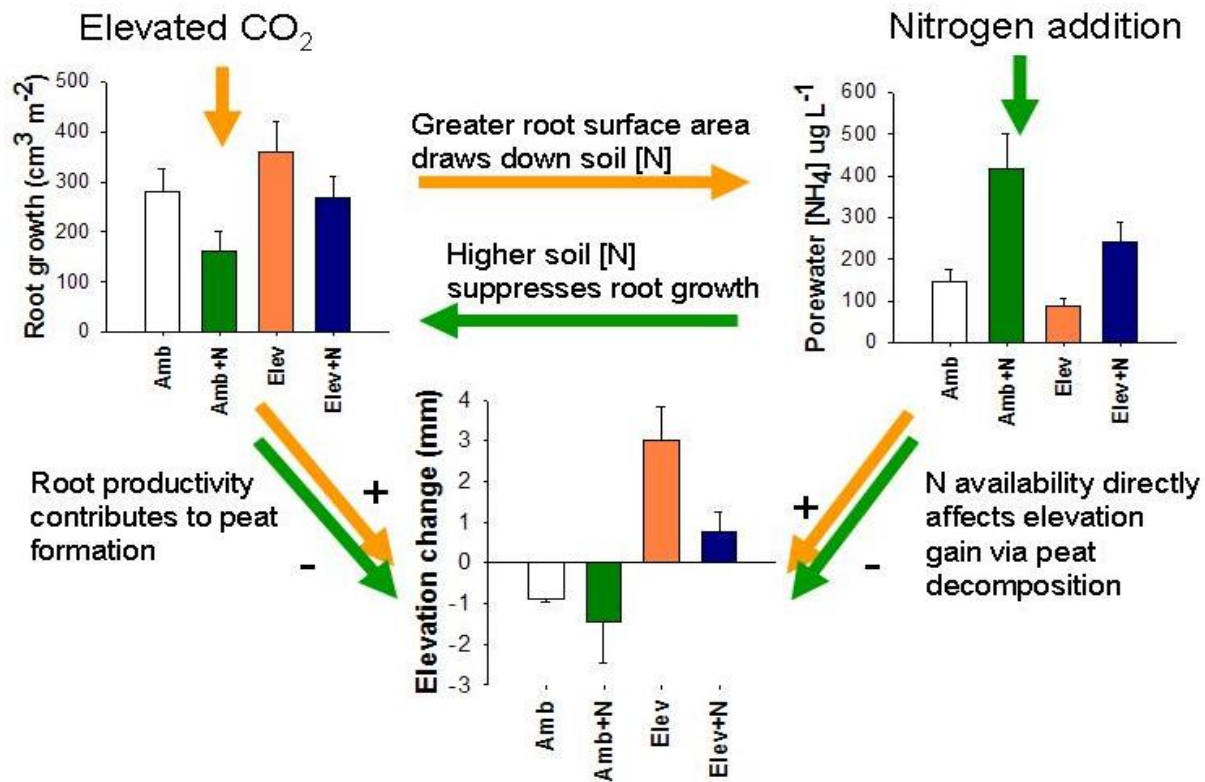
Fig. 12. Summary of results from a new 'long-term' study of elevated CO_2 and elevated N at the Global Change Research Wetland.

This rate will double with increased rates of sea level rise, which enhances detritus burial by increasing sediment deposition and reducing aerobic decomposition. Thus, coastal wetlands may provide an example of a negative feedback on global warming because the faster sea level rises the faster they sequester carbon. However, this feedback will only occur if the wetland can keep pace with sea level rise by accreting new soil surface. A wetland that cannot accrete at the same rate as sea level is rising will eventually break apart, and carbon sequestration will decline because of the loss of plant productivity. Because 70% of the world's population lives in coastal environments, the importance of carbon sequestration to the persistence of these systems impacts the economic well being, quality of life and the safety of many people.

Our long term goal was to determine the capacity of a terrestrial ecosystem to dampen the rate of CO_2 rise in the atmosphere by sequestering carbon in slowly-cycling pools. It has become clear over the 20 years of this study that answering this question requires a much better understanding of the physical, chemical and geomorphological characteristics of the system. With insights from the long-term interactions of these factors and elevated CO_2, we feel we were able to solve a number of puzzling patterns in the data. These include the great inter-annual variability in the CO_2 effect on photosynthesis and biomass, and the fate of the missing C we surmise from our NEE measurements. Our overall conclusion is that elevated CO2 will cause a large and persistent stimulation of plant productivity, increasing carbon sequestration from the atmosphere.

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