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Enhanced decomposition offsets enhanced productivity and soil carbon accumulation in coastal wetlands responding to climate change

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Abstract

Coastal wetlands are responsible for about half of all carbon burial in oceans, and their persistence as a valuable ecosystem depends largely on the ability to accumulate organic material at rates equivalent to relative sea level rise. Recent work suggests that elevated CO₂ and temperature warming will increase organic matter productivity and the ability of marshes to survive sea level rise. However, we find that organic decomposition rates increase by about 12% per degree of warming. Our measured temperature sensitivity is similar to studies from terrestrial systems, twice as high as the response of salt marsh productivity to temperature warming, and roughly equivalent to the productivity response associated with elevated CO₂ in C₃ marsh plants. Therefore, enhanced CO₂ and warmer temperatures may actually make marshes less resilient to sea level rise, and tend to promote a release of soil carbon. Simple projections indicate that elevated temperatures will increase rates of sea level rise more than any acceleration in organic matter accumulation, suggesting the possibility of a positive feedback between climate, sea level rise, and carbon emissions in coastal environments.

1 Introduction

Marshes are submerging at rates faster than they can transgress inland in many regions of the world, and some assessments predict that up to half of the world's tidal wetlands will submerge during this century (Nicholls et al., 2007). Understanding how coastal wetlands respond to global change is of broad concern since they improve water quality, support commercially important fisheries, and protect humans from storms – characteristics that make them one of the most valuable ecosystems in the world (Costanza et al., 1997). Tidal marshes also bury carbon at rates faster than almost any terrestrial ecosystem (Chmura et al., 2003), and together with mangroves and sea-grasses represent nearly half of all marine carbon burial today (Duarte et al., 2005). However, the persistence of this important ecosystem and its capacity as a carbon sink

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depends directly on the balance between organic matter production and decomposition in wetland soils (Charles and Dukes, 2009). Where mineral sediment is not readily available, peat accretion must exceed the rate of sea level rise for tidal wetlands to survive (Reed et al., 1995).

Recent work indicates that some aspects of global change may actually increase the productivity and resiliency of coastal wetlands (Erickson et al., 2007; Charles and Dukes, 2009; Cherry et al., 2009; Kirwan et al., 2009; Langley et al., 2009; Gedan et al., 2011). Both above-ground and below-ground components of *Spartina alterniflora* productivity appear to increase with moderate flooding (Morris et al., 2002; Mudd et al., 2009), and measurements of soil elevation indicate that enhanced root productivity allows C3 marshes grown under elevated CO₂ to survive higher rates of sea level rise than marshes under ambient conditions (Cherry et al., 2009; Langley et al., 2009). Above-ground plant growth is more rapid at warmer temperatures in C4 marsh plants, leading to the proposal of a similar feedback where enhanced productivity leads to more sediment trapping, and faster vertical accretion (Charles and Dukes, 2009; Kirwan et al., 2009; Gedan et al., 2011). Decomposition rates may be faster during warmer portions of the year (White et al., 1978; Montagna and Ruber, 1980; Christian, 1984), but recent experimental results suggest that warming does not lead to a significant change in decomposition rate relative to ambient temperatures (Charles and Dukes, 2009). Although research on carbon cycling in coastal regions is still in its infancy, these observations lead to the conclusion that marshes may survive faster rates of sea level rise in the future (Cherry et al., 2009; Langley et al., 2009), and that their ability to sequester CO₂ and provide ecosystem services will increase during the next century (Charles and Dukes, 2009; Mudd et al., 2009; Gedan et al., 2011). Here, we challenge this paradigm by demonstrating that organic decay rates in some marshes can be strongly temperature dependent, and that changes in productivity associated with elevated CO₂ and climate warming will be roughly offset by concomitant increases in decomposition.

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2 Materials and methods

To infer how the rate of organic matter decomposition in marshes will change in response to climate warming, we measured the mass loss of dried *Spartina alterniflora* stem and leaf material in a single marsh surrounding the upper portion of Phillips Creek, Virginia (37°26′38.49″ N, 75°52′04.99″ W).

This site is associated with other measurements of marsh productivity and decay associated with the Virginia Coast Reserve for Long Term Ecological Research (Blum, 1993; Blum and Christian, 2004). Our experiments were located in the upper reaches of the *S. alterniflora* vegetation zone, characterized by irregular tidal flooding and long term increases in elevation that exceed the local rate of sea level rise (Blum, 1993; Blum and Christian, 2004).

Sets of 5 litterbags, each containing 10.0 g of standing-dead plant leaves collected in February 2003, were placed in the marsh at weekly intervals for seven weeks between 1 May and 12 June 2003. The bags were buried in contact with the sediment surface, but underneath any accumulated plant litter. Each incubation period lasted four weeks and, because starting dates were staggered weekly, included different environmental conditions (e.g. temperature, precipitation) (Fig. 1).

At the end of each incubation period, samples were transported to the lab in a cooler and stored frozen at -80°C . Roughly half of each sample was used to measure moisture content and mass loss during the 4 week period, and the other half used to determine microbial abundance. To determine mass loss, organic material was dried in foil packets at 75°C , weighed, and then combusted in a muffle furnace to determine ash-free dry weight. Bacterial and fungal biovolumes were measured using Acridine Orange Direct Counting methods (Hobbie et al., 1977). Fungal biovolume was estimated by measuring the number, length, and diameter of fungal hyphae. Bacterial biovolume was calculated directly from measurements of cell width (w), and length (l), where total biovolume, $V = (\pi/4)w^2(l - w/3)$ (Krambeck et al., 1981).

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3 Results

Decay rates were lowest during the first four-week interval (15% total mass loss; 0.078 g day^{-1}) and increased steadily throughout the experiment, reaching a maximum decay rate during the last four-week interval (49% total mass loss; 0.114 g day^{-1}). Assuming the decay rate declines through time as an exponential function, our measurements yield decay coefficients (k) between 0.006 and 0.02 day^{-1} . These coefficients are significantly higher than long term estimates at the site since we measured only during spring and summer months, but are roughly consistent with short term measurements elsewhere (e.g. Marinucci et al., 1983; Morris and Bowden, 1986).

Although a variety of environmental variables were considered, the mean daily temperature of each experiment interval best explains the increase in decay rate through time. Simple linear regression yields a positive, significant ($p = 0.001$) relationship between temperature and decay rate equivalent to 0.2 g day^{-1} or an 11.6% increase in mass loss for each degree warming (Fig. 2a). Microbial mass (fungi and bacteria) did not increase throughout the experiment, suggesting that enhanced microbial activity rather than microbial abundance caused the acceleration in organic matter decay (Fig. 2b). Variability in precipitation and the moisture content of the litterbags cannot explain the steady increase in decay rate throughout the experiment; total precipitation and moisture content declined in the second half of the experiment when decay rates were highest (Fig. 1). Consequently, we conclude that the increase in decay rate through time is the result of warming.

4 Discussion

In this initial attempt to measure the sensitivity of decomposition rates to temperature warming in a coastal wetland, we have made several important assumptions. First, we assume that the temperature sensitivity of buried leaf and stem material to decay is similar to the temperature sensitivity of belowground material to decay. Second, we assume that measurements just beneath the litter layer are applicable to the shallow

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root zone in general. Finally, we assume that results from this short-term experiment at a single location are more broadly applicable. Previous work at the site indicates that organic matter buried just below the surface decays at rates similar to organic matter placed at depth (19), and that decomposition rates are relatively insensitive to flooding frequency and therefore exhibit only slight spatial variability throughout the marsh (Blum, 1993; Blum and Christian, 2004). Elsewhere, *Spartina* roots decay at rates similar to above ground material (Pozo and Colino, 1992). Nevertheless, our goal was to measure the sensitivity of the decay rate to temperature change, rather than simply determining the rate of decay. In situ measurements of sulfate reduction and oxygen uptake rates (proxies for organic decomposition rates) integrated over the entire root zone over 2 yrs suggest the temperature sensitivities we report here are more broadly applicable. In a *S. alterniflora* marsh at Great Sippewisset, Massachusetts, both metabolic processes increased with temperature at a rate similar to that reported here (0.1 moles $\text{SO}_4^{-2} \text{m}^{-2} \text{day}^{-1}$ to 0.17 moles $\text{SO}_4^{-2} \text{m}^{-2} \text{day}^{-1}$ between May and June as temperature increased from approximately 12 °C to 18 °C) (Howarth and Teal, 1979).

Despite these assumptions, the results of our short decay experiment in a salt marsh are also consistent with measures of temperature sensitivity predicted by biokinetics and observed in other ecosystems. The Q_{10} value, defined as the factor by which a reaction rate increases in response to a 10 °C increase in temperature, is typically around 2 for biological systems, meaning that reaction rates approximately double with every 10 °C increase in temperature (Davidson and Janssens, 2006). Our measurements yield a Q_{10} value of 2.16. Our local measurements of decomposition in coastal wetlands are therefore remarkably similar to that predicted by classic kinetics, and similar to, albeit higher than, an estimate of $Q_{10} = 1.5 \pm 0.4$ for global soil respiration (Bond-Lamberty and Thomson, 2010). We attribute our relatively high temperature sensitivity to the abundant soil moisture, nitrogen, and readily available carbon in tidal wetlands, factors that often limit decay rates at warmer temperatures in upland environments (Davidson et al., 2006).

The sensitivity of wetland decomposition rates to temperature warming that we report

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is in contrast with results from a recent field experiment in a Massachusetts salt marsh where decay rates were not sensitive to experimental warming (Charles and Dukes, 2009). Since temperature has long been thought an important control of decay rates in wetlands (White et al., 1978; Montagna and Ruber, 1980; Christian, 1984), we propose that regular tidal inundation by un-warmed water maintained soil temperatures in their experimental chambers even though air temperature and above-ground plant productivity were clearly enhanced. In any case, our work suggests that tidal wetlands behave like other ecosystems, and that estimates of warming-induced decomposition should be incorporated into assessments of how wetlands and their carbon storage potential respond to global change.

A relatively high sensitivity of decomposition rates to temperature warming has several implications for the future survival of tidal wetlands, and their role in carbon cycling. First, organic matter decay rates increase with temperature faster than rates of productivity, at least when expressed on a relative basis. Based on a latitudinal gradient, *S. alterniflora* above-ground productivity has been estimated to increase by $27 \text{ g m}^{-2} \text{ yr}^{-1}$ for each degree C warming (Kirwan et al., 2009), or by about $6\% \text{ degree}^{-1}$ for a typical mid-Atlantic salt marsh with productivity of about $450 \text{ g m}^{-2} \text{ yr}^{-1}$. Root to shoot ratios do not appear to change systematically with latitude (Gross et al., 1991), implying that the response of belowground productivity to temperature warming would be similar. Therefore, for a marsh where productivity and decomposition are roughly equal, our results (a $12\% \text{ degree}^{-1}$ increase in decomposition rate) suggest that temperature warming will lead to a net reduction of soil carbon and a loss of wetland elevation.

Recent work suggests that increases in organic matter production associated with elevated CO_2 will tend to make marshes more resilient to sea level rise (Cherry et al., 2009; Langley et al., 2009). For example, fine root growth of C_3 species in elevated CO_2 plots (720 ppm) is 26–48% greater than fine root growth in ambient plots (~ 380 ppm), resulting in a 3.9 mm yr^{-1} increase in the rate of soil accretion (Langley et al., 2009). However, CO_2 enrichment experiments do not typically facilitate the warming that would accompany a near doubling in atmospheric CO_2 . Global circulation

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models predict that an increase from 380 to 720 ppm would cause warming of mean annual temperatures by about 2.7 degrees (mean A2 scenario) (Meehl et al., 2007). Since we observe that decomposition rates increase by 12% degree⁻¹, our results suggest that elevated CO₂ and warmer temperatures would enhance organic matter decomposition rates by about 36%. At their most basic level, our results point to a situation where increases in productivity associated with enhanced CO₂ (mean = 37%) will be roughly offset by increases in decomposition rates associated with CO₂ driven warming (36%).

Historically, organic matter production has exceeded decomposition in most marshes worldwide, resulting in a net accumulation of soil carbon (Chmura et al., 2003). Where the balance is positive, an identical increase in productivity and decomposition rate expressed on a percentage basis will tend to slightly increase the absolute rate of organic matter accumulation. To determine whether this effect could be large enough to offset accelerated rates of sea level rise, we consider two *S. alterniflora* marshes where carbon budgets have been established. In the first example, our Phillips Creeks study site, productivity greatly exceeds decay resulting in net organic accumulation of about 590 g m⁻² yr⁻¹, or the equivalent of 5.9 mm yr⁻¹ (Blum and Christian, 2004). In the second example, Great Sippewissett Salt Marsh (Cape Cod, Massachusetts), productivity slightly exceeds decay resulting in net organic accumulation of about 108 g m⁻² yr⁻¹ or 1.1 mm yr⁻¹ (Howes et al., 1985). At both locations, we consider the effect of climate warming on the rate of sea level rise (Vermeer and Rahmstorf, 2009), and extrapolate the response of local carbon accumulation and its effect on organic accretion using the linear relationships discussed above between temperature and productivity (6% increase degree⁻¹) (Kirwan et al., 2009), and between temperature and decomposition (12% increase degree⁻¹). Although changes in sea level and marsh elevation clearly influence rates of mineral deposition, productivity, and decomposition (e.g. Morris et al., 2002; Mudd et al., 2009; Kirwan and Temmerman, 2009), the feedbacks are complex, and we instead focus on the isolated effect of temperature warming on organic matter accumulation.

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At Phillips Creek, organic accumulation rates increase slightly with warming ($590 \text{ g m}^{-2} \text{ yr}^{-1}$ to $685 \text{ g m}^{-2} \text{ yr}^{-1}$), even though the temperature sensitivity of decomposition is higher than the sensitivity of production (Fig. 3a). Nevertheless, the increase in organic accretion rate (5.9 mm yr^{-1} to 6.8 mm yr^{-1}) is extremely small when compared to rates of sea level rise predicted for concomitant changes in temperature. Therefore, the net effect of temperature warming at Phillips Creek is a shift from an organic accretion rate that exceeds the rate of sea level rise to an accretion rate that is less than the rate of sea level rise. At Great Sippewissett, the initially small positive balance between productivity and decay quickly diminishes and the accumulation rate of carbon becomes negative (Fig. 3b). In this marsh, an increasing sea level rise rate accompanied by a decreasing organic accretion rate results in rapid lowering of marsh elevations relative to sea level (Fig. 3c).

These results indicate that whether coastal wetland carbon accumulation rates increase or decrease in response to climate warming depends on the initial balance between productivity and decay (Fig. 3d). In the absence of feedbacks associated with inundation, marshes that produce much more carbon than is decomposed at current temperatures will accumulate even more carbon under warmer temperatures. Marshes with low accumulation rates, such as Great Sippewissett, will accumulate progressively lower amounts of carbon under warmer climate. However, in all cases, the acceleration in sea level rise induced by warming ($>20 \text{ mm yr}^{-1}$ by 2100) exceeds the ability of warming to enhance accretion rates. This suggests that the net effect of temperature warming (or by analogy, elevated CO_2) is to make marshes more vulnerable to sea level rise. Since vegetated coastal environments sequester more carbon than similar unvegetated environments (Duarte et al., 2005), our findings suggest that temperature warming will lead to a loss of coastal wetlands and carbon accumulation. Although we caution that these conclusions are based on a single set of experiments at a single site and neglect potential feedbacks between inundation and carbon storage, these preliminary comparisons favor a scenario much different than the paradigm that global change will lead to wetlands that are more resilient to sea level rise. In contrast, we

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hypothesize that when elevated CO₂, temperature warming, and the rate of sea level rise are considered together, there will tend to be a decrease in the amount of carbon buried in coastal wetland sediments. Our findings therefore open the possibility of a positive feedback in which a warming climate slows coastal carbon accumulation rates, and therefore causes additional warming and accelerated sea level rise.

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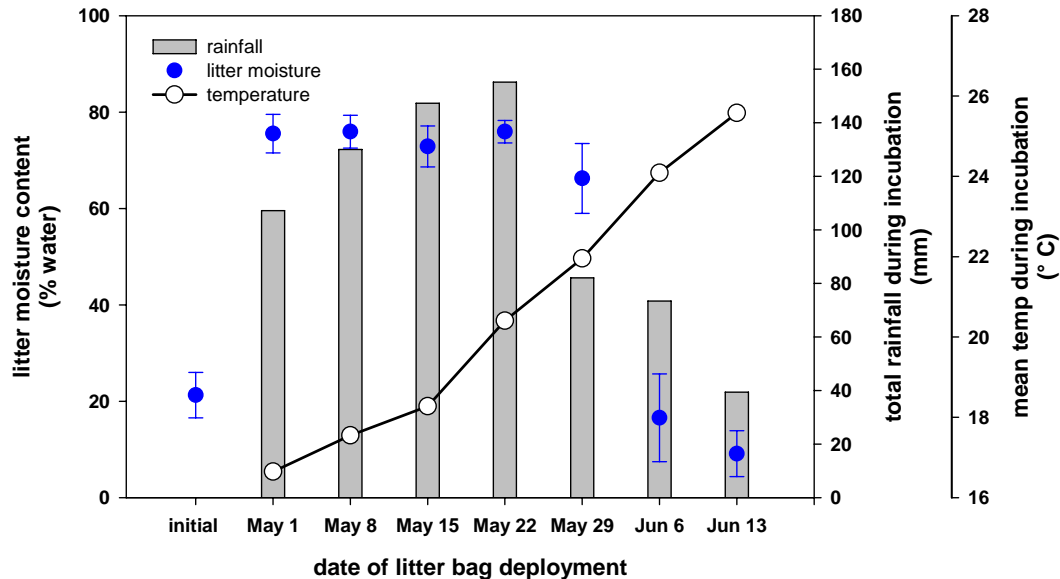


Fig. 1. Moisture content of organic matter contained in litter bags (blue circles) after 4 weeks of incubation ($n = 5$, error bars represent one SD), mean daily air temperature (open circles), and total rainfall during each 4-week incubation (vertical bar). Dates on the X-axis indicate the beginning of each incubation period; the label “initial” on the X-axis indicates the mean (\pm SD) initial moisture content of litter placed in bags at the beginning of each experiment.

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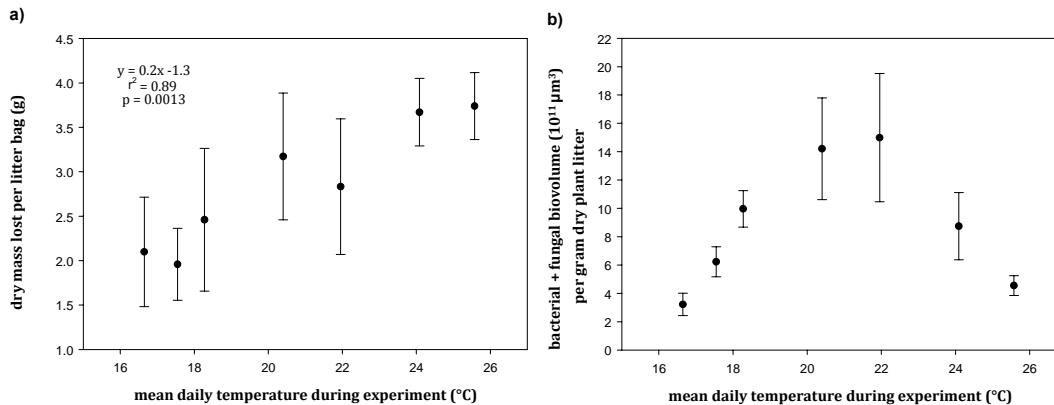
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Fig. 2. (a) Relationship between mean daily temperature and organic matter decay rate measured in litterbags. Each litterbag initially contained 10.0g of dry *Spartina alterniflora* material, and was subjected to 4 weeks of incubation, beginning one week apart. Each point represents the mean mass loss, and error bars represent the standard deviation, of 5 litterbag replicates during each incubation period. **(b)** Relationship between total microbial biovolume and mean daily temperature derived from fungal and bacterial counts on litter remaining at the end of each four-week experiment. In these experiments, the size of fungal hyphae dominates the size of bacteria, but neither bacterial or fungal abundance shows a statistically significant linear relationship with temperature. This suggests that the organic decay rate is controlled primarily by temperature and not the type or abundance of the microbial community.

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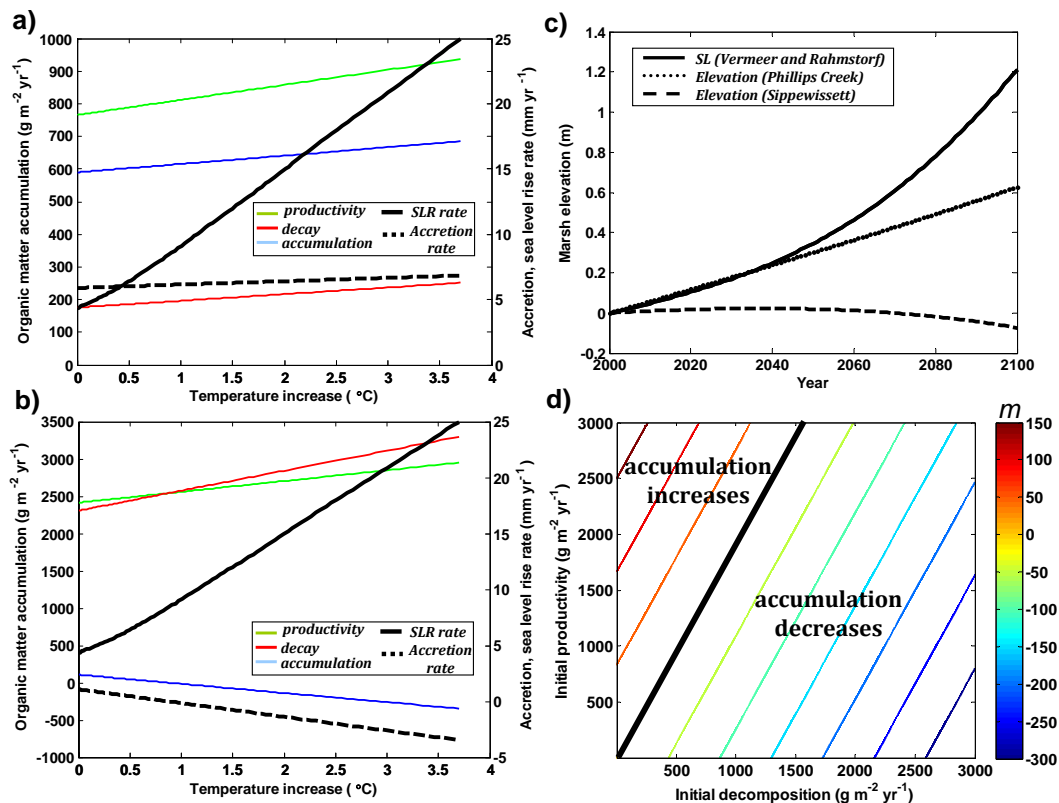
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Fig. 3. Estimated changes in organic matter accumulation, accretion rate, and sea level rise rate as a function of temperature at Phillips Creek, VA **(a)** and Great Sippewissett, MA **(b)**. Integrated changes in marsh elevation and sea level through time **(c)**. These projections begin with modern estimates of productivity and decomposition at each site (i.e. a large surplus at Phillips Creek, and a small surplus at Great Sippewissett). Productivity (p) and decomposition (d) rates increase as a function of temperature (T) according to the relationships defined in the text ($p(T) = 0.06 p_0 T$ and $d(T) = 0.116 d_0 T$). The organic accumulation rate equals $p - d$, and the organic accretion rate equals the accumulation rate divided by the dry bulk density of pure peat (0.1 g cm^{-3}). **(d)** The sensitivity of m to initial productivity and decomposition rates, where m describes the direction and magnitude of organic matter accumulation change with temperature ($m = 0.06 p_0 - 0.116 d_0$). Accumulation rates increase with temperature when m is positive, and decrease when m is negative.

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