

Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change

MATTHEW L. KIRWAN*, GLENN R. GUNTENSPERGEN† and JAMES T. MORRIS‡

*US Geological Survey, Patuxent Wildlife Research Center, Department of Environmental Science, University of Virginia, Charlottesville, VA 29904, USA, †US Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA,

‡Belle W. Baruch Institute for Marine & Coastal Sciences, University of South Carolina, Columbia, SC 20208, USA

Abstract

Marshes worldwide are actively degrading in response to increased sea level rise rates and reduced sediment delivery, though the growth rate of vegetation plays a critical role in determining their stability. We have compiled 56 measurements of aboveground annual productivity for *Spartina alterniflora*, the dominant macrophyte in North American coastal wetlands. Our compilation indicates a significant latitudinal gradient in productivity, which we interpret to be determined primarily by temperature and/or the length of growing season. Simple linear regression yields a $27 \text{ g m}^{-2} \text{ yr}^{-1}$ increase in productivity with an increase of mean annual temperature by 1°C . If temperatures warm $2\text{--}4^\circ \text{C}$ over the next century, then marsh productivity may increase by 10–40%, though physiological research suggests that increases in the north could potentially be offset by some decreases in the south. This increase in productivity is roughly equivalent to estimates of marsh lost due to future sea level change. If a warming-induced stimulation of vegetation growth will enhance vertical accretion and limit erosion, then the combined effects of global change may be to increase the total productivity and ecosystem services of tidal wetlands, at least in northern latitudes.

Keywords: biomass, climate, sea level, temperature, warming, wetland

Received 29 July 2008 and accepted 10 October 2008

Introduction

Coastal marshland in several regions worldwide is actively degrading in apparent response to relative sea level rise and reduced sediment delivery rates in several regions worldwide (Penland *et al.*, 2001; Kearney *et al.*, 2002; Van der Wal & Pye, 2004). Marsh platforms appear to be losing elevation relative to sea level (Morris *et al.*, 2005), channel networks are expanding (Hartig *et al.*, 2002), and vegetation characteristic of higher elevations is being replaced by vegetation associated with lower elevations (Warren & Niering, 1993; Donnelly & Bertness, 2001).

Recent work suggests that vegetation plays a critical role in determining the morphology and behavior of tidal marsh systems (D'Alpaos *et al.*, 2007; Kirwan & Murray, 2007; Temmerman *et al.*, 2007). For example, vegetation increases accretion rates by trapping inorganic sediment and contributing organic matter (Morris

et al., 2002; McKee *et al.*, 2007), and is thought to stabilize the width and length of channel networks (Kirwan & Murray, 2007; Kirwan *et al.*, 2008). Because vegetation growth exerts a first-order control on the stability of marshes adjusting to sea level change (Kirwan *et al.*, 2008), then any change in vegetation growth rate associated with climatic warming could impact the future stability of wetland landscapes.

The overall response of marshes to climatic warming is unclear. There are three types of measurements, each with advantages and disadvantages, from which to draw generalities about temperature effects. These include (1) physiological measurements of individual plants or leaves in controlled laboratory settings; (2) field-based measurements of productivity, canopy, or leaf level photosynthetic activity at a single site at different times of year; and (3) comparative analyses of field-based productivity measurements made across a latitudinal gradient. Laboratory experiments can never duplicate conditions in the field, but when done properly they reveal fundamental cause and effect relationships. *In situ* studies of productivity and phy-

Correspondence: Matthew L. Kirwan, tel. +1 540 808 5443, fax +1 434 924 4761, e-mail: mkirwan@usgs.gov

biology made over time are confounded by covariance among plant phenology and environmental drivers, but the net effect of these factors can be accurately measured. Similarly, comparisons across space are confounded by covariates that may include climate, relative elevation, tidal amplitude, sediment supply, and genetic adaptation.

In laboratory greenhouse experiments, increasing temperature by a few degrees tends to increase the aboveground productivity of marsh macrophytes (Seneca & Blum, 1984; Dunn *et al.*, 1987; Gray & Mogg, 2001). On the other hand, field-based gas exchange measurements indicate that rates of net photosynthesis and productivity are highest at typical summertime temperatures, but decline at higher temperatures (Shea, 1977; Giurgevich & Dunn, 1979). Finally, long-term measurements of annual productivity show no clear relation to either water or air temperature (Teal & Howes, 1996). While the response of marshes to sea level rise alone has been widely examined, these three contrasting scenarios (increased productivity, decreased productivity, and no change) illustrate a need to better understand how marsh productivity would respond to projected atmospheric temperature warming.

Because *Spartina alterniflora*, the dominant macrophyte in Atlantic and Gulf Coast marshes, grows abundantly from Texas through Nova Scotia, a latitudinal gradient could offer insight into the effect of temperature on its growth rate. Southern marshes have generally been considered to be more productive than northern marshes (e.g. Hatcher & Mann, 1975; Mendelssohn & Marcellus, 1976; Mendelssohn & Morris, 2000), but this observation is typically made from comparing a small number of marshes, often measured with different methodologies. In fact, our interpretation of the most extensive review of productivity in *S. alterniflora* dominated marshes (Turner, 1976), suggests that mid-Atlantic marshes may be no more productive than marshes as far north as Nova Scotia, and that a latitudinal gradient exists only between Gulf Coast and southern Atlantic marshes. Finding a clear gradient is inherently difficult. Productivity at a single site can easily double from year to year (e.g. Broome *et al.*, 1986; Morris & Haskin, 1990). At North Inlet, SC, for example, Morris & Haskin (1990) measured maximum annual standing biomass that varied between 209 and 694 g m⁻² yr⁻¹ over a 5-year period. Another difficulty in making comparisons between sites results from using different sampling methods; estimates of productivity within a single site and year may vary twofold depending on the sampling methods used (e.g. Kirby & Gosselink, 1976; Dai & Wiegert, 1996). Finally, because factors other than latitude (e.g. nutrients, salinity, herbivory) strongly determine the productivity of marsh grasses,

the large variation in productivity among nearby marshes could obscure any geographical gradient. Nevertheless, such comparisons reveal patterns that must be explained, and we have made maximum use of comparative analyses while drawing on the physiological literature to reach conclusions about likely temperature effects.

In this contribution, we expand Turner's (1976) pioneering review of aboveground *S. alterniflora* productivity, and use the resulting latitudinal gradient to infer the effect of temperature on *S. alterniflora*'s growth rate. Our results suggest that productivity will increase by 10–40% in the mid-Atlantic and northern latitudes in response to climatic warming over the next century, perhaps helping to offset losses in productivity from marsh lost due to sea level change and reductions in sediment delivery rates.

Materials and methods

We reviewed the literature for measurements of annual *S. alterniflora* aboveground productivity. In an effort to minimize variability associated with comparing productivity estimates derived from different methodologies, we only include measurements of the end of season living biomass, a proxy for annual productivity (Turner, 1976). Estimates from this method are commonly reported, or can be inferred from graphs of monthly biomass. In some cases, the original measurements did not include separate live and dead fractions of biomass. In these cases, we calculated the living fraction using regional or site specific live-to-dead ratios estimated from our literature search (please see supporting information Table S1 for details).

We excluded measurements of *S. alterniflora* located near a channel or described as tall form in order to compare measurements from similar topographic and hydrologic environments. In many regions, *S. alterniflora* grows in two distinct forms; a tall form typically occupies a narrow fringe along channel margins, and a short form typically occupies the expansive marsh interior. The channel adjacent form grows prolifically, with annual productivity that commonly exceeds interior marshland by up to an order of magnitude (e.g. Gallagher *et al.*, 1980; Dai & Wiegert, 1996). Therefore, our compilation of annual productivity should represent estimates from similar methodologies and hydrologic settings.

While environmental variables including salinity, marsh elevation, nutrient availability, and herbivory strongly influence the productivity of marshes, and may change from year to year, we hypothesize that climate-related gradients in productivity will emerge across the broader geographic range. Because factors

other than climate are likely to dominate local variability and obscure a clear geographic gradient, we average together all estimates of productivity that fall within a single degree of latitude (Table S1). The use of means for latitudinal analysis is appropriate because it removes variation due to unidentifiable factors (e.g. Middleton & McKee, 2004). We use this approach to identify a latitudinal gradient without the compounding influence of more local factors, but use the ungrouped estimates of productivity to determine the influence of climate.

In an effort to determine the influence of climate on the annual productivity of marshes, we compare measurements of productivity across the latitudinal gradient to several climatic variables using simple linear regression. We use monthly, seasonal, and annual means of precipitation and temperature from 1971 to 2000, reported in the climate summaries of local climate stations (Environment Canada, 2002; NCDC, 2004). In addition to precipitation and temperature metrics, we examined annual solar radiation (NREL, 1992), and the number of annual growing degree days (Environment Canada, 2002; NCDC, 2004). Growing degree days measure the number of degrees that daily temperatures exceed a threshold temperature necessary for significant plant growth, and therefore reflect both the temperature and duration of the growing season. We use 10 °C as a threshold for *S. alterniflora* growth, consistent with laboratory and field experiments (Long, 1990; Gray & Mogg, 2001).

Our compilation utilizes measurements of standing live biomass taken at the end of the growing season. This method assumes that all live biomass represents the current year's growth, and makes no attempt at incorporating the turnover of dead material into estimates of productivity. The method has been shown to significantly underestimate true productivity, particularly in southern marshes where the amount of turnover is generally high (e.g. Smalley, 1958; Kirby & Gosselink, 1976; Morris & Haskin, 1990). Therefore, our measurements of standing biomass should be considered minimum estimates of annual productivity. Moreover, because turnover increases southward (Turner, 1976), our estimate of the latitudinal gradient, and the corresponding response to temperature, is likely conservative.

Results

We compiled 56 measurements of *S. alterniflora* above-ground annual productivity from 48 different locations and 17 states and provinces (Fig. 1, Table S1). Estimates of productivity in North America span nearly an order of magnitude in our compilation, from 167 g m⁻² yr⁻¹ in



Fig. 1 Map of sampling locations used in compilation of *Spartina alterniflora* annual productivity estimates.

New Jersey to 938 g m⁻² yr⁻¹ in Texas. Local and temporal variability is high. For example, estimates of productivity for six marshes in Virginia range from 350 to 609 g m⁻² yr⁻¹. As stated earlier, this variability may correspond to local environmental differences including the effects of salinity, bed elevation, nutrient supply, and herbivory, or correspond to temporal variability between the years each marsh was measured.

Despite local and temporal variability, a significant ($r = 0.83$; $P < 0.000001$) latitudinal gradient of 25 g m⁻² yr⁻¹ per degree latitude exists across the entire geographic range of the compilation (Fig. 2). Linear regression explains as much variability as other methods (e.g. quadratic, exponential), suggesting that a simple linear relationship between latitude and productivity is reasonable. Annual productivity more than doubles across the gradient, with productivity in Texas and Louisiana averaging about 650 g m⁻² yr⁻¹ while productivity in New Hampshire, Maine, and Nova Scotia averages about 300 g m⁻² yr⁻¹. The latitudinal gradient in productivity appears to be driven by temperature. Annual productivity most significantly correlates with mean annual temperature ($r = 0.58$; $P = 0.000005$) and the annual number of growing degree days ($r = 0.58$; $P = 0.000005$), where 1 °C and 1 growing degree day correspond to 27 and 0.06 g m⁻² yr⁻¹ of productivity, respectively (Fig. 3). Other temperature metrics including spring, summer, and winter temperatures also significantly correlate with productivity (Table S2). Summer precipitation ($r = 0.37$; $P = 0.006$) and annual incident solar radiation ($r = 0.49$; $P = 0.0004$) correlate more weakly with productivity.

Discussion

Our results document a significant latitudinal gradient in *S. alterniflora* productivity existing throughout its

range in the United States and Canada. Based on Turner's (1976) compilation alone, a significant gradient was observed only in the southern United States, between about Texas and North Carolina (Fig. 2a). The lack of a significant gradient farther north may reflect the small number of measurements available, or a difference in the distribution of *S. alterniflora* between southern and

northern marshes. With increasing latitude, *S. alterniflora* becomes more restricted to channel margins where it occurs in a more productive, tall form. Because the Turner (1976) compilation utilizes marsh-wide averages, where less productive interior marshland is averaged together with channel adjacent marshland, the relatively high productivity of northern *S. alterniflora* could be biased by its restriction to channel margins. In our compilation we were careful to exclude productivity estimates that were clearly made along creekbanks. With this refinement and additional data, there is clearly a latitudinal productivity gradient.

The variability in productivity within a region (or even a single study site) can approach the total difference in productivity across the entire latitudinal gradient. This variability emphasizes the importance of factors other than latitude or temperature in determining the growth rate of marshland vegetation (e.g. Hatcher & Mann, 1975). Differences in salinity, herbivory, nutrient availability, and the elevation of the marsh relative to sea level all likely contribute to the local variability of annual productivity. Nevertheless, our relatively large sample size allows us to detect a significant and consistent latitudinal gradient in productivity that likely corresponds to temperature and/or the length of the growing season.

If we assume that the latitudinal gradient is a consequence of temperature and that local variables remain constant, we can estimate the response of *S. alterniflora* productivity to future increases in global temperature. Our results suggest that an increase in annual temperature of 2–4 °C by 2100 (IPCC, 2007) would cause productivity to increase by about 50–100 g m⁻² yr⁻¹ (Fig. 3). For mid-Atlantic and northern marshes with current

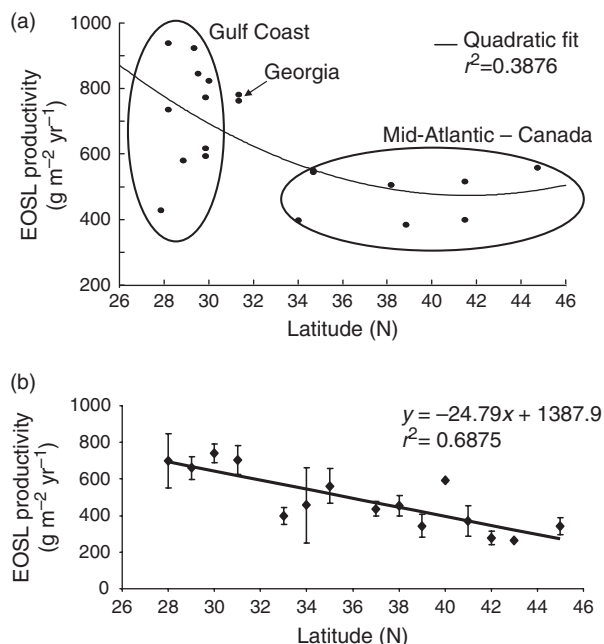


Fig. 2 Latitudinal gradient of *Spartina alterniflora* productivity (mean \pm 1 SE), estimated with End of Season Live (EOSL) method. (a) Data from Turner (1976) and suggests a disjunct gradient between Gulf and Atlantic Coast marshes, where mid-Atlantic marshes are no more productive than Canadian marshes. Our compilation (b) suggests a latitudinal gradient throughout the Atlantic and Gulf Coasts.

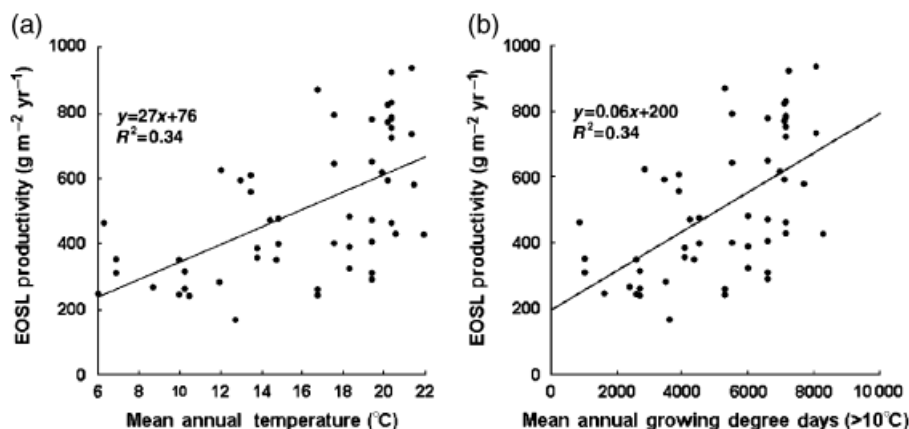


Fig. 3 End of season live (EOSL) *Spartina alterniflora* productivity compared with the mean annual temperature (a) and the average number of growing degree days (b) reported at local climate stations. Linear regressions indicate significant relationships ($P = 0.00003$) that correspond to a 26 g m⁻² yr⁻¹ increase in productivity for each degree increase in mean temperature, and a 60 g m⁻² yr⁻¹ increase in productivity for each 1000-day increase in the number of growing degree days.

productivity of 450 to 250 g m⁻² yr⁻¹ (Fig. 2b), this represents approximately a 10–40% increase in annual productivity. This is consistent with evidence that climate warming has already altered the phenology and productivity of forests, possibly contributing to increased plant production in the northern hemisphere (Norby *et al.*, 2003).

Extrapolation should not be made for the southernmost marshes because gas exchange measurements in Georgia indicate that the optimum temperature for net carbon assimilation (i.e. photosynthesis–photorespiration) in *S. alterniflora* is ~30–35 °C (Giurgevich & Dunn, 1979) and could be exceeded with additional warming. Similarly, *Spartina townsendii* in England has a temperature optimum of ~30 °C (Long *et al.*, 1975). Salinity stress can lower the temperature optimum, and conditions favoring low photosynthesis and high respiration have been measured even in Connecticut salt marsh pannes (Shea, 1977).

Because net carbon assimilation begins to decrease at temperatures typical of summer maximum daily temperatures in Georgia (Giurgevich & Dunn, 1979), it seems likely that southern marshes are near their optimum temperature and that future warming would cause a decline in their productivity and range contraction in the south. This is supported by reports of recent range expansion by mangroves into *Spartina* marshes in the Mississippi River deltaic plain (McKee *et al.*, 2004). At lower latitudes and warmer temperatures, mangroves replace *S. alterniflora* in coastal wetlands, perhaps indicating that below its current southern limit, *S. alterniflora* is a weak competitor limited by temperature or salinity. Other examples of high-temperature extremes limiting the productivity of vegetation at southern boundaries can be found, such as the work by Middleton & McKee (2004) on bald cypress. Finally, Shea's (1977) work in a Connecticut marsh leads us to caution that (1) physiology is proximally regulated by leaf temperature rather than air temperature, (2) leaf temperature may be considerably different from air temperature and is regulated by physiology, e.g. transpiration rate, and (3) plant physiological function can differ fundamentally across high and low ranges of temperature.

There is, however, uncertainty about the relative importance of temperature, length of growing season, and genetic adaptation on plant physiological processes. Length of growing season and temperature are closely related, and if recent research suggesting that trees maintain their leaves at nearly constant temperature across a wide range of latitude (Helliker & Richter, 2008) is generally applicable, then change in growing season may be the dominant mechanism responsible for the latitudinal gradient in productivity. Furthermore,

there is evidence for genetic differentiation of *Spartina* populations along this gradient. On the basis of the distribution of cpDNA haplotypes, it appears that *S. alterniflora* can be divided into northern, mid, and southern Atlantic coast groups, maintained by environmental selection, limited gene flow, legacy effects, or a combination of these factors (Blum *et al.*, 2007). With respect to genetic adaptation, there is evidence that variation within populations is high (Travis *et al.*, 2002), but the plasticity of these populations to environmental change is really unknown, and limited gene flow among populations could limit the range of response.

Field observations suggest that marshes worldwide are eroding and submerging in response to increasing rates of sea level rise and reduced sediment delivery (Penland *et al.*, 2001; Hartig *et al.*, 2002; Kearney *et al.*, 2002; Van der Wal & Pye, 2004). These observations are consistent with a number of numerical models that suggest an increase in sea level rise rate or reduction in sediment supply will lead to greater inundation, expansion of the channel network, and tend to convert marshland into subtidal mudflats (D'Alpaos *et al.*, 2007; Kirwan & Murray, 2007; Marani *et al.*, 2007). When subjected to future rates of sea level rise, numerical models and statistical projections predict that marshland worldwide will decline on the order of 10–50% during the next 50–100 years (Titus, 1988; Nicholls *et al.*, 1999; Reyes *et al.*, 2004; Kirwan & Murray, 2008). While determining the balance between erosion of marshland on the seaward margin and potential expansion of marshland upslope is difficult, such a decline could represent a catastrophic loss of ecosystem services by one of Earth's most valuable coastal environments (Costanza *et al.*, 1997).

Despite the tendency for marshes to erode and submerge under increased rates of sea level rise, our results contribute to the growing body of literature that suggests surviving northern marshland may actually increase its productivity in response to future global change. For example, Morris *et al.* (2002) find that *S. alterniflora* productivity is greatest during years of anomalously high sea level, provided that the relative elevation of the marsh is superoptimal for the growth of the vegetation. Additionally, marshes colonized by plants with C₃ photosynthetic pathways will likely experience greater productivity under enhanced atmospheric CO₂ levels. While C₄ communities (e.g. *Spartina*) show little response, *Scirpus olneyi* marsh grown under double ambient CO₂ conditions has a long-term 35% increase in net carbon assimilation, and a near doubling of aboveground biomass (Rasse *et al.*, 2005; Erickson *et al.*, 2007). On the other hand, *S. olneyi* productivity is low in years of high salinity (Erickson *et al.*, 2007), and

C₃ plants generally do not tolerate high temperatures (Dunn *et al.*, 1987).

Our estimates of the effect of temperature on *S. alterniflora* suggest that climatic warming will lead to increased productivity (10–40%) at a magnitude similar to that of marsh lost due to sea level change (10–50%). We caution, however, that processes controlling the submergence of marshland are inherently complex and nonlinear, and that ecosystem services may be related to characteristics beyond productivity (e.g. marsh area, species composition). Nevertheless, although we additionally recognize that increased aboveground productivity may not significantly increase accretion in sediment-deficient marshes, our conclusion that increased growth under a warming climate may compensate for the amount of productivity lost by eroding marshland could be conservative. Recent numerical models suggest that the growth rate of vegetation strongly influences the stability of some marshes responding to sea level change (Morris *et al.*, 2002; D'Alpaos *et al.*, 2007; Kirwan & Murray, 2007; Marani *et al.*, 2007; Kirwan *et al.*, 2008). In these models, increased vegetation growth will tend to promote higher marsh accretion rates, stabilize channel expansion, and decrease the ability for waves to erode the marsh platform. Although there is a clear need for future model and field-based experimentation to explicitly consider the coupled response of marshes to temperature and sea level change, the recognized ability of vegetation to stabilize marshes responding to sea level change suggests that temperature warming could reduce estimates of marsh loss, at least in middle and northern latitudes. If true, the combined impacts of future global change (e.g. sea level, temperature, CO₂) could actually increase the total productivity of marshland.

Acknowledgements

We appreciate the helpful reviews of Johan van de Koppel and an anonymous reviewer. This work was supported by the USGS Global Change Research Program and the National Science Foundation (OCE 0423565 and DEB 0316429).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Compiled estimates of *Spartina alterniflora* annual productivity, as measured by maximum standing live biomass. Position in Marsh heading refers to the elevation or vegetation characteristics of the portion of the marsh sampled. Middle and high elevation marshes assumed to be dominated by short form *S. alterniflora* rather than its tall form. We also assume that where reported as a 'marsh average,' the sampled vegetation is relatively homogenous and dominated by inland marsh far from edges of tidal creeks. We have specified 'homogenous average'

where this assumption can be confirmed. The source heading denotes whether the estimate was obtained directly from text or a table, interpreted from a figure, or obtained directly from the Turner, 1976 synthesis. An asterisk denotes that the productivity estimate represents an average of at least 2 years of data collection. Shading denotes locations of measurements that were averaged together in Figure 1b.

Table S2. Correlation statistics between *Spartina alterniflora* productivity and climatic variables.

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