Estuaries and Coasts
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A Landscape-Scale Assessment of Above- and Belowground Primary Production in Coastal Wetlands: Implications for Climate Change-Induced Community Shifts

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Abstract Above- and belowground production in coastal wetlands are important contributors to carbon accumulation and ecosystem sustainability. As sea level rises, we can expect shifts to more salt-tolerant communities, which may alter these ecosystem functions and services. Although the direct influence of salinity on species-level primary production has been documented, we lack an understanding of the landscape-level response of coastal wetlands to increasing salinity. What are the indirect effects of sea-level rise, i.e., how does primary production vary across a landscape gradient of increasing salinity that incorporates changes in wetland type? This is the first study to measure both above- and belowground production in four wetland types that span an entire coastal gradient from fresh to saline wetlands. We hypothesized that increasing salinity would limit rates of primary production, and saline marshes would have lower rates of above- and belowground production than fresher marshes. However, along the Northern Gulf of Mexico Coast in Louisiana, USA, we found that aboveground production was highest in brackish marshes, compared with fresh, intermediate, and saline marshes, and belowground production was similar among all wetland types along the salinity gradient. Multiple regression analysis indicated that salinity was the only significant predictor of production, and its influence was dependent upon wetland type. We concluded that (1) salinity had a negative effect on production within wetland type, and this relationship was strongest in the fresh marsh (0–2 PSU) and (2) along the overall landscape gradient, production was maintained by mechanisms at the scale of wetland type, which were likely related to plant energetics. Regardless of wetland type, we found that belowground production was significantly greater than aboveground production. Additionally, inter-annual variation, associated with severe drought conditions, was observed exclusively for belowground production, which may be a more sensitive indicator of ecosystem health than aboveground production.

Keywords Aboveground production · Belowground production · Climate change · Coastal wetlands · Landscape scale · Salinity gradient · Sea-level rise · Wetland type

Introduction

The effects of climate change are pervasive and have been documented in every continent, ocean, and major taxonomic group (IPCC 2013). Impacts from recent anthropogenic climate change have been expressed through changes in phenology, trophic-level interactions, range, community structure, and ultimately extinction (Parmesan 2006). Geographically restricted species can be especially sensitive to climate change, because they are vulnerable to reductions in range size, putting them at greater risk of extinction (Telwala et al. 2013). For example, montane species have experienced significant declines in population abundances along their lower elevation range boundaries (Franzen and Molander 2012). In Europe, warming has reduced the habitat of mountain-restricted butterfly species (Wilson et al. 2005) and resulted

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in the population extinction of some species such as the Apollo butterfly in France (Descimon et al. 2006).

Similarly, coastal wetlands, ecotones that occupy the land-sea interface, are restricted along the landward boundary and are also vulnerable to climate change-induced reductions in range size as sea level rises (Doyle 1998). Coastal wetland community composition is regulated by salinity and flooding regimes that create clear zonation patterns along landscape-scale salinity gradients (Snow and Vince 1984; Pennings et al. 2005; Silvestri et al. 2005). Therefore, as sea level rises, changes to salinity and flooding regimes will result in community restructuring (Warren and Niering 1993; Visser et al. 2002), and anthropogenic and geologic limits on transgression (Cahoon et al. 1999) will likely result in significant range contraction with an overall shift to more saline wetlands (Williams et al. 1999; Visser et al. 2013).

These community-level effects ultimately drive emergent ecological responses that include alterations in ecosystem function, such as productivity (Harley et al. 2006). For example, warming in the arctic has led to a shift from tundra to shrub-dominated communities and was linked to increased microbial activity and nutrient mineralization rates (Sturm et al. 2005). In coastal wetlands, a sea-level rise-induced shift from tree-dominated to herbaceous-dominated wetlands altered primary production (Cormier et al. 2013; Ensign et al. 2014) and nutrient mineralization rates (Noe et al. 2013). As sea-level rise causes shifts in community structure, variation in ecological function across wetland community types will have important implications for greenhouse gas flux and carbon storage potential (Krauss and Whitbeck 2012), which may eventually impact climate (Chapin et al. 2008).

Primary production in coastal wetlands plays an important role in complex feedback mechanisms that ultimately influence wetland sustainability (Morris et al. 2002; Kirwan and Guntenspergen 2012) and carbon cycling (Whiting and Chanton 1993; Mudd et al. 2009; Kirwan and Mudd 2012). Coastal wetlands maintain elevation relative to sea level through both surface and subsurface processes (Cahoon et al. 2006; McKee 2011). On the surface, accumulation of mineral sediments and organic matter are key processes that contribute to accretion (Neubauer 2008). Aboveground macrophyte production enhances mineral sedimentation (Ensign et al. 2014; Leonard 1997) and also contributes to autochthonous organic matter accumulation (Nyman et al. 1993). Belowground, biological processes, such as root and rhizome production, contribute to subsurface expansion and elevation gain (Kirwan and Guntenspergen 2012). Subsequently, elevation gain promotes favorable hydrologic conditions that feedback to increased primary production (McKee et al. 2007; Cherry et al. 2009).

It is critical to quantify primary production in multiple wetland types if we hope to predict the fate of wetlands and their ecosystem services as communities shift with sea-level rise. Despite the important role primary production plays in wetland ecosystem-level processes, relatively few studies have examined how this ecological function varies across multiple wetland types. An extensive literature review (Appendix 1) revealed that the majority of studies reporting aboveground production were conducted in saline marshes, and to a lesser extent in fresh marshes. We found 50–80 % fewer studies that reported belowground production, and the majority of these studies were constrained to saline marshes. Even fewer researchers measured both above- and belowground production, and we found only four studies that reported both above- and belowground production across multiple wetland types, none of which spanned the entire coastal landscape gradient from fresh to saline marsh.

Furthermore, although individual species-level responses to elevated salinity have been well-documented in greenhouse and manipulative field experiments, it remains untested whether landscape-scale responses will reflect these same patterns. Reduced primary production is one of the most evident species-level responses to elevated salinity (McKee and Mendelssohn 1989; Gough and Grace 1998; Willis and Hester 2004). At the landscape scale, salinization causes shifts to more salt-tolerant species (Herbert et al. 2015), and this tolerance comes at some cost, presumably growth and production (Grime 1988). To our knowledge, this is the first comprehensive study to quantify above- and belowground primary production rates in wetland types that span the entire coastal landscape gradient from freshwater to saline marsh. We hypothesized that increasing salinity would limit rates of primary production, and saline marshes would have lower rates of above- and belowground production than fresher marshes.

We address the following questions: (1) How do above- and belowground production vary across the landscape salinity gradient? (2) Does the relative contribution of above- and belowground production to total net primary production vary across the landscape gradient and over time? (3) How do environmental conditions change along the landscape gradient? and (4) Does the influence of environmental drivers on primary production vary across the landscape gradient?

Methods

Study Site and Experimental Design

To characterize primary production dynamics at the landscape scale, we estimated above- and belowground primary production along a salinity gradient that incorporated changes in wetland type. The landscape gradient included four wetland types defined by salinity range and dominant macrophyte species (Visser et al. 2002). Fresh marshes (0–0.5 PSU) were dominated by *Panicum hemitomon* and *Typha latifolia*, intermediate marshes (0.5–5 PSU) were dominated by *Sagittaria lancifolia* and *Schoenoplectus americanus*, brackish marshes (5–12 PSU) were dominated by *Spartina patens* and

S. americanus, and saline marshes (12–20 PSU) were dominated by *Spartina alterniflora* and *Juncus roemerianus*.

We selected 24 sites that encompassed the four wetland types across two hydrologic basins in coastal Louisiana (Fig. 1). All sites were co-located with monitoring sites maintained by the Coastwide Reference Monitoring System (CRMS) (Steyer et al. 2003). Within each wetland type, six sites were selected, three in each basin, and within each site, we established five replicate plots. Replicated plots within each site were randomly established along a transect that was situated perpendicular to the waterbody and extended up to 50 m inland. The experimental design was a randomized complete block design with sampling, where the hydrologic basin represented random block-level effects ($r = 2$) and wetland type represented fixed treatment-level effects ($t = 4$). Sites were replicated in each block-by-treatment combination ($n = 3$) and included subsampling within each site ($s = 5$, total N = trns, experimental error = tr(n−1), total error = trn (s−1)).

Above- and Belowground Production

Within each replicate plot, we established one subplot for each sampling event at the beginning of the study to ensure that the same plot was not clipped or cored more than once over the duration of the 2-year study. Nine subplots were established 2 m apart in parallel with the water body. In each replicate plot, above- and belowground biomass was harvested seasonally (approximately every three months) from June 2012 to July 2014. Aboveground biomass was clipped at the soil surface from 0.25 m^2-quadrats, separated into total live and total dead components, and weighed after drying to a constant mass at 60 °C (Mendelssohn 1979). We used a serial coring technique to estimate belowground production (Neill 1992). After aboveground biomass was removed from the plot, we used a sharpened 10-cm PVC corer to collect belowground biomass from the center of the quadrat. The cores were taken to a maximum depth of 30 cm or the entire mat thickness. Cores were divided into three depth intervals (0–7.5 cm, 7.5–15 cm and 15–30 cm) and washed in a 0.5-mm sieve to remove soil particles. Live roots and rhizomes were separated from dead roots and rhizomes and the remaining matrix of dead organic material. Live roots and rhizomes were identified according to turgor, buoyancy, and white color. All material was dried at 60 °C to a constant mass and weighed. Only live and dead roots and rhizomes were included in production calculations, whereas the remaining matrix of dead organic material was not considered in these estimations (Neill 1992). Above- and belowground biomass samples were not sorted by species.

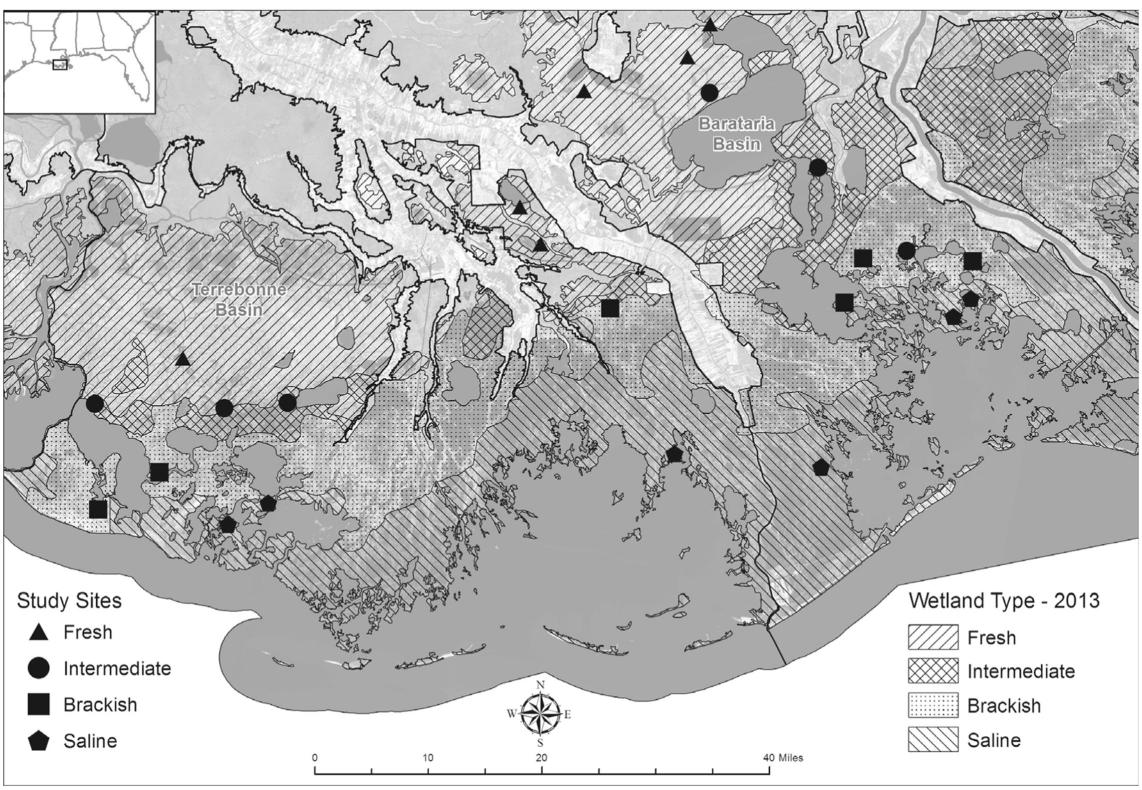

Fig. 1 Site locations of above- and belowground production measurements within four wetland types along the northern Gulf of Mexico coast in Louisiana. Study sites were located within two hydrologic basins, Terrebonne and Barataria, whose boundaries are identified by *solid black lines*. Wetland-type boundaries for 2013 were defined using publically available vegetation classification data provided by the Coastwide Reference Monitoring System (CRMS; http://lacoast.gov/crms2/Home.aspx)

Above- and belowground production rates for year 1 (June 2012–June 2013) and year 2 (July 2013–July 2014) were estimated using the Smalley (1959) method with an adjustment for missing samples. The average change in live and dead biomass over time was used to generate a rate of net annual primary production (NAPP; g biomass m^{-2} $year^{-1}$) for each plot (N = 120). Traditionally, when using the Smalley (1959) method, an interval (Δ) is defined as the sum of the change in live ($B_{\mathrm{live}\,,\,t}$) and dead ($B_{\mathrm{dead}\,,\,t}$) material between two sampling events (t_i) (Eq. 1), and production rate (P) is calculated as the sum of all intervals in one annual cycle (Eq. 2),

$$\Delta B_{t_i} = \left(B_{\mathrm{live},t_{i+1}} - B_{\mathrm{live},t_i}\right) + \left(B_{\mathrm{dead},t_{i+1}} - B_{\mathrm{dead},t_i}\right) \quad (1)$$

$$P = \sum_{i=1}^{T-1} \Delta B_{t_i} \quad (2)$$

where T is the total number of sampling events in a complete annual cycle. However, using this method potentially results in large errors associated with missing data. For example, if data is missing from one sampling period, it can potentially affect two interval calculations. Therefore, we adjusted for missing samples by using the average of observed intervals, or those intervals that contained observed, not missing, data, multiplied by the total number of intervals to calculate production (Eq. 3),

$$P = \frac{T-1}{T_o-1} \sum_{i=1}^{T_o-1} \Delta B_{t_i} \quad (3)$$

where T_o is the number of observed sampling events.

Root-to-shoot ratios (R/S) were calculated using average annual live belowground and aboveground biomass values. Belowground biomass values are the sum of all depth intervals (0–30 cm).

Environmental Parameters

All 24 sites were co-located with CRMS stations (http://lacoast.gov/crms2/Home.aspx), where continuous in-situ surface water salinity and water-level data were collected hourly using a YSI 600LS or equivalent continuous recorder with a vented cable (Folse et al. 2008). Elevations of all plots were surveyed with real-time kinematic (RTK) surveying instrumentation and rectified to the North American Vertical Datum of 1988 (NAVD88), which we used to calculate hydroperiod for each plot in each site.

Additional discrete soil and porewater samples were taken to measure a suite of environmental parameters in October 2012 and 2013. At each site, two soil cores were collected near each of the five sample plots. One soil core (5 × 30 cm) was used to measure soil bulk density, % organic matter, % moisture, electrical conductivity (EC), and pH. A second soil core (5 × 30 cm) was used to measure soil total C, N, and P, soil extractable nutrients (NH_4–N, PO_4–P), and other elements of interest (including Fe, K, Mg, Mn, Na, P, and S). All soil cores were immediately placed on ice in the field and transported back to the laboratory for analysis. After homogenization, the soil was dried to a constant weight at 60 °C, ground in a Wiley Mill (Model no. 4, 20 mesh (850 μm)) and separated into several scintillation vials for multiple analyses. Soil total N and total C were measured using a Costech ® 4010 Elemental Combustion analyzer (Nelson and Sommers 1982; EPA Method 440). Extractions were performed for the following analyses: soil total P (HCl, Aspila et al. 1976), PO_4–P (Bray-2, Olsen and Sommers 1982), NH_4–N (KCl, Keeney and Nelson 1982), and other elements of interest (H_2NO_3, American Public Health Association 2005a). Soil total P, PO_4–P samples and NH_4–N were measured on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA; EPA Method 365.5; EPA Method 350.1). The remaining extracts were analyzed with an inductively coupled argon plasma optical emission spectrometer (ICP-OES) (Varian-MPX, Agilant, USA; American Public Health Association 2005b).

At the time of soil sampling, three separate aliquots of porewater were also collected from each sample plot at a depth of 15 cm using a sipper-tube method (Vasilas et al. 2013). The first aliquot of water was used to measure porewater pH and electrical conductivity (EPA Methods 150.1 and 120.1, respectively) and porewater total N and total P following persulfate oxidation (D'Elia et al. 1977; Ebina et al. 1983) on a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). The third aliquot was filtered through a 0.45-μm filter to measure NH_4–N and PO_4–P using a segmented flow AutoAnalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA; EPA Method 365.5; EPA Method 350.1), and the third aliquot was filtered and acidified to pH <2 to measure other elements of interest using ICP as described above. Filtration and acidification procedures were performed in the field, and all porewater samples were immediately placed on ice and transported back to the laboratory for analysis.

Statistical Analyses

A mixed-model ANOVA was used to estimate variance in production across wetland type, time, and depth (belowground only) using PROC MIXED in SAS 9.3 (SAS Institute 2011). Statistical analysis of root-to-shoot ratios followed the framework described in Robinson et al. (2010). Root biomass is described as a power function of shoot biomass (Eq. 4),

$$R = \beta S^{\alpha} \quad (4)$$

where R is root biomass, S is shoot biomass, β is the allometric coefficient, and α is a scaling exponent that describes the shape of the relationship between root and shoot biomass and in this case represents the ratio of relative growth rates (Hunt and Nicholls 1986). To test the hypothesis that allocation between roots and shoots differed across wetland type and between years, we fit the linear model (Eq. 5)

$$\log(R) = \log(\beta) + \alpha\log(S) \tag{5}$$

where β and α were allowed to vary by wetland type and year (i.e., wetland type by year interaction).

Principle component analysis (PCA) incorporating all measured environmental parameters was conducted to characterize general trends of primary environmental drivers across wetland type (Table 1). Environmental data from both years 1 and 2 were included in PCAs. A subsequent PCA was also performed to generate principle components (PCs) for use in the multiple regression analysis. Because parameters associated with salinity and nutrients were loaded onto the same PC in the initial PCA, we removed all salinity parameters from the second PCA so that we could include salinity and nutrients as separate predictive variables in the multiple regression analysis. The data from the subsequent PCA, which did not include salinity, can be found in Appendix 2. We conducted an analysis of similarity (ANOSIM) for each PC, to determine whether the compositional dissimilarities of factor scores among wetland type were significantly greater than those within wetland type. We conducted multiple linear regression analysis using the glm function, with a gamma distribution and a log link function. The regression modeled the log of aboveground NAPP as a function of annual surface water salinity (salinity), wetland type, and the three PCs used to quantify soil and porewater quality. Goodness of fit was estimated using McFadden's pseudo-R^2 (McFadden 1974). All statistical analyses were conducted using R software (R Core Team 2013), unless otherwise stated.

Results

Spatial Variation in Production Rate

Aboveground production rates varied significantly across wetland type ($p = 0.0004$, $F = 6.4$, $df = 3$), and the brackish marsh had the greatest rate of aboveground production compared with all other wetland types (Fig. 2a). Similarly, there was a significant difference in belowground production rates across wetland type ($p = 0.0135$, $F = 3.64$, $df = 3$). The greatest difference in belowground production occurred between the fresh marsh, which had the lowest production rate, and the brackish marsh, which had the highest production rate (Fig. 2b).

Table 1 Principal component analysis results

Environmental parameter	PC1: salinity/nutrients (42 %)	PC2: metals (16 %)	PC3: flooding (10 %)
Pw pH	*0.81*	0.32	−0.06
Pw electrical conductivity	*0.88*	0.33	0.01
Pw ammonium	*0.74*	0.35	0.09
Pw phosphate	*0.65*	0.27	0.25
Pw total nitrogen	*0.66*	0.34	0.08
Pw total phosphorus	*0.53*	0.24	0.23
Pw iron	0.34	*0.53*	0.16
Soil copper	*0.89*	0.28	0.01
Soil iron	0.49	0.19	0.23
Soil zinc	−0.24	0.15	0.15
Soil pH	*−0.63*	0.28	0.34
Soil phosphate	*−0.91*	0.23	−0.06
Soil ammonium	*−0.89*	0.31	−0.05
Soil total phosphorus	*−0.90*	0.30	−0.06
Soil total nitrogen	−0.11	*−0.50*	0.04
Soil organic matter	0.44	*−0.76*	0.03
Soil total carbon	0.60	*−0.70*	0.03
Annual surfacewater salinity	0.55	*−0.76*	0.03
Soil electrical conductivity	*0.82*	0.37	−0.07
Marsh surface elevation	−0.19	−0.25	*0.87*
Annual %time flooded	−0.08	0.25	*−0.89*
Eigenvalue	8.7	3.4	2.1

Data presented are correlation coefficients for the soil and porewater (PW) parameters (rows) and PCs (%variance, columns). Correlation coefficients greater than 0.45 (set in italics) were used to define the PCs

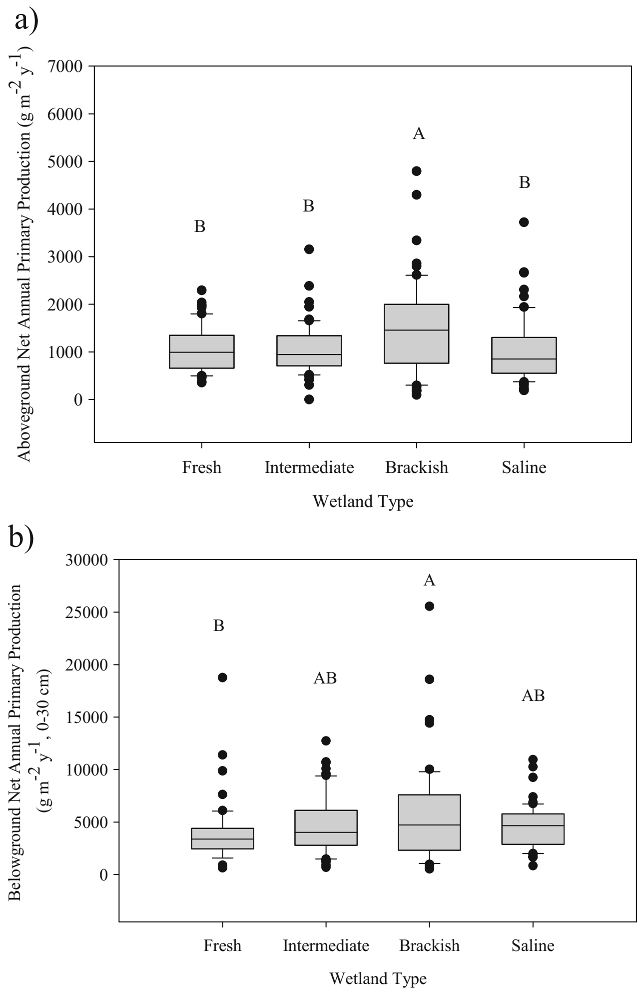

Fig. 2 Net annual primary production rate of **a** aboveground and **b** belowground plant components. *Box plot boundaries closest to zero* represent the 25th percentile, the *line within the boxes* indicates the median, and *boundaries farthest from zero* represent the 75th percentile. The *whiskers* indicate the 90th and 10th percentiles. *Black dots* represent outlying points. *Letters* denote statistical significance of post hoc multiple comparisons of means (Fisher's protected LSD, $\alpha = 0.05$)

Belowground production rate did not vary significantly with depth below the soil surface ($p = 0.0884$, $F = 5.05$, $df = 2$; data not shown), but there were clear differences between live and dead biomass stock trends across the depth profile that were dependent upon wetland type ($p = 0.0012$, $F = 3.71$, $df = 6$). Live biomass stocks were greatest in the top 7.5 cm and declined significantly with depth. Dead biomass stocks were greater, overall, compared with live biomass stocks and increased significantly with depth. Although the interaction of depth, condition and wetland type was significant, the trends in live and dead biomass with depth were similar across all wetland types (Fig. 3).

Relative Contributions

Belowground primary production rates were significantly greater than aboveground primary production rates regardless

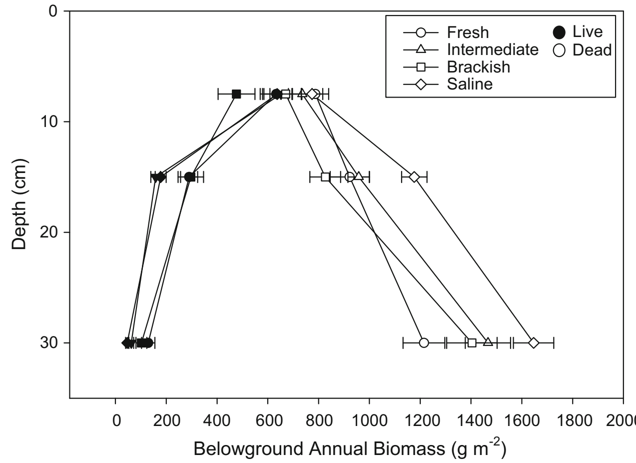

Fig. 3 Annual live and dead belowground biomass, with respect to depth, in each wetland type. *Error bars* represent standard errors

of wetland type. Additionally, the ratio of relative growth rates between roots and shoots did not significantly vary across wetland type ($p = 0.846330$, $F = 0.2709$, $df = 3$).

Trends in above- and belowground production over time were consistent across all wetland types (three-way interaction $p = 0.1863$, $F = 1.61$, $df = 3$). Even though belowground production declined considerably from years 1 to 2, and aboveground production remained constant, belowground production was still significantly greater than aboveground production ($p < 0.0001$, $F = 23.3$, $df = 1$; Fig. 4). Total (aboveground + belowground) production rates reflected belowground trends and also declined in year 2 (Fig. 5). Accordingly, the ratio of relative growth rates between roots and shoots significantly declined in year 2 ($p < 0.0001$, $F = 96.5354$, $df = 1$), but root-to-shoot ratios remained greater than one (Fig. 5).

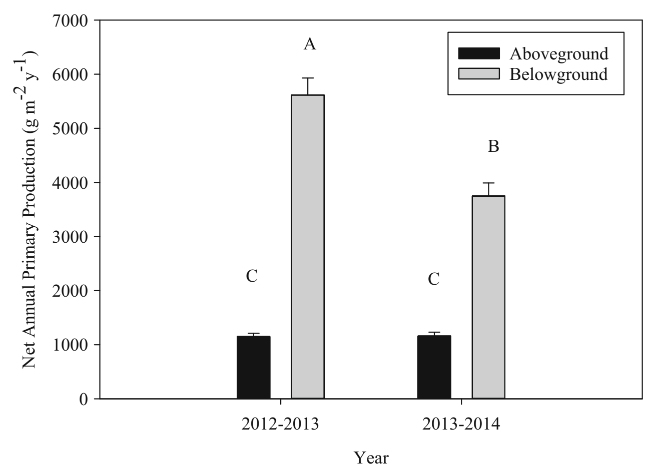

Fig. 4 Above- and belowground production rates in year 1 (2012–2013) and year 2 (2013–2014), averaged over wetland type. *Error bars* represent standard errors. *Letters* denote statistical significance of post hoc multiple comparisons of means (Fisher's protected LSD, $\alpha = 0.05$)

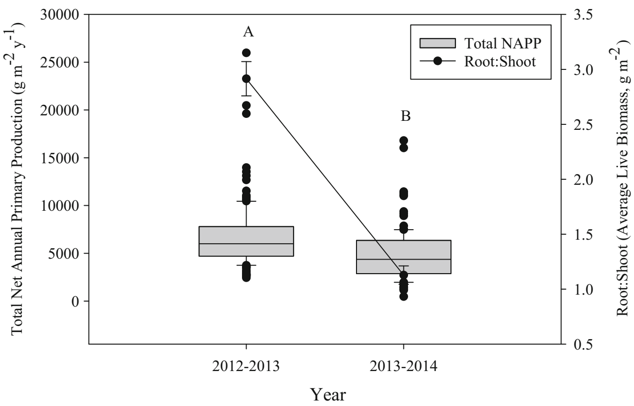

Fig. 5 Total NAPP (aboveground + belowground production) and root-to-shoot ratios in year 1 (2012–2013) and year 2 (2013–2014). *Box plot boundaries closest to zero* represent the 25th percentile, the *line within the boxes* indicates the median, and *boundaries farthest from zero* represent the 75th percentile. The whiskers indicate the 90th and 10th percentiles. *Black dots* represent outlying points. *Letters* denote statistical significance of post hoc multiple comparisons of means (Fisher's protected LSD, $\alpha = 0.05$)

Hydro-edaphic Parameters

The first principal component (PC1-salinity/nutrients) was highly correlated with salinity variables such as porewater electrical conductivity (EC), soil EC and annual surface water salinity, and nutrient variables, such as soil total nutrients, soil extractable nutrients, porewater nutrients, and soil total carbon and organic matter. The second PC (PC2-metals) was highly correlated with soil total metals such as iron, copper, and zinc and soil pH. The third PC (PC3-flooding) was defined by wetland surface elevation and flood duration (Table 1). There was a clear separation of the factor scores among wetland type along the PC1 (salinity/nutrients, $R = 0.1004$, $p = 0.001$) and PC3 (flooding, $R = 0.05$, $p = 0.001$) axes. Fresh and intermediate marshes were associated with lower pore- and surface water salinity and higher concentrations of organic nutrients (total N, total P), brackish and saline marshes were associated with higher salinity and inorganic nutrients (NH_4, PO_4) (Fig. 6a, b). There was no significant partitioning of factor scores among wetland type along the PC2 (metals) axis ($R = -0.012$, $p = 0.97$; Fig. 6b, c).

Multiple Regression

McFadden's pseudo-R^2, used to estimate the goodness of fit of the multiple regression model, was 0.16, which is relatively good based on the suggestion that values between 0.2 and 0.4 represent very good fit of the model (Louviere et al. 2000).

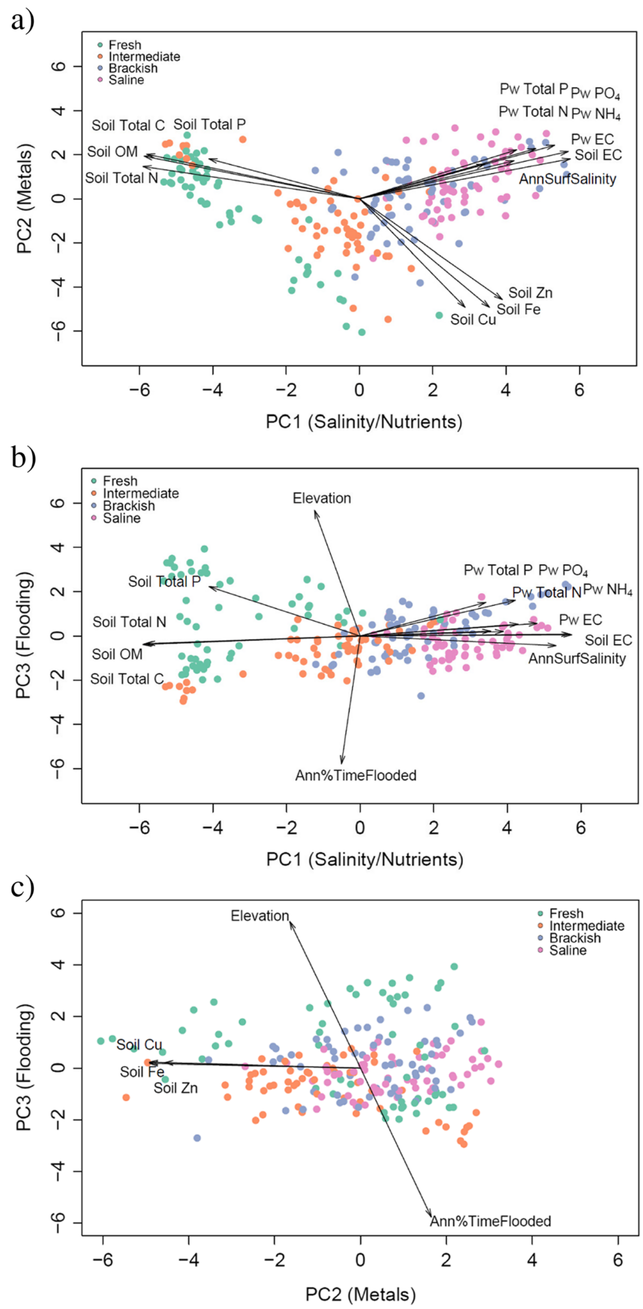

Fig. 6 Principal component analysis biplots of hydro-edaphic observation projections, or factor scores, in component space for all comparisons between principal components (*PCs*) 1, 2, and 3. In each plot, factor scores are grouped by wetland type. A subset of highly correlated vectors from each PC overlay the factor scores

The multiple regression illustrated that there was no significant effect of the PCs that represented nutrients, metals, or flooding on aboveground NAPP (Tables 2 and 3). However, there was a significant effect of salinity on production, which was dependent upon wetland type (Table 2; Fig. 7). The model predicted a negative relationship between salinity and production, with the strongest response observed in the fresh marshes (Table 3; Fig. 7).

Table 2 Analysis of deviance estimating effects of wetland type and environmental drivers on aboveground production rates

Source	*df*	Deviance	Residual *df*	Residual deviance	*F* value	*p* value
Null			229	81.131		
PC1 (nutrients)	1	0.7302	228	80.401	2.6472	0.105173
PC2 (metals)	1	0.4568	227	79.944	1.6558	0.199524
PC3 (flooding)	1	0.0055	226	79.939	0.0198	0.888327
Wetland type	3	5.5595	223	74.379	6.7179	0.000234
Salinity	1	3.6861	222	70.693	13.3624	0.000321
Wetland type × salinity	3	2.5504	219	68.143	3.0817	0.028297

Discussion

To predict how wetland ecosystem services, such as carbon storage, will be affected by climate change-induced changes in wetland type, it is imperative that we quantify the differences in critical ecological functions, such as primary production, at a landscape scale (Odum 1988; Crain 2007). Although above- and belowground macrophyte production have been thoroughly described in saline marshes (Valiela et al. 1976; Schubauer and Hopkinson 1984), we still lack a comprehensive understanding of total macrophyte production across multiple wetland types that are common along coastal landscape gradients.

Our estimates of aboveground production were similar to literature reports from fresh, intermediate, brackish, and saline wetlands (Table 4). Estimates of belowground production using the Smalley (1959) method were similar to relevant studies in brackish and saline marshes. It was more difficult to find equivalent belowground estimates in fresh and intermediate marshes, because most studies using the Smalley (1959) method were conducted at higher latitudes, and comparatively our estimates were much higher. Our estimates of belowground production in fresh and intermediate marshes were more similar, albeit still higher, compared with estimates from studies in the same geographic region, and differences in methodology likely account for the remaining disparity (Ket et al. 2011; Graham and Mendelssohn 2014).

We found that the brackish marsh had the highest aboveground production rates compared with all other wetland types, which were all similar to each other. Other studies have found higher biomass in brackish marshes compared with both fresh (White and Simmons 1988) and saline (Valiela et al. 1976; Linthurst and Reimold 1978a; Elsey-Quirk et al. 2011) marshes. Different photosynthetic pathways may have contributed to observed variation in production (Cheng et al. 2006; Cherry et al. 2009; Drake 2014). Brackish marshes, dominated by the C_4 plant *S. patens*, had higher production rates than the fresh and intermediate marshes, which were dominated by C_3 plants. Our results are consistent with the findings of others that C_4 plants have greater photosynthetic efficiency (Long 1999; Still et al. 2003) and water use efficiency (D'Antonio and Vitousek 1992), than C_3 plants, which can lead to greater rates of production in C_4 plants (Lopez Rosas et al. 2005). However, this relationship does not explain the difference between the brackish and saline marshes, both of which were dominated by C_4 plants.

While the variation in production among wetland types was statistically significant (aboveground $p = 0.0004$, $F = 6.4$, $df = 3$; belowground $p = 0.0135$, $F = 3.64$, $df = 3$), post hoc pairwise comparisons did not show clear separation in belowground production among brackish, intermediate, and saline marshes (Fig. 2b). Furthermore, it is possible that higher above- and

Table 3 Multiple regression parameter estimations

Parameter	Estimate	Standard error	*t* value	*p* value
PC1 (nutrients)	−0.036932	0.027002	−1.368	0.1728
PC2 (metals)	−0.006269	0.027391	−0.229	0.81918
PC3 (flooding)	0.021078	0.033477	0.630	0.5296
Fresh marsh × salinity	−1.593550	0.520917	−3.059	0.0025
Int. marsh × salinity	1.561648	0.520778	2.999	0.00302
Brackish marsh × salinity	1.530393	0.523174	2.925	0.0038
Saline marsh × salinity	1.513353	0.520728	2.906	0.00403

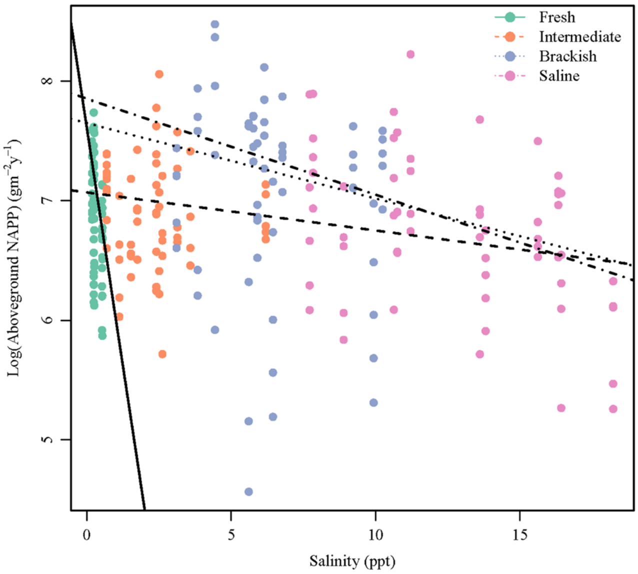

Fig. 7 Results of the multiple linear regression illustrating the significant interactive effect of salinity and wetland type on aboveground production rates

belowground production rates in brackish marshes, specifically those dominated by *S. patens*, may be a function of high variability associated with the marsh structure. The heterogeneous microtopography of *S. patens* marshes is characterized by a hummock/hollow structure that is maintained through a hydrogeomorphic feedback loop (DeLaune et al. 1994; Windham 1999), resulting in a landscape where *S. patens* growth is highly concentrated on hummocks, and very little vegetation is found in the hollows (Windham 2001). We used a randomized sampling design that captured production in both hummocks and hollows, resulting in high variation in our estimates of NAPP, with elevated production rates in the hummocks and low production rates in the hollows. High rates of production in the hummocks, when extrapolated over a larger spatial scale, may have contributed to the overall differences observed between the brackish marsh and other wetland types that had a more even spatial distribution of growth (Roman and Daiber 1984). In support of this, we observed in a post hoc analysis that production in brackish marshes with hummock/hollow microtopography was best described by a log-normal distribution with the same location parameter (7.11) as the brackish marshes without hummock/hollow topography. However, the scale parameter, which describes variation in the model, was significantly larger in the hummock/hollow model (2.56 vs. 1.63, Likelihood ratio test: $X^2 = 9.023$, $df = 1$, $p = 0.003$), indicating that the source of greater variation was associated with hummock/hollow topography.

Nevertheless, decades of species-level research has illustrated the importance of environmental drivers on wetland primary production, and based on our understanding of salinity and flooding impacts to individual species, we expected to observe a significant decline in production with increasing salinity across this landscape-scale gradient. Direct negative impacts of elevated salinity and prolonged flooding on production have been demonstrated for the fresh, intermediate and brackish species studied here (McKee and Mendelssohn 1989; Broome et al. 1995; Webb and Mendelssohn 1996; Baldwin and Mendelssohn 1998; Gough and Grace 1998; Willis and Hester 2004; Spalding and Hester 2007). Furthermore, salinity and flooding have been shown to limit production even in the most salt-tolerant species (Naidoo et al. 1992). For example, elevated salinity in flooded, anaerobic, conditions promotes the production of sulfides (Postgate 1959), which can inhibit ammonium uptake (Bradley and Morris 1990, 1991; Koch et al. 1990) and limit wetland plant production, including *S. alterniflora* (Koch and Mendelssohn 1989). Although the gradient studied here represents the shift to more salt-tolerant communities (Osmond et al. 1987), the energy required to survive in stressful conditions should eventually come at the cost of growth and reproduction (Grime 1988). Therefore, our findings, which demonstrated statistically similar rates of production between fresh, intermediate, and saline marshes, were unexpected.

We performed regression analysis to ascertain which environmental parameters were influencing production rates along this landscape-scale gradient. We found that the best-fit model was an interaction model, where salinity was the only significant predictor of production, and its influence was dependent upon wetland type. Our results indicate that the relative influence of salinity changed along the landscape gradient, was strongest in the fresh marsh (0–2 PSU), and other environmental parameters (nutrient availability, metals, flooding) were not significant predictors of production. Given the interaction with wetland type, there are two conclusions to be drawn from these results: (1) salinity has a negative effect on production within wetland type, but along the overall landscape gradient, production is maintained with shifts to more salt-tolerant wetland types, and (2) mechanisms at the scale of wetland type are responsible for the maintenance of production along the gradient of increasing stress. For example, we found that, although nutrient availability did change across the landscape gradient, production did not vary greatly, indicating that plant energetics may differ between wetland types (Elsey-Quirk et al. 2011). Nitrogen resorption efficiency, which is an important mechanism for supplying nitrogen to marsh

Table 4 Summary of studies that measured above- and/or belowground production in fresh (0–0.5 ppt), intermediate (0.5–5 ppt), brackish (5–12 ppt), and saline (12–20 ppt) wetlands using the Smalley (1959) method

Wetland type	Dominant species	Above/ below	Production (g m^{-2} year^{-1})	Location	Study
Fresh	*Panicum hemitomon*, *Typha latifolia*	Above	1047	Louisiana, USA	Current study
Fresh	*Cladium jamaicense*	Above	2361	Florida, USA	Daoust and Childers (1998)
Fresh	*Eleocharis* spp.	Above	296	Florida, USA	Daoust and Childers (1998)
Fresh	*P. hemitomon*	Above	1641	Louisiana, USA	Pezeshki and DeLaune (1991)
Fresh	*Sagittaria lancifolia*	Above	1241	Louisiana, USA	White and Simmons (1988)
Fresh	*Scirpus maritimus*	Above	452	Rhone Delta, France	Ibanez et al. (1999)
Fresh	*Typha angustifolia*	Above	2989	Rhone Delta, France	Ibanez et al. (1999)
Fresh	*T. latifolia*	Above	1284–1604	Michigan, USA	Dickerman et al. (1986)
Intermediate	*S. lancifolia*, *Schoenoplectus americanus*	Above	1056	Louisiana, USA	Current study
Intermediate	*Eleocharis* spp.	Above	4.5	Quebec, Canada	Giroux and Bedard (1988)
Intermediate	*S. lancifolia*	Above	23.8	Quebec, Canada	Giroux and Bedard (1988)
Intermediate	*S. lancifolia*	Above	1243	Louisiana, USA	Graham and Mendelssohn (2010)
Intermediate	*S. lancifolia*	Above	1745	Louisiana, USA	Graham and Mendelssohn (2010)
Intermediate	*Scirpus americanus*	Above	73.2	Quebec, Canada	Giroux and Bedard (1988)
Intermediate	*Zizania aquatica*	Above	35.6	Quebec, Canada	Giroux and Bedard (1988)
Brackish	*Phragmites australis*, *Scirpus* spp.	Above	824	Rhone Delta, France	Ibanez et al. (1999)
Brackish	*Spartina patens*, *Schoecnoplectus americanus*	Above	1487	Louisiana, USA	Current study
Brackish	*Carex lyngbyei*	Above	687	British Columbia, Canada	Kistritz et al. (1983)
Brackish	*P. australis*	Above	2215–3664	Delaware, USA	Roman and Daiber (1984)
Brackish	*P. australis*	Above	876	Po Delta, Italy	Scarton et al. (2002)
Brackish	*S. patens*	Above	4411	Louisiana, USA	Cramer et al. (1981a, b)
Brackish	*S. patens*	Above	3677	Louisiana, USA	Pezeshki and DeLaune (1991)
Brackish	*S. patens*	Above	705–1473	Delaware, USA	Roman and Daiber (1984)
Brackish	*S. patens* dominant	Above	2259	Louisiana, USA	White and Simmons (1988)
Saline	*Spartina alterniflora*, *Juncus roemerianus*	Above	1034	Louisiana, USA	Current study
Saline	*Distichlis spicata*	Above	648–922	Delaware, USA	Roman and Daiber (1984)
Saline	*D. spicata*	Above	1291	Louisiana, USA	White et al. (1978)
Saline	*D. spicata*	Above	1274	Delaware, USA	Linthurst and Reimold (1978b)
Saline	*D. spicata*	Above	1258	Georgia, USA	Linthurst and Reimold (1978b)
Saline	*Halimione portulacoides*	Above	952	Cantabrian Sea, Spain	Benito and Onaindia (1991)
Saline	*Juncus gerardii*	Above	562–1940	Maine, USA	Linthurst and Reimold (1978b)
Saline	*J. gerardii*	Above	884	Delaware, USA	Linthurst and Reimold (1978b)
Saline	*J. roemerianus*	Above	2500	Georgia, USA	Gallagher et al. (1980)
Saline	*J. roemerianus*	Above	1740	Louisiana, USA	White et al. (1978)
Saline	*Phragmites communis*	Above	1501	Delaware, USA	Linthurst and Reimold (1978b)
Saline	*Salicornia ramosissima*	Above	486	Cantabrian Sea, Spain	Benito and Onaindia (1991)
Saline	*Sarcocornia fruticosa*	Above	683	Venice Lagoon, Italy	Scarton et al. (2002)
Saline	*S. alterniflora*	Above	1160	Cantabrian Sea, Spain	Benito and Onaindia (1991)
Saline	*S. alterniflora*	Above	449–466	Maryland, USA	Cahoon (1975)[a]

Table 4 (continued)

Wetland type	Dominant species	Above/ below	Production (g m^{-2} year^{-1})	Location	Study
Saline	*S. alterniflora*	Above	2318–2720	California, USA	Callaway and Josselyn (1992)
Saline	*S. alterniflora*	Above	113	Paranagua Bay, Brazil	Da Cunha Lana et al. (1991)
Saline	*S. alterniflora*	Above	5445	South Carolina, USA	Dame and Kenny (1986)
Saline	*S. alterniflora*	Above	1281	Louisiana, USA	Darby and Turner (2008)
Saline	*S. alterniflora*	Above	700–2300	Georgia, USA	Gallagher et al. (1980)
Saline	*S. alterniflora*	Above	505–980	Delaware, USA	Hardisky et al. (1984)
Saline	*S. alterniflora*	Above	1231	Louisiana, USA	Kaswadji et al. (1990)
Saline	*S. alterniflora*	Above	1006–1410	Louisiana, USA	Kirby and Gosselink (1976)
Saline	*S. alterniflora*	Above	758–763	Maine, USA	Linthurst and Reimold (1978b)
Saline	*S. alterniflora*	Above	426	Delaware, USA	Morgan (1961)[a]
Saline	*S. alterniflora*	Above	2008–3683	Louisiana, USA	Pezeshki and DeLaune (1991)
Saline	*S. alterniflora*	Above	295–995	Virginia, USA	Reidenbaugh (1983)
Saline	*S. alterniflora*	Above	561–1539	Delaware, USA	Roman and Daiber (1984)
Saline	*S. alterniflora*	Above	225	North Carolina, USA	Shew et al. (1981)
Saline	*S. alterniflora*	Above	643–1098	Georgia, USA	Smalley (1959)[a]
Saline	*S. alterniflora*	Above	804–851	Louisiana, USA	Stagg and Mendelssohn (2010)
Saline	*S. alterniflora*	Above	350–820	Connecticut, USA	Steever (1972)[a]
Saline	*S. alterniflora*	Above	329–1296	North Carolina, USA	Stroud and Cooper (1968a, b)[a]
Saline	*S. alterniflora*	Above	360–720	Massachusetts, USA	Valiela et al. (1975)[a]
Saline	*S. alterniflora*	Above	1527	Louisiana, USA	White et al. (1978)
Saline	*S. alterniflora*	Above	637	Maine, USA	Gordon et al. (1984)
Saline	*Spartina cynosuroides*	Above	2789	Georgia, USA	Linthurst and Reimold (1978b)
Saline	*Spartina foliosa*	Above	349–418	California, USA	Callaway and Josselyn (1992)
Saline	*Spartina maritima*	Above	296	Cantabrian Sea, Spain	Benito and Onaindia (1991)
Saline	*S. patens*	Above	3523	Maine, USA	Linthurst and Reimold (1978b)
Saline	*S. patens*	Above	980	Delaware, USA	Linthurst and Reimold (1978b)
Saline	*S. patens*	Above	1674	Georgia, USA	Linthurst and Reimold (1978b)
Saline	*S. patens*	Above	1136–1158	Delaware, USA	Roman and Daiber (1984)
Saline	*S. patens*	Above	1342	Louisiana, USA	White et al. (1978)
Fresh	*P. hemitomon, T. latifolia*	Below	3883	Louisiana, USA	Current study
Fresh	*Scolochloa festucacea*	Below	1115	Manitoba, Canada	Neill (1992)
Intermediate	*S. lancifolia, S. americanus*	Below	4679	Louisiana, USA	Current study
Intermediate	*Eleocharis* spp.	Below	7.3	Quebec, Canada	Giroux and Bedard (1988)
Intermediate	*S. lancifolia*	Below	30.5	Quebec, Canada	Giroux and Bedard (1988)
Intermediate	*S. americanus*	Below	130.4	Quebec, Canada	Giroux and Bedard (1988)
Intermediate	*Z. aquatica*	Below	5.5	Quebec, Canada	Giroux and Bedard (1988)
Brackish	*S. patens, S. americanus*	Below	5609	Louisiana, USA	Current study
Brackish	*P. australis*	Below	5100–6400	Delaware, USA	Roman and Daiber (1984)
Brackish	*P. australis*	Below	2263	Po Delta, Italy	Scarton et al. (2002)
Brackish	*S. alterniflora*	Below	4300–6600	Delaware, USA	Roman and Daiber (1984)
Brackish	*S. patens*	Below	4500–7300	Delaware, USA	Roman and Daiber (1984)
Saline		Below	4593	Louisiana, USA	Current study

Table 4 (continued)

Wetland type	Dominant species	Above/ below	Production (g m^{-2} year^{-1})	Location	Study
	S. alterniflora, *J. roemerianus*				
Saline	*S. fruticosa*	Below	1260	Venice Lagoon, Italy	Scarton et al. (2002)
Saline	*S. alterniflora*	Below	2363–5445	South Carolina, USA	Dame and Kenny (1986)
Saline	*S. alterniflora*	Below	11,676	Louisiana, USA	Darby and Turner (2008)
Saline	*S. alterniflora*	Below	4473	Georgia, USA	Hopkinson and Schubauer (1984)
Saline	*S. alterniflora*	Below	4400–7700	Delaware, USA	Roman and Daiber (1984)
Saline	*S. alterniflora*	Below	4780	Georgia, USA	Schubauer and Hopkinson (1984)
Saline	*S. cynosuroides*	Below	4628	Georgia, USA	Schubauer and Hopkinson (1984)
Saline	*S. patens*	Below	2500–4100	Delaware, USA	Roman and Daiber (1984)

[a] Citation within Turner (1976) review

species, has been shown to differ between species and growth forms (Aerts 1996). Additionally, Linthurst and Seneca (1981) found that as salinity increased, nutrient tissue concentrations declined as production increased, indicating greater nutrient use efficiency with increased stress. More research is needed to elucidate the wetland type-level mechanisms that are contributing to the maintenance of production rates across this gradient. Furthermore, we might expect significantly different landscape patterns of production in regions where these wetland types are dominated by other species.

Regardless of wetland type, belowground production was significantly greater than aboveground production, and root-to-shoot ratios were greater than or equal to one (Good et al. 1982), illustrating that belowground biomass is clearly an important contributor to total net primary production (de la Cruz and Hackney 1977; Smith et al. 1979). Greater allocation to belowground biomass has been reported for all wetland types studied here (Smith et al. 1979; Bellis and Gaither 1985; Giroux and Bedard 1988; Karagatzides and Hutchinson 1991). Profuse belowground production is an adaptive strategy for plants living in stressful environments (Barko and Smart 1978), where water and nutrient uptake are limited in low nutrient and low soil oxygen environments (Shaver and Billings 1975; Wielgolaski 1975; William and Black 1994; Clevering 1998). Additionally, wetland halophytes adapt to the further stress of elevated salinity and low water potential by increasing belowground biomass (Waisel 1972).

However, when stressful conditions extend beyond a plant's zone of tolerance, or adaptive ability, belowground biomass production will eventually decline (Mendelssohn and Seneca 1980; Bandyopadhyay et al. 1993; Howard and Mendelssohn 1995; Brown et al. 2006). In the current study, belowground production declined from year 1 (2012–2013) to year 2 (2013–2014). The consistent decline across all wetland types suggests a response to a large-scale stressor, such as drought. National Climatic Data Center (NCDC) climate data for the Southeast Louisiana climate region document severe to extreme drought in the winter of 2012 according to the Palmer Severity Drought Index, and severe drought continuing through the spring of 2012 according to the Palmer Modified Drought Index (NCDC 2016; Appendix 3). Furthermore, climate data from the year preceding the study, 2011, illustrate sustained incipient to severe drought conditions in this climate division. We hypothesize that the temporal variation in production was due to variation in climatic controls (Mendelssohn and Morris 2000), and the decline in belowground production observed across all wetland types in 2013–2014 was a response to severe drought conditions experienced in the years leading up to the study.

Severe drought has the potential to impact coastal wetlands at the individual plant and ecosystem scale. Previous research has shown that severe drought diminishes photosynthesis and growth of coastal marsh species (Brown and Pezeshki 2007). Moreover, severe drought has been linked to large-scale disturbances, such as Sudden Vegetation Dieback (McKee et al. 2004), which can significantly impair ecosystem function (Stagg and Mendelssohn 2010). Recent studies have shown that changes in macro-climate drivers, such as precipitation and temperature, have the potential to impact coverage of foundation species in coastal wetlands (Osland et al. 2016). Drier conditions are predicted to cause declines in foundation species coverage (Osland et al. 2014), and our findings underscore the need for a better understanding of how ecological function at the landscape scale will be impacted by changes in macroclimate drivers.

Other studies have also shown that the ratio of belowground to aboveground biomass declines under stressful conditions (Grace and Wetzel 1982; Grace 1989; Turner et al. 2004; Martin and Shaffer 2005; Shi et al. 2015), suggesting that translocation of energy from belowground reserves to the photosynthesizing parts of the plant is a critical mechanism for maintaining resilience (Gallagher 1983). In this study, trends in belowground production reflected trends in total production, which declined from years 1 to 2; however, aboveground production remained constant over time. The observed inter-annual variation of belowground production may be an example of translocation in response to changing resource limitations (Bloom et al. 1985; Chapin et al. 1993; Shipley and Meziane 2002) resulting in consistent aboveground production rates over time (Howard and Mendelssohn 1995). This implies that ecosystem-level responses to changes in environmental parameters will be more apparent in belowground biomass dynamics compared with aboveground biomass dynamics, and that belowground production is a better indicator of ecosystem health than aboveground production (Turner et al. 2004).

Furthermore, the potential for long-term storage of carbon in wetlands is greater in the belowground biomass pool (Howes et al. 1985; Connor and Chmura 2000), where saturated soils limit decomposition of organic matter (Blum 1993). Across all wetland types studied here, live root and rhizome biomass declined with increasing depth (de la Cruz and Hackney 1977; Smith et al. 1979), whereas dead biomass increased with increasing depth (Windham 2001; Graham and Mendelssohn 2014). It is likely that greater soil aeration and nutrient availability in the top 7.5 cm of the soil profile contributed to more favorable conditions for the production of live roots (Valiela et al. 1976; Mendelssohn et al. 1981) and simultaneously enhanced decomposition of dead biomass (Hackney and de la Cruz 1980), which demonstrates the importance of how complementary forces, such as production and decomposition, can interact to influence net carbon production.

Although we found that above- and belowground production rates were generally constant across the landscape gradient (with the exception of the brackish marsh), other studies have shown that soil carbon accumulation does vary across different wetland types (Neubauer 2008; Turner et al. 2000; Nyman et al. 1993, 2006). The accumulation of soil organic matter is the net result of "inputs," e.g., primary production, and "outputs," e.g., decomposition. Therefore, given that there is no change in the inputs across these communities, it is clear that the output processes are contributing to differential accumulation rates, indicating that decomposition processes are important in these systems (Kirwan and Mudd 2012). Ecological function at the landscape scale will have important implications for carbon storage (Chmura et al. 2003, Cheng et al. 2006) and emissions (Turetsky et al. 2014) given predicted changes in wetland habitat distribution with increasing sea level. For example, model simulations of vegetation type distribution in coastal Louisiana under multiple SLR scenarios predicted stability in fresh and intermediate wetland habitats and expansion of saline wetlands at the expense of brackish wetlands (Visser et al. 2013). Therefore, if the higher rates of brackish aboveground production identified in this current study are not an artifact of sampling variation, declines in brackish wetland coverage could translate to a decrease in aboveground primary production and potentially carbon storage. If we hope to manage ecosystems services in dynamic wetland communities that are responding to climate change, it is critical that we understand and quantify all of the processes that contribute to these emergent ecosystem properties. Furthermore, our conclusion that species-level responses to environmental drivers are not analogous to landscape-level responses emphasizes the need for further research to quantify the mechanisms controlling landscape-scale ecological function.

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Appendix 1

Table 5 Summary of studies that report above- and/or belowground production in fresh (0–0.5 ppt), intermediate (0.5–5 ppt), brackish (5–12 ppt), and saline (12–20 ppt) wetlands

Study	Wetland type	Above/below	Production estimation method	Location
Auclair et al. (1976)	Fresh	Above	Peak total	Quebec, Canada
Bartsch and Moore (1984)	Fresh	Above	EOS live	Quebec, Canada
Bernard and Gorham (1978)	Fresh	Above	EOS total	New York, USA
Bernard and Hankinson (1979)	Fresh	Above, below	Max-min total	New York, USA
Bernard and MacDonald (1974)	Fresh	Above	Max-Min total	New York, USA
Bernard and Solsky (1977)	Fresh	Above, below	Peak total	New York, USA
Bernard (1974)	Fresh	Above, below	Max-min total	Minnesota, USA
Birch and Cooley (1982)	Fresh	Above, below	Lomnicki et al. (1968), max-min total	Georgia, USA
Boyd and Vickers (1971)	Fresh	Above	Peak total	South Carolina, USA
Boyd (1971)	Fresh	Above	Peak total	South Carolina, USA
Bray et al. (1959)	Fresh	Above	EOS total	Minnesota, USA
Cahoon and Stevenson (1986)	Fresh	Above	Modified peak total	Chesapeake Bay, USA
Daoust and Childers (1998)	Fresh	Above	Milner and Hughes (1968), Smalley (1959), modified Wiegert and Evans (1964)	Florida, USA
Daoust and Childers (2004)	Fresh	Above, Below	EOS Total, Milner and Hughes (1968)	Florida, USA
de la Cruz (1974)	Fresh	Above	Milner and Hughes (1968)	Mississippi, USA
Dickerman et al. (1986)	Fresh	Above	Allen Curve, Milner and Hughes (1968), Peak Total, Smalley (1958), Wiegert and Evans (1964)	Michigan, USA
Ewe et al. (2006)	Fresh	Above	Daoust and Childers (1998)	Florida, USA
Ferreira et al. (2009)	Fresh	Above	Dickerman and Wetzel (1985)	Taim Wetland Ecosystem, Brazil
Good and Good (1974)	Fresh	Above, below	Peak total	New Jersey, USA
Gorham and Somers (1973)	Fresh	Above	Peak Total	Alberta, Canada
Hogeland and Killingbeck (1985)	Fresh	Above, below	Lomnicki et al. (1968), Max-Min, Wiegert and Evans (1964)	Rhode Island, USA
Ibanez et al. (1999)	Fresh	Above	Smalley (1959)	Rhone Delta, France
Jervis (1969)	Fresh	Above	Peak total	New Jersey, USA
Ket et al. (2011)	Fresh	Above, below	Allometry, EOS total	Georgia, USA
Klopatek and Stearns (1978)	Fresh	Above	EOS Live	Wisconsin, USA
Klopatek (1975)	Fresh	Above	EOS Live	Wisconsin, USA
Muthuri et al. (1989)	Fresh	Above	Dickerman et al. (1986)	Lake Naivasha, Nairobi
Neill (1992)	Fresh	Below	Gallagher (1983), Smalley (1959), Dahlman and Kucera (1965)	Manitoba, Canada
Pezeshki and DeLaune (1991)	Fresh	Above	Smalley (1959)	Louisiana, USA
Pratolongo et al. (2005)	Fresh	Above	Peak total, allometry	Parana River, Argentina
dos Santos and de Assis Esteves (2002)	Fresh	Above	Dickerman et al. (1986)	Rio de Janeiro, Brazil
Sasser and Gosselink (1984)	Fresh	Above	Lomnicki et al. (1968)	Louisiana, USA
Thorman and Bayley (1997)	Fresh	Above	Peak live	Alberta, Canada
Wetzel and Howe (1999)	Fresh	Above, below	Peak total	Alabama, USA

Table 5 (continued)

Study	Wetland type	Above/below	Production estimation method	Location
Wetzel and Pickard (1996)	Fresh	Above	Allen Curve, other cohort estimation methods, peak total, summed shoot maximum	Minnesota, USA
Whigham and Simpson (1977)	Fresh	Above	Peak total	New Jersey, USA
Whigham and Simpson (1992)	Fresh	Above	Peak total	New Jersey, USA
White and Simmons (1988)	Fresh	Above	Smalley (1959)	Louisiana, USA
White (1993)	Fresh	Above	Peak total	Louisiana, USA
Bellis and Gaither (1985)	Intermediate	Above, below	Max-min live	North Carolina, USA
Ewing (1986)	Intermediate	Above	Peak total	Washington, USA
Giroux and Bedard (1988)	Intermediate	Above, below	Max-min total, peak total, Smalley (1959)	St. Lawrence Estuary
Graham and Mendelssohn (2010)	Intermediate	Above	Smalley (1959)	Louisiana, USA
Graham and Mendelssohn (2014)	Intermediate	Below	Peak total	Louisiana, USA
White and Simmons (1988)	Intermediate	Above	Smalley (1959)	Louisiana, USA
Crain (2007)	Brackish	Above	Peak total	Maine, USA
Cramer et al. (1981a, b)	Brackish	Above	Smalley (1959), Wiegert and Evans (1964)	Louisiana, USA
de la Cruz (1974)	Brackish	Above	Milner and Hughes (1968)	Mississippi, USA
Ewing (1986)	Brackish	Above	Peak total	Washington, USA
Hopkinson et al. (1980)	Brackish	Above	Williams and Murdoch (1972)	Louisiana, USA
Ibanez et al. (1999)	Brackish	Above	Smalley (1959)	Rhone Delta, France
Karagatzides and Hutchinson (1991)	Brackish	Above, below	Peak total	Canada
Keefe and Boynton (1973)	Brackish	Above	Peak total	Virginia-Maryland, USA
Kistritz et al. (1983)	Brackish	Above	Smalley (1959)	British Columbia, Canada
Pezeshki and DeLaune (1991)	Brackish	Above	Smalley (1959)	Louisiana, USA
Roman and Daiber (1984)	Brackish	Above, below	Peak live, Smalley (1959)	Delaware, USA
Scarton et al. (2002)	Brackish	Above, below	Smalley (1959)	Po Delta, Italy
White and Simmons (1988)	Brackish	Above	Smalley (1959)	Louisiana, USA
Wigand et al. (2004)	Brackish	Above, below	EOS total	Rhode Island, USA
Windham (2001)	Brackish	Above, below	Peak live	New Jersey, USA
Allen (1971)[a]	Saline	Above	EOS total	Louisiana, USA
Anisfeld and Hill (2012)	Saline	Below	Gallagher (1983)	Connecticut, USA
Bellis and Gaither (1985)	Saline	Above, below	Max-min live	North Carolina, USA
Benito and Onaindia (1991)	Saline	Above	Smalley (1959)	Cantabrian Sea, Spain
Blum (1993)	Saline	Below	Max-min live	Virginia, USA
Cahoon (1975)[a]	Saline	Above	EOS live	Maryland, USA
Callaway and Josselyn (1992)	Saline	Above	Smalley (1959)	California, USA
Connor and Chmura (2000)	Saline	Below	Peak total	Dipper Harbor, Canada
Good (1965)[a]	Saline	Above	EOS total	New Jersey, USA
Gordon et al. (1984)	Saline	Above	Smalley (1959)	Maine, USA
Gosselink et al. (1975)[a]	Saline	Above	EOS total	Louisiana, USA
Groenendijk and Vink-Lievaart (1987)	Saline	Below	Dahlman and Kucera (1965)	Netherlands, USA
Gross (1966)[a]	Saline	Above	EOS total	Connecticut, USA
Hardisky et al. (1984)	Saline	Above	Milner and Hughes (1968), peak total, Smalley (1959)	Delaware, USA
Hatcher and Mann (1975)[a]	Saline	Above	EOS total	Canada, USA
Hopkinson et al. (1978)	Saline	Above	Wiegert and Evans (1964)	Louisiana, USA
Karagatzides and Hutchinson (1991)	Saline	Above, below	Peak total	Canada

Table 5 (continued)

Study	Wetland type	Above/below	Production estimation method	Location
Kaswadji et al. (1990)	Saline	Above	Lomnicki et al. (1968), peak total, Milner and Hughes (1968), Smalley (1959), Wiegert and Evans (1964)	Louisiana, USA
Keefe and Boynton (1973)[a]	Saline	Above	EOS total	Virginia-Maryland, USA
Kirby and Gosselink (1976)	Saline	Above	Peak total, Milner and Hughes (1968), Smalley (1959) , Wiegert and Evans (1964)	Louisiana, USA
Kirby (1972)[a]	Saline	Above	EOS total, max-min live, Smalley (1959)	Louisiana, USA
Kruczynski et al. (1978)	Saline	Above	Smalley (1959)	Florida, USA
Linthurst and Reimold (1978b)	Saline	Above	Milner and Hughes (1968), peak total, Smalley (1959), Wiegert and Evans (1964)	Maine, Delaware, Georgia, USA
Linthurst and Reimold (1978a)	Saline	Above	Modified Smalley (1959), Smalley (1959), Wiegert and Evans (1964)	Maine, Delaware, Georgia USA
Livingstone and Patriquin (1981)	Saline	Below	Peak total	Nova Scotia, Canada
Marshall (1970)[a]	Saline	Above	EOS total	North Carolina, USA
Mendelssohn (1973)[a]	Saline	Above	EOS total	Virginia, USA
Morgan (1961)[a]	Saline	Above	EOS total	Delaware, USA
Morris and Haskin (1990)	Saline	Above	Modified Dickerman et al. (1986)	South Carolina, USA
Nixon and Oviatt (1973)[a]	Saline	Above	EOS total	Rhode Island, USA
Udell et al. (1969)[a]	Saline	Above	EOS total	New York, USA
Odum and Fanning (1973)[a]	Saline	Above	EOS total	Georgia, USA
Pezeshki and DeLaune (1991)	Saline	Above	Smalley (1959)	Louisiana, USA
Reidenbaugh (1983)	Saline	Above	Milner and Hughes (1968), Smalley (1959)	Virginia, USA
Roman and Daiber (1984)	Saline	Above, below	Peak live, Smalley (1959)	Delaware, USA
Ruber et al. (1981)	Saline	Above	Wiegert and Evans (1964)	Massachusetts, USA
Scarton et al. (2002)	Saline	Above, below	Smalley (1959)	Venice Lagoon, Italy
Schubauer and Hopkinson (1984)	Saline	Above, below	Smalley (1959)	Georgia, USA
Shew et al. (1981)	Saline	Above	Lomnicki et al. (1968), Milner and Hughes (1968), peak total, Smalley (1959), Wiegert and Evans (1964)	North Carolina, USA
Smalley (1959)[a]	Saline	Above	Smalley (1959)	Georgia, USA
Smith et al. (1979)	Saline	Above, below	Dahlman and Kucera (1965)	New Jersey, USA
Squiers and Good (1974)[a]	Saline	Above	EOS total	New Jersey, USA
Stagg and Mendelssohn (2010)	Saline	Above, below	Gallagher (1983), Smalley (1959)	Louisiana, USA
Steever (1972)[a]	Saline	Above	EOS total, Smalley (1959)	Connecticut, USA
Stroud and Cooper (1968a, b)	Saline	Above, below	Max-min live, peak total	North Carolina, USA
Stroud (1976)	Saline	Below	Max-min live	North Carolina, USA
Trilla et al. (2009)	Saline	Above	Peak total	Bahia Blanca, Argentina
Turner and Gosselink (1975)[a]	Saline	Above	EOS total	Texas, USA
Turner et al. (2004)	Saline	Above, Below	Peak live, peak total	Louisiana, USA
Valiela et al. (1975)[a]	Saline	Above	EOS total, Smalley (1959)	Massachusetts, USA
Valiela et al. (1976)	Saline	Above, Below	Allometry, max-min total	Massachusetts, USA
Visser et al. (2006)	Saline	Above	EOS total, peak total	Louisiana, USA
Wass and Wright (1969)[a]	Saline	Above	EOS total	Virginia, USA

Table 5 (continued)

Study	Wetland type	Above/below	Production estimation method	Location
White et al. (1978)	Saline	Above	Peak total, Smalley (1959), Wiegert and Evans (1964)	Louisiana, USA
Williams and Murdoch (1969)[a]	Saline	Above	EOS total, max-min live	South Carolina, USA

Allen Curve estimates cohort production using a relationship between plant density and biomass. Allometry estimates production using established relationships between plant biomass and structural characteristics such as height. End of season (EOS) live estimates production as the value of live biomass collected at the end of the growing season. End of season (EOS) total estimates production as the value of total live and dead biomass collected at the end of the growing season and is analogous to end of season standing crop. Max-min total estimates production as the difference between the maximum total biomass and the minimum total biomass collected during an annual cycle. Max-min live estimates production as the difference between the maximum live biomass and the minimum live biomass collected during an annual cycle. Peak live estimates production as the maximum live biomass collected during an annual cycle. Peak total estimates production as the maximum total live and dead biomass collected during an annual cycle and is analogous to peak standing crop. Summed shoot maximum estimates production as the sum of maximum shoot biomass and includes a correction for mean leaf turnover.

[a] Citation within Turner (1976) review

Appendix 2

Table 6 Results from second principal component analysis subsequently used in the multiple regression analysis

Environmental parameter	PC1: nutrients (40 %)	PC2: metals (17 %)	PC3: flooding (12 %)
Pw pH	*0.73*	-0.45	−0.09
Pw ammonium	*0.68*	−0.52	0.05
Pw phosphate	*0.61*	−0.42	0.21
Pw total nitrogen	*0.62*	−0.52	0.04
Pw total phosphorus	*0.52*	−0.42	0.19
Soil pH	0.23	*−0.57*	0.14
Soil phosphate	0.46	−0.31	0.20
Soil ammonium	−0.24	−0.14	0.14
Soil total phosphorus	*−0.67*	−0.17	0.34
Soil total nitrogen	*−0.92*	−0.09	−0.06
Soil organic matter	*−0.92*	−0.17	−0.06
Soil total carbon	*−0.93*	−0.15	−0.06
Pw iron	−0.01	*0.51*	0.06
Soil copper	0.61	*0.61*	0.03
Soil iron	0.73	*0.56*	0.04
Soil zinc	0.71	*0.60*	0.04
Marsh surface elevation	−0.15	0.29	*0.90*
Annual %time flooded	−0.12	−0.23	*−0.90*
Eigenvalue	6.8	3.0	2.1

This analysis did not include salinity parameters. Data presented are correlation coefficients for the hydro-edaphic parameters (rows) and PCs (columns). Correlation coefficients greater than 0.5 (set in italics) were used to define the PCs. Primary attribute(s) and % variance explained are identified for each PC

Appendix 3

Table 7 National Climatic Data Center, climate indices data for Climate Division: Louisiana (16), Southeast (9) during water years (October–October) from 2010 to 2014

Year	Month	PCP (mm)	TAVG (°C)	PDSI	PHDI	ZNDX	PMDI	TMIN (°C)	TMAX (°C)
2010	10	23.88	21.39	−1.54	−1.54	−1.90	−1.54	15.39	27.39
2010	11	115.06	16.89	−1.44	−1.44	−0.19	−1.44	11.50	22.33
2010	12	51.82	10.39	−2.02	−2.02	−2.17	−2.02	4.78	16.00
2011	1	86.36	10.39	−2.07	−2.07	−0.79	−2.07	5.17	15.56
2011	2	45.72	12.89	−2.53	−2.53	−2.02	−2.53	7.44	18.33
2011	3	136.65	18.61	−2.33	−2.33	−0.18	−2.33	13.28	23.94
2011	4	10.67	22.28	−3.08	−3.08	−2.97	−3.08	17.28	27.22
2011	5	12.70	24.17	−3.97	−3.97	−3.60	−3.97	19.22	29.06
2011	6	86.36	28.78	−4.47	−4.47	−2.72	−4.47	23.89	33.67
2011	7	306.07	28.50	−3.05	−3.05	2.86	−1.90	24.22	32.78
2011	8	60.96	29.94	−3.91	−3.91	−3.52	−3.91	25.17	34.67
2011	9	332.74	25.17	−2.01	−2.01	4.50	−0.20	20.39	30.00
2011	10	8.64	19.89	−2.40	−2.40	−1.80	−1.30	13.78	26.06
2011	11	42.93	17.39	−2.72	−2.72	−1.71	−2.21	12.11	22.67
2011	12	35.56	13.83	−3.49	−3.49	−3.16	−3.49	9.06	18.61
2012	1	50.04	15.00	−4.11	−4.11	−2.92	−4.11	9.39	20.67
2012	2	119.89	15.61	−3.92	−3.92	−0.69	−3.92	11.61	19.61
2012	3	179.07	20.67	0.17	−3.34	0.52	−3.08	15.89	25.39
2012	4	178.56	21.67	0.59	−2.56	1.30	−1.74	16.61	26.72
2012	5	75.95	25.28	−0.54	−2.84	−1.63	−2.60	20.39	30.22
2012	6	185.42	27.28	0.28	−2.27	0.85	−1.65	22.78	31.78
2012	7	280.67	28.00	1.25	−1.04	2.98	0.71	23.67	32.22
2012	8	458.47	27.72	4.03	4.03	8.75	4.03	23.78	31.67
2012	9	132.84	26.28	3.49	3.49	−0.40	3.27	21.94	30.61
2012	10	24.13	20.67	2.63	2.63	−1.49	1.79	15.22	26.17
2012	11	51.05	15.28	1.96	1.96	−1.19	0.64	9.28	21.33
2012	12	82.30	14.72	1.20	1.20	−1.70	−0.72	9.28	20.17
2013	1	213.11	13.72	1.98	1.98	2.71	1.05	9.11	18.33
2013	2	183.90	14.44	2.29	2.29	1.56	1.81	9.72	19.17
2013	3	14.22	14.06	1.16	1.16	−2.68	−0.27	8.22	19.83
2013	4	249.68	19.50	2.17	2.17	3.39	1.80	14.94	24.00
2013	5	190.75	22.61	2.70	2.70	2.25	2.70	18.28	26.94
2013	6	115.82	27.83	−0.18	2.24	−0.54	1.95	23.61	32.00
2013	8	142.49	27.61	−0.58	1.37	−0.90	0.42	23.50	31.67
2013	9	140.72	27.06	−0.77	0.98	−0.74	−0.27	22.61	31.56
2013	10	72.39	22.11	−0.89	0.68	−0.60	−0.75	17.50	26.78
2013	11	82.04	15.11	−0.99	−0.99	−0.58	−0.99	10.28	20.00
2013	12	101.60	12.72	−1.17	−1.17	−0.84	−1.17	8.11	17.33
2014	1	73.66	8.06	−1.35	−1.35	−0.90	−1.35	2.11	14.06
2014	3	138.18	14.33	0.50	−0.58	0.56	0.45	9.22	19.44
2014	2	158.75	12.89	0.35	−0.86	1.06	−0.17	7.83	17.94
2014	4	94.23	19.94	0.30	−0.68	−0.46	0.11	15.28	24.61
2014	5	219.46	23.17	1.24	1.24	2.91	1.24	18.39	27.89
2014	6	175.77	27.11	1.48	1.48	1.12	1.48	23.22	31.00
2014	7	165.86	27.61	−0.04	1.29	−0.12	1.14	23.28	31.89
2014	8	119.13	28.33	−0.50	0.69	−1.40	−0.28	24.17	32.50

Table 7 (continued)

Year	Month	PCP (mm)	TAVG (°C)	PDSI	PHDI	ZNDX	PMDI	TMIN (°C)	TMAX (°C)
2014	9	114.30	26.78	−0.88	−0.88	−1.29	−0.88	22.72	30.89
2014	10	56.90	22.22	−1.14	−1.14	−1.05	−1.14	16.72	27.78

The climate indices data for this region were collected from 62 stations within the geographical division. (Source: http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#, accessed September 2016)

PCP mean monthly precipitation (mm), *TAVG* mean monthly temperature (°C), *PDSI* Palmer Drought Severity Index, *PHDI* Palmer Hydrological Drought Index, *ZNDX* Palmer Z Index, *PMDI* Modified Palmer Drought Severity Index, *TMIN* monthly minimum temperature (°C), *TMAX* monthly maximum temperature (°C)

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