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Microspatial Differences in Soil Temperature Cause Phenology Change on Par with Long-Term Climate Warming in Salt Marshes

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ABSTRACT

Phenology studies mostly focus on variation across time or landscapes. However, phenology can vary at fine spatial scales, and these differences may be as important as long-term change from climate warming. We used high-frequency ''PhenoCam'' data to examine phenology of *Spartina alterniflora*, a foundation species native to salt marshes on the US East and Gulf coasts, and a common colonizer elsewhere. We examined phenology across three microhabitats from 2013 to 2017 and used this information to create the first spring green-up model for *S. alterniflora*. We then compared modern spatial variation to that exhibited over a 60-year climate record. Marsh interior plants initiated spring growth 17 days earlier than channel edge plants and spent 35 days more in the green-up phenophase and 25 days less in the maturity phenophase. The start of green-up varied by 17 days among 3 years. The best spring green-up model was based on winter soil total growing degree days. Across microhabitats, spring green-up differences were caused by small elevation changes (15 cm) that drove soil temperature variation of 0.8°C. Preliminary evidence indicated that high winter belowground biomass depletion triggered early green-up. Long-term change was similar: winter soil temperatures warmed 1.7 ± 0.3°C since 1958, and green-up advanced 11 ± 6 days, whereas contemporary microhabitat differences were 17 ± 4 days. Incorporating local spatial variation into plant phenology models may provide an early warning of climate vulnerability and improve understanding of ecosystem-scale productivity. Microscale phenology variation likely exists in other systems and has been unappreciated.

Key words: digital camera imagery; global climate change; coastal tidal marsh; Georgia Coastal Ecosystems LTER; microhabitat; PhenoCam; *Spartina alterniflora*; *Sporobolus alterniflorus*; soil temperature gradient; spring green-up.

HIGHLIGHTS

- Winter soil temperature gradients drove spring green-up in *Spartina alterniflora*.
- Microspatial phenology variation was similar to effects of 60 years of climate warming.

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- Similar phenology variation likely exists in other systems and may be unrecognized.

INTRODUCTION

Studies of plant phenology inform our understanding of plant growth and productivity and how these may shift with climate change (Goulden and others 1996). Historically, accurate phenological models were limited by the labor required to collect high-frequency data that allow precise identification of phenophase transitions. Technologies such as repeat digital image photography create temporally dense vegetation time series from which we can analyze phenology trends and have ushered in a new era of plant phenology studies. For example, researchers have demonstrated that landscape heterogeneity is linked to phenophase transitions in deciduous forests (Klosterman and others 2014) and that precipitation can drive grassland phenology (Zelikova and others 2015). However, few studies have examined how phenology varies within sites at small spatial scales. An open challenge, then, is to gain a better understanding of intraspecific variation in phenology to improve our ability to forecast the effects of changing temperature and precipitation regimes on ecosystem function.

Studies of plant phenology trace their roots back to the origins of human agriculture (Schwartz 2013). Annual plant cycles have often been defined as consisting of four phenophases (Zhang and others 2004): green-up, maturity, senescence, and dormancy, with the first three comprising the growing season. Although plants may not enter true physiological dormancy when conditions are mild (Vegis 1964), the dormancy period can be operationally defined as the winter period with minimal growth. Transitions among phenophases are often described with empirical models based on climate factors, and phenophase transition models typically rely on accumulated temperature (total growing degrees days—TDD). Many investigators have examined variation in phenology across large environmental gradients such as along mountain ranges or across latitudes (Stanton and others 1997; Zhang and others 2004; Schwartz and others 2006). However, few studies have examined whether microspatial environmental variation can drive phenology in landscapes with low topographic variation over short distances.

This study focused on a salt marsh dominated by *Spartina alterniflora* Loisel (Kartesz 2015; USDA and NRCS 2019) (= *Sporobolus alterniflorus*; Peterson and others 2014a, b), a perennial salt marsh grass. Salt marshes dominated by *S. alterniflora* are well suited as a test case for examining microspatial phenology differences because these plants typically occur in monoculture and are highly clonal, but still exhibit growth structured by environmental factors (Mendelssohn and Morris 2002; Travis and Hester 2005). They are also low-stature plants that grow in full sun, such that one camera image can capture several microhabitats across a site. These facts allow us to assign phenology variation across microhabitats to environmental conditions. Here, we used data from the ''GCESapelo'' PhenoCam to describe the phenological cycle of *S. alterniflora* on Sapelo Island, GA. The camera's field of view spans three microhabitats (channel edge, mid-marsh and marsh interior), where environmental variables such as elevation and tidal flooding vary. We used PhenoCam data to assess spatial variation in phenology across these microhabitats over four annual cycles (2013–2017).

Understanding *S. alterniflora* phenology is valuable for evaluating how salt marshes will respond to climate change over the long-term. This is in part because *S. alterniflora* is a dominant native plant within salt marshes on the East and Gulf coasts of North America (Pennings and Bertness 2001) and is an important colonizing species on the US Pacific coast, most of the coast of China, and elsewhere (Strong and Ayres 2016). Accumulation of *S. alterniflora* belowground biomass improves marsh resilience against sea level rise by increasing vertical marsh accretion (Kirwan and Guntenspergen 2012). Thus, identifying the environmental cues that drive *S. alterniflora* phenology may improve our understanding of marsh plant ecology and geomorphological resilience, and how both will respond to climate change. However, no empirical phenology model yet exists for *S. alterniflora*.

Our overarching goal was to evaluate microspatial variation in phenology in *S. alterniflora* and identify environmental parameters related to spring green-up. Spring green-up is commonly modeled in other systems (Cannell and Smith 1983; Hänninen 1987; Murray and others 1989; Hunter and Lechowicz 1992) and is likely a key phenological transition driving the timing of other phenophases and growing season length. Differences in phenology among microhabitats also need to be put into a long-term context to determine their importance. Therefore, once we identified a suitable model for predicting spring green-up, we used it to hindcast long-term change in *S. alterniflora* to put the microhabitat differences into context and provide insight into how habitat variation will interact with ecosystem outcomes and future global climate change.

To accomplish this, we (1) used PhenoCam data to examine spatial and temporal differences in *S. alterniflora* phenophases across a salt marsh edge to marsh interior gradient; (2) parameterized an empirical phenology model that could accurately estimate *S. alterniflora* spring green-up, and (3) used the best phenology model to hindcast spring green-up dates over a 60-year climate record, allowing us to place modern microhabitat differences within the context of long-term change.

Materials and Methods

Study Area

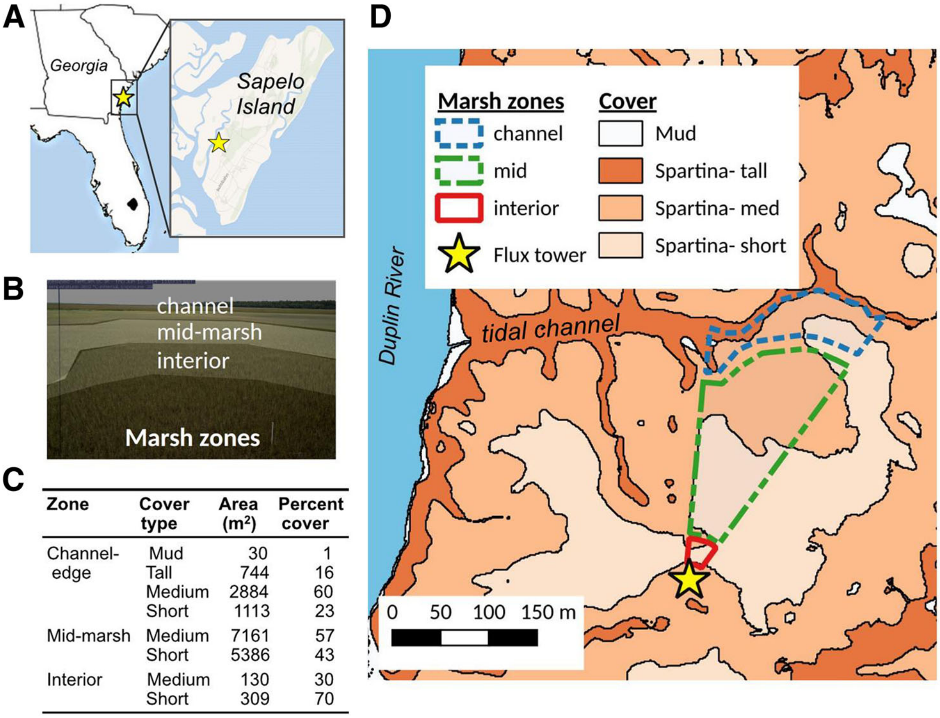
Our study marsh was a monoculture of *S. alterniflora* on Sapelo Island, GA, adjacent to a flux tower operated by the Georgia Coastal Ecosystems Long-Term Ecological Research (GCE-LTER) program (lat: 31.441°, long: − 81.284°, data hosted at https://gce-lter.marsci.uga.edu). We used data from the flux tower instruments as part of this work, including air temperature (probe model 107, Campbell Scientific Instruments, located ~ 1 m up from the tower platform) and soil temperature (two averaging soil thermocouple probes, model TCAV-L, Campbell Scientific Instruments, located ~ 10 m into the marsh interior from the tower, each buried 5–10 cm and approximately 1.5 m apart), as well as the ''GCESapelo'' PhenoCam (StarDot NetCam SC 5MP IR, StarDot Technologies, Buena Park, CA USA), a digital camera mounted on the flux tower roughly 6.2 m from the marsh surface (data hosted at https://phenocam.sr.unh.edu/webcam/sites/gcesapelo/). Tides at this site are semi-diurnal with a range of 2–3 m, such that high tides flood the marsh platform up to 1.2 m deep.

Spatial and Temporal Differences in *S. alterniflora* phenophases

To estimate spatial and temporal patterns in *S. alterniflora* phenophases, we used PhenoCam data, which consisted of year-round repeat digital images of the study marsh taken every half-hour during daylight at an oblique angle (Figure 1). We analyzed images from September 17, 2013, through September 22, 2017, except when the camera was off-line July 16, 2014, through September 2, 2014, and February 1, 2016, through February 29, 2016. To reduce solar variation in illumination, we limited analyses to images collected between 10:00 and 14:30 H. We also applied the smart classifier, a salt marsh-specific algorithm we developed to calculate cloud cover and marsh flooding within PhenoCam imagery (O'Connell and Alber 2016). This allowed us to identify and remove images depicting more than 1% marsh flooding or more than 30% cloud cover, leaving only optimal images for analysis (O'Connell and Alber 2016). Information from the remaining images was then averaged into a single value for each day, resulting in a time series of 1341 daily observations. We used the R platform for all image processing and statistical analysis (version 3.4.2).

We divided the PhenoCam imagery field of view into three marsh zones: channel edge, mid-marsh and interior, which were used as separate regions of interest (ROIs) in our analyses (Figure 1B). To place these ROIs, we had some physical constraints. We used a tidal creek in the background of the PhenoCam field of view to determine the distal edge of the channel edge zone, and a reference panel that appeared in the foreground of some PhenoCam images to determine the proximal edge of the interior marsh zone. We also made these ROIs roughly parallel to the tidal creek in the image background and roughly equivalent in terms of PhenoCam image area. Because the PhenoCam takes oblique angle images, closer objects appear larger than background objects in the images. Thus, these ROIs have different actual map areas (Figure 1D).

These ROIs also have different mean plant heights (Figure 1C, D). Although plant height is continuous, *S. alterniflora* is often classified into three height forms, where shorter plants are more typical of the marsh interior and taller plants of the marsh edge. Hladik and others (2013) created a habitat map for marshes adjacent to Sapelo Island in which they categorized plants as tall (> 1 m in height), medium (0.5–1 m) and short (< 0.5 m). Based on this classification, the channel and mid-marsh zones were both dominated by medium-form plants, whereas the interior was dominated by short-form plants (Figure 1). Tall-form plants were only present in the channel edge zone. We had monthly vegetation plot data for each marsh zone from a nearby location (see Supporting Information). We used this data in combination with the habitat map of Hladik and others (2013) to create a weighted average of estimated plant heights across the marsh zone ROIs. From this, we estimated that maximum plant heights (mean from all years ± SD) were 48 ± 7, 36 ± 5, and 32 ± 3 cm, respectively, in the channel edge, mid-marsh and marsh interior zones.



Zone	Cover type	Area (m^2)	Percent cover
Channel-edge	Mud	30	1
	Tall	744	16
	Medium	2884	60
	Short	1113	23
Mid-marsh	Medium	7161	57
	Short	5386	43
Interior	Medium	130	30
	Short	309	70

Figure 1. **A** The location of the flux tower on Sapelo Island, GA, where the ''GCESapelo'' PhenoCam is mounted. **B** An example PhenoCam image. **C** Approximate area (m^2) of cover types within each marsh zone region of interest (ROI). Tall, medium, and short refer to *S. alterniflora* growth forms, and mud refers to areas of bare soil. **D** A cover type map of the PhenoCam field of view for the interior, mid-marsh, and channel marsh zone ROIs. Cover type map and table information adapted from Hladik and others (2013).

To extract information from each marsh zone, we created ROI image masks and used the biOps package in R (Bordese and Alini 2013) to convert PhenoCam jpeg images into numerical arrays representing the amount of red, green and blue (RGB, on a scale of 0–255) in each pixel for each ROI and averaged these to daily RGB values for each ROI. We then calculated greenness indices, such as the green chromatic coordinate (GCC) for each ROI, fit logistic curves to each period of phenology index increase or decrease and took the derivative of each curve to determine the date of phenophase transition (see Supporting Information).

To compare phenology results among zones and years, we used a generalized linear model (GLM) with period length (days) or start of phenophase (day of year) as the response variable and either year or marsh zone (channel edge, mid-marsh or interior) as the predictor for each phenophase (green-up, maturity, senescence or dormancy). Similarly, we compared total growing season length (days) by marsh zone and year, where growing season was the sum of days for green-up, maturity and senescence. Finally, we confirmed PhenoCam-derived microspatial differences in spring green-up through an analysis of Landsat 8 estimates of monthly percent change in aboveground biomass (Supporting Information).

Parameterization of an Empirical Spring Green-Up Model

Once we described the phenological patterns, the next step was to parameterize a green-up phenology model for *S. alterniflora*. A common approach for modeling phenology uses empirical models that relate plant development to climate factors (De Réaumur 1735; Chuine and others 2013; Richardson and others 2013), especially temperature because temperature increases plant development rates (De Réaumur 1735; Arnold 1959) and often explains much of phenology variation (Chuine and others 2013). Phenophase transition models that only rely on temperature variation can be considered a kind of null model. These have been called the growing degree day model, or, when applied to the spring green-up phenophase, the spring warming model (Arnold 1959; Hunter and Lechowicz 1992). This basic model can be modified to include other environmental parameters, such as the degree of winter chilling, either sequentially or in parallel with temperature (Hänninen 1987; Hunter and Lechowicz 1992). To identify the best spring green-up model, we parameterized the spring warming model and compared it to more complex models. Ultimately, the spring warming model had the strongest evidence, and we show only its parameterization here. The parameterization of other models and the model selection procedure can be found in the Supporting Information.

In the spring warming model, TDD (cumulative temperature sums) accumulate above a base temperature that begins once days are lengthening, typically January 1. Green-up occurs when a TDD accumulation threshold is crossed (Hunter and Lechowicz 1992). Following Arnold (1959), we calculated the base temperature (for example, the temperature below which development does not occur) by regressing mean temperature for the phenophase, in this case dormancy, against the phenophase development rate (100/total phenophase length). The base temperature is then:

$$\text{base temp} = \frac{-\text{slope}}{x \ \text{intercept}} \tag{1}$$

where Eq. 1 parameters are extracted from the linear regression (Arnold 1959). Plants with the same base temperature should fall along a straight line with a positive slope (Arnold 1959). We compared Eq. 1 regressions based on either air or soil temperature to see which best fit the data. Air temperature was recorded at the flux tower and soil temperature estimates came from a transect of temperature probes. As described in the results, preliminary analyses indicated that spatially explicit soil temperatures yielded better predictions for *S. alterniflora* green-up than air temperatures measured from a single location. Further, we could predict soil temperature as a function of elevation and tidal flooding for each marsh ROI, where elevation explained most of the variation in soil temperature because the marsh was usually exposed (Supporting Information). We therefore used soil temperatures for all of the following calculations.

Once the base temperature was established, starting from January 1 (that is, after days were lengthening), we calculated TDD as:

$$\text{TDD} = \sum (T - B)\frac{1}{288} \tag{2}$$

where T is the 5 min temperature observation and B is the calculated base temperature from Eq. 1. A requirement of Eq. 2 is that $T > B$. When $T < B$, 0 is substituted for the expression $(T - B)$ in Eq. 2 (for example, the observation is excluded from the temperature sum). For the spring warming model, green-up occurs when TDD crosses a threshold value, calculated as the mean of all the observed TDD values at green-up for all years and zones. We observed one outlier in the regression relationships, based on a Cook's distance of more than 1 (Cook and Weisberg 1982), and did not include it in our estimate of base temperature. To examine the influence of the outlier, all phenology model analyses were conducted with and without it included.

The PhenoCam-based methods above suggested that small elevation changes caused soil temperature differences and that soil temperature was the appropriate variable for modeling spring green-up. We confirmed that differences in spring green-up were related to elevation more broadly across the marsh through an analysis of Landsat 8 data. We also used this same analysis to ask whether physiological differences related to plant height-form could be a better explanation than elevation for spring green-up and could not find evidence of this (Supporting Information).

We also developed a model to explain the 2014 outlier, which we called the Spring warming + belowground biomass depletion model. We needed this model because of the outlier in the marsh interior in 2014 where green-up was much earlier than predicted by any of the other empirical models we tried. We hypothesized that high dormancy phenophase temperatures associated with this observation led to high respiration and belowground biomass depletion rates, potentially triggering earlier green-up to avoid critical losses in belowground resources. We therefore conducted an exploratory data analysis wherein we modified the spring warming model to include belowground biomass depletion rate (Supporting Information). We consider this a preliminary estimate because we had only one very high depletion event (for example, the 2014 early spring green-up).

Hindcast Spring Green-Up Dates Over a 60-Year Climate Record

We placed observed microspatial variation in context by hindcasting spring green-up changes. For this, we acquired a 60-year record of daily climate summaries collected at the University of Georgia Marine Institute on Sapelo Island, GA from the National Weather Service (GHCND:USC00097808; www.ncdc.noaa.gov; gce-lter.marsci.uga.edu; https://www.ncdc.noaa.gov/cdo-web/datasets/GHCN

D/stations/GHCND:USC00097808/detail) (May 1957–2017), where data gaps were filled with data from the nearby Brunswick-Malcolm McKinnon Airport (GHCND:USW00013878; https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USW00013878/detail). Air temperature from the climate summaries was correlated with soil temperature at the flux tower, which was then used in combination with information on flooding to generate a single historical soil temperature record averaged across the zones (Supporting Information). We calculated root mean squared error (RMSE) in predicted versus observed soil temperatures by comparing long-term estimates to modern soil temperature estimates (averaged across all zones) for overlapping years (2013–2017).

We used the spring warming model to estimate green-up dates from the 60-year soil temperature time series. To calculate TDD from daily summary data, we estimated the average daily temperature as the (maximum temperature + minimum temperature)/2 (Cannell and Smith 1983). TDD was then the sum of the daily temperature means minus the base temperature, excluding days where the daily mean was less than the base temperature (Cannell and Smith 1983). We calculated RMSE in predicted green-up date by comparing green-up estimates to PhenoCam observations (averaged across all zones) for overlapping years (2013–2017). Finally, we estimated the change in green-up date over the 60-year record by fitting a linear model with green-up day as the response and year as the predictor.

RESULTS

Spatial and Temporal Differences in *S. alterniflora* phenophases

Phenophases in *S. alterniflora* differed in both timing and length across the three marsh zones. Averaged over all years, plants in the interior initiated green-up on Julian day 39 (Feb 8), which averaged 17 days earlier than those in the mid-marsh or channel edge ($P < 0.001$; Figure 2A). In contrast, the other transition dates were statistically similar among zones: on average, the onset of maturity was on July 4, the onset of senescence on August 23 and the onset of dormancy on December 6. Differences in phenophase length were more common, particularly between the interior and channel edge zones (Figure 2B). Plants at the channel edge spent more than a month less in green-up than those in the marsh interior (162 vs. 128 days; $P < 0.001$). Channel edge plants also spent 25.5 days longer in maturity than the other two zones (67 days vs. 41 and 42 days in the mid-marsh and interior zones, respectively; $P = 0.001$). For senescence, there was weak support for a biologically significant difference between the channel edge and mid-marsh, such that channel edge plants spent 18 fewer days in senescence ($P = 0.09$). For dormancy, the largest differences were once again between the channel edge and marsh interior, such that marsh interior plants spent 17 fewer days in dormancy ($P = 0.01$). However, total growing season length did not differ significantly among zones ($P > 0.1$).

There were also interannual differences in phenology (Figure 3). In 2016, the marsh reached maturity on May 30 and senescence on July 21, which was almost two months earlier than the two previous years (maturity on July 23 and 19 and senescence on September 7 and 9 in 2015 and

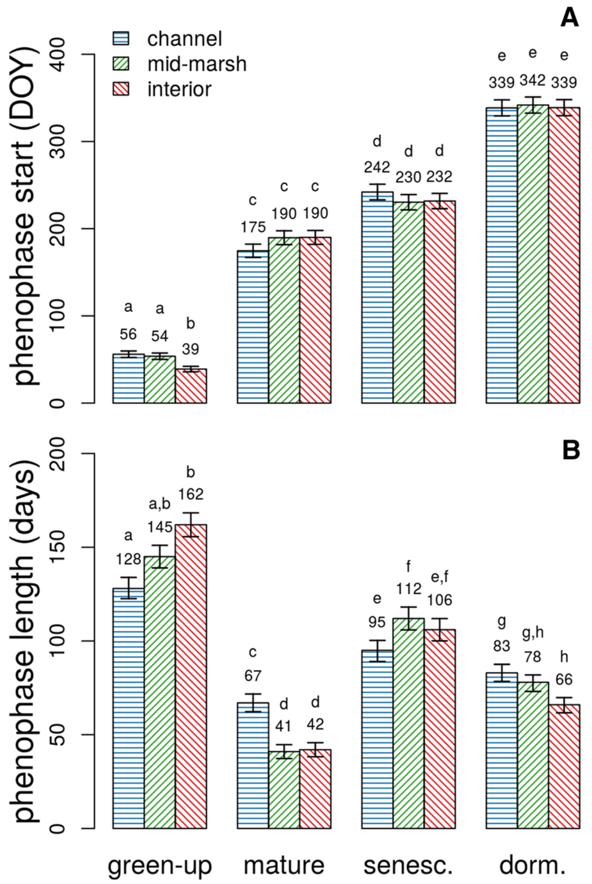


Figure 2. Spatial trends in **A** phenophase start (day of year) and **B** phenophase length (days). Trends were captured starting fall 2013 and ending summer 2017. Error bars represent 1 SE. Significant differences across groups are indicated by different Latin letters above each bar. Numbers above each bar indicate the mean value in days.

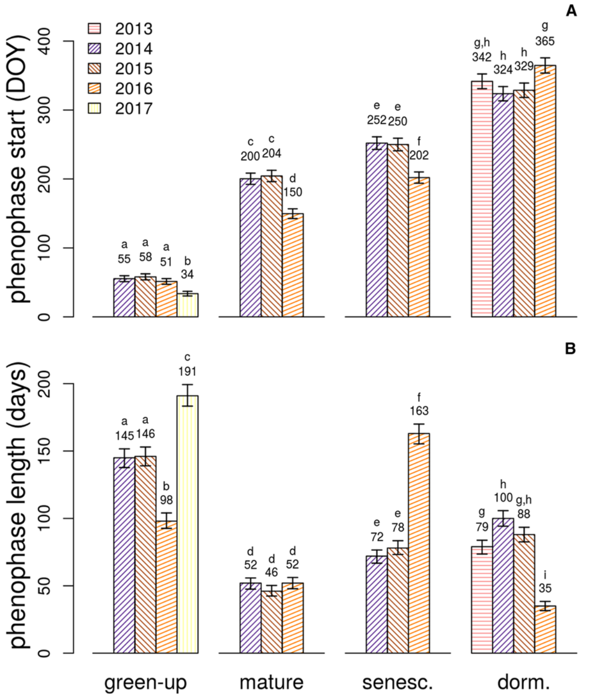


Figure 3. Annual trends in **A** phenophase start (day of year) and **B** phenophase length (days). Trends were captured starting fall 2013 and ending summer 2017. Error bars represent 1 SE. Significant differences across groups are indicated by different Latin letters above each bar. Numbers above each bar indicate the mean value in days.

2014, respectively) (Figure 3A). Green-up in 2017 was on February 3, as compared to the last week in February for all other years, a range of 17 days. The length of time in the various phenophases also varied from year to year, with 47.5 fewer days in green-up in 2016 as compared to previous years (98 vs. 145 and 146 days; $P < 0.001$) and more time in 2017 (192 days; $P < 0.001$) (Figure 3B). The senescence phenophase was nearly twice as long in 2016 as in previous years (163 days vs. 78 and 72 days; $P < 0.001$); the dormancy period starting in 2016 was 54 days less than other years (35 as compared with 79–100 days; $P < 0.001$). The overall growing season length was significantly longer in 2016 than in other years ($P = 0.001$), mostly as a result of a longer senescence period during 2016.

Parameterization of an Empirical Spring Green-Up Model

To parameterize a phenology model for spring green-up of *S. alterniflora*, we first identified a base temperature for calculating TDD (Eq. 1). We began with air temperature for this calculation, resulting in a base temperature of 3.8°C (outlier excluded; $R^2 = 0.77$). However, there was a zonal bias, such that the marsh interior was always above the best fit line and the channel edge marsh always below (Figure 4A). This disappeared when we calculated the base temperature from spatially variable estimates of soil temperature rather than air temperature (Figure 4A). The resulting base temperature was 9.9°C, which is in keeping with values (5–15°C) typically reported for other plants (Cannell and Smith 1983, for example, Murray and others 1989; Hunter and Lechowicz 1992). The soil temperature relationship also explained more of the variability in the data than air temperature (outlier excluded; R^2 0.94) (Figure 4B). We therefore used soil temperature to calculate TDD for green-up models.

We ultimately selected the spring warming model as the best fit model because it had the lowest RMSE and the fewest parameters (Table S1). The basic spring warming model assumed green-up occurred when a TDD threshold of 202 (outlier excluded) was exceeded (Figure S5) and predicted green-up day of year well, with a RMSE of 6.7 days without the outlier and 6.9 days with it (Table S1; Figure 5A).

We also explored a spring warming + biomass model, primarily to explain the 2014 early green-up outlier in the marsh interior. We found that belowground biomass depletion rates were related to winter precipitation and soil temperature, with precipitation accounting for most of the variation (Supporting Information: Figure S6). Adding a threshold biomass depletion rate as an alternate trigger for the spring warming model reduced the RMSE (outlier included) from 6.9 to 3.9 d (Figure 5B, Table S1). However, because this model was based on a single event, further observations are necessary for firm conclusions.

Hindcast Spring Green-Up Dates Over a 60-Year Climate Record

To place microspatial variation in context, we used a 60-year time series to hindcast soil temperature as well as the resulting change in spring green-up dates. The gap-filled record of soil temperature showed an overall increase of 1.7 ± 0.3°C from 1958 to 2017 ($P < 0.001$), from an estimated 12.8 to 14.5°C at 10 cm depth (Figure 6A). The estimated soil temperatures corresponded to the observations derived from the flux tower (RMSE = 0.5°C), which overlapped from 2014 to 2017 (Figure 6A).

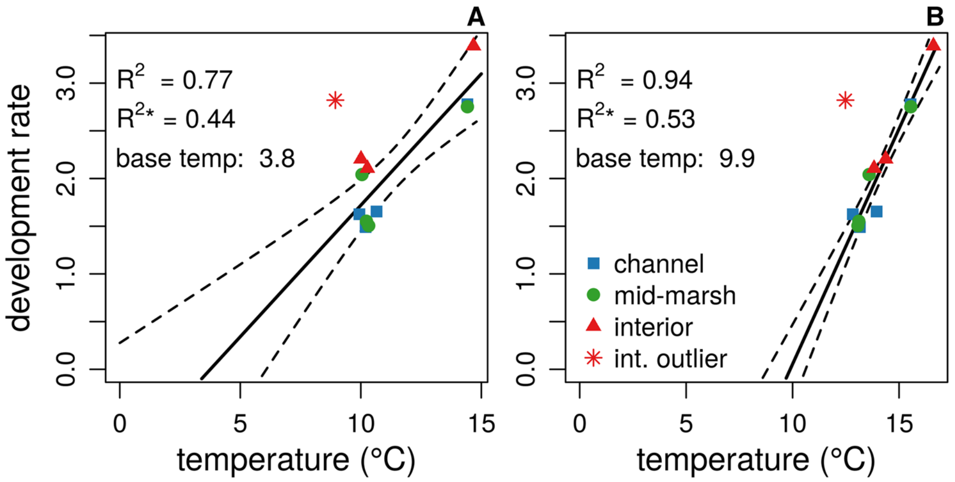


Figure 4. Base temperature extracted as the x-intercept in the relationship between development rate and mean daily temperature. In **A** the data were plotted against air temperature. In **B** data were plotted against estimated soil temperature, which provided a better fit. Goodness of fit for the relationships also are presented, where R^2 and R^{2*} is with and without the outlier included, respectively. The dashed lines represent the 95% CI for the fit.

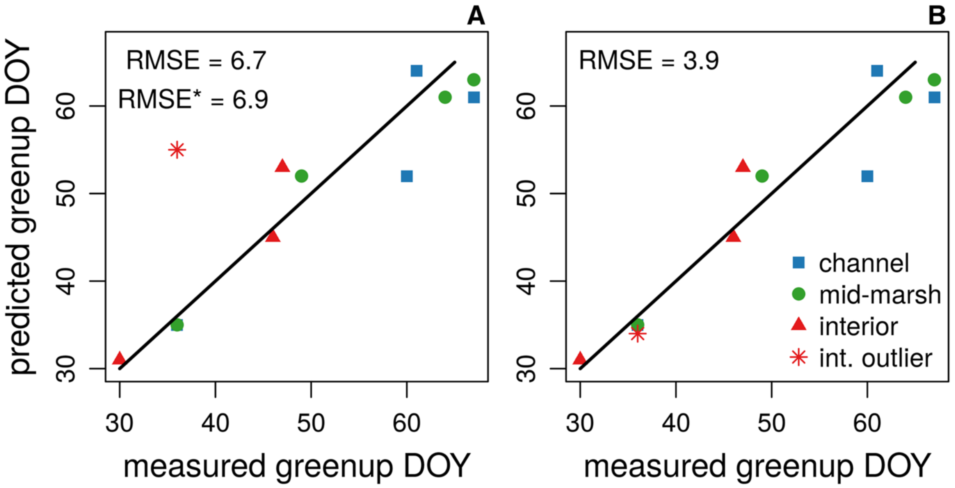


Figure 5. **A** Goodness of fit and RMSE in days between the PhenoCam-measured green-up day of year (DOY) and the spring warming model estimated green-up DOY calculated with and without (*) the outlier included and **B** the spring warming model modified by biomass depletion rate, which includes the outlier by definition.

For the period that overlapped the modern observations, the spring green-up model estimated green-up dates from the long-term climate data with a RMSE of 6.1 days, which was similar to the PhenoCam-estimated green-up RMSE (Figure 6B). There was considerable variation in green-up dates over the 60-year time series, ranging from as early as January 27 (in 1974) to as late as March 19 (in 1978), a 51 day difference. From this, we estimated a mean green-up advancement of 10.8 ± 6 days from 1958 to 2017 (Figure 6B), which is similar to the observed green-up spatial difference between channel edge and marsh interior in the modern PhenoCam data (17 ± 4 days).

Discussion

This study demonstrated that aspects of *S. alterniflora* phenology varied by more than 1 month along microspatial gradients across a salt marsh. We also provided a spring green-up model for *S. alterniflora*, based on winter soil temperatures. When we applied the green-up model, we found that finescale spatial soil temperature differences caused modern green-up variation across the marsh, and that when compared to historic trends, those effects were on par with change caused by long-term climate warming. These findings suggest that microspatial variation in phenology should be

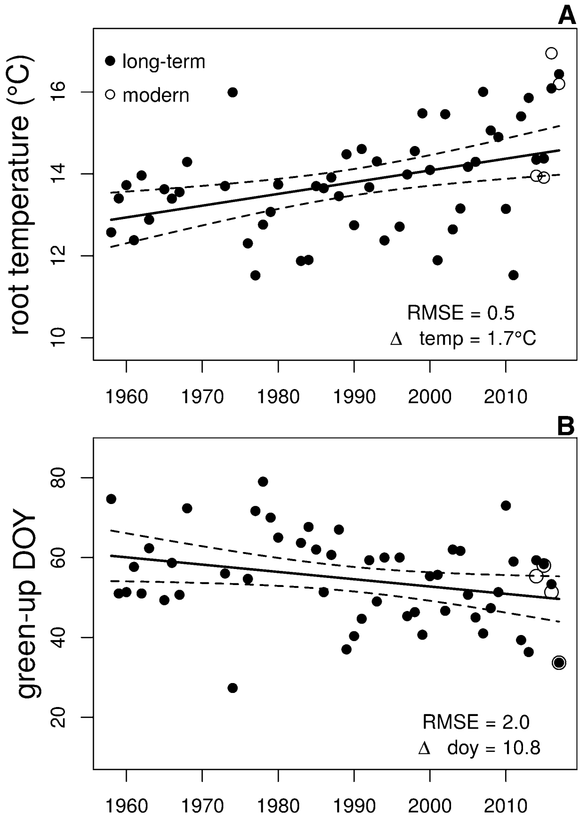


Figure 6. A Long-term record of change in estimated mean winter soil temperatures from the gap-filled and site-calibrated 60-year climate data, estimated as the mean of all marsh zones during December and January. Modern data estimated from the flux tower are also superimposed and RMSE is provided for the difference between modern and long-term estimates for overlapping years. The best fit line (solid line) estimating the increase in temperature with time is presented ($P < 0.001$) where the dashed lines represent the 95% CI for the fit. **B** Long-term change in green-up day of year (DOY) predicted from the climate record in panel A through the use of the spring warming model. The best fit line (solid line) for change in green-up DOY with respect to year also is indicated ($P < 0.001$). The dashed lines represent the 95% CI for the fit. Modern green-up dates from the PhenoCam (mean of all zones) also are superimposed and RMSE is provided for the difference between modern and long-term estimates for overlapping years.

incorporated into our understanding of marsh plant ecology as well as into phenology-dependent calculations, such as productivity. Similar variation in microhabitats likely drives phenology in other systems and is not always recognized.

To create a detailed description of *S. alterniflora* microspatial phenophases differences, we took advantage of the high-frequency (every 30 min) observations provided by the ''GCESapelo'' PhenoCam. This type of high-frequency phenology data has not been easily available before PhenoCams for any plant and allows documentation of phenophase transitions with an accuracy that is difficult to obtain from sampling programs with less dense temporal data (Richardson and others 2007). We also used PhenoCam data in a new way, by examining within image phenology variation, allowing us to report microspatial variation within a habitat. This was possible because our PhenoCam captures a largely clonal grass monoculture, allowing us to ask questions about how environmental gradients interact with its phenology. The PhenoCam also revealed patterns that were difficult to observe through field campaigns. For example, during preliminary analyses, we found that monthly field measures of biomass were not sufficient because key phenological transitions occurred between the monthly observations. Similarly, available satellite data such as Landsat and MODIS were spatially coarse so that finescale spatial phenology differences were difficult to observe. Satellite datasets also had missing observations from tides and clouds, especially during the summer, a key part of the growing season. Thus, the ''GCESapelo'' PhenoCam uniquely allowed us to observe the interaction of phenology and the environment at fine temporal and spatial scales.

Phenophase lengths were spatially variable across zones. Although we have not yet examined other phenophase transitions, the phenophase contributing the most to zonal differences appeared to be green-up onset date, which was largely controlled by spatial variation in winter soil temperature (discussed below). Thus, green-up onset was 1.5–3 weeks earlier in the marsh interior than in the mid-marsh or channel edge and the green-up phenophase lasted more than a month longer in the marsh interior than in other habitats. Similarly, Landsat-estimated aboveground biomass from the PhenoCam field of view also changed faster in the marsh interior early in the year (Supporting information), demonstrating that PhenoCam marsh zone differences can be observed in other data sources. The next phenophase, maturity, was nearly a month longer at the channel edge than elsewhere. Channel edge plants may reach maturity quickly because they initiate growth later in the growing season when there are higher air temperatures that can increase shoot metabolism (Arnold 1959) and photosynthetic rates (Saxe and others 2001). Senescence length and dormancy onset were the least spatially variable parameters, suggesting that the marsh was synchronized by the end of the growing season and that dormancy onset had the least mutable trigger. A combination of temperature and photoperiod is thought to control bud growth cessation in many woody species (Saxe and others 2001), and is a likely trigger of flowering in *S. alternflora* (which is tied to the end of the growing season) (Seneca 1974; Somers and Grant 1981). Thus, photoperiod and temperature are probably related to *S. alterniflora* senescence and dormancy onset as well. In fact, photoperiod plays an implicit role in any model based on thermal sums because we always begin TDD sums by selecting a common day on which to start the analysis. Flowering onset itself likely did not play a role in the senescence and dormancy patterns we observed. Flowers were rare, similar in color to background vegetation, and spatially heterogeneous in terms of both timing and proportion (earlier timing and greater flowering for medium and tall-form plants than short form), whereas, in contrast, senescence and dormancy onset were spatially homogeneous. However, the best fit model for senescence and dormancy onset in *S. alterniflora* remains to be determined.

The broader implications of these spatial differences in phenophase timing are unclear. Early green-up may expose plants to stress from freeze events (Saxe and others 2001; Badeck and others 2004), whereas later green-up may concentrate growth during the most favorable part of the year for photosynthetic rates, allowing more rapid carbohydrate accumulation (Gu and others 2003). Ultimately, green-up date represents a trade-off between the number of growing days and the rate of growth. As *S. alterniflora* nearly uses up its belowground reserves during spring green-up to create aboveground canopies (Gallagher 1983; Jung and Burd 2017), spring may be a particularly vulnerable time for plants. Further, early spring green-up may not predict increases in productivity. Gu and others (2003) compared five sites (one evergreen forest, three deciduous forest and a tall-grass prairie) and found that plant communities that reached peak CO_2 assimilation soon after green-up had greater total CO_2 assimilation, and that this variable was more important than growing season length for determining total C uptake. Future work should account for spatial phenology variation in plant productivity models to understand how this affects carbon assimilation.

These results also have implications for restoration managers because they may help improve models that predict marsh resiliency, productivity, or other ecosystem services monitored as part of restoration trajectories. Most current models either use one temperature estimate or do not explicitly mention temperature (Morris and others 2002; Gifford 2003; Swanson and others 2014); we believe that accounting for spatial temperature variation will make these models more accurate and provide better information to managers. Overall, microspatial differences in soil temperature and phenology need to be monitored so that we have baseline data to understand how they are changing and how they contribute to important ecosystem outcomes.

To model green-up onset for *S. alterniflora*, we ultimately selected the spring warming model, based on soil temperatures at 10 cm depth, because this model was able to predict the date of green-up onset for *S alterniflora* within approximately one week (Figure 5). To apply this green-up model for *S. alterniflora,* the steps are to estimate soil temperature and then calculate TDD with a base temperature of 9.9°C and assume a phenophase transition when TDD crosses the 202 threshold. Phenology models based on soil temperature summed from a particular day are quite old (De Réaumur 1735; Chuine and others 2013) and typically are important for explaining phenology variation.

Microspatial differences in winter soil temperature were important for predicting *S. alterniflora* green-up, with the marsh interior averaging 0.8°C warmer than the channel edge. Early green-up in the marsh interior likely resulted from lower average elevation in this zone vs the channel edge (− 15 cm), as we found that elevation had strong negative relationships with soil temperature on the marsh platform (Alber and O’Connell 2019; Supporting Information: Figure S3). Thus, the low-lying marsh interior zone accumulated TDD more rapidly and initiated green-up sooner than elsewhere. Similarly, Landsat-derived estimates of broader-scale early spring aboveground biomass also showed that biomass accumulated faster in warmer, lower elevation marsh areas (Supporting Information). Although we commonly think of elevation as a driver of marsh plant growth because of its influence on tidal flooding, soil salinity, and sediment deposition (Mendelssohn and Morris 2002; Kirwan and Guntenspergen 2012; Voss and others 2013; O’Donnell and Schalles 2016), our results also suggest that elevation-driven temperature differences can drive important spatial variation in plant phenology, with largely unexamined consequences.

Although the spring warming model and its close relatives was best for estimating green-up date, unusual environmental conditions may cause additional variance in this model. In particular, we found preliminary evidence that a high belowground biomass depletion rate may have influenced the early green-up onset in the marsh interior during 2014. The marsh interior experiences greater plant stresses, including anoxic soils, high soil salinity, and high soil concentrations of toxic soluble sulfides (Mendelssohn and Morris 2002), which may have played a role in creating the conditions for early green-up by accelerating plant maintenance costs. Additionally, others have suggested that plant resources can influence phenology (Kikuzawa 1995; Zheng and others 2016). We could robustly associate belowground biomass depletion rates with warm soils and, especially, high winter precipitation (Supporting Information: Figure S6). We have not experimentally explored the mechanisms for early green-up and intend to follow up. One hypothesis is that warming directly increases physiological activity (Laidler 1984), and precipitation does so indirectly by reducing soil salinity (Mendelssohn and Morris 2002). However, we need more observations of these circumstances before we can conclude that belowground biomass depletion can stimulate an early green-up. Belowground biomass is a large component of marsh accretion and carbon sequestration potential, so this will be important to resolve.

We estimated that marsh soil temperatures have increased approximately 1.7°C over a 60-year interval. Although long-term advancement in green-up from global change has been documented in other habitats, such as alpine cold deciduous plants (Badeck and others 2004; Schwartz and others 2006), it has not been previously evaluated for coastal marshes. The rate of increase we observed was similar to that suggested by Hansen and others (2006), who noted a 0.2°C decade^{-1} increase in global air temperature over the past 30 years (a total of 1.2°C over a 60-year period). Although there was a great deal of interannual variability, the increased soil temperature we observed corresponded to an estimated 11-day advancement in green-up date, or 1.8 days decade^{-1} (Figure 6). This is in keeping with other long-term studies, which have reported spring green-up advancements of more than 1 day decade^{-1} (Walther and others 2002; Schwartz and others 2006). Advancements in green-up have far-reaching and complex implications for the life histories of insects, birds, and other organisms (Primack and others 2009). The ecological consequences of variation in green-up need to be evaluated for salt marshes.

Others may also wish to estimate microspatial phenology in order to improve estimates of plant phenology-related outcomes. The first step is to estimate spatial variation in soil temperature. Where detailed information from soil temperature probes is lacking, Landsat 8 estimates of land surface temperature can provide a first order approximation of this variation (Alber and O'Connell 2019) and USGS now provides these data as provisional Analysis Ready Data (ARD) products (earthexplorer.usgs.gov). This can provide information on relative temperature differences. These can then be combined with detailed winter soil temperature data from a single location to estimate soil temperature time series across a vegetated habitat, similar to what we did here. This information can then be used to estimate soil temperature-driven microspatial phenology variation.

Although many studies have examined how climate change may alter phenology at broad scales (Zhang and others 2004; Schwartz and others 2006), few have examined finescale differences within a habitat and associated these with environmental gradients. Our results suggest that as temperatures rise, we can expect green-up at the channel edge to approach the current timing of the marsh interior and that of the marsh interior green-up to continue to advance. Thus, plants at low elevations may provide a space for time substitution to forecast stress from warming winter temperatures and will bear close monitoring. However, predicting the effect of future climate change on *S. alterniflora* salt marsh phenology is not straightforward. The southeastern USA has been warming since 1960 and temperatures are projected to increase a further 1.9–2.4°C by 2065 (USGCRP 2017), which should directly affect soil temperatures and advance spring green-up. Elevation-driven gradients in soil temperature (Alber and O'Connell 2019) will also affect the rates of biological reactions such as nutrient processing, with implications for phenology. In addition, precipitation is also thought to be increasing in the southeastern USA (USGCRP 2017), which when coupled with increased temperature, may accelerate the winter depletion of belowground biomass with concomitant increases in ecosystem vulnerability during spring when belowground resources are lowest (Gallagher 1983). In addition, sea level rise will increase flooding, which will affect soil temperature and phenology in complex ways. For example, moderate sea level rise can stimulate plant growth and thus marsh accretion, but can drown plants when sea level rise is high (Nyman and others 1993; Voss and others 2013). Increased flooding from sea level rise will also change winter soil temperatures, cooling them in warmer climates such as the southeastern USA, but likely warming them in more northerly latitudes. Ultimately, these influences can cause changes in green-up and growing season length, and particularly if they affect belowground biomass, will likely affect plant carbon uptake, marsh accretion, and the carbon storage potential of salt marshes (Goulden and others 1996; Mudd and others 2009; Kirwan and Megonigal 2013).

CONCLUSIONS

We found that spatial variation in *S. alterniflora* phenology was considerable over short distances in the natural environment, and also demonstrated that soil temperature, rather than air temperature, was the appropriate variable for understanding spatial change in spring green-up. Intraspecific differences in spring green-up phenology based on microhabitat were similar in magnitude to variation among years and to differences caused by 60 years of global warming. This indicates that studies need to examine spatial gradients as well as temporal change to properly understand plant phenology. Studies from mountain slopes have long demonstrated that the ecology of the same species can differ along abiotic gradients (Stanton and others 1997; Dunne and others 2003). Here we show that similar variation exists among plants only a few meters apart and differing in elevation by only a few centimeters. Similar microhabitat differences likely drive phenology in many other systems and have been unrecognized.

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REFERENCES

Alber M, O'Connell JL. 2019. Elevation drives gradients in surface soil temperature within salt marshes. Geophysical Research Letters 46:5313–22.

Arnold CY. 1959. The determination and significance of the base temperature in a linear heat unit system. Proceedings of the American Society for Horticultural Science 74:430–45.

Badeck F-W, Bondeau A, Böttcher K, Doktor D, Lucht W, Schaber J, Sitch S. 2004. Responses of spring phenology to climate change. New Phytologist 162:295–309.

Bordese M, Alini W. 2013. biOps: Image processing and analysis.

Cannell MGR, Smith RI. 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. Journal of Applied Ecology 20:951–63.

Chuine I, de Cortazar-Atauri IG, Kramer K, Hänninen H. 2013. Plant development models. Phenology: an integrative environmental science. Dordrecht: Springer. p 275–93.

Cook RD, Weisberg S. 1982. Residuals and influence in regression. New York: Chapman and Hall.

De Réaumur R. 1735. Observation du thérmomètre, faites à Paris pendant l'année 1735, comparées avec celles qui ont été faites sous la ligne, à l'Isle de France, à Alger et en quelquesunes de nos isles de l'Amérique. Memoires de l'Académie des Sciences de Paris.

Dunne JA, Harte J, Taylor KJ. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. Ecological Monographs 73:69–86.

Gallagher JL. 1983. Seasonal patterns in recoverable underground reserves in *Spartina alterniflora* Loisel. American Journal of Botany 70:212–15.

Gifford RM. 2003. Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Functional Plant Biol 30:171–86.

Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC. 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biology 2:169–82.

Gu L, Post WM, Baldocchi D, Black TA, Verma SB, Vesala T, Wofsy SC. 2003. Phenology of vegetation photosynthesis. Phenology: an integrative environmental science. Tasks for Vegetation Science. Dordrecht: Springer. p 467–85.

Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M. 2006. Global temperature change. Proceedings of the National Academy of Sciences 103:14288–93.

Hänninen H. 1987. Effects of temperature on dormancy release in woody plants. Silva Fennica 21(3):279–99.

Hladik C, Schalles J, Alber M. 2013. Salt marsh elevation and habitat mapping using hyperspectral and LIDAR data. Remote Sensing of Environment 139:318–30.

Hunter AF, Lechowicz MJ. 1992. Predicting the timing of budburst in temperate trees. Journal of Applied Ecology 29:597–604.

Jung Y, Burd A. 2017. Seasonal changes in above- and belowground non-structural carbohydrates (NSC) in *Spartina alterniflora* in a marsh in Georgia, USA. Aquatic Botany 140:13–22.

Kartesz JT. 2015. The Biota of North America Program (BONAP). Chapel Hill, NC, USA: North American Plant Atlas. http://bonap.net/napa.

Kikuzawa K. 1995. Leaf phenology as an optimal strategy for carbon gain in plants. Canadian Journal of Botany 73:158–63.

Kirwan ML, Guntenspergen GR. 2012. Feedbacks between inundation, root production, and shoot growth in a rapidly submerging brackish marsh. Journal of Ecology 100:764–70.

Kirwan ML, Megonigal JP. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. Nature 504:53–60.

Klosterman ST, Hufkens K, Gray JM, Melaas E, Sonnentag O, Lavine I, Mitchell L, Norman R, Friedl MA, Richardson AD. 2014. Evaluating remote sensing of deciduous forest phenology at multiple spatial scales using PhenoCam imagery. Biogeosciences 11:4305–20.

Laidler KJ. 1984. The development of the Arrhenius equation. Journal of Chemical Education 61:494.

Mendelssohn IA, Morris JT. 2002. Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In: Weinstein MP, Kreeger DA, Eds. Concepts and controversies in tidal marsh ecology. Netherlands: Springer. p 59–80.

Morris JT, Sundareshwar PV, Nietch CT, Kjerfve B, Cahoon DR. 2002. Responses of coastal wetlands to rising sea level. Ecology 83:2869–77.

Mudd SM, Howell SM, Morris JT. 2009. Impact of dynamic feedbacks between sedimentation, sea-level rise, and biomass production on near-surface marsh stratigraphy and carbon accumulation. Estuarine, Coastal and Shelf Science 82:377–89.

Murray MB, Cannell MGR, Smith RI. 1989. Date of budburst of fifteen tree species in britain following climatic warming. Journal of Applied Ecology 26:693–700.

Nyman JA, Delaune RD, Roberts HH, Patrick WH. 1993. Relationship between vegetation and soil formation in a rapidly submerging coastal marsh. Marine Ecology Progress Series 96:269–79.

O'Connell JL, Alber M. 2016. A smart classifier for extracting environmental data from digital image time-series: applications for PhenoCam data in a tidal salt marsh. Environmental Modelling & Software 84:134–9.

O'Donnell JPR, Schalles JF. 2016. Examination of abiotic drivers and their influence on *Spartina alterniflora* biomass over a twenty-eight year period using Landsat 5 TM satellite imagery of the central Georgia coast. Remote Sensing 8:477.

Pennings SC, Bertness MD. 2001. Salt marsh communities. In: Hay ME, Gaines SD, Bertness MD, Eds. Marine community ecology. Sunderland: Sinauer Associates. p 550.

Peterson PM, Romaschenko K, Arrieta YH, Saarela JM. 2014a. A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoideae: Sporobolinae). Taxon 63:1212–43.

Peterson PM, Romaschenko K, Arrieta YH, Saarela JM. 2014b. Proposal to conserve the name Sporobolus against Spartina, Crypsis, Ponceletia, and Heleochloa (Poaceae: Chloridoideae: Sporobolinae). Taxon 63:1373–4.

Primack RB, Ibáñez I, Higuchi H, Lee SD, Miller-Rushing AJ, Wilson AM, Silander JA. 2009. Spatial and interspecific variability in phenological responses to warming temperatures. Biological Conservation 142:2569–77.

Richardson AD, Jenkins JP, Braswell BH, Hollinger DY, Ollinger SV, Smith M-L. 2007. Use of digital webcam images to track spring green-up in a deciduous broadleaf forest. Oecologia 152:323–34.

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. Agricultural and Forest Meteorology 169:156–73.

Saxe H, Cannell MGR, Johnsen Ø, Ryan MG, Vourlitis G. 2001. Tree and forest functioning in response to global warming. New Phytologist 149:369–99.

Schwartz MD, Ahas R, Aasa A. 2006. Onset of spring starting earlier across the Northern Hemisphere. Global Change Biology 12:343–51.

Schwartz MD, Ed. 2013. Phenology: an integrative environmental science. Dordrecht: Springer.

Seneca ED. 1974. Germination and seedling response of Atlantic and Gulf Coasts populations of *Spartina alterniflora*. American Journal of Botany 61:947–56.

Somers GF, Grant D. 1981. Influence of seed source upon phenology of flowering of *Spartina alterniflora* Loisel. and the likelihood of cross pollination. American Journal of Botany 68:6–9.

Stanton ML, Galen C, Shore J. 1997. Population structure along a steep environmental gradient: consequences of flowering time and habitat variation in the Snow Buttercup, Ranunculus Adoneus. Evolution 51:79–94.

Strong DR, Ayres DA. 2016. Control and consequences of Spartina spp. invasions with focus upon San Francisco Bay. Biological Invasions 18:2237–46.

Swanson KM, Drexler JZ, Schoellhamer DH, Thorne KM, Casazza ML, Overton CT, Callaway JC, Takekawa JY. 2014. Wetland Accretion Rate Model of Ecosystem Resilience (WARMER) and its application to habitat sustainability for endangered species in the San Francisco Estuary. Estuaries and Coasts 37:476–92.

Travis SE, Hester MW. 2005. A space-for-time substitution reveals the long-term decline in genotypic diversity of a widespread salt marsh plant, *Spartina alterniflora*, over a span of 1500 years. Journal of Ecology 93:417–30.

USDA, NRCS. 2019. The PLANTS Database. National Plant Data Team.

USGCRP. 2017. Climate science special report. In: Wuebbles DJ, Fahey DW, Hibbard KA, Dokken DJ, Stewart BC, Maycock TK, Eds. Washington D.C.: U.S. Global Change Research Program.

Vegis A. 1964. Dormancy in higher plants. Annual Review of Plant Physiology 15:185–224.

Voss CM, Christian RR, Morris JT. 2013. Marsh macrophyte responses to inundation anticipate impacts of sea-level rise and indicate ongoing drowning of North Carolina marshes. Marine Biology 160:181–94.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. Nature 416:389–95.

Zelikova TJ, Williams DG, Hoenigman R, Blumenthal DM, Morgan JA, Pendall E. 2015. Seasonality of soil moisture mediates responses of ecosystem phenology to elevated CO_2 and warming in a semi-arid grassland. Journal of Ecology 103:1119–30.

Zhang X, Friedl MA, Schaaf CB, Strahler AH. 2004. Climate controls on vegetation phenological patterns in northern mid- and high latitudes inferred from MODIS data. Global Change Biology 10:1133–45.

Zheng S, Shao D, Asaeda T, Sun T, Luo S, Cheng M. 2016. Modeling the growth dynamics of *Spartina alterniflora* and the effects of its control measures. Ecological Engineering 97:144–56.