Potential effects of sea-level rise on plant productivity: species-specific responses in northeast Pacific tidal marshes

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ABSTRACT: Coastal wetland plants are adapted to varying degrees of inundation. However, functional relationships between inundation and productivity are poorly characterized for most species. Determining species-specific tolerances to inundation is necessary to evaluate sea-level rise (SLR) effects on future marsh plant community composition, quantify organic matter inputs to marsh accretion, and inform predictive modeling of tidal wetland persistence. In 2 macrotidal estuaries in the northeast Pacific we grew 5 common species in experimental mesocosms across a gradient of tidal elevations to assess effects on growth. We also tested whether species abundance distributions along elevation gradients in adjacent marshes matched productivity profiles in the mesocosms. We found parabolic relationships between inundation and total plant biomass and shoot counts in *Spartina foliosa* and *Bolboschoenus maritimus* in California, USA, and in *Carex lyngbyei* in Oregon, USA, with maximum total plant biomass occurring at 38, 28, and 15% time submerged, respectively. However, biomass of *Salicornia pacifica* and *Juncus balticus* declined monotonically with increasing inundation. Inundation effects on the ratio of belowground to aboveground biomass varied inconsistently among species. In comparisons of field distributions with mesocosm results, *B. maritimus*, *C. lyngbyei* and *J. balticus* were abundant in marshes at or above elevations corresponding with their maximum productivity; however, *S. foliosa* and *S. pacifica* were frequently abundant at lower elevations corresponding with sub-optimal productivity. Our findings show species-level differences in how marsh plant growth may respond to future SLR and highlight the sensitivity of high marsh species such as *S. pacifica* and *J. balticus* to increases in flooding.

KEY WORDS: Marsh organs · Plant biomass · Root-to-shoot ratio · Tidal wetlands · Zonation

INTRODUCTION

Vascular plant production is central to many important ecosystem processes in tidal wetlands. In addition to fueling coastal food webs (Parker et al. 2008), plant material also accumulates in sediments to contribute to the production of new soils (Neubauer 2008, Callaway et al. 2012). With long residence times in anoxic wetland sediments, non-labile organic matter constitutes a coastal carbon storage pool (Ouyang & Lee 2014), while wetland loss can release large quantities of sequestered carbon into the atmosphere (Pendleton et al. 2012). The aboveground physical structure of salt marsh plants also provides other important coastal ecosystem services such as attenuating wave energy (Shepard et al. 2011), facil-

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itating sediment accretion (Gleason et al. 1979, Mudd et al. 2010), and providing habitat for wetland-dependent vertebrates (Sustaita et al. 2011).

Incorporation of estuarine plant material into wetland soils is one of the key elements of the biophysical processes that determine tidal wetland elevation relative to changing sea levels (Morris et al. 2002). For example, belowground root growth (or expansion of the base of shoots) contributes to the vertical growth of the marsh surface (Nyman et al. 2006, Cherry et al. 2009). However, vascular plant production is inundation-dependent, potentially leading to spatial heterogeneity in organic matter inputs to soils or aboveground trapping of inorganic sediment particles. Inundation gradients impact soil salinity and porewater sulfide concentrations (Mahall & Park 1976a, Bertness & Ellison 1987) — factors demonstrated to affect plant physiology (Bradley & Dunn 1989, Hester et al. 2001).

Various inundation–productivity relationships have been reported for tidal marsh plants, including parabolic responses (Kirwan & Guntenspergen 2012, 2015, Schile et al. 2014, Watson et al. 2015), linearly declining monotonic relationships (Voss et al. 2013), or exponentially declining relationships (Watson et al. 2014, Snedden et al. 2015). However, research to date has mainly focused on common marsh species found along the Atlantic coast of North America (but see Schile et al. 2014 for multi-species biomass data in California, USA). Since marshes in other regions of the world typically have different tidal ranges, species composition, and climatic regimes, relationships between inundation and plant growth may vary by species or region.

Accurate understanding of relationships between inundation and productivity is essential for implementation of mechanistic models of sea-level rise (SLR) effects because of the role that vegetation plays in the ecogeomorphic feedbacks that maintain marsh surface elevation in the tidal frame (Marani et al. 2010, Schile et al. 2014, Swanson et al. 2014). Morris et al. (2002) posited a unimodal relationship between productivity and inundation for Atlantic coast *Spartina alternifora*, suggesting that increasing inundation up to a threshold stimulates plant growth, thus enhancing marsh vertical growth, while flooding beyond this threshold negatively affects production and leads to the loss of the marsh as a stable ecosystem. Some wetland SLR models incorporate this basic unimodal functional relationship into projections of future marsh elevation (Schile et al. 2014, Swanson et al. 2014), but productivity in other marsh species may respond differently to changing inundation. In the absence of sufficient *in situ* vertical growth to keep pace with SLR, marshes will need to migrate upslope to persist over the long term (Kirwan & Megonigal 2013).

The present study determined how productivity in 5 common marsh species is affected by a wide range of inundation conditions at 2 estuaries on the Pacific coast of North America. Using intertidal mesocosms that isolated effects of submergence from potential inter-specific interactions, we quantified functional relationships between inundation and plant biomass and vegetative growth in individual species. To evaluate potential inundation effects on plant contributions to ecosystem processes, we tested the hypothesis that greater inundation had a disproportionately negative impact on belowground versus aboveground growth in each species. We additionally determined inundation effects on flower and seed production (reported in the supplementary material). Finally, we tested whether peak species abundance in the field (where both the biological interactions and various abiotic conditions potentially affect plant abundance) coincided with inundation levels of maximum productivity observed in the mesocosms.

MATERIALS AND METHODS

Study sites

We used mesocosms to grow plants at a range of elevations in 2 estuaries along the west coast of the United States during the 2014 growing season (Fig. 1). We deployed the mesocosms along the south-facing banks of Tule Slough in the Petaluma marsh, Sonoma County, California, USA (38.1901° N, 122.5489° W) and Millport Slough in the Siletz Estuary, Lincoln County, Oregon, USA (44.8877° N, 123.9971° W). Both sites are relatively undisturbed areas representative of brackish emergent tidal marsh in the northern San Francisco Bay estuary and outer coast of the US Pacific Northwest with mixed semi-diurnal tides.

Vegetation at Petaluma marsh is dominated by perennial pickleweed *Salicornia pacifica* (Takekawa et al. 2013), but includes other common species such as coyote brush *Baccharis pilularis* DC., jaumea *Jaumea carnosa* (Lessing) A. Gray, California cordgrass *Spartina foliosa* Trin., and saltmarsh bulrush *Bolboschoenus maritimus* (L.) Palla. The site has a tidal range of 1.92 m between mean lower low water (MLLW) and mean higher high water (MHHW) (NOAA tide station 9415423, http://tidesandcurrents. noaa.gov). The region has a Mediterranean climate
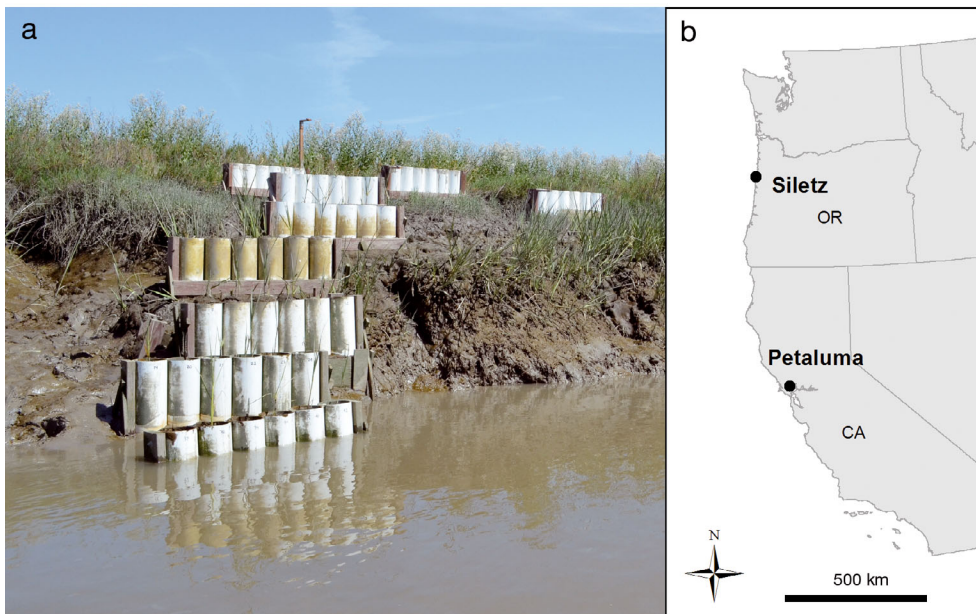
Fig. 1. (a) Mesocosms at Petaluma, and (b) study locations at Petaluma marsh, California, and Siletz marsh, Oregon, along the west coast of the USA. Photo: C. N. Janousek

with pronounced wet and dry seasons. Mean monthly salinities during higher tides range from about 3 ppt in late winter to 25 ppt in fall (Takekawa et al. 2013). During our study period, mean water column salinity at Petaluma at the beginning of the growing season was mesohaline (6–10 ppt in early April) but gradually increased to euhaline conditions by late June (≥30 ppt). Mean water temperatures in Tule Slough ranged from 13.3 to 23.6°C (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m548p111_supp.pdf). Average daily air temperatures for the study period (excluding a 13 d data gap) at a nearby weather station in the Petaluma Valley ranged from 8.1 to 21.9°C; total precipitation during the same period totaled 72 mm (CIMIS station 144, www.cimis.water.ca.gov).

The Siletz Estuary is a macrotidal, drowned river-mouth estuary on the central Oregon coast (Lee & Brown 2009). In Millport Slough, emergent wetland vegetation is composed of several dozen herbaceous and woody species with tufted hairgrass *Deschampsia cespitosa* (L.) Beauv., Baltic rush *Juncus balticus* Willdenow ssp. *ater* (Rydb.) Snogerup, Pacific silverweed *Potentilla anserina* L. and creeping bentgrass *Agrostis stolonifera* L. being common (Brophy et al. 2011). At nearby Salmon River Estuary and Depot Bay (to the north and south of Siletz Bay, respectively), MLLW–MHHW tidal ranges are 2.17 and 2.51 m, respectively (NOAA tide stations 9436381 and 9435827; http://tidesandcurrents.noaa.gov). The Oregon coast has a Maritime climate with higher total annual rainfall than central California. During

our study period in 2014, Siletz was oligohaline until late May (<5 ppt) and mean water column salinities did not exceed 20 ppt for the rest of the experiment. Daily mean water temperatures in Millport Slough during the study period ranged from 9.4 to 20.7°C (Fig. S1 in Supplement 1). Mean daily air temperatures at nearby South Beach along the central Oregon coast ranged from 8.7 to 22.5°C; total precipitation at South Beach during the study period was 190 mm (http://weather.hmsc.oregonstate.edu/weather/weatherproject/hmsc_weather.html).

Experimental design

The mesocosms in this study followed the 'marsh organ' designs used previously in studies of tidal inundation effects on marsh productivity in the eastern USA (e.g. Voss et al. 2013, Kirwan & Guntenspergen 2015), except that individual rows of the 'organs' (different elevation treatments) were physically separated and installed along natural elevation gradients found at the edges of tidal channels to accommodate the larger tidal amplitude of north Pacific marshes. Each 'module' in the experiment consisted of 6 vertical PVC pipes (15 cm diameter, 40 cm length) linearly arranged in a wooden frame. All pipes were open on the bottom, with the bottom of the tubes resting on ambient sediment, enabling physical support of the sediment inside the tubes and allowing vertical (but not horizontal) hydrologic connectivity with the sediment below (see discussion in

Kirwan et al. 2013). The mesocosm approach allows precise quantification of inundation duration and the ability to carefully quantify belowground biomass responses (because roots of experimental plants are separated from other plants), but may artificially slow soil drainage and isolates plants from belowground interactions with neighboring vegetation. We filled the mesocosms completely with sediment obtained from the adjacent tidal channels.

We deployed the modules at 6 (Siletz) or 7 (Petaluma) elevations spanning the range of tidal elevations over which tidal marsh vegetation is typically found at the 2 sites, with the uppermost modules above the nearby marsh plain and the lowest modules at approximately the lowest extent of marsh vegetation (Fig. 1). The vertical separation between treatment levels was 27 cm at Petaluma and 33 cm at Siletz. We installed 3 modules per elevation at Petaluma (21 total modules) and 2 modules per elevation at Siletz (12 total modules), giving 6 replicate mesocosms per elevation per species. Water level data collected during the experiment (described below) showed that the highest platform level at Siletz did not flood during the duration of the experiment, so we omitted those samples from further analysis.

To determine the elevation of each installed module, we averaged multiple survey-grade Real-Time Kinematic (RTK) GPS measurements using Leica Viva GS15 and RX1250X GNSS rovers (Leica Geosystems) conducted over the course of the experiment (n = 4–11 per module). Rover positions were received from the Leica Smartnet RKT network in California (https://www.smartnetna.com/index.cfm) and the Oregon Real-Time RTK network (www.oregon.gov/ODOT/HWY/theorgn/Pages/Maps.aspx). We determined orthometric heights (North American Vertical Datum of 1988, NAVD88) with geoid models 09 (Petaluma) and 12A (Siletz). Rover precision was determined with replicate measurements at a reference benchmark and it varied among the 2 rovers between 0.013 and 0.023 m (standard deviation). We measured probable minor sinking of some platforms (<10 cm) over the course of the experiment; thus we used the mean elevation of all measurements of each module for analyses.

We measured changes in water column conditions in the adjacent tidal channels at each site over the course of 1 growing season. We determined water levels every 12 min with Solinst water level loggers (Levelogger; Solinst Canada) set inside stilling wells, with sensor positions 10 cm below the lowest experimental elevation at each site. We corrected raw water level data for atmospheric variation with a time series of local barometric pressure readings obtained with additional loggers above the intertidal. We determined the percent time each individual module was inundated over the course of the experiments from the NAVD88 elevations of each module and the time series of water level at each site. We recorded water column conductivity and temperature with Odyssey conductivity sensors (Dataflow Systems) also deployed at the elevation of the lowest module. We first converted raw logger output (specific conductance values) to salinity and then (because logger accuracies can vary by several percent from sensor to sensor), obtained final time series by adjusting logger salinity and temperature values with logger-specific linear regression equations generated across a range of temperatures and salinities under carefully measured laboratory conditions (Janousek & Mayo 2013).

Plant cultivation

We used species that are major components of tidal marsh floras in their respective regions. At Petaluma we collected small shoots of *Spartina foliosa* (Poaceae) and *Bolboschoenus maritimus* (Cyperaceae) including intact sections of rhizome in March 2014, and placed them in Cone-tainers (Stewe & Sons) with sediment from the field site, to grow in a greenhouse at the US Geological Survey field station in Vallejo, California, USA. We also collected ~10 to 20 cm long green shoot cuttings of *Salicornia pacifica* (Chenopodiaceae) during the same time period and placed the stems directly into sediment to promote root formation. We grew plants in shallow plastic bins with the bottom half of the Cone-tainers submerged in fresh water. We periodically watered all plants with fresh water, until about 1 wk prior to transplantation, at which time we raised salinity to 5 ppt and then 10 ppt. We did not note any obvious shock to the plants by raising the salinity over the course of a week. After 2 to 4 wk in the greenhouse, on 2 April we planted healthy plants (with single shoots) randomly across elevation treatments and mesocosm position within the modules. We sacrificed 6 additional plants of each species to estimate initial dry mass at the time of planting. Total dry mass values (mean ± SD) were 0.79 ± 0.27, 2.30 ± 1.20, and 0.29 ± 0.13 g for *S. foliosa*, *B. maritimus* and *S. pacifica*, respectively.

At Siletz, we collected small marsh plugs (~10 × 10 cm, 10 cm deep) containing roots, rhizomes and shoots of *Carex lyngbyei* (Cyperaceae) and *Juncus balticus* (Juncaceae) on 11 April 2014 and added them to pots for maintenance under fresh water in an

outdoor greenhouse at Oregon State University in Corvallis, until transplantation into the field. We removed shoots from non-target species that grew from the plugs. The site was relatively fresh at the time of transplantation with mean daily salinities ranging from 0.7 to 4.8 ppt the first week after planting. We removed all but 2 or 3 shoots of *C. lyngbyei* and *J. balticus*, respectively, before planting the 72 replicate plugs on 23 April, assigning plants to mesocosms randomly. We sacrificed 6 additional plants of each species to estimate initial dry mass (shoots only) at the time of planting. Shoot dry mass (mean ± SD) was 0.47 ± 0.06 and 0.64 ± 0.28 g for *J. balticus* and *C. lyngbyei*, respectively.

End of growing season measurements

We surveyed growth and health of the plants by monitoring them every 2 to 4 wk from planting until the end of the experiments. At approximately the end of the growing season (11–12 August for Petaluma; 26 August for Siletz), we assessed plant status (healthy, almost dead, dead, missing), the total number of shoots (for all species except *S. pacifica*), incidence of flower production, and number of seeds (*J. balticus* only) in each mesocosm. We then harvested the plants to determine above- and belowground biomass. We washed plants in tap water over 500 or 1000 μm sieves to remove soil and organic debris from belowground roots and rhizomes and removed belowground biomass of non-target species (e.g. *Triglochin maritima*) that were present in the Siletz samples. We did not retain very small root fragments during sample processing, which constituted a small fraction of total root mass. We dried above- and belowground fractions at about 55 to 60°C for approximately 4 d prior to weighing on an analytical balance (model AND HR-202i; A&D Company). At Siletz, we recovered above- and belowground biomass for all replicates in the experiment. At Petaluma, 14% of plants were missing shoots (or all structures), and many of these replicates died during the course of the experiment. However, we treated missing structures at the end of the study as missing values, not as zero values, because many plants grew for weeks or months before they were lost from the mesocosms and therefore had net gains in biomass. We reanalyzed these Petaluma samples by treating missing structures as zero biomass or zero shoot counts, but this had no qualitative, and little quantitative, effect on study results (Supplement 2 at www. int-res.com/articles/suppl/m548p111_supp.pdf).

Species distributions in the adjacent marshes

We conducted field surveys with 0.25 m^2 quadrats to compare *in situ* distributions of the 5 species with the mesocosm results. At Petaluma, we surveyed percent cover of *S. foliosa*, *B. maritimus* and *S. pacifica* in 120 plots from 14 to 17 July. Because most of the site consists of a relatively high-elevation marsh plain dominated by *S. pacifica*, we sampled 30 transects (~6 m length) randomly positioned along 3 major tidal channels in the area to capture enough plots across a range of elevations. Along each transect (oriented perpendicular to the channel axis) we measured percent cover and plot elevation with RTK GPS in 4 plots spaced about 2 m apart from the vegetation boundary at the channel edge onto the marsh plain.

At Siletz, we sampled percent cover of *C. lyngbyei* and *J. balticus* in 126 plots between 25 August and 4 September along parallel transects spaced relatively uniformly across the marshes between Millport Slough and the Siletz River. Plots were sampled typically at ~100 m intervals. As at Petaluma, we measured plot elevation with RTK GPS. Most of the vegetated tidal wetland surveyed at the site was relatively high in elevation, so the surveys captured only a subset of the elevation range present in the mesocosm experiment. At both sites we used RTK-derived elevations with local water level data to estimate duration of inundation for each field plot. We also determined the elevation of each plot relative to local MHHW using tidal datums in Brophy et al. (2011) for Siletz and published geodetic and tidal elevations (www.ngs.noaa.gov) for 3 tidal benchmarks near the Petaluma marsh. Site-specific relationships between MHHW and time inundated are shown in Fig. S2 in Supplement 3 at www.int-res.com/articles/suppl/m548p111_supp.pdf.

Statistical analyses

We tested the effects of percent time inundated on end-of-growing-season total plant dry mass, shoot dry mass, root + rhizome dry mass, natural log-transformed ratios of root-to-shoot biomass (Hedges et al. 1999), and total shoot counts, with a second order polynomial regression for each species (function 'lm', package 'base', R v.3.1.2, The Comprehensive R Archive Network; https://cran.r-project.org). We used polynomial regression to accommodate non-linear relationships, consistent with previous studies (e.g. Kirwan & Guntenspergen 2012). For total biomass and shoot count data, we estimated the inundation level

corresponding with maximum productivity for those species exhibiting distinct unimodal relationships.

To estimate the elevations at which maximum abundance occurred for each species along elevation gradients at the sites, we used non-linear quantile regression splines (functions 'rq' and 'ns' in packages 'quantreg' and 'splines', R v.3.1.2). We used the upper 90th percentile of the distribution (tau = 0.9) to estimate maximum percent cover, because some plots may have had low cover at otherwise favorable elevations due to other factors affecting species distribution (e.g. Cade & Noon 2003). We used natural cubic splines, a method which uses polynomial fits to discreet quantiles of the distribution depending on the number of 'internal knots' selected, while constraining the fit beyond the ends of the distribution ('boundary knots') to be linear. We used 4 internal knots (df = 5) to fit the splines, which generally provided satisfactory curve smoothness but did not overfit noise in the distribution. We qualitatively compared inundation–productivity relationships for each species from the mesocosms (estimated from the polynomial relationships with total biomass) with abundance distributions in the field.

RESULTS

Plant survivorship and growth

Plant survivorship in the experiments varied by species and inundation treatment. At Petaluma, *Bolboschoenus maritimus* shoots grew rapidly during the first month of the experiment, but ceased growing taller thereafter; *Salicornia pacifica* and *Spartina foliosa* grew steadily over the growing season (data not shown). By the end of the growing season most individuals of *S. pacifica* and *S. foliosa* were alive, but 36 and 21% of the mesocosms, respectively, had dead plants or were missing all shoots. *B. maritimus* survivorship was poor: 12% of plants were alive, 33% were near death, 45% were dead, and 10% were missing shoots. In contrast, all *Carex lyngbyei* and *Juncus balticus* plants survived at Siletz.

Plant biomass

Growth responses to the inundation gradients in our experiments varied by species. End-of-season total dry mass of *S. foliosa* and *B. maritimus* had unimodal relationships with tidal inundation (Fig. 2) — *S. foliosa*: $R^2_{adj} = 0.60$, p < 0.0001; *B. maritimus*: $R^2_{adj} = 0.33$, p =

0.0004). Peak dry mass was estimated at 38% inundation for *S. foliosa* and 28% for *B. maritimus*. Total dry biomass of *S. pacifica* was highest at about 0 to 10% inundation, but non-linearly declined with increased submergence ($R^2_{adj} = 0.61$, p < 0.0001). *S. pacifica* total mass was very low when inundation exceeded about 30%. Total dry biomass of *J. balticus* was variable (though generally high) between 0 and 5% flooding, but declined at greater levels of inundation, reaching nearly zero above 35% submergence ($R^2_{adj} = 0.49$, p < 0.0001). The response of *C. lyngbyei* to flooding followed a unimodal pattern with maximum total mass at 15% inundation ($R^2_{adj} = 0.31$, p = 0.003). For all species, above- and belowground dry mass had similar functional relationships with inundation as observed with total dry mass (Fig. 2, Supplement 2).

Allocation of biomass between belowground versus aboveground structures varied non-linearly with tidal flooding, but again patterns differed among species (Fig. 3). *S. pacifica* tended to have low root-to-shoot ratios at low inundation, indicating allocation of most resources to shoot growth. At greater inundation, root-to-shoot ratios were higher ($R^2_{adj} = 0.18$, p = 0.02). In *B. maritimus*, *S. foliosa* and *J. balticus*, root-to-shoot ratios were lowest at intermediate levels of inundation but higher under either infrequent or frequent inundation (*B. maritimus*: $R^2_{adj} = 0.31$, p = 0.0007; *S. foliosa*: $R^2_{adj} = 0.15$, p = 0.02; *J. balticus*: $R^2_{adj} = 0.15$, p = 0.04). In *C. lyngbyei*, root-to-shoot ratios declined monotonically with increasing inundation ($R^2_{adj} = 0.33$, p = 0.002).

Vegetative growth and fecundity

Inundation effects on end-of-growing season total shoot counts in *S. foliosa*, *B. maritimus*, *C. lyngbyei* and *J. balticus* were similar to species-specific results obtained for total dry mass (Fig. 4). *B. maritimus* and *S. foliosa* produced the most shoots at intermediate levels of inundation ($R^2_{adj} = 0.15$, p = 0.02 and $R^2_{adj} = 0.35$, p = 0.0002, respectively). Maximum shoot production was estimated at 38% inundation in *S. foliosa* and 36% in *B. maritimus*. Shoot production in *C. lyngbyei* also had a unimodal relationship with flooding ($R^2_{adj} = 0.27$, p = 0.006), and maximum shoot production occurred at 7% inundation. *J. balticus* shoot production declined nearly linearly from the lowest to highest levels of inundation ($R^2_{adj} = 0.30$, p = 0.003). Inundation effects on plant flowering incidence for all species and on seed production in *J. balticus* are presented in Supplement 4 at www.int-res.com/articles/suppl/m548p111_supp.pdf.
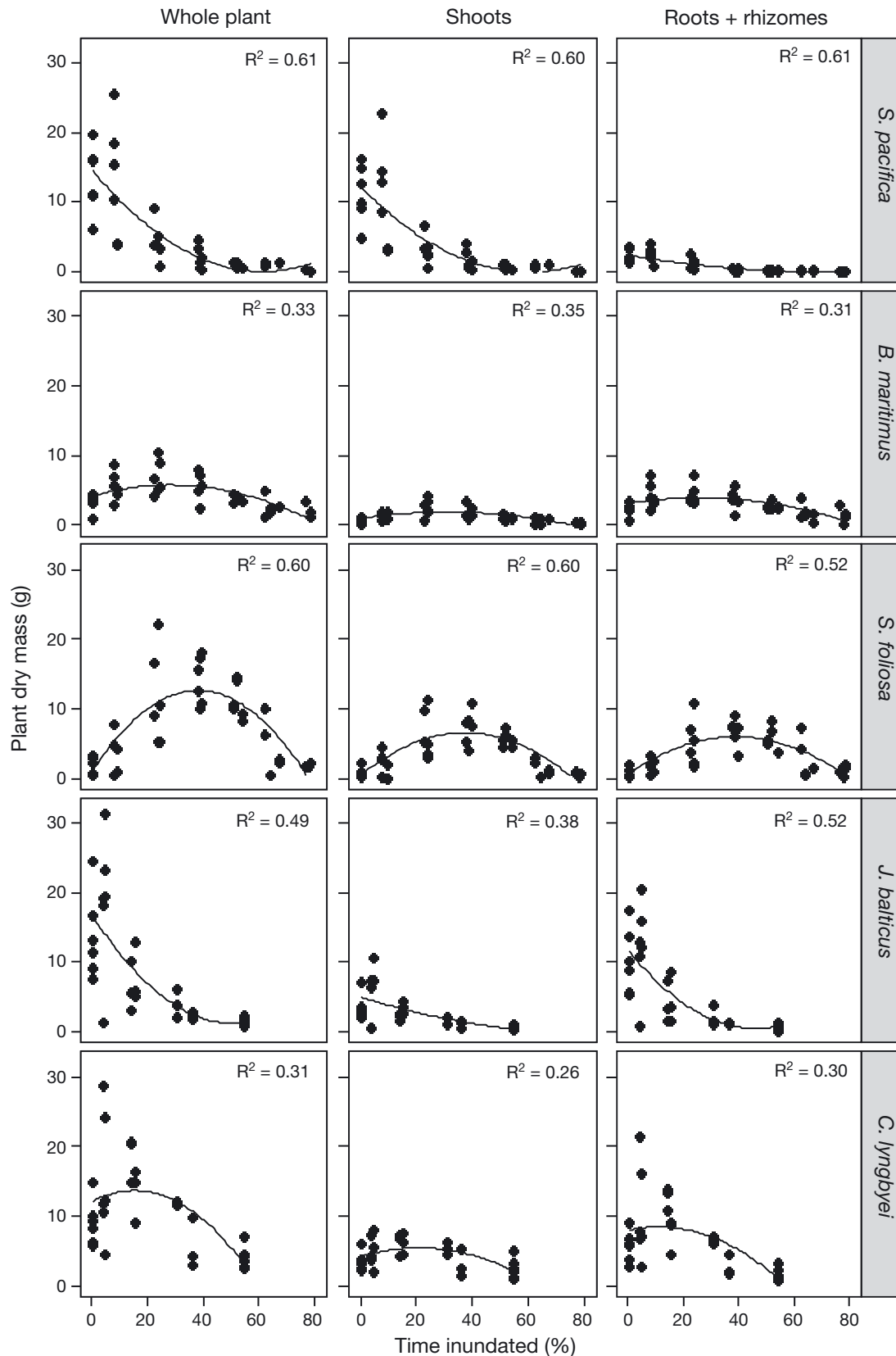
Fig. 2. End-of-growing-season dry mass of whole plants, shoots and roots + rhizomes relative to total time inundated in *Salicornia pacifica*, *Bolboschoenus maritimus*, and *Spartina foliosa* at Petaluma, and *Juncus balticus* and *Carex lyngbyei* at Siletz. Lines and adjusted R^2 values are least-squares second order polynomials fit to the data
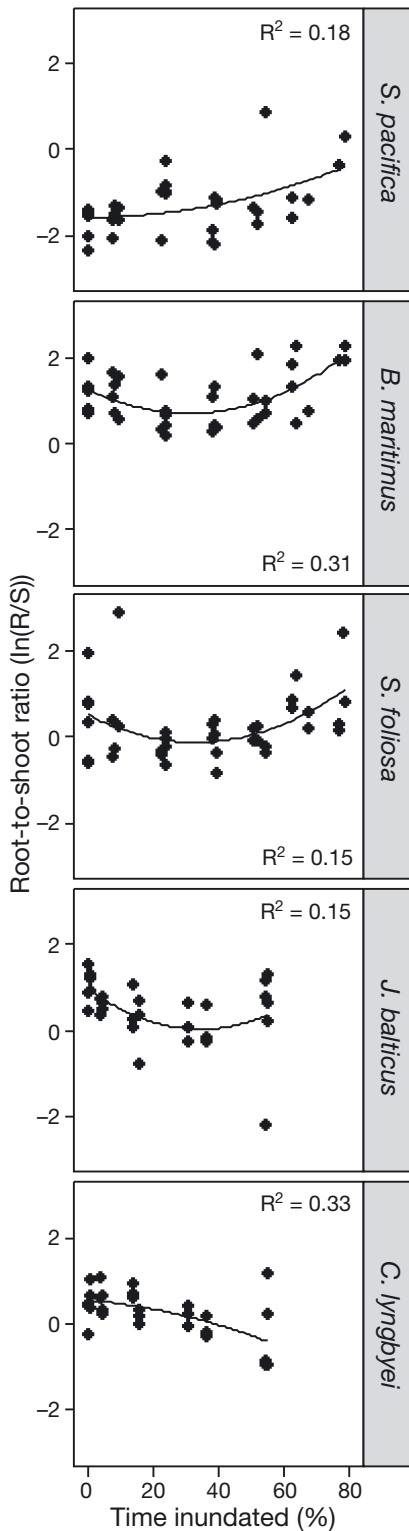
Fig. 3. Inundation effects on end-of-growing season root-to-shoot (R/S) ratios in *Salicornia pacifica*, *Bolboschoenus maritimus*, and *Spartina foliosa* from Petaluma, and *Juncus balticus* and *Carex lyngbyei* from Siletz. Lines and adjusted R[2] values are least-squares second order polynomials fit to the data
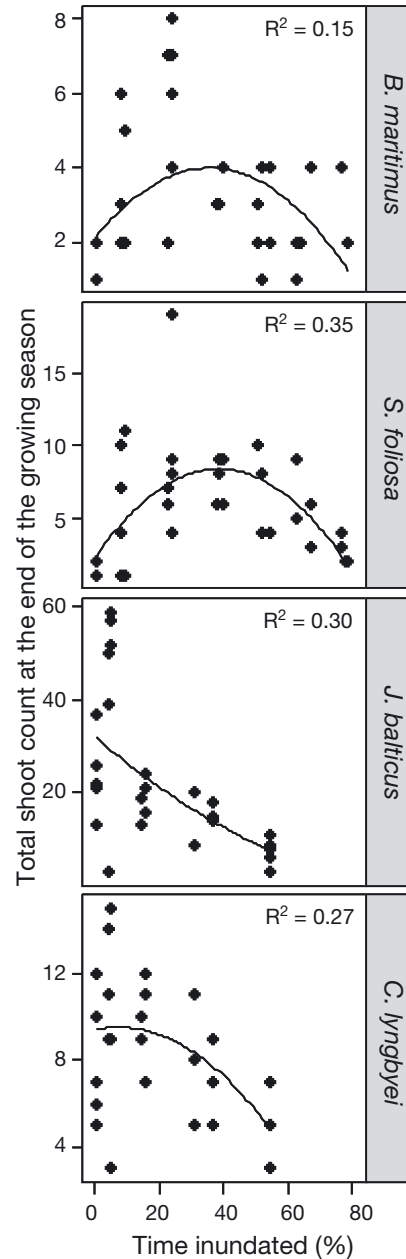

Fig. 4. Total shoot count in *Bolboschoenus maritimus* and *Spartina foliosa* along inundation gradients at Petaluma, and in *Juncus balticus* and *Carex lyngbyei* along inundation gradients at Siletz. Lines and adjusted R[2] values are least-squares second order polynomials fit to the data

Plant distributions in adjacent marshes

Species in the study tended to occupy distinct tidal zones, particularly at Petaluma. *S. foliosa* and *B. maritimus* frequently occurred in monospecific patches at lower tidal elevations, with the latter sometimes co-occurring with *S. pacifica*. *S. foliosa* was present
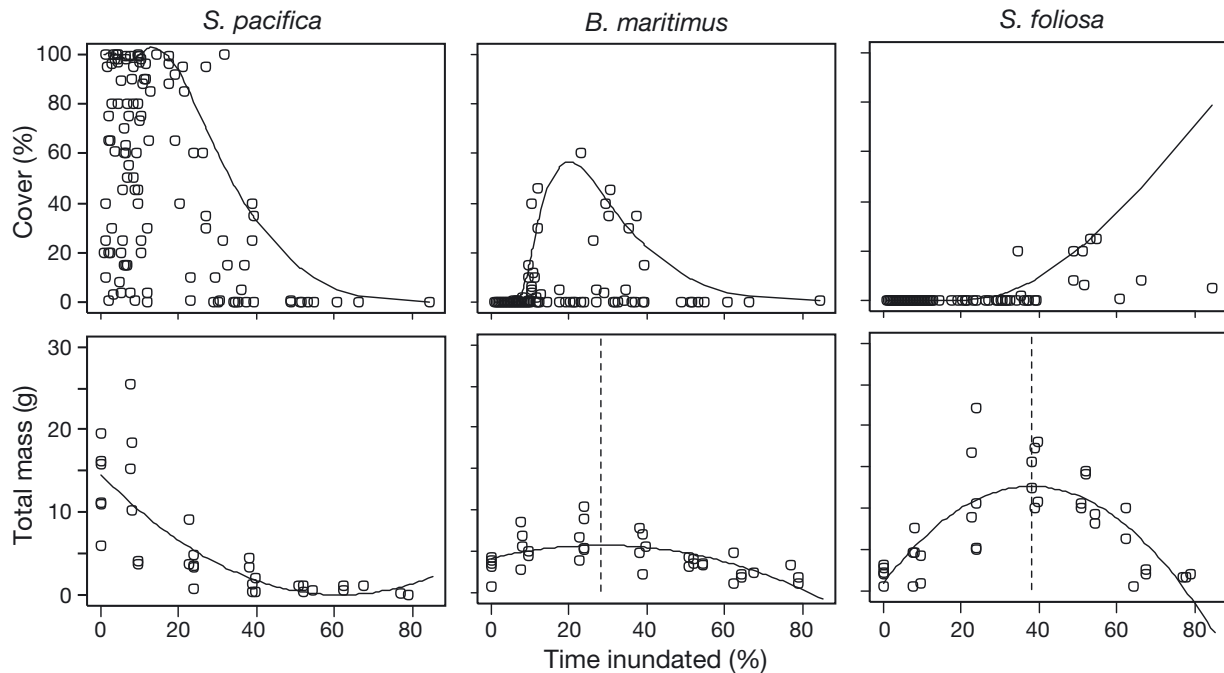
Fig. 5. Comparison of *in situ* species cover versus inundation, along with indundation–biomass relationships in the mesocosm experiments at Petaluma marsh. Distribution of maximum cover with inundation was modeled using 90% quantile natural regression splines with 4 internal knots (top panels, solid lines); biomass was modeled with least-squares second order polynomials (bottom panels, solid lines), and estimated peak productivities for *Spartina foliosa* and *Bolboschoenus maritimus* are shown with vertical dashed lines. The increasing tail of the *S. foliosa* model fit at high inundation is thought to be an artifact of fitting quantile regression to a limited sample size; higher inundation usually corresponds with unvegetated mudlfat or tidal channels at the site

between −0.46 and −1.48 m MHHW, corresponding to 35 to 84% inundation (Fig. 5, Supplement 3). However, most occurrences of the species were at greater levels of inundation (≥49%). *B. maritimus* was distributed from +0.09 to −1.48 m MHHW, with moderate to high cover (≥25%) occurring between −0.02 and −0.51 m MHHW (10–37% inundation). Peak abundance was estimated by splinal quantile regression to occur at ~20% flooding. Cover was zero or at trace levels at >40% flooding. *S. pacifica* tended to occur higher than the other species at the site, though it had a broad distribution, occurring from +0.25 to −0.77 m relative to MHHW. It occurred as monospecific assemblages or mixed with other species. Its highest abundance (≥50% cover) occurred between +0.21 and −0.41 m MHHW, elevations that corresponded to 1 to 32% inundation. Splinal regression summaries are reported in Table S5 in Supplement 5 at www.int-res.com/articles/suppl/m548p111_supp.pdf.

At Siletz, *C. lyngbyei* often occupied lower elevation tidal marsh, ranging from near monocultures to mixed assemblages with other species. It was distributed from +0.24 to −0.47 m relative to local MHHW (Fig. 6).

It had high cover (≥50%) between −0.13 and −0.47 m MHHW but we did not survey any plots lower than −0.47 m MHHW at the site. The elevation range of high cover corresponded with 5 to 18% inundation. *J. balticus* typically occurred as one component of mixed species plots. It was present in plots ranging from +0.38 to −0.21 m MHHW, with high abundance (≥50% cover) occurring from +0.21 to −0.20 m MHHW (corresponding to 1 to 7% inundation).

DISCUSSION

We found major differences in responses to inundation gradients among the Pacific coast marsh species examined in this study. Three species had unimodal functional relationships with inundation but peak production at different tidal levels, while production in 2 species declined monotonically with increasing inundation. Ratios of root-to-shoot dry mass varied non-linearly with tidal inundation and inconsistently among species. By comparing plant distributions in adjacent marshes with mesocosm results, we determined that 2 species common in Cali-
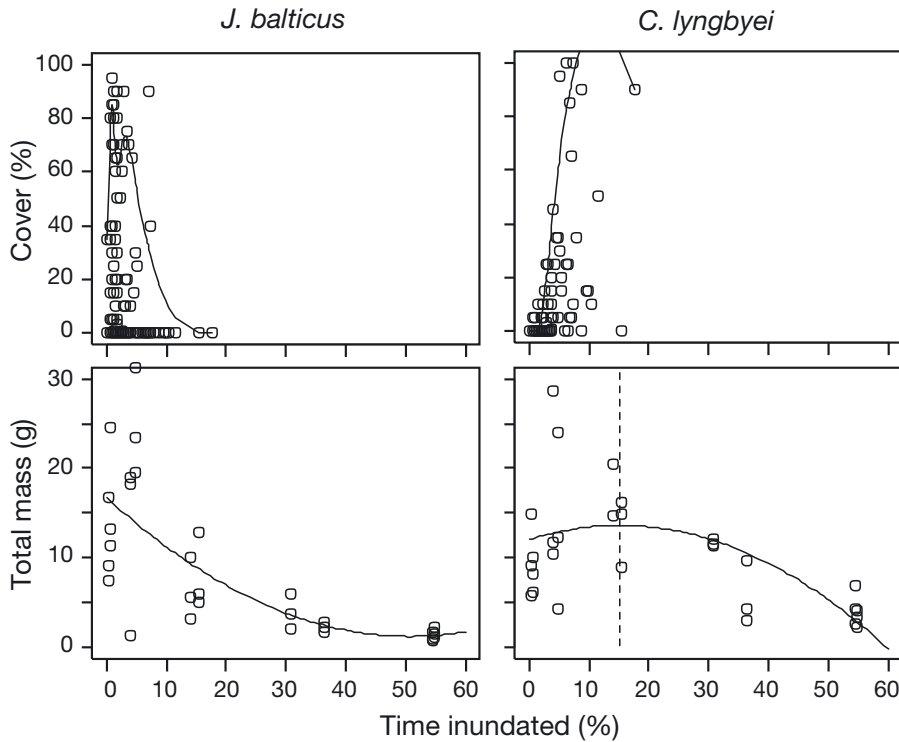
Fig. 6. Comparison of *in situ* species cover versus inundation, along with indundation–biomass relationships in the mesocosm experiments at Siletz. Distribution of maximum cover with inundation was modeled using 90% quantile natural regression splines with 4 internal knots (top panels, solid lines), biomass was modeled with least-squares second order polynomials (bottom panels, solid lines), and estimated peak productivity for *Carex lyngbyei* is shown with a vertical dashed line

fornia marshes — *Salicornia pacifica* and *Spartina foliosa* — were often abundant at intertidal elevations below their optimal productivity. The other species in the study had highest abundance in the field at elevations corresponding with their preferred inundation levels. These divergent functional responses to inundation, and distribution relative to optimal inundation conditions, suggest unique species responses to future sea-level rise on the Pacific coast.

Biomass–inundation relationships

Middle- to lower-marsh species in our study (*Bolboschoenus maritimus* and *S. foliosa* in California; *Carex lyngbyei* in Oregon) had unimodal productivity–inundation relationships, qualitatively similar to previous findings for *Schoenoplectus americanus* on the Atlantic coast of the USA (Kirwan & Guntenspergen 2012, 2015). Although the 3 Pacific coast species had similarly-shaped functional responses to inundation, estimated peak biomass occurred at different inundation levels. *S. foliosa* had the greatest tolerance of higher inundation, consistent with its usual occurrence at lower elevations than other species in many California marshes (Zedler 1977, Takekawa et al. 2013).

Productivity of 2 common high marsh species (*S. pacifica* in California and *Juncus balticus* in Oregon)

declined monotonically with increasing inundation. Both species maintained relatively high productivity at <5 to 10% inundation, but growth declined steeply with increasing submergence. A recent greenhouse study with adult *S. pacifica* also found that plant height declined monotonically with increasing inundation (Woo & Takekawa 2012). *S. pacifica* dominates tidal marsh vegetation throughout much of California where it typically occurs on the high marsh plain. At Petaluma for example, it is abundant between mean high water (MHW) and MHHW (Takekawa et al. 2013). *S. pacifica* is a foundation species in many California tidal wetlands, providing important habitat for marsh-dependent wildlife (Thorne et al. 2012) and likely contributing large amounts of organic matter to salt marsh soils. *J. balticus* is a common species in Pacific Northwest tidal marshes, found particularly in lower-salinity, high-elevation soils (Janousek & Folger 2014).

Like *S. pacifica* and *J. balticus* in this study, experimental work with the high marsh species *Spartina patens* from Chesapeake Bay showed declining production with increasing inundation (Kirwan & Guntenspergen 2015). Productivity in the lower-elevation Atlantic species *Spartina alterniflora* was initially hypothesized to have a unimodal relationship with inundation (Morris et al. 2002), though experimental data from North Carolina did not strongly support this relationship (Voss et al. 2013) and data from New

England and Louisiana show a monotonic decline in production with greater flooding (Watson et al. 2014, Snedden et al. 2015).

Our species-specific data on productivity–inundation relationships have several implications for understanding SLR effects on Pacific coast tidal wetlands. First, similar to emerging patterns for Atlantic salt marshes, our results suggest that marshes with differing species composition may have fundamentally different responses to changing inundation gradients. For instance, in *S. pacifica*-dominated high marshes, small increases in relative SLR are expected to reduce, not enhance, productivity, in contrast to predictions of the conceptual model in Morris et al. (2002). At Petaluma, relative SLR of 20 cm would nearly double inundation times at current MHHW (10 to 19%) with an expected decrease in *S. pacifica* total biomass. Loss of local productivity may initiate a negative feedback between inundation and marsh accretion because of a reduction in inorganic particle trapping and a decrease in organic matter inputs to marsh soils (Morris et al. 2002).

Second, our data suggest that mechanistic models of SLR may be more effective if they account for differences in vegetation composition and their feedbacks to tidal marsh elevation. Under conditions of constant inorganic sediment availability, spatial differences in marsh production can affect the rate at which marshes are impacted by rising sea levels (Schile et al. 2014). The WARMER model, used to estimate SLR effects on Pacific coast marshes, currently uses a unimodal productivity–inundation relationship hypothesized for *S. alterniflora* which places maximum production at mid-marsh elevations and assumes that productivity approaches zero at the upland-marsh boundary (Swanson et al. 2014). This generalized functional relationship may work well for modeling sites dominated by similarly-responding species such as *C. lyngbyei* in some Pacific Northwest estuaries (Hutchinson 1988), but may inaccurately estimate organic matter contributions to soil formation for areas dominated by high marsh species such as *S. pacifica* in California, *J. balticus* in some mature Pacific Northwest marshes, or *S. patens* in some Atlantic marshes (Kirwan & Guntenspergen 2015). These species have maximum production essentially at near-zero inundation levels, a substantial difference from the assumptions of some current models.

Finally, our data have implications for potential changes in tidal marsh plant composition that may occur with relative sea-level rise. One expected consequence is that the inundation gradients affecting species distributions in tidal marshes may change in magnitude or spatial location, leading to changes in the relative abundance of marsh species. For instance, in California, *S. pacifica*-dominated marshes that gradually become subject to higher inundation may be eventually colonized by *Spartina foliosa* or other more flooding-tolerant species such as the nonnative *S. alterniflora* and *S. alterniflora × foliosa* hybrid that have recently invaded the San Francisco Bay estuary (Callaway & Josselyn 1992, Daehler & Strong 1997). The pace and magnitude of compositional changes will likely be affected by how quickly individual species more tolerant of inundation are able to disperse to areas occupied by species less tolerant of flooding and outcompete established, but less productive, vegetation. Where *Spartina* spp. cannot invade, drowning *S. pacifica* marshes may become unvegetated mudflat.

Changes to marsh assemblage composition are also likely to be determined by how broadly tolerant different species are to a range of inundation conditions, not just differences in their inundation optima. In the diverse tidal marshes of the Pacific Northwest, for example, the distribution of some species such as *Agrostis stolonifera* or *Triglochin maritima* were found to be relatively insensitive to differences in marsh elevation and might therefore be little affected by increasing inundation (Janousek & Folger 2014). More generally, species largely restricted to high marsh elevations may be particularly vulnerable to SLR because small increases in relative SLR could result in a several-fold increase in flooding.

One additional important consequence of elevated SLR may be changes to other abiotic factors that affect plant composition, including the potential for increasing wetland salinity to accompany SLR (Cloern et al. 2011, Ross et al. 2015). Rising salinity may favor more salt tolerant species (Ryan & Boyer 2012, Snedden et al. 2015), decrease productivity (Pearcy & Ustin 1984, Hester et al. 2001), and reduce plant diversity in marsh assemblages (Engels & Jensen 2009). Increasing inundation may also be associated with lower soil redox potential (Bertness & Ellison 1987), which in turn may correspond with differences in marsh species composition (Sánchez et al. 1998).

We hypothesized that root-to-shoot ratios would decline with increasing inundation as observed in several other tidal marsh studies (e.g. Rozema & Blom 1977, Kirwan & Guntenspergen 2012, Janousek & Mayo 2013, Langley et al. 2013). However, of the 5 species examined, this response was only observed in *C. lyngbyei*. In contrast, *S. pacifica* root-to-shoot ratios appeared to increase with greater inundation,

and ratios in *B. maritimus*, *J. balticus* and *S. foliosa* increased above ~30 to 40% inundation, similar to findings of increased flooding effects on biomass allocation patterns in Mediterranean *Spartina maritima* (Wong et al. 2015). Kirwan & Guntenspergen (2015) found that root-to-shoot ratios were largely invariant along inundation gradients in *S. americanus* and *S. patens*. In our study, inundation effects on root-to-shoot ratios were relatively weak, and variable responses among species suggest different growth responses to inundation. For instance, increasing flooding affected *S. pacifica* shoots more strongly than roots, but *J. balticus* roots + rhizomes more strongly than shoots (Fig. 3).

Elucidating above- versus belowground growth responses to inundation gradients is important for evaluating SLR effects on different vascular plant functions in tidal wetlands. For example, disproportionate loss of aboveground biomass may reduce trapping and deposition of inorganic material in surface soils, rendering wetlands more dependent on belowground organic matter inputs to maintain elevation with rising water levels. Declines in shoot growth may also impact plant canopy complexity with negative consequences for marsh-dependent fauna. In contrast, significant loss of belowground production with relative SLR may destabilize marsh soils, particularly at channel edges where waves and tidal currents may weaken soil cohesion (see Deegan et al. 2012 for a nutrient example), even if aboveground capacity to trap sediments remains unaffected.

Other abiotic and biotic factors are likely to interact with inundation to determine spatial patterns of plant productivity in tidal marshes. For instance, recent work by Schile et al. (2011) on *S. pacifica* in northern California suggests that soil drainage patterns, not just total inundation time, may be an important determinant of plant production. Plants in well-drained soils were more productive than those on the marsh plain. Elevated salinity, an important abiotic stressor for vascular plants, may also interact with flooding to negatively impact production (Janousek & Mayo 2013, Snedden et al. 2015). In fact, variation in inundation may create vertical salinity gradients (through evaporation in warmer areas, or fluvial contributions in estuaries with high freshwater inputs) that also affect productivity. Langley et al. (2013) found that addition of nitrogen, or nitrogen + CO_2, modified the elevation at which *S. patens* showed maximum production and increased production in *S. americanus* at higher flooding levels relative to controls. In contrast, Wong et al. (2015) determined that the negative effects of increased flooding on *S. maritima* growth were greatest under elevated nutrient conditions.

Interspecific plant interactions (not present in our mesocosms because we isolated plants from neighbors) may also affect plant growth along inundation gradients, much as they impact overall plant distribution in tidal marshes (Pennings et al. 2005). There are few published data available on inundation effects on mixed species assemblages in controlled experiments. However, Langley et al. (2013) used field mesocosms to study inundation, nitrogen and CO_2 effects on a mixed assemblage of *S. americanus* and *S. patens* and found that the relative abundance of the species changed along the inundation gradient. Variation in flooding may contribute to a shift in the competitive balance among co-occurring species, as seen in a greenhouse manipulation of inundation and nutrients with *Distichlis spicata* and *S. patens* (Watson et al. 2015). To better understand how whole marsh assemblages may respond to SLR, other experimental designs such as manipulation of marsh inundation by passive weirs may be useful (Cherry et al. 2015).

Productivity versus field abundance

Determining current patterns of plant distributions with respect to conditions for optimal productivity are important for evaluating near versus long-term effects of SLR on marsh structure and function. We found high abundance of *C. lyngbyei*, *J. balticus* and *B. maritimus* in field plots at elevations at (or above) those coinciding with maximum productivity in the mesocosm experiments, suggesting that small near-term increases in relative SLR may have little impact on growth of these species. In contrast, both *S. pacifica* and *S. foliosa* were often abundant in the field at elevations below their estimated maximum productivity levels in the mesocosm experiment. Thus, small levels of relative SLR such as the 17 to 28 cm rise projected to occur under mid SLR scenarios for several USA west coast locations by the year 2050 (NRC 2012) may have a greater negative effect on marshes dominated by *S. pacifica* and *S. foliosa*. Similarly, Voss et al. (2013) found that *S. alterniflora* and *Juncus roemerianus* in a North Carolina marsh organs study occurred on adjacent marshes below their optimal productivity levels.

For species particularly sensitive to soil saturation, however, the marsh organ experimental design may exacerbate the negative effects of inundation on plant growth because horizontal drainage during low

tide may be impeded in the PVC pipes. This may affect estimates of optimal productivity in some species such as *S. pacifica*, which has been shown to be sensitive to soil drainage (Schile et al. 2011, but see Mahall & Park 1976b, who suggested that the distribution of *S. pacifica* is insensitive to soil oxygen availability). If the mesocosms contained more anoxic sediment than un-manipulated marsh at the same tidal elevation, optimal productivity may have been shifted higher in the tidal frame relative to the marsh.

Alternatively, species interactions and inter-specific differences in abiotic tolerances may explain why *S. foliosa* and *S. pacifica* both commonly grew at apparently sub-optimal elevations in the field relative to the mesocosms. *S. foliosa* may be distributed at lower elevations than its peak productivity because it is outcompeted by *S. pacifica* and/or *B. maritimus* at higher elevations, similar to *S. alterniflora* zonation on the Atlantic coast (Bertness 1991). Along the edges of tidal channels where soil drainage may be greater than on the marsh plain (Schile et al. 2011), *S. pacifica* may be able to outcompete *S. foliosa*. As the dominant species in the Petaluma marsh, *S. pacifica* probably tolerates a broad range of soil conditions (including high salinity sediments; Mahall & Park 1976a), so it may frequently grow under sub-optimal conditions. It may be a competitive sub-dominant in local patches (e.g. some high marsh areas occupied by large woody species such as *Grindelia stricta* and *Baccharis pilularis*). Our study provides important general data on how several major Pacific coast marsh species respond to gradients of tidal inundation, but further experimentation incorporating variation in soil drainage and salinity, neighbor effects, or other factors will help refine understanding of contemporary ecosystem structure and potential changes with SLR.

CONCLUSIONS

Above- and belowground plant production are important components of the biogeomorphic response to inundation that shapes tidal wetland elevation (Morris et al. 2002) and of other essential ecosystem functions maintained by tidal marsh vegetation. Our data show species-level differences in functional responses with inundation, suggesting that marsh vegetation composition will play an important role in determining relative SLR effects on specific tidal marshes. In particular, growth of high marsh species such as *Salicornia pacifica* that are most sensitive to elevated inundation may be least tolerant of relative SLR. Loss of production in marshes dominated by these species will potentially reduce marsh capacity to keep up with SLR. Relative SLR may also induce shifts in vegetation composition, with drowning marshes becoming more dominated by more flooding-tolerant species. We suggest that incorporation of species-specific productivity–inundation relationships into mechanistic SLR models will produce more accurate projections of local marsh vulnerability to SLR.

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