Inundation and precipitation effects on growth and flowering of the high marsh species

Juncus gerardii

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Abstract

Accelerated sea level rise threatens coastal wetland plant communities where coastal development restricts transgression, and inundation increases and declining sediment supplies limit the capacity of coastal wetlands to build in elevation. *Juncus gerardii* Loisel., black needle rush, is a high latitude cosmopolitan plant species and, within salt marshes of the U.S. mid-Atlantic and New England coasts, it occupies a narrow belt along the marsh-upland border. Examination of historic aerial photography, vegetation resurveys, and peat composition analysis for U.S. Northeastern marshes have shown vegetation change patterns indicative of increased inundation, including decline of *J. gerardii*. To interpret loss patterns for *J. gerardii* in southern New England, we conducted a factorial experiment to

establish its sensitivity to inundation and drought. A strong relationship was found between inundation and growth for *J. gerardii*, which together with marsh elevation and water level data, suggests that growth is reduced by current flooding patterns. Examination of *J. gerardii* flowering also indicates that floret and inflorescence density vary with inundation, suggesting that negative impacts of sea level rise on *Juncus* may extend to seed production. Late spring and summer drought impacted neither *J. gerardii* growth nor its flowering, implying that *J. gerardii* is insensitive to below-average precipitation or drought during this time of year. We conclude that current inundation patterns are incompatible with robust growth for *J. gerardii*, and recommend conservation actions be focused on the marsh-upland border to facilitate the upslope migration of *J. gerardii* and other transitional high marsh plant species.

Keywords

vegetation change, dieback, storms, sea level rise

1. Introduction

Coastal wetland plant communities are vulnerable to accelerated sea level rise where coastal development limits transgression, and increases in flooding and the duration of inundation exceed the capacity of salt marshes to build in elevation. In southern New England (USA), salt marshes are exceptionally vulnerable due a developed coastline, low sediment supply (Roman et al. 2000; Weston 2014), and high rates of sea level rise (3-4 times the global average; Sallenger et al. 2012), which collectively limit adaptive responses (Watson et al. 2014). Sediment accumulation simulation models predict a state change from salt marsh to tidal flat for current sea level rise rates for the region, primarily due to low suspended sediment concentrations (e.g., 2 mg L⁻¹; Morton 1972), which are at the extreme lower boundary for stable salt marsh (Kirwan et al. 2010). Studies of salt marsh vegetation change have revealed species composition shifts consistent with a response to increased inundation for the U.S. northeastern states of Connecticut, Rhode Island, New York, and Massachusetts over the twentieth century as historic rates of sea level rise (1 mm y⁻¹; Donnelly et al. 2004) have increased, and accretion deficits have developed (Warren and Niering 1993).

Historic southern New England salt marsh landscape patterns were comprised of a mosaic of vegetation communities (Miller & Egler 1950; Redfield 1972; Nixon 1982) where environmental stresses (i.e., soil anoxia and flooding) were thought to control the lower elevation boundaries of individual species, with competitive interactions a more common control at higher elevations (Bertness 1991). The marsh-upland border was composed of *Phragmites australis* (Cav.) Trin. Ex Steud at the irregularly flooded upland edge, while *Iva frutescens* L. was associated with more regular flooding. A belt of *Juncus gerardii* Loisel.,

most noticeable during spring, was typically seaward of *Iva*. On the high marsh, *Spartina patens* (Aiton) Muhl. was typically the most expansive species, and was found in mixed stands with *Distichlis spicata* (L.) Greene. *Salicornia depressa* Standley, an annual succulent and short-term colonizer, occupied disturbed locations. The tall ecotype of *Spartina alterniflora* (Loisel) was found adjacent to the shoreline and tidal channels. Botanical nomenclature follows Haines (2001).

A combination of vegetation resurveys and peat analyses for U.S. Northeastern marshes have shown patterns suggestive of increased inundation. A decline in the upper marsh *J. gerardii* belt and replacement of the high marsh species *S. patens* by *S. alterniflora* has been noted in the Wequetequock-Pawcatuck marshes of Connecticut (Niering and Warren 1980; Warren and Niering 1993), and landward movement of *S. alterniflora* through the twentieth century is concurrent with declines in high marsh vegetation in Rhode Island (Donnelly and Bertness 2001). Likewise, historic reports of vegetation composition for sites on Long Island suggest a shift in dominance from the high marsh species *S. patens* and *J. gerardii* to *S. alterniflora* between 1938 and 1972 (Nixon 1982). Analysis of historic air photos from Cape Cod also reveals loss of high marsh vegetation since the 1980s (Smith 2009).

In addition to increased inundation associated with accelerated sea level rise, climate model simulations corresponding to Intergovernmental Panel on Climate Change emissions scenarios suggest that by the end of this century, one to three month droughts could occur as frequently as once per summer in the U.S. Northeast (Wehner 2004; Frumhoff et al. 2007). As drought conditions have been associated with coastal marsh die-off events (McKee et al. 2004; Silliman et al. 2005), a process that has affected *Juncus*

gerardii (Alber et al. 2008), this shift in precipitation patterns may accelerate loss of high marsh vegetation. In particular, *Juncus gerardii* is thought be sensitive to drought, as previous studies have shown growth reductions in *Juncus gerardii* in response to increased salinity or low precipitation conditions (Rozema and Blom 1977; de Leeuw et al. 1990).

This study documents the interactive effects of inundation and precipitation on growth and flowering of the high marsh species *J. gerardii*, or black needle rush. Plants were field collected in early spring and propagated through the growing season in a greenhouse factorial experiment, using flow through seawater to simulate tidal inundation. Based on field studies that have suggested a loss of *J. gerardii* as a consequence of increased inundation in combination with accretion deficits (e.g. Warren and Niering 1993), we hypothesized that growth would be most vigorous under treatments where tidal inundation occurred less frequently than under typical field conditions. Because previous studies have also identified *J. gerardii* growth reductions with increased salinity or reduced precipitation (Rozema and Blom 1977; de Leeuw et al. 1990), we further hypothesized that reductions in precipitation would similarly result in reduced growth. This study aimed to determine the sensitivity of *Juncus gerardii* to current and future climate change impacts, and whether specific environmental sensitivities can explain the ongoing loss of *Juncus gerardii* from New England coastal wetlands.

2. Materials and methods

A factorial greenhouse experiment was conducted to test our hypotheses that flooding and drought impact *J. gerardii* growth. Sods were propagated for 125 days (7 May to 9 September 2013) during the summer growing season in three 700 L tanks with

simulated semi-diurnal tides (Fig. 1). The greenhouse experiment used a 5 x 3 factorial design, replicated three times, for a total of 45 experimental units. Five inundation regimes were created by housing pots on shelves within tanks (Fig 1). Seawater used for the experiment was drawn from lower Narragansett Bay (Rhode Island, USA), was low in nutrient concentration ($\sim 6\mu\text{M}$ dissolved inorganic nitrogen; $< 2\mu\text{M}$ phosphate), and of moderate salinity (23-30 psu). Tides simulated were semi-diurnal: tanks remained at tide levels (high/low) for two hours, with four hour fill and drain cycles. No supplemental lighting was used; day length at 41°N ranged from about 13h at the beginning and end of the experiment period to 16h on the summer solstice. Temperature was not controlled but automated greenhouse window vents allowed equilibration with outside temperatures. Local air temperature during the coolest and warmest months was $10\text{-}20^\circ\text{C}$ in May 2013; and $20\text{-}30^\circ\text{C}$ in July 2013; local water temperature was $10\text{-}15^\circ\text{C}$ in May 2013; and $21\text{-}24^\circ\text{C}$ in July 2013.

Sods containing a *Juncus gerardii* monoculture were collected 7 May 2013 from Colt State Park, Bristol, RI (41.68°N , 71.30°W). Sods were separated using an electric knife into $5 \times 5 \times 10$ cm plugs for planting; shoot density ranged from 17 to 59, with a mean of 35, and standard deviation of 10. Plugs were planted in circular pots 10 cm in width, and 40 cm in length, to hold constant volume available for root growth, and fitted with a basal collar and nylon screen to allow water exchange through the soil column. To reduce environmental impacts, and to provide a more homogenous soil matrix, sods were planted in a mixture of native marsh soils collected in small batches from four salt marsh ponds (Mary Donovan Marsh, Little Compton, RI; 41.55°N , 71.21°W ; Galilee Bird Sanctuary, Narragansett, RI; 41.38°N , 71.50°W ; Old Mill Cove, Warwick, RI; 41.71°N , 71.37°W ; Round Marsh,

Jamestown, RI; 41.51°N, 71.38°W) mixed using a cement mixer. Soils had a mean organic content of 12.2%, and were 15.7% sand, 75.4% silt, and 8.9% clay. Pots were assigned randomly to one of 15 inundation and precipitation treatment combinations, and position was distributed between tanks so that each tank contained a mixture of treatments (Fig. 1).

For each set of nine pots grown at each elevation, three each received the following precipitation treatments: no precipitation ('drought'), ambient precipitation (50 cc rainwater, 3 times weekly), or an intermediate precipitation treatment (25 cc rainwater, 3 times weekly). The volume of rainwater used for the ambient treatment was calculated from mean rainfall figures for Narragansett, RI multiplied by pot area. Pots were watered with rainwater from roof collectors.

To relate laboratory treatments to field conditions, water levels were monitored for a five month period at five Narragansett Bay salt marshes using pressure transducers (one Aquatroll 200 and four Solinst Leveloggers, compensated for atmospheric pressure using a Solinst Barologger). Site-specific values of mean high water (MHW) during the time of deployment were calculated and marsh elevation profiles were expressed relative to MHW using a combination of static GPS surveys (differentially corrected using the public Continuously Operating Reference Station network) and differential surveys using a rotary laser and stadia rod.

Variables associated with growth and flowering for *J. gerardii* were monitored. Growth response was measured as shoot height and density monthly (7 May, 11 June, 11 July, and 14 Aug) and as dry aboveground biomass at the conclusion of the experiment (9 Sept 2013). The number of shoots supporting inflorescence, and the number of florets per inflorescence were recorded once, on 11 June 2013, just after a synchronous pulsed

flowering event occurred. Aboveground biomass was harvested, rinsed of salts and adherent materials, dried, weighed, and converted to biomass per square meter through multiplication by a constant.

Variables from the factorial experiment (dry aboveground end of season biomass, shoot density at peak biomass [mid August], mean shoot height at peak biomass, percent flowering, floret density) were analyzed using multivariate analysis of covariance (MANCOVA) using SPSS Statistics (version 22, IBM, Armonk, NY, USA). The model included precipitation and elevation as main effects and an interaction term (precipitation x elevation). To control for variation in initial shoot density, density measures (from 7 May 2013) were included in the model as a covariate. Analysis was completed on natural log transformations of three variables (peak biomass, percent flowering, mean stem height) to ensure normality of error terms. Where main or interaction terms were significant, post-hoc tests (one-way ANCOVAs) were carried out for each response variable, again using initial density measures as a covariate. Growth and flowering responses were described using linear regression functions. Polynomial functions were used when data violated linear regression assumptions (homoscedasticity of residuals).

3. Results

The MANCOVA model demonstrated a statistically significant effect on the combined dependent variables for inundation ($F = 6.831$, $p < 0.005$; Wilks' $\Lambda = 0.041$). A statistically significant effect was not found for precipitation ($F = 1.019$, $p = 0.442$; Wilks' $\Lambda = 0.690$), nor was there a significant precipitation-inundation interaction ($F = 0.879$, $p = 0.673$; Wilks' $\Lambda = 0.304$).

Plant growth response variables were found to co-vary with inundation (Fig 2A), with higher elevations and lower inundation levels associated with enhanced growth, and low elevations and higher immersion times associated with reduced growth. Inundation was found to have had a statistically significant impact on end of season aboveground biomass (ANCOVA; $F = 33.298$, $p < 0.001$), August shoot density (ANCOVA; $F = 23.567$, $p < 0.001$), and shoot height (ANCOVA; $F = 24.131$, $p < 0.001$). The shape of growth response functions varied with plant response variable. The aboveground biomass-inundation relationship formed a polynomial function, while the shoot density-inundation relationship circumscribed a linear function. The mean stem height-inundation relationship showed a threshold relationship, below which mean stem height was reduced, and above which, mean stem height was insensitive to inundation.

Plant flowering response variables were also found to co-vary with inundation (Fig 2B). Inundation was found to have had a statistically significant impact on floret density ($F = 8.302$, $p < 0.001$), but not on the percentage of shoots with inflorescence ($F = 1.325$, $p = 0.278$). Floret density responded linearly to tidal height, with the highest elevations supporting the highest floret densities. Qualitative examination of *J. gerardii* inflorescence at field sites revealed a similar relationship between tidal height and flowering density.

Equating simulated high water with field measured mean high water (abbreviated MHW), allows comparability between treatment and field conditions. Plotting the distribution of marsh elevations found at field sites relative to MHW reveals that marsh elevations fall into the range where both growth and flowering of *Juncus gerardii* are especially sensitive to inundation.

4. Discussion

In this study, inundation was found to strongly impact growth and flowering for the high marsh plant species, *Juncus gerardii*, with the highest rates of growth and flowering found at elevations well above MHW. Previous experimental studies have also found strong detrimental impacts of waterlogged conditions on growth of *J. gerardii* (Rozema and Blom 1977; Cooper 1982), suggesting that its position in the upper portion of the salt marsh ecotone is a function of its inability to tolerate frequent inundation. As inundation-flowering interactions in salt marsh plants are not well studied, and previous reports on the response of *J. gerardii* to tidal inundation have not extended to flowering patterns, the observation that seed production may be impacted by increased inundation associated with accelerated sea level rise provides new information on coastal response patterns. In addition, because *Juncus* seeds are heavily grazed by marsh insect fauna (Bertness et al. 1987), this finding suggests sea level rise may also be impacting salt marsh trophic interactions.

Results reported here are also consistent with previous studies that credit the disappearance of *Juncus gerardii* and other high marsh taxa from southern New England coastal marshes to accelerated sea level rise coupled with accretion deficits (Orson et al. 1998; Warren and Niering 1993; Donnelly and Bertness 2001). Where inundation increases are not compensated for by marsh accumulation, taxa that are able to persist under more inundated conditions will replace flood-intolerant species (Reed 1995).

In contrast with inundation, reduced precipitation and drought were not found to significantly impact growth or flowering, nor were significant interactions identified between precipitation and inundation treatments. If true, drought tolerance may indicate

resilience of *J. gerardii* to high marsh dieback events, which have been associated with drought conditions, particularly in the U.S. Southeast (Silliman et al. 2005; Alber et al. 2008). However, these results generally contradict previous studies, which have found rainfall deficits associated with reduced *J. gerardii* biomass (de Leeuw et al. 1990), and negative impacts of increased salinity (Rozema and Blom 1977; Cooper 1982). Alternatively, *J. gerardii* in New England may be relatively insensitive to below-average precipitation during the months of June through September, but still possess sensitivity to precipitation variability from March to June (when shoots emerge), as the cessation of shoot emergence in June has been attributed to increasing evapotranspiration (Bouzillé et al. 1997).

Our results indicate that the upper marsh species *J. gerardii* is experiencing reduced growth and abundance related to current inundation patterns. The decline in *J. gerardii* noted for the twentieth century in southern New England, and linked here to sea level rise, raises conservation concerns. As a reversal of high marsh loss patterns is unlikely, and widespread accretion subsidies (i.e., thin layer dispersal; Frame et al. 2006) are impractical, we urge salt marsh conservation organizations in the region to identify migration opportunities and strategies. Such approaches might include reduced mowing of marsh edges, barrier removal where hard structures prevent upland transgression, and shifts in land use, such as discontinuing driving or parking on areas that now support coastal wetland plant taxa. Towns, cities, and land trusts might additionally consider acquiring parcels especially suitable for migration. Over the past century the status of *Juncus gerardii* in New England salt marshes has apparently declined from being the second

244 most common species to that of a minor component of the plant community. It is likely that
245 the status of this species will continue to decline without active conservation efforts.

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References

- Alber, M., Swenson, E. M., Adamowicz S.C., Mendelssohn, I.A. 2008. Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science* 80, 1-11.
- Bertness, M.D., Wise, C., Ellison, A.M. 1987. Consumer pressure and seed set in a salt marsh perennial plant community. *Oecologia* 71, 190-200.
- Bertness, M.D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72, 125-137.
- Bouzillé, J.B., Bonis, A., Clément, B., Godeau, M. 1997. Growth patterns of *Juncus gerardi* clonal populations in a coastal habitat. *Plant Ecology* 132, 39-48.
- Cooper, A. 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytologist* 90, 263-275.
- de Leeuw, J., Olff, H., Bakker, J.P. 1990. Year-to-year variation in peak above-ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. *Aquatic Botany* 36, 139-151.
- Donnelly, J. P., Bertness, M.D. 2001. Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. *Proceedings of the National Academy of Sciences* 98, 14218-14223.
- Donnelly, J.P., Cleary, P., Newby, P., Ettinger R. 2004. Coupling instrumental and geological records of sea-level change: evidence from southern New England of an increase in the rate of sea-level rise in the late 19th century. *Geophysical Research Letters* 31, GL018933
- Frame, G.W., Mellander, M.K., Adamo, D.A. 2006. Big Egg marsh experimental restoration in Jamaica Bay, New York. In: Harmon, D. (Ed.), *People, Places, and Parks: Proceedings*

- of the 2005 George Wright Society Conference on Parks, Protected Areas, and Cultural Sites. The George Wright Society, Hancock, MI, pp. 123-130.
- Frumhoff, P.C., McCarthy, J.J., Melillo, J.M., Moser, S.C., Wuebbles, D.J. 2007. Confronting Climate Change in the Northeast: science, impacts, and solutions. Union of Concerned Scientists, Cambridge, MA, USA.
- Haines, A. 2011. *Flora Novae Angliae: a manual for the identification of native and naturalized higher vascular plants of New England*. Yale University Press, New Haven, CT, USA.
- Kirwan, M.L., Guntenspergen, G.R., D'Alpaos, A., Morris, J.T., Mudd, S.M., and Temmerman, S. 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37, L23401.
- McKee, K.L., I.A. Medelssohn, and M.D. Materne. 2004. Acute salt marsh dieback in the Mississippi deltaic plain: a drought-induced phenomenon? *Global Ecology and Biogeography* 13: 65-73.
- Miller, W.R., Egler, F.E. 1950. Vegetation of the Wequetequock-Pawcatuck tidal-marshes, Connecticut. *Ecological Monographs* 20, 143-172.
- Morris, J.T., K. Sundberg, and C.S. Hopkins. 2013. Salt marsh primary production and its responses to relative sea level and nutrients in estuaries at Plum Island, Massachusetts, and North Inlet. *Oceanography* 26, 78-84.
- Morton, R.W. 1972. Spatial and temporal distribution of suspended sediment in Narragansett Bay and Rhode Island Sound. *The Geological Society of America Memoir* 133, 131-141.
- Niering, W.A., Warren, R.S. 1980. Vegetation patterns and processes in New England salt

- marshes. *BioScience* 30, 301-307.
- Nixon, S.W. 1982. The ecology of New England high salt marshes: a community profile. No. FWS/OBS-81/55. National Coastal Ecosystems Team, Washington, DC (USA); University of Rhode Island, Kingston, RI (USA).
- Orson, R.A., Warren, R.S., and Niering, W.A. 1998. Interpreting sea level rise and rates of vertical marsh accretion in a southern New England tidal marsh. *Estuarine Coastal and Shelf Science* 47, 419-429.
- Reed, D.J. 1995. The response of coastal marshes to sea level rise: survival or submergence? *Earth Surface Processes and Landforms* 20, 39-48.
- Redfield, A.C. 1972. Development of a New England salt marsh. *Ecological Monographs* 42, 201-237.
- Roman, C.T., Jaworski, N., Short, F.T., Findlay, S., Warren, R.S. 2000. Estuaries of the Northeastern United States: habitat and land use signatures. *Estuaries* 23, 743-764.
- Rozema, J., Blom, B. 1977. Effects of salinity and inundation on the growth of *Agrostis stolonifera* and *Juncus gerardii*. *Journal of Ecology* 65, 213-222.
- Sallenger, A.H., Jr, Doran, K.S., Howd, P.A. 2012. Hotspot of accelerated sea-level rise on the Atlantic coast of North America. *Nature Climatic Change* 2, 884-888.
- Silliman, B.R., Van de Koppel, J., Bertness, M.D., Stanton, L.E., Mendelssohn, I.A. 2005. Drought, snails, and large-scale die-off of southern US salt marshes. *Science* 310, 1803-1806.
- Smith, S.M. 2009. Multi-decadal changes in salt marshes of Cape Cod, MA: photographic analyses of vegetation loss, species shifts, and geomorphic change. *Northeastern Naturalist* 16, 183-208.

- 328 Warren, R.S., Niering, W.A. 1993. Vegetation change on a northeast tidal marsh: interaction
329 of sea-level rise and marsh accretion. *Ecology* 74, 96-103.
- 330 Watson, E.B., Oczkowski, A.J., Wigand, C., Hanson, A.R., Davey, E.W., Crosby, S.C. Johnson,
331 R.L., Andrews, H.M. 2014. Nutrient enrichment and precipitation changes do not
332 enhance resiliency of salt marshes to sea level rise in the Northeastern US. *Climatic*
333 *Change* 125: 501-509.
- 334 Wehner, M.F. 2004. Predicted twenty-first-century changes in seasonal extreme
335 precipitation events in the parallel climate model. *Journal of Climate* 17, 4281-4290.
- 336 Weston, N.B. 2014. 2014. Declining sediments and rising seas: an unfortunate convergence
337 for tidal wetlands. *Estuaries and Coasts* 37, 1-23.

Figures Captions

Figure 1. Experimental design showing inundation treatments and pot elevation relative to water levels (A), tank set up, where flow-through seawater was used to simulate tidal inundation (B), and assignment of treatments within tanks. We equate mean high tide with mean high water (MHW). Tanks were not drained at low tide, as coastal marsh groundwater levels typically do not fall more than a few decimeters below the marsh surface (Watson et al. 2014). Each tank contained 15 pots at five elevations. For each elevation, each set of three individual pots received either an ambient, drought, or intermediate precipitation treatment.

Figure 2. *Juncus gerardii* growth and flowering as a function of tidal height: Aboveground biomass at the time of harvest, August shoot density and mean shoot height as a function of elevation for all precipitation treatments (A), and percentage of stems supporting inflorescence and floret density per inflorescence as a function of elevation (B). Box and whisker plot shows marsh elevation (interquartile range, median, mean, and standard error) for five Narragansett Bay salt marshes relative to MHW measured during the summers of 2011 and 2012 (n=1220 points). Error bars show standard error.

Figure 2