

Spatial patterns of plant litter in a tidal freshwater marsh and implications for marsh persistence

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Abstract. The maintenance of marsh platform elevation under conditions of sea level rise is dependent on mineral sediment supply to marsh surfaces and conversion of above- and belowground plant biomass to soil organic material. These physical and biological processes interact within the tidal zone, resulting in elevation-dependent processes contributing to marsh accretion. Here, we explore spatial pattern in a variable related to aboveground biomass, plant litter, to reveal its role in the maintenance of marsh surfaces. Plant litter persisting through the dormant season represents the more recalcitrant portion of plant biomass, and as such has an extended period of influence on ecosystem processes. We conducted a field and remote sensing analysis of plant litter height, aboveground biomass, vertical cover, and stem density (collectively termed plant litter structure) at a tidal freshwater marsh located within the Potomac River estuary, USA. LiDAR and field observations show that plant litter structure becomes more prominent with increasing elevation. Spatial patterns in litter structure exhibit stability from year to year and correlate with patterns in soil organic matter content, revealed by measuring the loss on ignition of surface sediments. The amount of mineral material embedded within plant litter decreases with increasing elevation, representing an important tradeoff with litter structure. Therefore, at low elevations where litter structure is short and sparse, the role of plant litter is to capture sediment; at high elevations where litter structure is tall and dense, aboveground litter contributes organic matter to soil development. This organic matter contribution has the potential to eclipse that of belowground biomass as the root:shoot ratio of dominant species at high elevations is low compared to that of dominant species at low elevations. Because of these tradeoffs in mineral and organic matter incorporation into soil across elevation gradients, the rate of marsh surface elevation change is remarkably consistent across elevation. Because of the role of plant litter in marsh ecosystem processes, monitoring and assessment of these dynamic geomorphic marsh landscapes might be streamlined through the measurement of plant litter structure, either via LiDAR technologies or field observation.

Key words: light detection and ranging; organic matter; plant litter; sea level rise; sediment; tidal freshwater marsh; wetlands.

INTRODUCTION

The accumulation of organic matter in terrestrial and wetland soils builds soil surfaces through time, thereby maintaining ecosystem structure and function. The accumulation of organic matter is dynamic in space and time and depends on feedbacks between biotic and abiotic processes. Thus, soil surfaces are never constant but shift and adapt to changing environmental conditions. Tidal marsh ecosystems are a quintessential example of such shifting landscapes as they accumulate mineral sediments and organic matter to maintain elevation relative to sea level (Friedrichs and Perry 2001, Marani et al. 2013). Tidal marsh surface development is viewed and often

modeled as depending on interacting inputs in the form of allochthonous and autochthonous sediments that can be either inorganic or organic in origin (Redfield 1972, Morris et al. 2002, D'Alpaos et al. 2007, Kirwan and Murray 2007, Fagherazzi et al. 2012, Mariotti and Fagherazzi 2013a). Despite their simplicity, these models have been remarkably successful in simulating marsh surface development and maintenance in salt marshes where plant diversity is low relative to tidal freshwater systems. Organic matter accumulation in salt marshes may therefore be a simple function of plant biomass, which is tightly coupled to elevation and inundation time. However, tidal freshwater marshes are more diverse, with both annual and perennial plant species exhibiting a range in root:shoot ratios of over an order of magnitude (Whigham and Simpson 1978). Therefore, organic matter accumulation and soil development in tidal freshwater marshes may be a more spatially complex process, which

Manuscript received 17 October 2014; revised 5 June 2015; accepted 17 August 2015. Corresponding Editor: D. Schimel.

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depends more strongly on the conversion of aboveground plant biomass to plant litter and subsequently to soil. It follows, therefore, that the spatial variability of plant litter will be useful for identifying the critical processes determining marsh persistence with rising sea level.

Tidal freshwater marshes are highly productive systems that produce new aboveground biomass annually. This aboveground biomass senesces entirely each autumn and is subsequently converted to plant litter (Zedler and Kercher 2004). Despite being ubiquitous, plant litter is spatially variable in biomass and vertical structure, creating challenges in assessing standing stocks and understanding its impact on ecosystem functioning (Marani et al. 2006). Casual observations and detailed field studies alike have shown that spatial and temporal patterns in plant litter are due to both environmental (often simplified as water depth at high tide; Kirwan and Murray 2007) and biological variables. For example, variability in litter biomass is influenced by contrasting plant species such as *Impatiens* spp. and *Typha* spp., which exhibit highly contrasting C:N ratios in plant tissue, leading to differing rates of decomposition (Davis and Vandervalk 1978, Kuehn and Suberkropp 1998, Christensen et al. 2009). The structure of plant litter varies due to species-level differences, but also different types of disturbance causing canopy collapse. When collapse occurs, plant litter forms thick mats on the marsh surface, distinctly different than areas where stems continue to stand throughout the winter. This variability in structure can, in combination with litter biomass, have a significant effect on ecosystem processes (Vaccaro et al. 2009).

The ecosystem process of greatest perceived importance to tidal freshwater marshes experiencing sea level rise is the development of soil such that marsh platform elevation can be maintained in the tidal frame (Perry and Hershner 1999). This occurs through two processes, both of which are potentially influenced by plant litter structure. First, sediment deposition occurs during each tidal cycle, and its magnitude typically declines with increasing elevation owing to differences in inundation (higher elevations are flooded less often and for shorter durations; e.g., Palinkas et al. 2013). Plant stems (litter during winter) influence sedimentation rates directly by intercepting sediment and indirectly by slowing tidal flows and allowing sediment to settle out of suspension (Morris et al. 2002, Nardin and Edmonds 2014). Marsh areas of intermediate plant stem density are reported to be the most effective at intercepting sediments and facilitating deposition (Nardin and Edmonds 2014). Secondly, soil development and marsh platform elevation maintenance depend on annual inputs of plant biomass to form soil organic matter (SOM). This process will depend strongly on the ratios of above- to belowground biomass, the C:N ratios of these tissues, and the relative efficiency of aerobic and anaerobic mineralization of organic matter. Plants exhibiting a high C:N ratio in aboveground biomass might be important to soil development because plant litter that develops in autumn has the

potential to be maintained (despite spatial variation in structure) throughout the winter, influencing many processes before decomposing over the following growing season. While belowground biomass might still contribute significant SOM to soil when averaged across large areas and over time, the annual transitions of aboveground biomass from live plant tissues, to plant litter, and to SOM are critical processes that interact with sediment capture and deposition, potentially influencing long-term marsh persistence.

Recent work tracking elevation-dependent gains over two decades in a tidal freshwater marsh has confirmed the ability of these marshes to maintain elevation despite sea level rise (Cadot et al. 2014). However, this work also shows that elevation gain is not uniform across elevations, but rather is greatest at two separate elevation ranges: low elevations (centered at -0.2 m) that are inundated for 16 h/d, and higher elevations (centered at 0.4 m) that are inundated for 7 h/d and exhibit dense plant litter throughout the winter. Intrigued by these results and the implied importance of plant litter on marsh elevation gain, we designed a study with the following objectives. (1) We sought to establish and compare a suite of methods for quantifying plant litter density and structure during the winter at a tidal freshwater marsh. (2) We then used these observations to study the relationship between plant litter, elevation, and organic matter content in litter and soil. (3) Finally, we applied our results within the context of rising sea levels and marsh restoration efforts to provide science-based management guidance. We accomplished these objectives by advancing the science of interpreting Light Detection and Ranging (LiDAR) surveys, and their application to the measurement of marsh elevation and plant litter structure. LiDAR data have been used with success to inventory and monitor aboveground carbon pools and fluxes in forested systems (Beets et al. 2011, 2012, Hudak et al. 2012, d'Oliveira et al. 2012). In *Spartina alterniflora*-dominated salt marshes where vegetation is sufficiently sparse to enable LiDAR penetration to the ground surface, LiDAR is primarily used to map elevation, with accuracy measured to be within 4 cm (Montane and Torres 2006). To date, these advancements have not been successfully transferred to the study of freshwater marshes due to greater vegetation density during the growing season and high persistent litter biomass in the non-growing seasons. This living and non-living plant biomass inhibits LiDAR penetration to the mineral soil surface, which presents significant challenges for developing accurate elevation models for marshes and, hence, for monitoring changes in marsh surface elevations.

METHODS

Site description

The study was conducted at Dyke Marsh Wildlife Preserve (DMWP), which is a portion of the George

Washington Memorial Parkway, administered by the National Park Service (NPS). DMWP is a naturally occurring marsh located on the Virginia, USA shore of the Potomac River estuary (Fig. 1). The United States Geologic Survey determined that the marsh is ~530 yr old and has experienced a mean accretion rate of 3.1 mm/yr over that time (Litwin et al. 2011). Cores from the marsh show that a base of fluvial gravels and sands underlie ~3 m of marsh sediment. In the early 20th century, the area of emergent marsh habitat at DMWP was ~0.75 km². However, portions of the marsh were dredged for sand and gravel in the period 1940–1970, immediately reducing the area of the marsh by ~50%. Shoreline erosion has continued to reduce marsh area, as the result of wave action (during storm events) on shorelines left in an unstable configuration

following the period of dredging. Shoreline erosion rates are between 1 and 3 m/yr, with the most rapidly eroding areas in the southern portions of the marsh (Litwin et al. 2011). In 2013, the area of the marsh was ~0.24 km².

The NPS and scientific partners have actively monitored accretion and net elevation change through (1) the use of sediment and erosion tables (SETs) and feldspar clay horizons (both introduced in 2005), (2) repeat Total Station (theodolite and electronic distance meter; Topcon Positioning Systems GR-3 antenna, Livermore, CA United States) and Real Time Kinematic (RTK) Global Position System (GPS) surveys spanning two decades (Cadot et al. 2014), and (3) a sea level gauge (Campbell Scientific, Logan, UT, USA) located at Belle Haven, Virginia, USA marina (38.7770364° N, 77.0486278° W) installed in May 2004. This work has demonstrated that the marsh surface is gaining elevation at a rate approximately equal to historical sea level rise (3.9 mm/yr), except in areas exposed to the Potomac River and associated wave action. Recent efforts to synthesize these observations have demonstrated elevation change with elevation. Two elevations of peak elevation change occur, one at -0.20 m elevation and a second at 0.40 m elevation. The lower peak in elevation gain corresponds with an area primarily consisting of a tidal-channel network that radiates through the marsh from a central large channel. Channels support a low-marsh plant community dominated by *Nuphar lutea*, *Pontedaria cordata*, and *Zizania aquatica*. The higher peak in elevation gain is associated with the transition to a high-marsh plant community (Cadot et al. 2014). This area is a broad, relatively flat high-marsh platform dominated by *Typha angustifolia*, *Bolboschoenus fluvialis*, *Peltandra virginica*, *Acorus americanus*, *Impatiens capensis*, and *Bidens laevis* (Hopfensperger and Engelhardt 2008).

The vulnerability of this marsh to sea level rise and shoreline erosion is of acute interest to National Park Service resource managers. In 2013, a decision was made to allocate restoration funds made available following hurricane sandy to the creation of a new expanse of marsh platform at the southern end of Dyke Marsh. As proposed, the new restored marsh surface would be designed to trap additional sediment and block wave action originating in the Potomac River estuary (National Park Service 2014). Decisions on the placement and elevation profile of the restored marsh surface would ideally be based on current scientific observations and understanding. Further, monitoring of the restored and existing marsh has been proposed to ensure that changes to the hydraulics of the system do not inadvertently cause negative impacts.

Elevation and litter height survey

An extensive survey of marsh elevation and litter structure was conducted in two dormant-season field campaigns. The first was intended to coincide with a Light Detection and Ranging (LiDAR) survey flown in

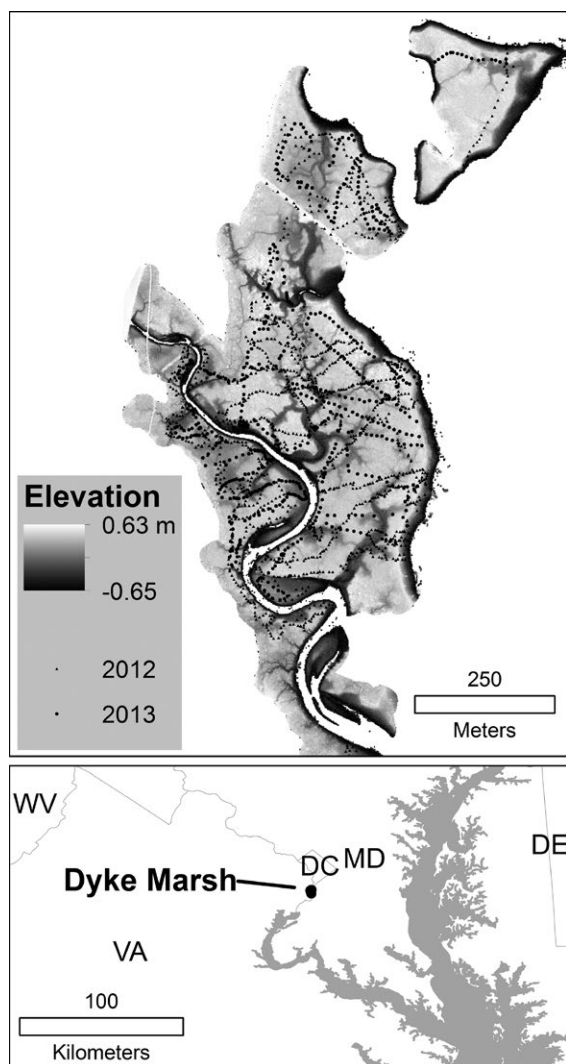


FIG. 1. The study marsh, Dyke Marsh Wildlife Preserve (DMWP), is located on the Virginia shore of the Potomac River, ~20 km south of Washington, D.C., USA. Shown are the extents of two Real Time Kinematic (RTK) GPS field surveys that were conducted in February 2012 and 2013. The image is oriented so that north is up.

2012 (see *LiDAR survey and digital elevation model generation* for a description of the LiDAR survey); the second was conducted 1 yr following the LiDAR survey. In each case, the marsh was traversed in a zig-zag pattern with an RTK GPS device (Topcon Positioning Systems GR-3 antenna), with manufacturer-reported horizontal accuracies of $10 \text{ mm} + 10^{-6}$ times the distance from rover to base station and vertical accuracies of $15 \text{ mm} + 10^{-6}$ times the distance from rover to base station. In practice, we observed as much as 22 mm of vertical elevation variation for points reoccupied on multiple days, even for points <1 km from the base station. Every 10 paces (~8 m) a geographic position (in three dimensions, referenced to NAD83 [horizontal] and NAVD88 [vertical] datum) was recorded at the mineral soil surface (Fig. 1). All elevations given in this work are similarly referenced to the NAVD88 vertical datum. The RTK GPS was mounted on a carbon fiber poll; great care was taken to place the tip of the poll exactly at the mineral soil/litter interface. In February 2012, 1344 positions were recorded (806 high marsh and 538 low marsh) and in February 2013, 815 positions were recorded (441 high marsh and 374 low marsh).

For each of the two field campaigns a measurement of litter structure was recorded at each RTK GPS location. For low marsh, where no litter was present at the time of the field campaign, a value of null (i.e., 0) was recorded. Where litter existed, the dominant species were typically *T. angustifolia* and *B. fluvialis*. Both commonly maintain vertical plant stems well into the winter. For this work, we desired an estimate for litter structure that would have the best chance of correlating with the importance of litter in ecosystem processes, but could also be predicted from LiDAR data. Although maximum litter height was our initial choice, we considered the long, slender upper stems and leaves of plant litter, which frequently extended above one meter, to be too small to be reliably detected by airborne LiDAR. We therefore adopted a technique commonly employed in grasslands to rapidly estimate aboveground biomass, in which a plywood board of standard surface area and mass is lowered onto the litter canopy ('t Mannetje and Jones 2000). The board flattens the tallest stems and leaves and eventually becomes supported by the vegetation above the ground at a height that is measured and compared to plot-based field measurements of litter biomass and density (see following section). The "litter board height" seemed to produce meaningful measurements in a variety of settings. For example, when stems were sparse, the board flattened existing litter to a greater extent than it did when stems were dense. Litter board height also returned a meaningful measurement of the thickness of litter mats remaining after canopy collapse (i.e., litter with stems laying horizontally), and therefore integrated observations of standing and down litter. For this procedure we used a 1.3 cm thick plywood board with dimensions of $80 \times 80 \text{ cm}$, weighing 3.8 kg. A graduated pole passing through a hole in the middle of the board provided lateral support. Held at the top and resting on

the marsh surface at the bottom, the centrally located pole enabled consistent height measurements even when the board came to rest at a slant.

Plot-based field observations

We envisioned litter board height to be an efficient method for rapidly measuring litter structure, enabling its use in conjunction with a fast-paced RTK survey that encompassed a large area. However, we sought evidence that litter board height accurately reflected other measures of how much litter was present at a given site. We also wished to compare litter board height with measures of organic and inorganic inputs to sediments. We therefore used fine-scale plot-based field measurements made at the same time as the 2012 survey to complement the broadscale LiDAR, field elevation, and litter board height surveys. The 58 study plots were co-located with those used in previous studies (Hopfensperger and Engelhardt 2008, Palinkas et al. 2013). Plots were distributed across the marsh and located to capture known elevation and plant community patterns. At each $1 \times 1 \text{ m}$ plot, a combination of vegetation and soil measurements were recorded. Four measurements were made related to vegetation biomass and structure.

- (1) Litter board height was measured using the plywood board as described previously.
- (2) Vertical litter cover (i.e., the fractional cover of litter as viewed from the side through 1 m of canopy) was measured by positioning a 10 cm wide and 100 cm tall wooden board ($A_b = 1000 \text{ cm}^2$, where A refers to area) painted blue vertically through the canopy and acquiring a horizontal photograph of the board from ground level 1 m from the board. From the photograph, the visible area of the blue paint, A_{vis} , was measured and the complement of this area recorded as the percent vertical cover: $((A_b - A_{\text{vis}})/A_b) \times 100$.
- (3) The number of plant stems in each plot was counted. For stems to remain standing into February, the stems needed to be strong enough to not collapse immediately after senescence of the plant in October. Hence, all stems could be unambiguously counted within each plot.
- (4) After measuring these aspects of litter structure, aboveground biomass (AGB; all of which was senescent material) was harvested to the mineral/litter interface. Litter fragments that were embedded in sediment were left at the plot. However, sediment that clung to or was embedded within standing litter, and all litter that was clearly separate from the mineral layer (i.e., an air space was observed between the litter and mineral layer) was collected with the litter biomass. These litter samples were stored in large plastic bags, labeled, and transported to the laboratory.

In May 2012, we returned to the marsh and extracted sediment push cores from a subset of the marsh plots

($n = 26$). Push cores were 5 cm in diameter and 10 cm in depth. Plant litter that was clearly embedded in sediment was allowed to be collected in the core, however, all litter that was separate from the mineral soil surface was pushed aside before extracting the core.

In the laboratory, aboveground biomass samples were dried for over 36 h at 60°C and weighed. Organic content of each biomass sample was determined via mass loss during combustion at 450°C for 4 h (i.e., the loss on ignition [LOI] method was employed; Nelson and Sommers 1996). Push cores were divided into 1-cm increments. The top 1-cm increment was dried for 24 h at 60°C before measuring its mass. Organic/inorganic content of the soil samples was also determined via LOI using the same protocols as for litter samples.

All plot-based litter and LOI measurements were related to LiDAR litter board height and marsh elevation (calculation of LiDAR metrics described in the following section) using linear regression in the R statistical software environment (R Core Team, 2014).

LiDAR survey and digital elevation model generation

A LiDAR survey was conducted on 14 March 2012 at low tide. An Optech ALTM 3100 LiDAR instrument was flown on a Piper Navajo twin-engine aircraft (Piper, Vero Beach, Florida, USA) at an altitude of 915 m and at a mean speed of 70 m/s. A maximum of four returns (including the intensity of each return) per laser pulse were recorded, referenced to NAD83 (horizontal) and NAVD88 (vertical) datum. Repeated overlapping flight lines achieved a median return density of 10 returns/m². The LiDAR operator estimate of vertical error was 0.06 m, based on a selection of nine RTK GPS elevation measurements of hard surfaces. An analysis of return density at the locations of near-concurrently acquired RTK GPS positions determined that a grain size of 1 m/grid cell provided the optimum balance between the number of returns per grid cell and the mean error associated with using the lowest return as the ground return. We initially attempted to use a ground-filtering algorithm provided by the LiDAR operator to determine the ground return (i.e., mineral soil/litter interface) from the lowest return, but found that due to dense litter biomass the ground-filtering algorithm removed all returns from large areas of the high-marsh platform. This was deemed unacceptable, but not uncharacteristic of these data (e.g., Wang et al. 2009).

Further inspection of the relationship between the minimum LiDAR return and the elevation of the mineral/litter interface revealed a nonlinear relationship that approximated linear at elevations below ~0.25 m, but at higher elevations tended to curve in the direction of a LiDAR over-prediction (Fig. 2). Our interpretation was that as elevation increased, litter height and density also increased, increasing the degree to which the mineral soil/litter interface was obscured from LiDAR penetration. The difference in elevation between the minimum LiDAR

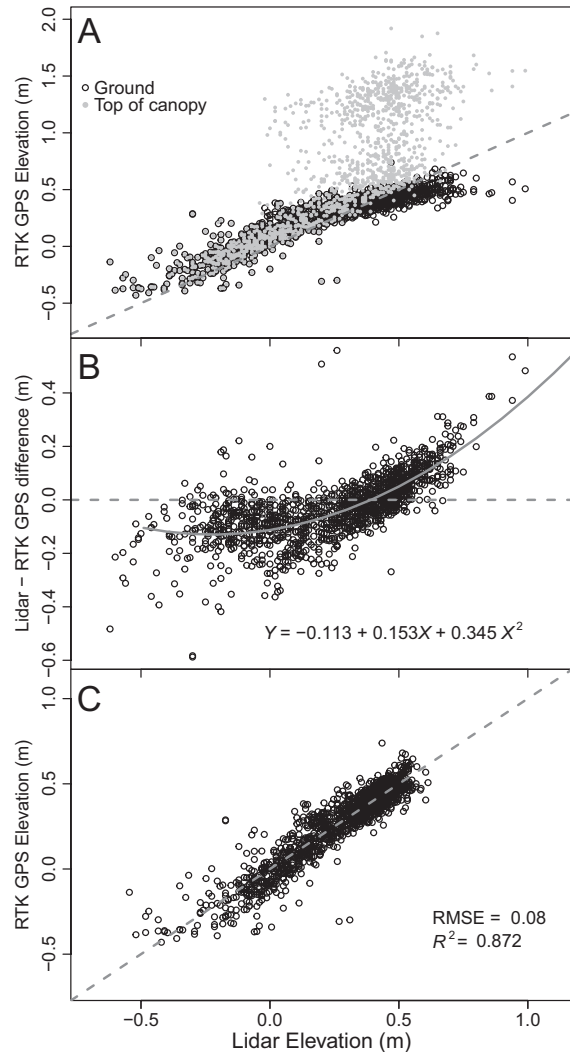


FIG. 2. A comparison of RTK GPS ground elevation and top of canopy elevation (i.e., ground elevation plus field litter board height) with LiDAR elevation (both collected in 2012) for 1341 locations at Dyke Marsh showing (A) that as litter board height becomes greater (i.e., top of canopy symbols separate from the ground symbols), LiDAR penetration to the soil surface is reduced causing the ground returns to deviate from the 1:1 line. Consequently, (B) the difference between the minimum LiDAR return and the RTK GPS elevation is a polynomial function of the minimum LiDAR return elevation (Table 1). The effect of plant litter can be corrected for by subtracting the correction factor, represented as a gray line in (B), from the minimum LiDAR return elevation, resulting in (C) a more accurate representation of marsh surface elevation. Root mean squared error (RMSE) is shown.

return and the RTK GPS elevation was slightly negative (LiDAR under-prediction) in low-marsh habitats but increased nonlinearly above 0.25 m. This relationship was seen as a statistically robust pattern and therefore was applied as a correction factor when creating a LiDAR DEM from the minimum LiDAR returns (Fig. 2; see Results for details on this correction factor). We returned to the marsh in 2013, 1 yr after our initial survey. Ground

TABLE 1. Results of a polynomial regression model predicting the difference between Real Time Kinematic (RTK) GPS elevation and the elevation of the minimum LiDAR return for each grid cell containing an RTK GPS elevation observation.

Parameters	Sum of Squares	Estimate	P
Intercept		-0.113 ± 0.003	<0.0001
Min LiDAR elevation	1.15	0.153 ± 0.011	<0.0001
(Min LiDAR elevation) ²	1.29	0.345 ± 0.024	<0.0001

Notes: Residual SS = 8.59. For parameters, $n = 1341$ and $R^2 = 0.52$.

surface elevation was measured at 815 locations in 2013, and we used these data to validate the LiDAR digital elevation model of ground surface elevation derived from the 2012 survey. This validation assumed negligible increases in elevation between 2012 and 2013, an assumption that appeared to be upheld by the 2013 RTK GPS data.

Litter board height model generation

The 1344 RTK GPS locations with associated observations of litter height acquired concurrently with the 2012 LiDAR survey were used to train a nonparametric model of litter board height that was subsequently projected to the entire marsh surface. To understand the improvement in model performance with model complexity, we first calculated litter board height as the difference between the highest LiDAR return and the modeled ground surface (described in the previous section), which we termed “adjusted LiDAR litter board height.” Seeing that this estimate underestimated litter board height at low elevations and overestimated litter board height at higher elevations (Fig. 3A), we sought additional variables that might help explain these errors. Because casual observation of the marsh suggested that litter board height correlated with elevation, we included the elevation of the first and lowest LiDAR return. Several recent authors have shown that the intensity of LiDAR returns can yield useful information about vegetation structure and habitat (e.g., Goetz et al. 2010). Therefore, for each RTK GPS training location we also extracted the intensity of the first and lowest LiDAR return. We also included the total number of returns and the adjusted LiDAR elevation, bringing the total number of LiDAR-derived training observations to six.

Visible imagery can also provide important information on vegetation structure. For example, green vegetation in the spring must grow beyond the height of plant litter (standing since the previous growing season) before it can be observed from above. A spring image of Dyke Marsh acquired by the Commonwealth of Virginia in 2012 was used to extract the red, green, and blue intensity for each of the 1344 RTK GPS positions. These observations brought the total number of independent

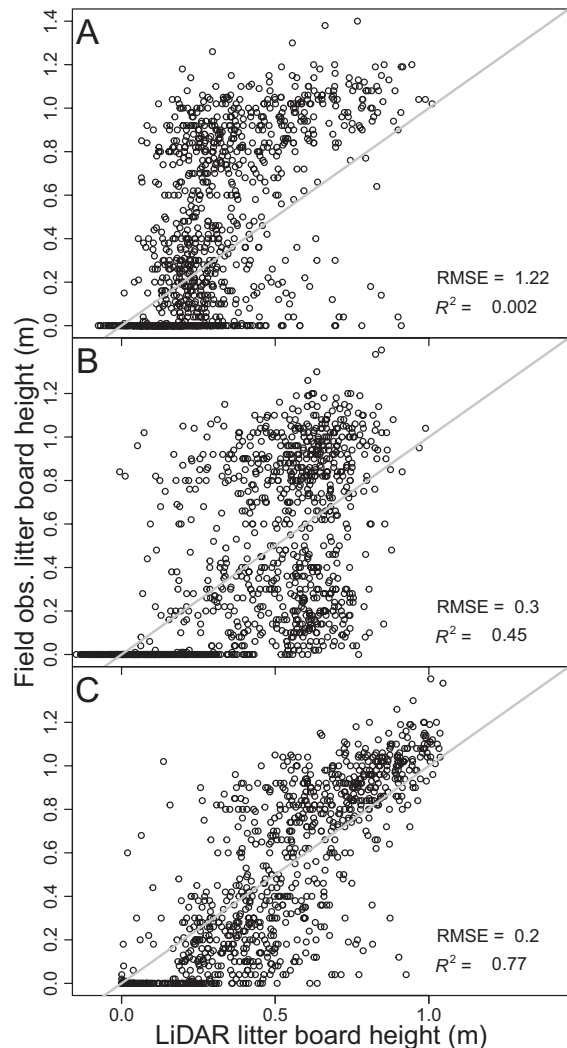


FIG. 3. Three models predicting field litter board height from map variables. (A) The difference between maximum and minimum LiDAR return elevations in each grid cell (after adjusting for litter interference shown in Fig. 2). (B) A multiple linear regression model incorporating return intensity and the position of lowest and highest return (coefficients presented in Table 2). (C) A nonparametric random forest model, exhibiting a RMSE of 0.20 cm.

variables to nine: (1) elevation of lowest return, (2) elevation of first return, (3) adjusted LiDAR litter board height, (4) total number of returns, (5) intensity of lowest return, (6) intensity of first return, (7) red image band, (8) green image band, and (9) blue image band. In the R statistical programming environment, we used these nine variables to train two statistical models to predict field-measured plant litter height. The first model was a linear regression model that included all nine model effects. From this model, we removed model effects that were not significant predictors of litter height (total number of returns, red image band, blue image band), bringing the reduced model to six effects.

In an attempt to further improve our ability to model litter height, we applied an ensemble decision tree method called “random forest” to the same nine variables discussed above. Random forest, which has been used in numerous applications of LiDAR to predictive modeling in ecology (e.g., Martinuzzi et al. 2009, Goetz et al. 2010), is a machine-learning implementation of decision tree modeling in which many decision trees are constructed from different bootstrapped random samples of the input data. In this application we used 500 trees, each constructed from a randomly selected subset of five of the nine input variables. We chose to use the random forest implementation, cforest, provided in the R party package.

To evaluate the LiDAR litter board height model, we compared it against the 2013 field survey. Areas of the marsh exhibiting consistent and, alternatively, different litter structure between 2012 and 2013 were identified. To evaluate the correlation of LiDAR litter board height and elevation, we built an image mask that included marsh surfaces above 0 m elevation (where litter would be expected to exist) and excluded swamp forest that existed in the same elevation range as marsh. To explore how the litter–elevation relationship depended on spatial resolution, we incrementally degraded the resolution of the LiDAR litter board height map from 1 m to 32 m/pixel and recalculated the correlation at each resolution.

RESULTS

LiDAR estimates of elevation and plant litter board height

At the time of the March 2012 LiDAR survey, all plants were in dormancy and the low-marsh plant community exhibited a field litter board height of 0 m (evident by the identical positions of black and gray symbols in Fig. 2A for elevations less than 0 m, corresponding with a mean daily inundation time of ~15 h). LiDAR returns at these lower elevations (low-marsh vegetation) generally underestimated the ground surface elevation compared with RTK GPS (mean offset for low marsh = 12 cm; Fig. 2B). This was assumed to be caused by the combined effects of microtopography and random positional errors inherent to the LiDAR and RTK GPS data, which result in a range of LiDAR elevations within each 1-m grid cell. If the lowest return in this range is taken as the elevation of the entire 1-m grid cell, the LiDAR elevation will always underestimate the RTK GPS elevation for that grid cell (Wang et al. 2009), which is why most LiDAR-derived DEMs are formed from the mean or median ground return elevation within each grid cell. Above 0 m elevation, the difference between the high and low LiDAR returns was larger due to the presence of plant litter. Plant litter board height abruptly increased to greater than 0 m at almost all elevations >0.25 m to a maximum of just over 1 m around 0.5 m elevation (Fig. 2A). Through this elevation range of increasing litter board height, the lowest LiDAR return increasingly

TABLE 2. Results of a linear regression model predicting litter board height with selected map variables.

Parameters	SS	Estimate	P
Intercept		0.33 ± 0.09	0.0001
Adjusted LiDAR litter board height	0.33	0.76 ± 0.28	0.0059
Intensity of lowest return	92.40	0.004 ± 0.0003	<0.0001
Intensity of first return	1.47	−0.002 ± 0.0003	<0.0001
Elevation of lowest return	3.10	0.968 ± 0.219	<0.0001
Elevation of first return	0.46	−0.780 ± 0.275	0.0046
Green image band	1.76	−0.002 ± 0.0005	<0.0001

Notes: Residual SS = 119.44. For parameters, $n = 1341$ and $R^2 = 0.45$

over-predicted the ground elevation. This bias towards an over prediction of the ground surface elevation was so consistent that the difference between LiDAR and RTK GPS estimates of elevation was satisfactorily predicted by LiDAR elevation alone (Fig. 2B; Table 1). After adjusting for this elevation-dependent bias due to microtopography and positional uncertainty (low elevations), and litter density and height (high elevations), we arrived at our model of ground elevation (Fig. 2C; $R^2 = 0.87$; $P < 0.0001$). This model exhibited root mean squared error (RMSE) of 8.0 cm, representing small contributions from random positional errors that could not be removed through this approach.

We first estimated litter board height directly by subtracting the adjusted lowest LiDAR elevation (Fig. 2C) from the highest LiDAR return (presumably representing the top of the litter canopy). However, this direct estimate of litter board height did not adequately explain variance

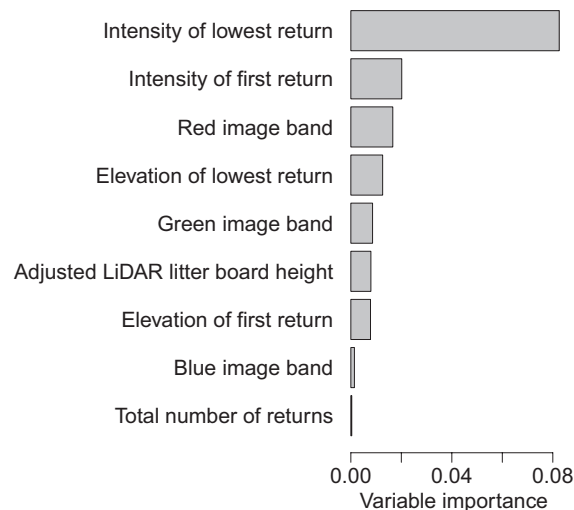


FIG. 4. Unbiased estimates of variable importance in the random forest model.

in field litter board height (Fig. 3A; $R^2 = 0.002$, $P = 0.15$). At marsh surface elevations around 0.25 m, the direct estimate was unable to differentiate between short (<75 cm) and tall stands (>75 cm) of litter observed in the field. At higher elevations, the direct estimate underestimated litter board height by up to 30 cm. Variance in field litter board height was better explained by a multilinear model (Fig. 3B; $R^2 = 0.45$, $P < 0.0001$), which assigned a near-zero plant litter height to low-marsh grid cells. The significant model effects (Table 2) were those most related to litter height (elevation of the lowest and highest LiDAR return) and litter presence/absence (LiDAR intensity of the low and high return and the intensity of the green image band from air photography).

The random forest procedure resulted in a model that best explained variance in field litter board height ($R^2 = 0.76$; $P < 0.0001$; Fig. 3C). Most low-marsh grid cells devoid of plant litter were assigned a plant litter board height of 0 m by the random forest model. An analysis of unbiased variable importance showed that LiDAR intensity of the low and high returns were the most important variables in the model (Fig. 4). The red image band from air photography was the next most important variable, followed by LiDAR elevation. The predicted uncertainty of this final model of LiDAR litter board height had an RMSE of 0.2 m, which could be used as an uncertainty value for each grid cell (e.g., ± 0.2 m uncertainty bounds). When projected to the marsh surface, the random forest model produced a map of litter board height (Fig. 5) that clearly delineated the low-marsh boundaries (white; Fig. 5) and the regions of tall, dense plant litter (e.g., the red areas in the northeastern portion of the marsh; Fig. 5). Unless otherwise noted, the term “LiDAR litter board height” is used throughout this study in reference to the random forest model output.

Interannual variability of litter board height

The 2013 RTK GPS survey data was similar to data from 2012 in that below an elevation of ~ 0.25 m, the lowest LiDAR return under-predicted the RTK GPS elevation by ~ 12 cm. Above 0.25 m elevation, RTK GPS elevations did not exhibit as great a range as LiDAR elevations, causing an over-prediction by LiDAR (Fig. 6A). When the 2012 adjustment factor (see Fig. 2B and Table 1) was applied to the 2013 data, the resulting relationship between RTK GPS and LiDAR elevation was significant and similar to that observed in 2012 ($R^2 = 0.86$; $P < 0.0001$), thus validating the elevation-dependent correction factor approach using independent data. The RMSE on this model is 9 cm (Fig. 6B).

The comparison between 2012 and 2013 field-measured litter board height and 2012 LiDAR litter board height exhibited similar patterns. Although there was considerable deviation from the 1:1 line, areas of discrepancy were consistent between years suggesting that litter structure is remarkably consistent from year to year. Areas of the marsh exhibiting tall standing litter at the

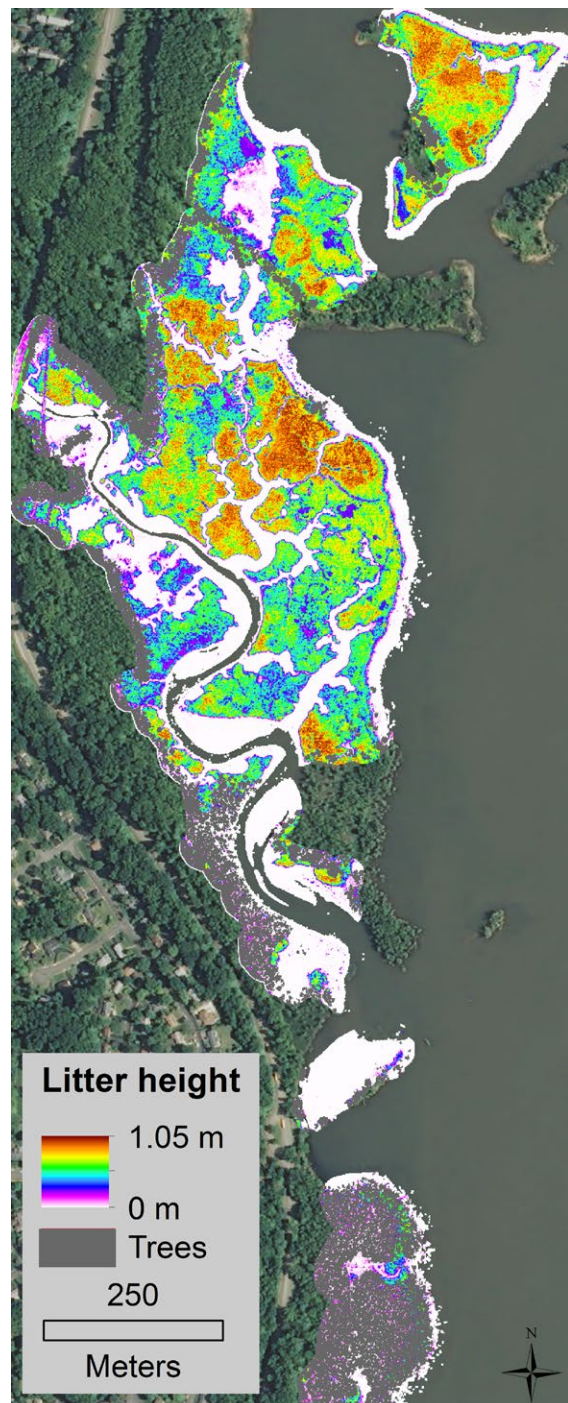


FIG. 5. A map of litter board height produced by projecting the random forest unbiased decision tree based on LiDAR and air photography variables to the study region. The image is oriented so that north is up.

end of the winter in 2012 also exhibited tall standing litter in 2013. The one noted exception to this observation was selected areas that were >1 m tall in 2012, but became ~ 0.80 m shorter in 2013. Litter board height of collapsed

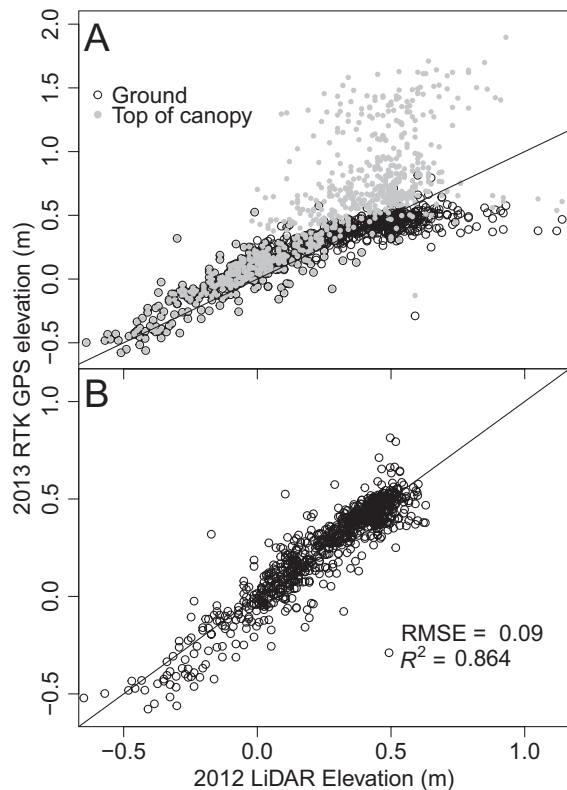


FIG. 6. (A) Comparison of elevation via RTK GPS collected in 2013 and elevation via LiDAR collected in 2012 showing the same relationship for both ground and top of canopy positions as was seen in 2012 field data (Fig. 2). (B) Ground comparison after correcting for the effect of litter obstructing LiDAR returns from the ground surface.

litter typically ranged from 10 to 30 cm, thus areas of standing litter in 2012 that were collapsed in 2013 occupied a new region in the plot of field vs. LiDAR litter board height (lower circle in Fig. 7).

Observations of litter and elevation

Litter board height, litter biomass, vertical plant cover, and the number of plant stems measured at 58 plots across the marsh all correlated with LiDAR litter board height (Fig. 8). Among these variables, field litter board height was most highly correlated with LiDAR litter board height ($R^2 = 0.76$; $P < 0.0001$), followed by vertical plant cover ($R^2 = 0.70$; $P < 0.0001$). Aboveground litter biomass increased with increasing LiDAR litter board height ($R^2 = 0.52$; $P < 0.0001$), although variability in the relationship increased with increasing LiDAR litter board height. Likewise the number of plant stems (all standing dead at the time of this sampling) increased with increasing LiDAR litter board height ($R^2 = 0.47$; $P < 0.0001$).

All measures of litter structure measured at the 58 plots correlated with elevation, though these correlations were all weaker than exhibited between field-measured litter structure and LiDAR litter board height (Fig. 9).

Field-measured litter board height was often 0 m at low elevation, but was consistently nonzero at greater elevation ($R^2 = 0.32$; $P < 0.0001$). Similarly, litter biomass ($R^2 = 0.39$; $P < 0.0001$), plant vertical cover ($R^2 = 0.33$; $P < 0.0001$), and the number of litter stems ($R^2 = 0.2$; $P = 0.0004$) all increased with increasing LiDAR elevation.

When the entire marsh surface was considered, LiDAR litter board height was near zero at all elevations below 0 m and increased with increasing elevation above 0 m (Fig. 10A). Because litter is not expected below 0 m elevation, we restricted our linear regression analysis to locations above 0 m elevation ($n = 347225$; after removing areas of tree cover). For this area, LiDAR litter board height was correlated with elevation ($R^2 = 0.50$; $P < 0.0001$). However, within any narrow elevation range, there was considerable variability in LiDAR litter board height. Aggregating LiDAR litter board height pixels to 5 m/pixel produced an improved correlation with elevation ($R^2 = 0.65$; $P < 0.0001$; Fig. 10A). The litter–elevation correlation increased with increasing pixel sizes, reaching a maximum of just under $R^2 = 0.70$ at ~10–15 m/pixel (Fig. 10B). Therefore, this broader analysis of the litter–elevation correlation across a range in spatial resolution revealed that variability at the scale of meters partially accounts for litter variability at any one elevation.

Relationships between plot organic matter and inundation time

Marsh surface elevations (low and high marsh) ranged from <0 m to 0.60 m. This elevation range corresponds to an inundation time from 15 to 3 h/d at the Belle Haven

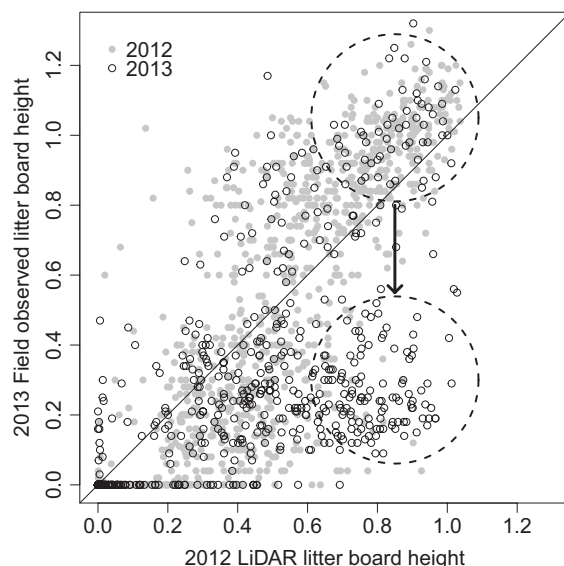


FIG. 7. 2013 and 2012 field-observed litter board height vs. 2012 LiDAR litter board height (via random forest modeling). The density of points in 2012 became more sparse above the 1:1 line and became more dense below the 1:1 line, likely representing locations that were “blown down” in 2013 but not 2012.

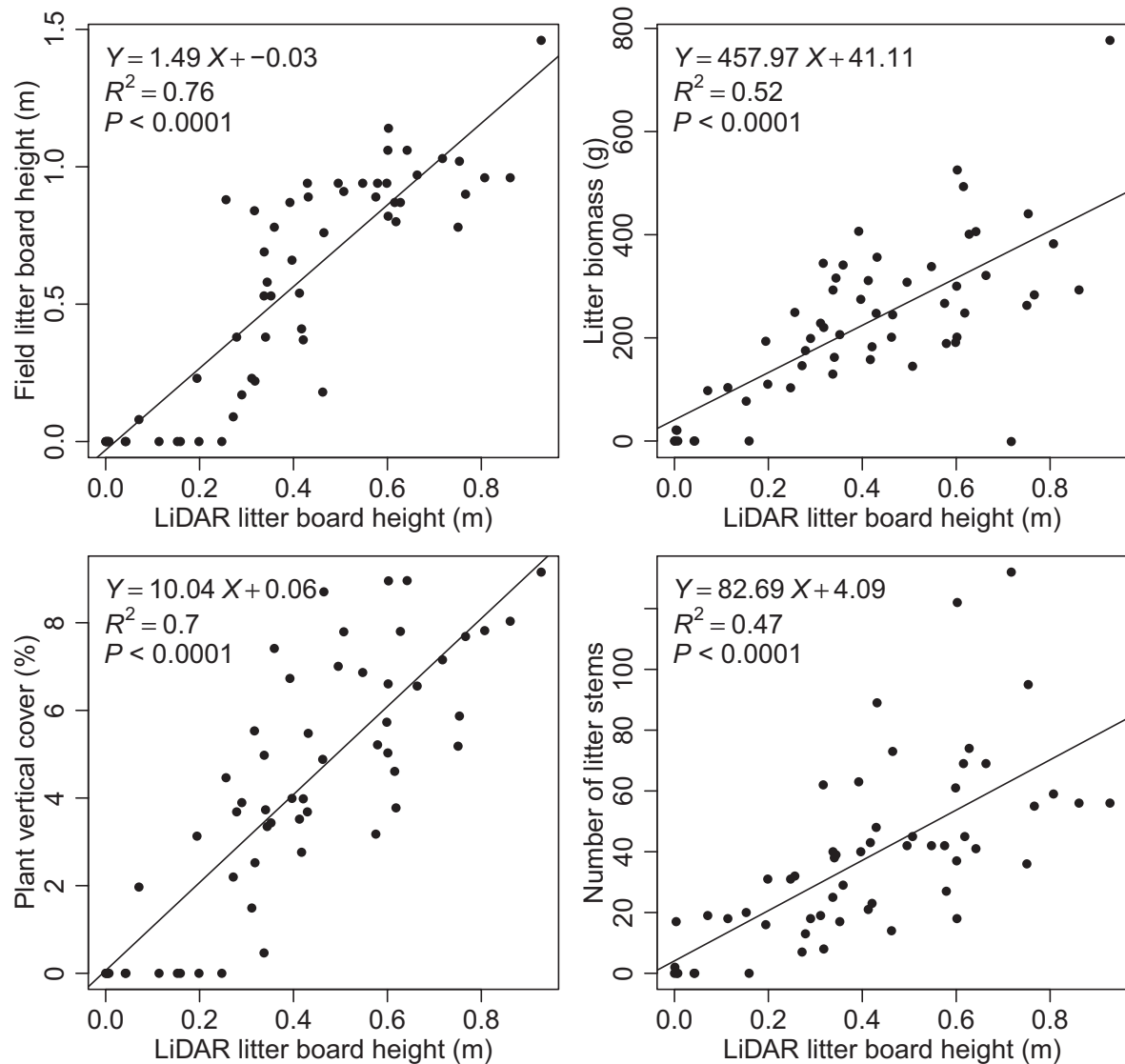


FIG. 8. Four measurements of vegetation structure measured at the 58 field plots plotted against LiDAR litter board height.

Marina tide gauge (Fig. 10A). At the low elevation end of this gradient, we found only sparse and sporadic litter cover; at the high end of this gradient we found tall, dense litter. The relationship between inundation time and elevation is largely linear across this entire range, though a slight deviation towards higher inundation time (i.e., above a strictly linear trend) is seen between an elevation of 0.2 and 0.5 m. The elevation range of high marsh, exhibiting LiDAR litter board height consistently above 0 m, roughly corresponds to the elevation range of slightly elevated inundation time.

Loss on ignition of surface soils increased with increasing LiDAR elevation ($R^2 = 0.38$; $P = 0.0007$; Fig. 11A) from a minimum of just under 20% to a maximum of 60%. These values reflect the high organic matter content of these wetland soils, but also demonstrate the

influence of elevation on soil composition. The LOI of plant litter (AGB) collected from these plots also increased with LiDAR elevation ($R^2 = 0.15$; $P = 0.0007$; Fig. 11B). LOI of plant litter increased from ~70% to 95%, showing that in total plant litter at lower elevations intercept a greater proportion of mineral sediments. However, mineral mass per stem was not correlated with elevation.

DISCUSSION

Plant litter is a major feature of this tidal freshwater marsh, where live plants grow up from the ground surface every year and senesce in the autumn, contributing copious amounts of plant litter to the marsh surface. Despite this high productivity, however, we found that

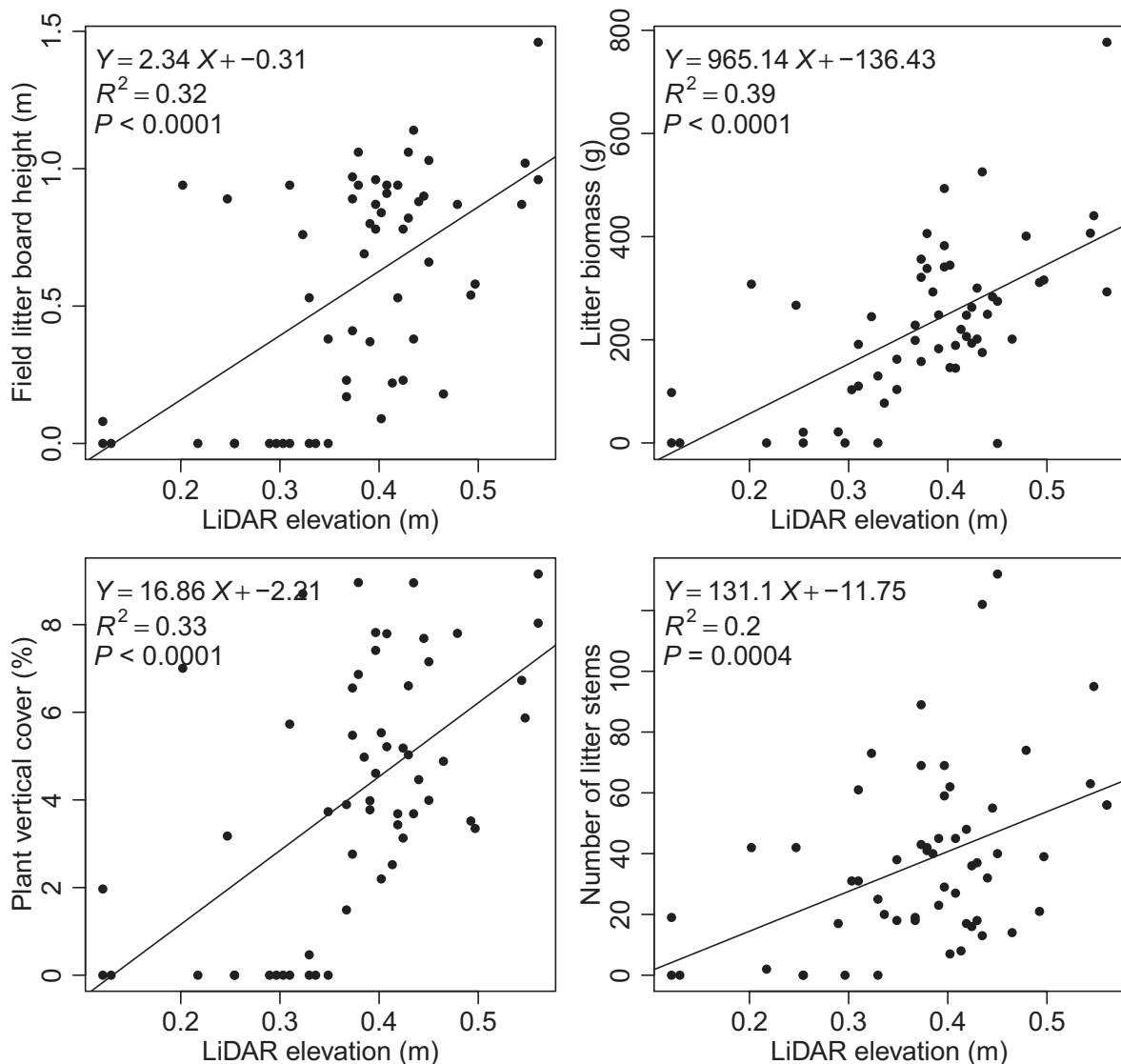


FIG. 9. Four measurements of vegetation structure measured at the 58 field plots plotted against LiDAR elevation.

plant litter is not distributed uniformly across the marsh surface (Fig. 5). Rather, due to trait differences among species (Whigham and Simpson 1978, Gardner et al. 2014, Sutter et al. 2015) and elevation-driven species turnover (Hopfensperger and Engelhardt 2008), plant litter board height and density varies significantly across marsh surfaces. Species turnover is also driven by complex spatial interactions among species (Gardner and Engelhardt 2008), likely affecting plant litter production even at fine spatial scales.

Low-marsh plant communities are dominated by species characterized by high root:shoot ratios (Whigham 1978), and, due to tidal flushing and rapid decomposition, exhibit little aboveground biomass during winter. At the transition between low and high marsh, plant litter is largely a function of *Typha angustifolia* cover, which

can be patchy, and exhibit variable height and density. At this intermediate elevation, existing litter has the opportunity to interact with a large volume of tidal channel water as tides inundate these areas for greater than 10 h/d. At the highest marsh elevations, the marsh exhibits tall stands of plant litter throughout the winter and spring, primarily consisting of *T. angustifolia* stems and leaves, which exhibits a low root:shoot ratio of 0.55 (Whigham 1978). Plant litter remains standing or becomes lodged as 10–30 cm thick mats on the marsh surface, influencing mineral and organic sediment deposition through the winter and into spring.

These descriptive characteristics of plant litter are supported by empirical observations. At the scale of 1-m field plots, elevation explains between 20% and 33% of the variation in litter board height, vertical cover, biomass,

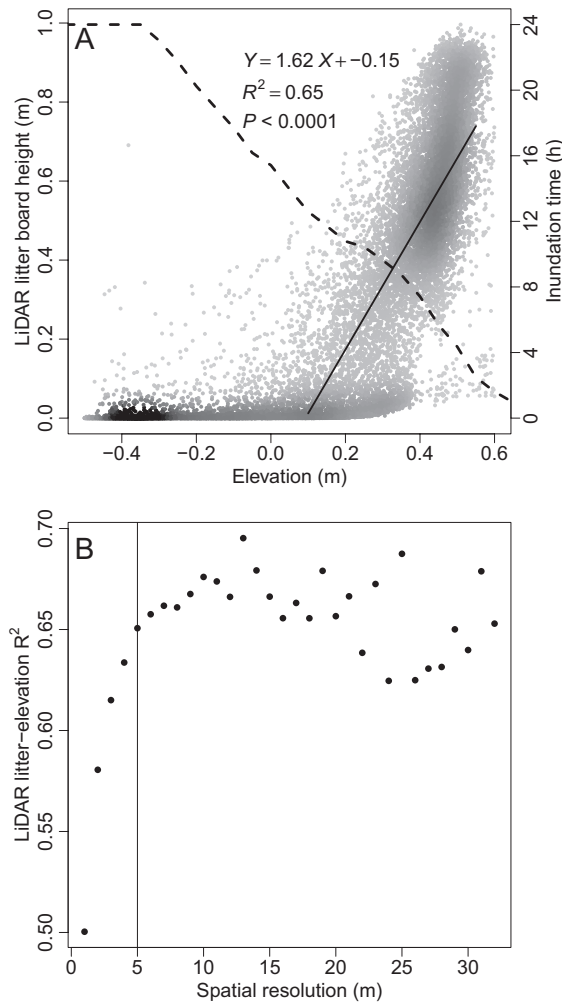


FIG. 10. (A) Inundation time (dashed black line) and LiDAR litter board height as a function of elevation, and (B) the R^2 of the LiDAR litter board height vs. elevation relationship as a function of spatial resolution.

and stem density, and depending on spatial resolution, elevation explains between 50% and 70% of the variation in LiDAR litter board height. Therefore, after accounting for observed fine-scale variability, elevation is an important predictor of plant litter. This finding has implications for our understanding of ecosystem functioning in tidal freshwater marshes. First, plant litter, which increases with elevation, interacts with tidal inundation, which decreases with elevation. It follows that sediment trapping by plant litter is maximized at intermediate elevations. Second, when the plant litter originates from plants with a high C/N ratio, as is the case at high elevations, more organic matter has the potential to be incorporated into the marsh's soil horizon before being decomposed at the soil surface. Thus, plant litter at mid-to high elevations is critical for the continued evolution of marsh surfaces, especially in plant communities where root:shoot ratios are low and therefore do not contribute

a belowground build-up of biomass. These findings contrast with observations made in southeastern United States salt marshes, where productivity and stem density increase with decreasing elevation due to interactions with salinity (Morris et al. 2002). Thus, as water depth rises, as it would with increasing sea level, these salt marshes become more productive at lower elevations and thereby counteract the effects of sea level rise with greater organic matter incorporation into soil (Marani et al. 2006, Kirwan and Megonigal 2013). In the absence of salt water, our results suggest the opposite effect based on the observation of increasing litter board height, stem density, vertical cover, and biomass with increasing elevation. These measures of vegetation productivity and structure suggest that this marsh would become less productive and contributions from plant biomass to soil development would decrease each year as the water depth at high tide increased.

Belowground biomass contributes to soil development in a way that likely counters the elevation-dependent effects of aboveground biomass, measured here as senesced material in winter. Studies of root:shoot ratios of freshwater marsh plant species have revealed important trends that are correlated with elevation. Low-marsh communities (exhibiting no aboveground plant litter in winter) include perennial plants with some of the highest root:shoot ratios of all marsh plant species. For example, *Peltandra virginica*, with a high root:shoot ratio of 8.42 (Whigham and Simpson 1978), occurs throughout the marsh but becomes more abundant at lower elevations. Other low-marsh species have reported root:shoot ratios close to 1 such as *Nuphar lutea* (0.86), *Pontedaria cordata*

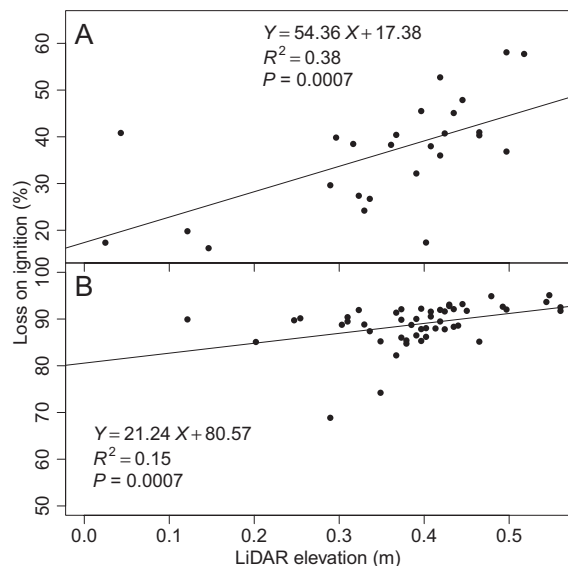


FIG. 11. Loss on ignition (LOI) expressed as a percent of total sample mass vs. LiDAR elevation for (A) push cores (upper 1 cm of soil) sampled in spring 2012 ($n = 26$); and for (B) plant litter (AGB) ($n = 58$). Litter samples were collected in February 2012.

(1.3), and *Sagittaria latifolia* (0.94) (Whigham and Simpson 1978). Annual plants with very low root:shoot ratios (e.g., Hemminga et al. 1996) are more common in high-marsh plant communities (Hopfensperger and Engelhardt 2008). The most common perennial in the high marsh, *T. angustifolia*, exhibits a very low root:shoot ratio of 0.55, although its competitor *Bolboschoenus fluvialis* (representing on average 10% of plant litter; KAM Engelhardt, unpublished data) has a high root:shoot ratio of 3.64 (Whigham and Simpson 1978). In whole, these values from the literature support the idea that tradeoffs between above- and belowground litter biomass may help to maintain more or less consistent soil organic matter inputs to soil across elevation gradients.

Plant biomass just above the mineral soil surface interacts with tidal water, slowing flood and ebb tides, reducing erosion, and increasing the capture of sediments. Plant litter that remains above the marsh soil surface through winter integrates these sedimentation properties over a longer time. Modeling studies have shown that plant stems are most effective at enhancing sedimentation at medium densities (Nardin and Edmonds 2014). Therefore, the medium-density litter we observed at the low- to high-marsh transition is likely effective at enhancing sedimentation through the entire year, rather than just the growing season. This idea was upheld by empirical data that showed that LOI of surface soils decreased (mineral content increased) with decreasing elevation ($R^2 = 0.38$; $P = 0.0007$; Fig. 11A). Unpublished measurements of the composition of sediments deposited on tiles at Dyke Marsh exhibit considerable spatial and temporal variability, from 25% to 75% mineral content (C. Palinkas, unpublished data). This suggests that the elevation gradient we see in LOI in surface sediments occurs despite spatially variable organic matter in suspended sediment, which is likely partially composed of autochthonous plant litter. We also found that the mineral content of plant litter (estimated by loss on ignition) increased with decreasing elevation. This observation is consistent with the idea that plant litter intercepts mineral sediments suspended in tidal waters throughout the winter, and that these sediments become entrained in the decomposing plant litter. Our data show that the “per stem” entrapment of sediments is virtually constant with increasing elevation ($R^2 = 0.01$; $P = 0.52$). Therefore, despite decreasing water depth and inundation time with increasing elevation, the increased stem density found at higher elevations works to maintain mineral input to soils. This statement is corroborated by slightly longer inundation times at elevations exhibiting dense plant litter (observed as a small deviation from a straight line in the elevation range of tall plant litter in Fig. 10A), evidence of the hydrologic effects of plant stems on tidal water. However, mineral content at higher elevations is diluted by increasing litter biomass, leading to higher organic matter content in soils at higher elevations. The consistency of these spatial processes has led to stable patterns of soil organic matter content and marsh elevation change, maintaining the form and function of this marsh

for centuries (D’Alpaos et al. 2007, Fagherazzi et al. 2012, Mariotti and Fagherazzi 2013b).

Syntheses of marsh elevation gain under conditions of sea level rise have come to the conclusion that given sufficient sediment supply, salt and freshwater marshes are not vulnerable to being submerged as sea levels rise. This tendency to increase sedimentation in response to increased water depth requires interactions between tidal water and vegetation, enhancing sedimentation rates at elevations most prone to flooding. Observations of elevation change over time in our study system confirm the ability of this marsh to maintain elevation above sea level (Cadot et al. 2014). However, the elevation trend of marsh surface elevation gain found at this site exhibits two elevations where elevation gain is locally higher. The elevation gain peak near -0.2 m elevation is likely the result of low-marsh vegetation that contributes enhanced belowground biomass, captures sediment during the growing season, but is otherwise dependent on a large sediment supply from outside the marsh, delivered as suspended sediment in tidal water. Elevations above 0.2 m, however, are unlikely to receive significant allochthonous sediment, thus requiring greater dependence on in situ biomass production for elevation gain. Due to the generally low root:shoot ratios of high-marsh species (discussed earlier), it follows that the copious amounts of aboveground plant litter, found in this study to increase with elevation, are important in ecosystem processes determining elevation gain. The increasing elevation gain rate from ~ 0.2 to 0.35 m correlates with the transition from LiDAR litter board heights of around 0 m to upward of 0.8 m. If this peak in elevation gain were exclusively driven by enhanced sediment capture at the edge of the denser high-marsh canopy we would expect a rapid drop off in elevation gain, as waters reaching the higher elevations of the marsh interior became starved of sediment. Instead, we observe a gradual decline in elevation gain, with even a possible increase at 0.6 m elevation, though it should be noted that the uncertainty near the edge of the elevation range is very high due to the smoothing procedure used to produce the elevation gain curve (Cadot et al. 2014). Therefore, the maintenance of high elevation gain rates into the marsh interior is best explained by plant litter, which contributes increasing amounts of biomass to the soil at these higher elevations. While other processes are certainly at work, neither increased belowground biomass (due to low root:shoot ratios) nor sedimentation (elevated LOI of surface sediments) can fully explain the elevation gain observed over time at elevations at and above 0.35 m.

The finding that litter board height, vertical cover, biomass, and stem count increases with elevation has methodological implications for using LiDAR and field observations to assess the vulnerability of this site, and likely other fresh water tidal marshes, to sea level rise. We found that due to increasing density of plant litter, LiDAR laser penetration decreased (i.e., reached the mineral soil interface less often) with increasing elevation.

This effect was so consistent across the study area that we were able to use it to our advantage, adjusting the elevation of the lowest LiDAR return to account for decreasing laser penetration with increasing elevation. This adjustment effectively lowered the LiDAR elevation of the marsh in areas of high litter density. The resulting digital elevation model compared favorably with the RTK GPS elevation data concurrently collected in Feb 2012, but also for data collected the following year ($R^2 = 0.86$; $P < 0.0001$). Without the calculated correction to account for litter density, we would have overestimated the elevation of the marsh surface at all elevations above 0.5 m (*sensu* Chassereau et al. 2011). Consequently, we have advanced methods used to correct LiDAR data for the effect of vegetation. The lack of these methods to date, have resulted in accurate digital elevation models only being available for areas lacking dense vegetation. In salt marshes, where much of marsh LiDAR work has focused, vegetation is typically of much lower density. But even in salt marshes, the effect of vegetation hinders accurate DEM generation to some extent (Wang et al. 2009, Chassereau et al. 2011).

Our results can be used to inform the restoration of Dyke Marsh and possibly other marsh restoration efforts. The National Park Service is in the final planning stages of a restoration effort that will use a suite of containment materials including stone and riprap breakwaters, coir biologs, hay bales, and sand-filled geotextile tubes to create cells that will be filled with clean sediment (National Park Service 2014). The outer edges of cells will be sloped to mimic a natural marsh surface, and native vegetation will be established at appropriate elevations. Such approaches depend on marsh vegetation becoming established such that natural processes develop that enhance sedimentation and future soil development. Vegetation and elevation monitoring are key to assuring the investment in restoration is achieving the desired results (e.g., Hopfensperger et al. 2007, Staszak and Armitage 2013), and our work suggests that LiDAR surveys might be ideally suited to this task. We identified an elevation profile of plant litter in winter that appears to be indicative of healthy marsh functioning, contributing to marsh functioning by increasing sediment capture at low elevations and increasing organic matter development in soils at high elevations. Thus, monitoring litter density could be a key management tool for assessing restoration success. The functioning of vegetation at different stem densities has already been considered in modeling work (Nardin and Edmonds 2014); the suggestion here is that this could be taken one step further by considering the elevation dependence of plant litter across continuous gradients in elevation.

CONCLUSIONS

The combination of airborne and field observations provided a unique perspective on the interactions between environment, plant litter, and soil development that will aid future studies aiming to model and understand the

co-evolution of tidal freshwater marsh surfaces and marsh plant communities. In particular, we show that plant litter exhibits strong gradients with elevation, which interacts with mineral sediments in the development of soil surfaces to maintain annual increases in elevation across a broad range in elevation. At lower elevations, mineral sediment deposition dominates whereas at higher elevations, organic matter accumulation dominates. At this freshwater tidal marsh, the contribution from aboveground biomass appears to be more important than previously recognized. Thus, plant biomass and sediment supply are important in tidal freshwater marshes, similar to salt marsh systems; however, their relative importance switches along the elevation gradient in tidal freshwater marshes due to spatial and temporal variability in litter structure. These observations are consistent with the idea that freshwater marsh elevation is maintained above sea level rise as long as sediment delivery via suspension in tidal waters (at low elevations) and organic matter delivery via plant litter (at high elevations) is maintained. Perturbations to either process are expected to threaten marsh persistence under conditions of sea level rise.

ACKNOWLEDGMENTS

We thank Steven Guinn and Kara Hawkins for assistance with data processing and management, and Jason Cessna for assistance with fieldwork. This work was supported by the National Science Foundation (Division of Environmental Biology award DEB-0841394).

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DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.m96d0>