The temperature sensitivity of organic matter decay in tidal marshes

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Abstract

Approximately half of marine carbon sequestration takes place in coastal wetlands, including tidal marshes, where organic matter contributes to soil elevation and ecosystem persistence in the face of sea level rise. The long-term viability of marshes, and their carbon pools, depends in part on how the balance between productivity and decay responds to climate change. Here, we report the sensitivity of labile soil organic matter decay in tidal marshes to seasonal and latitudinal variations in temperature measured over a 3-year period. We find a moderate increase in decay rate at warmer temperatures (3-6% per °C, Q_{10}=1.3-1.5). Despite the profound differences between microbial metabolism in wetlands and uplands, our results indicate a strong conservation of temperature sensitivity. Moreover, simple comparisons with organic matter production suggest that elevated atmospheric CO_2 and warmer temperatures will accelerate carbon accumulation in marsh soils, and potentially enhance their ability to survive sea level rise.

1 Introduction

Coastal marshes are among the most productive ecosystems on Earth and bury carbon at rates approximately an order of magnitude faster than terrestrial forest soils on a per area basis [*Duarte et al.*, 2005]. The high productivity of marsh vegetation protects coastal regions by dissipating energy associated with storms, traps mineral sediment and pollutants, supports marine fisheries, and sequesters carbon [*Barbier et al.,* 2011]. However, marshes are submerging at rates faster than they can transgress inland in several regions of the world, and there is widespread concern over their ability to survive faster rates of sea level rise in the future [*Kirwan et al.,* 2010]. Organic matter accumulation is a primary mechanism regulating marsh elevation, particularly in the sediment-deficient estuaries most vulnerable to sea level rise [*Turner et al.,* 2000, *Langley et al.*, 2009, *Nyman et al.*, 2006, *Neubauer* 2008]. Thus, the fate of these ecosystem services under future sea-level rise depends largely on the balance between organic matter production and decay, and how it will respond to climatic warming and other global change drivers.

Complex interactions between soil elevation relative to sea level and vegetation characteristics control the response of coastal carbon pools to climate change [*Kirwan & Mudd* 2012, *Langley & Megonigal* 2010]. Long term elevated CO_2 experiments demonstrate a sustained increase in belowground organic matter production [*Erickson et al.,* 2007], and an increase in the rate of marsh elevation gain that can counteract the effects of sea level rise in brackish marshes dominated by C_3 plants [*Langley et al.*, 2009]. Warming may have a similar impact on salt marshes dominated by C_4 plants, where enhanced aboveground productivity would presumably lead to enhanced mineral sediment deposition [*Charles & Dukes*, 2009; *Kirwan et al.,* 2009; *Gedan et al.*, 2011; *Mudd et al.*, 2010]. Moderate increases in flooding frequency associated with sea level rise may increase rates of above and belowground productivity in both salt and brackish marshes [*Morris et al.*, 2002; *Kirwan & Guntenspergen* 2012] without altering decomposition rates [*Blum & Christian*, 2004; *Kirwan et al.*, 2013]. Together, these processes may increase the amount of carbon buried in the coastal zone over the next few decades [*Kirwan & Mudd* 2012].

Accelerated rates of soil organic matter decomposition largely offset increases in biomass production associated with elevated CO_2 and warmer temperatures in terrestrial ecosystems [*Davidson & Janssens* 2006, *Conant et al.*, 2011]. However, the extent to which warmer temperatures accelerate decomposition in wetland ecosystems is virtually unknown. Many terrestrial ecosystems yield a similar temperature sensitivity (Q_{10}=1.3-1.5) for ecosystem respiration [*Mahecha et al.,* 2010]. Preliminary experiments designed to measure decomposition sensitivity to warming in marshes have yielded results ranging from no sensitivity [*Charles & Dukes*, 2009] to a Q_{10} greater than many terrestrial studies [*Kirwan & Blum*, 2011]. However, these previous studies examined decomposition of aboveground litter placed above the soil surface whereas the organic matter inputs that sustain tidal wetlands and contribute to carbon burial are primarily belowground and subjected to a fundamentally different biogeochemical environment [*Nyman et al.,* 2006; *Cherry et al.,* 2009]. Therefore, a poor understanding of the impact of warming on organic matter decay limits our ability to predict how marshes and their carbon pools will respond to interacting components of climate change.

Here, we use environmental temperature gradients through space and time to assess the temperature sensitivity of decomposition rates in tidal marsh soils and find that apparent Q_{10} values are much lower than previously reported, but consistent with results from terrestrial ecosystems.

2 Methods

2.1 Latitudinal gradient experiment

We estimated the rate of cellulose decomposition at 14 sites along a latitudinal gradient from South Carolina to Nova Scotia. Each site is mesohaline, and located at an elevation where *Spartina patens* and *Schoenoplectus americanus* converge (Figure 1a). The loss of tensile strength in standardized cellulose material, such as cotton strips, is a widely used proxy for labile decay in soils of many ecosystems since cellulose comprises about 70% of the organic material in plants [*Harrison et al.,* 1988; *Mendelssohn et al.,* 1999; *Slocum et al.,* 2009]. The use of a standardized material eliminates variations in substrate quality that potentially influence decomposition, helping to isolate the effect of environmental factors such as temperature across a latitudinal gradient. Following typical cotton strip assay methods for wetlands [*Mendelssohn et al.,* 1999; *Slocum et al.,* 2009], we inserted 2, 30 cm strips of artist canvas into the marsh soil vertically at each site, and left them in the ground for 8-89 days depending on the initial soil temperature (longer for cooler locations) so that the loss of tensile strength ranged between 50 – 75% of their initial tensile strength. Cotton strips were deployed during the middle of each site’s growing season, generally in June or July of each year. Two control strips were installed at the same time as the sample strips but removed immediately. Upon retrieval, each strip was washed in deionized water to remove soil particulate material, and air dried to a constant weight. Strips were then cut into 2 cm increments, and analyzed on a Dillon Quantrol Snapshot tensiometer to measure tensile strength and loss of tensile strength with depth. Soil temperature was measured at 4 cm depth at the beginning and end of each deployment, and averaged together. The experiment was repeated in 2008, 2009, and 2010.

2.2 Seasonal warming experiment

In a second experiment, we deployed bags containing soil organic matter at a single location to measure the influence of seasonal temperature warming on decomposition. This experiment was done at our Blackwater River site (38.41°N, 76.08°E) near the midpoint of the latitudinal gradient. The Blackwater marshes are microtidal (astronomical tides < 50 cm), mesohaline, and dominated by the C_3 macrophyte, *Schoenoplectus americanus.* Following *Kirwan et al.* [2013], decomposition bags were 6 x 6 x 1 cm, constructed of a non-reactive synthetic membrane (Versapor©; Pall Corporation, Port Washington, NY) with 5 um pore size to allow access to water and microbes but prevent exogenous particulate matter, such as roots and sediment, from entering the bags. Each bag contained approximately 3.5 g of *S. americanus* roots and rhizomes. To better understand the effects of organic matter quality on sensitivity of decay to temperature, we used two sources of soil organic matter, each dried at 40°C, milled and homogenized. In one set of experiments, we used *S. americanus* root and rhizome material harvested from a previous mesocosm experiment [*Kirwan & Guntenspergen* 2012]. In the other set of experiments, we used *S. americanus* root and rhizome material collected from the adjacent marshland in February, 2012. Sets of 5 decomposition bags of each organic material source were deployed at approximately monthly intervals from April 11, 2012 through January 7, 2013. Decomposition bags were oriented so that they were exposed to the upper 6 cm of the soil profile. To understand the relationship between cotton strip tensile strength loss and native organic material mass loss, sets of 5 cotton strips were deployed concurrently with the decomposition bags. At the end of each monthly interval, soil organic matter bags and cotton strips were retrieved, dried at 40°C, and weighed to measure mass loss or analyzed for tensile strength loss. Continuous soil temperature measurements were made with Hobo Pendant thermometer data loggers inserted in the soil at 4 cm depth.

2.3 Analytical methods

The decomposition of cotton strip material was calculated as the loss of tensile strength in deployed strips relative to the control strips, and divided by the duration of each experiment (i.e. percent loss per day) [*Slocum et al.,* 2009]. Tensile strength loss measurements in the upper 6 cm of each strip were averaged together to determine an average rate of tensile strength loss near the soil surface (i.e. 0-6 cm) that could be directly compared with mass loss of decomposition bags. Measurements of mass loss in decomposition bags were converted to decay coefficients to account for subtle differences in initial bag weight and duration of experiments. According to exponential decay, the decay coefficient $k = [-\ln(C_t / C_o)]/t$ where Co and Ct are the mass of organic matter at the beginning and end of the experiment, and t is the duration of the experiment. Results from replicate cotton strips and decomposition bags were averaged together, and then compared to soil temperature via regression, assuming an exponential relationship between the decay rate, *k* and temperature, *T* [e.g. *Davidson & Janssens*, 2006]. Analysis of covariance revealed that the relationship between mass loss and soil temperature for the two organic material sources was not significantly different (p=0.87), so data from both sources was combined. We used linear regression to relate loss of tensile strength in cotton strips to mass loss in the decomposition bags for the seasonal warming experiment at our Blackwater study site, and used this relationship to calibrate the latitudinal gradient in tensile strength loss to units of mass loss. Finally, Q_{10} values were calculated according to $Q_{10} = e^{10a}$ where a= ln (k)/T [*Langley et al.*, 2005].

3 Results

In the latitudinal experiment, average soil temperatures during each deployment period varied from 13°C at the Kouchibouguac (Nova Scotia) study site to 29°C at the Blackwater (Maryland) study site (Figure 1). Cellulose strips lost tensile strength at rates ranging from 1.1% day^{-1} to 6.5 % day^{-1}, where the variation was positively and significantly correlated with soil temperature ($r=0.83$, $p<0.01$) (Figure 1b). The relationship between temperature and decay rate was similar in 2008, 2009, and 2010 (Figure 1b).

In the seasonal warming experiment, average soil temperatures ranged from 26.6°C in the July 2012 deployment to 6.8°C in the December 2012 deployment which encompass the temperature range of the latitudinal experiment (Figure 2a). Both indices of decay followed seasonal variations in soil temperature (Figure 2a), where cotton strips lost tensile strength at rates between 1.1 % day^{-1} (winter) and 2.8 % day^{-1} (summer), and decomposition bags lost mass according to decay coefficients between 0.003 day^{-1} and 0.007 day^{-1} (Figure 2b). Other environmental factors including precipitation ($r=0.52$, $p=0.12$) and flooding frequency ($r=0.46$, $p=0.18$) were not significantly correlated with decomposition rates (Figure 2a). Finally, the loss of tensile strength in cotton strips was significantly related to mass loss of the decomposition bags in the seasonal experiment (r=0.63, p=0.04) (Figure 2c), allowing us to calibrate the tensile strength data from the latitudinal experiment in terms of mass loss.

Both experimental approaches demonstrate a consistent relationship between temperature and organic matter decomposition rate. In the seasonal warming experiment, organic matter decay was significantly and positively correlated (r=0.74, p=0.01) with soil temperature, equivalent to a 3.0 percent increase in decay rate per °C, and a Q_{10} value of 1.27 (Figure 3a). Decay coefficients estimated from the calibrated cotton strip measurements across latitude were also significantly related to the temperature at each study site (r=0.81, p=0.003), where decay coefficients increased from 0.004 to 0.010 day^{-1}, equivalent to a 5.6% increase in decay rate per °C, and a Q_{10} value of 1.51 (Figure 3b).

4 Discussion

Each of our decomposition experimental approaches has important limitations. For example, our latitudinal experiments were conducted with standardized cellulose material not necessarily reflective of native soil organic matter. Sites were selected without regard to environmental factors that could obscure or complicate trends with latitude such as nutrient availablity, and only loosely selected with regard to flooding frequncy (i.e. located at the ecotone between *S. Patens and S. americanus*). The seasonal experiments suffer from lack of generality since they were conducted at a single site and in a single year. However, the parallel experiments complement each other and relieve many of the potential issues in either individual approach. For example, the seasonal experiment at a single site controls for environmental factors that could vary along the latitudinal gradient, and uses native root and rhizome material. The latitudinal experiment confirms that the sensitivity of decomposition to temperature is similar from year-to-year, and that the relationship between temperature and decay measured at one site is more generally applicable to brackish marshes along the Atlantic Coast.

Our measurements of root and rhizome decay in the seasonal experiment (k=0.003-0.007 day^{-1} or k=1.1-2.6 year^{-1}) and in the calibrated latitudinal gradient (k=0.004-0.010 day^{-1} or k=1.5-3.7 yr^{-1}) are similar to other short-term measurements of decay rate, suggesting that our experimental design adequately measured the early stages of decay. For example, *Kirwan & Blum* [2011] reported decay coefficients between 1.5 and 5.9 yr^{-1} in a similar seasonal experiment, and *Christian* [1984] reported decay coefficients between 1.0 and 9.1 yr^{-1} from 11 marshes throughout the United States. Our rates are similar, but slightly lower, perhaps reflecting their use of above-ground material from the salt marsh plant species *S. alterniflora*. Our decay rates are higher than for root and rhizome decomposition measured over longer durations at our study site (k=0-0.38 yr^{-1}) [*Kirwan et al.*, 2013] and elsewhere in the mid-Atlantic (k=0.11-0.51 yr^{-1} ; k=0.25-0.57 yr^{-1}) [*Blum & Christian*, 2004 ; *Windham*, 2001] because our monthly measurements include only the most rapid, initial phases of decay (i.e. leaching of soluble compounds and decomposition of cellulose) [*Valiela* 1985].

The goal of this research was to measure the sensitivity of wetland decomposition to temperature, rather than to quantify the long-term rate of decay itself. The regressions in Figure 3 imply a 3% and 6% increase in decay rate per °C in the seasonal and latitudinal experiments, respectively. Our results therefore confirm that temperature plays a significant role in wetland decomposition rates, contrasting early experimental findings [*Charles & Dukes*, 2009], but suggest a much lower sensitivity than previously reported [*Kirwan & Blum*, 2011]. Previous experiments reporting a 20% per °C sensitivity were based on similar observations of monthly decay throughout the growing season but were conducted with above-ground portions of *S. alterniflora* plants placed directly on the soil surface in a rarely flooded salt marsh [*Kirwan & Blum* 2011]. The temperature sensitivity of decomposition that we report (Q_{10}=1.3-1.5) is also less than the sensitivity reported for ecosystem respiration of a freshwater marsh (Q_{10}=3.0-3.6) [*Neubauer, 2013*], presumably because our estimate corresponds to heterotrophic respiration, whereas ecosystem fluxes include autotrophic and heterotrophic respiration from plants and soil. In contrast, the sensitivity we report (Q_{10}= 1.3 – 1.5) is very similar to the range of estimated temperature sensitivities of CO_2 emissions from freshwater wetland soils (Q_{10}=1.3-2.5) [*Inglett et al.*, 2012] and salt marsh soils (Q_{10}=1.5-1.8) [*Morris and Whiting*, 1986].

In addition to implications for viability of coastal wetlands, the results provide insight into climate-carbon cycle feedbacks, which have rarely been examined in wetlands. Decomposition studies in uplands have yielded a wide range of temperature sensitivities [*Craine et al.*, 2013], begetting a large uncertainty in the strength of the climate-carbon feedback. The temperature sensitivity of decomposition in wetlands is particularly important in future climate because wetlands sequester carbon at rates an order of magnitude faster than upland ecosystems [*Mcleod et al.*, 2011]. However, increasing temperatures could accelerate decomposition rates and slow or potentially reverse the wetland carbon sink. The temperature sensitivities we report agree generally with a global average temperature sensitivity of respiration derived from ecosystem flux measurements over mostly upland sites (Q_{10} = 1.3 – 1.5) [*Bond-Lamberty & Thomson* 2010; *Mahecha et al.,* 2010]. That we find similar temperature sensitivity in such a biogeochemically distinct environment, and with a different experimental approach supports the idea that there may be fundamental determinants to temperature sensitivity of ecosystem carbon loss [*Allison et al.,* 2010].

The sensitivity of decomposition to warming in upland soils may ultimately depend on the production and diffusion rates of carbon substrates to soil microbes, which can be limited by water availability [*Davidson et al.,* 2006]. Q_{10} estimates based on temperature fluctuations are confounded because fluctuations in soil water often correlate with soil temperature. Therefore, Q_{10} studies in saturated wetland soils offer unique insight because diffusion of dissolved carbon substrates is not limited by water availability. However, soil microbes in wetlands consume oxygen more rapidly than it can be replenished through diffusion from the atmosphere and plant aerenchyma, or through direct advection of oxygen and aerated water. The resulting scarcity of oxygen reduces decomposition rates, allowing organic matter to accumulate in wetland soils. Even though anaerobic metabolism, which dominates organic matter decomposition in many wetland soils, may operate in absence of available molecular oxygen, the oxidative status of the alternate electron acceptors, and therefore the efficiency of metabolism, still ultimately depends on interaction with available oxygen [*Megonigal et al.,* 2003]. If oxygen diffusion represents the rate-limiting step in decomposition of wetland soil organic matter, then the temperature dependence of wetland decomposition should resemble the temperature dependence of oxygen diffusion. Based on an empirical relationship between oxygen diffusivity in water and temperature [*Han & Bartels*, 1996], Figure 4 illustrates that the Q_{10} of oxygen diffusivity (1.25-1.4) matches our measurements of Q_{10} for decomposition (1.3-1.5). Moreover, the Q_{10} of oxygen diffusivity declines with increasing temperature, as do Q_{10} values for respiration across a wide range of ecosystem types [*Lloyd & Taylor*, 1994].

Soil carbon accumulation is a primary mechanism regulating marsh elevation and the vulnerability of marshes to sea level rise [*Turner et al.,* 2000; *Langley et al.,* 2009; *Nyman et al.,* 2006; *Neubauer,* 2008]. Manipulative experiments indicate that warmer temperatures and moderate increases in rates of sea level rise tend to increase organic matter production [*Gedan et al.,* 2011; *Kirwan & Guntenspergen,* 2012]. Elevated CO_2 experiments indicate a sustained increase in rates of C_3 organic matter production and marsh elevation gain [*Erickson et al.,* 2007; *Langley et al.*, 2009], but do not facilitate the warming and higher decomposition rates that are likely to accompany higher greenhouse gas concentrations. Our results indicate that belowground labile organic matter in C_3 dominated marshes is indeed sensitive to temperature but suggest the sensitivity of decomposition is relatively small compared to climate factors that influence production (Figure 5). These simple comparisons do not include important long-term constraints on the concentration of carbon within a wetland soil [*Kirwan & Mudd*, 2012], changes in carbon quality [*Ball and Drake*, 1997], interactions between multiple components of global change [*Langley and Megonigal*, 2010] or various feedbacks between climate, biota and sea level rise [*Wolf et al.*, 2007; *Weston et al.*, 2011; *Kirwan & Mudd*, 2012]. How temperature sensitivities of labile carbon decomposition relate to the more refractory carbon that is important for long-term carbon burial, is poorly understood [*Fang et al., 2005*; *Craine et al.*, 2010]. Nevertheless, the relatively low sensitivity of decomposition to temperature adds qualitative support to the idea that marshes will become more efficient carbon sinks under climate change, and therefore more resilient to sea level rise.

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Figure captions

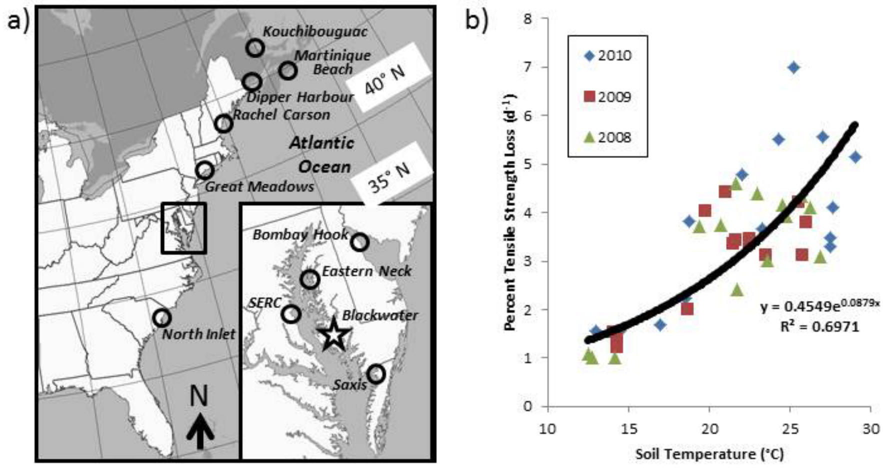

Figure 1. (a) Map of deployment locations for the latitudinal cotton strip experiment. Star denotes location of seasonal warming experiment, and 4 cotton strip deployment sites in the vicinity of the Blackwater and Transquaking Rivers, MD. (b) Relationship between soil temperature and cotton strip tensile strength loss measured across the latitudinal gradient in 2008 (triangles), 2009 (squares), and 2010 (diamonds). The markers and solid trend line correspond to tensile strength loss measurements averaged over the upper 6 cm of the soil profile.

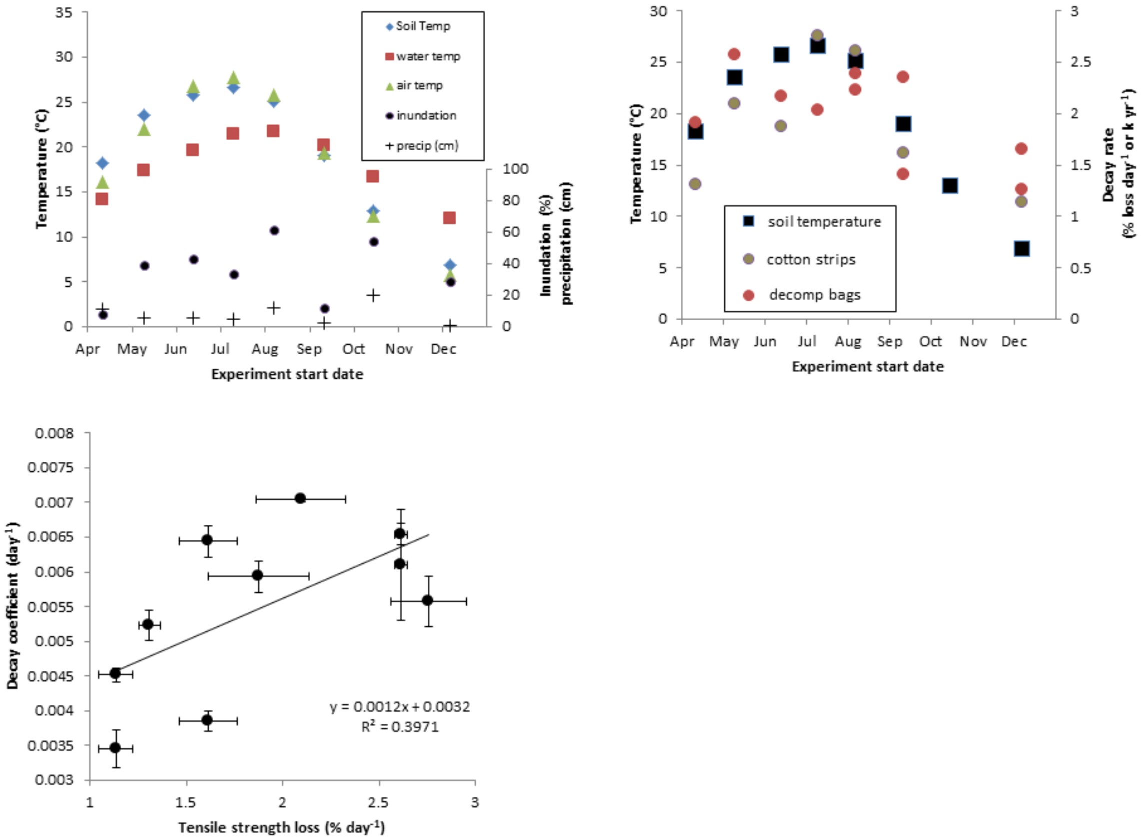

Figure 2. Temperature change and its effect on decay in seasonal Blackwater experiments. (a) environmental conditions during each experiment. (b) Variation in decay rate throughout the experiments measured by cotton strips (% loss of tensile strength day^{-1}, gray circles) and decomposition bags (k, yr^{-1}, red circles). (c) relationship between cotton strip tensile strength loss and the decay coefficients measured in the decomposition bags.

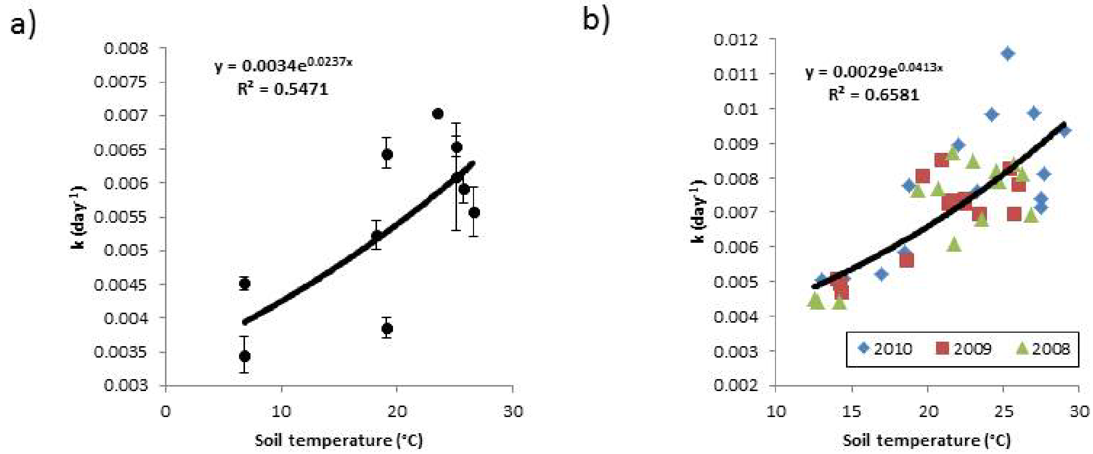

Figure 3. Relationship between decay coefficient (k) and temperature as measured in seasonal decomposition bag experiment (a) and in calibrated cotton strips across latitudinal gradient (b). Tensile strength loss in cotton strips was converted to decay coefficients of mass loss with the regression in Figure 2c.

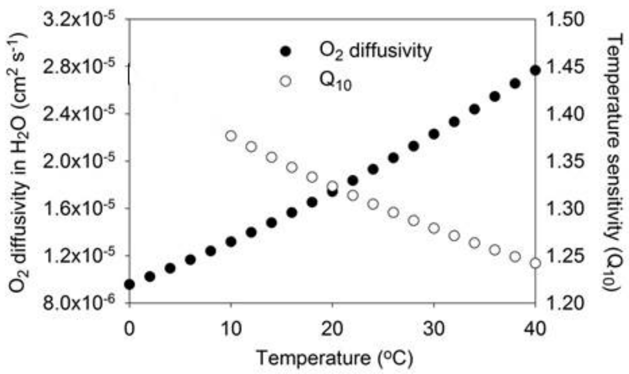

Figure 4. The diffusivity of O_2 in water and the temperature sensitivity of diffusivity expressed as Q_{10}. Diffusivity is estimated from an empirical formula:

$\log_{10}$(Diffusivity) = -4.410+773.8/T – $(506.4/T)^2$ where D is diffusivity in $cm^2\ s^{-1}$ and T is temperature in Kelvin (Han and Bartels 1996). The Q_{10} was calculated as diffusivity at T divided by the diffusivity at (T-10). Because the observed relationship between diffusivity and temperature deviates from exponential, the calculated Q_{10} decreases as temperature increases.

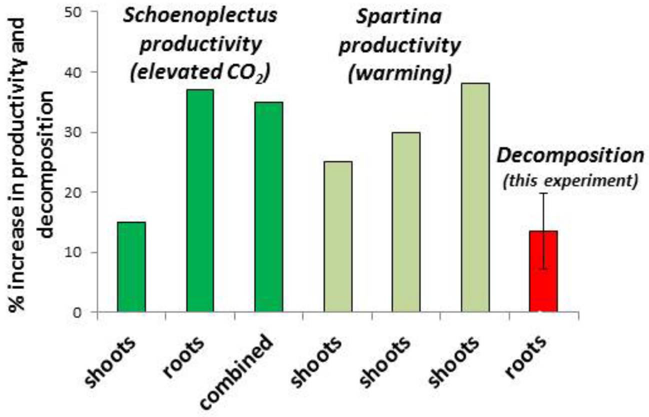

Figure 5. Response of marsh organic matter production (green bars) and decomposition (red bar) to individual components of global change. Dark green bars represent response of *Schoenoplectus americanus* marsh to CO_2 fertilization (720 ppm), light green bars represent response of *Spartina alterniflora* and *S. patens* marshes to elevated temperatures (+ 3 °C). Red bar represents decomposition response to 3°C warming, which we assume is roughly equivalent to the near doubling of [CO2] considered in CO2 fertilization experiments (Stocker et al., 2013). These are simplistic comparisons and do not address potential interactions, such as warming impact on *S. Americanus* productivity, or the influence of CO_2 fertilization on decomposition rate. Data sources from left to right: *Schoenoplectus americanus* shoots (Langley et al., 2009), *S. americanus* roots (Langley et al., 2009), *S. americanus* shoots and roots (Erickson et al., 2007), *Spartina alterniflora* shoots (Kirwan et al., 2009), *S. alterniflora* shoots (Gedan et al., 2011), *S. patens* shoots (Gedan et al., 2010).