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The relationship between inundation duration and *Spartina alterniflora* growth along the Jiangsu coast, China

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Abstract

The above-ground biomass of *Spartina alterniflora* salt marsh meadows is influenced by numerous interacting factors, among them elevation, tidal range and inundation duration. Bio-geomorphological models make use of either linear or quadratic equations, but it is important to be aware that the variables are area specific and hence not generic. In order to explore the vegetation growth pattern and its influencing factors along the Jiangsu coast, China, field surveys were conducted in two typical *S. alterniflora* marshes along the coast of Dafeng and Rudong. To combine the influence of elevation and the effect of tidal range, the inundation ratio (*IR*) is introduced as a novel parameter, which is the ratio between inundation duration and the duration of the whole tidal period concerned. The relationship between above-ground biomass and *IR* can be expressed by a quadratic equation. The optimal inundation ratio for *S. alterniflora* along the Jiangsu coast ranges from 0.21~0.26, which is much lower than, for example, that for the marsh of North Inlet (0.35), South Carolina, and the Virginia Coast Reserve (0.41), USA. Tidal range plays a significant role in that a larger tidal range leads to a smaller optimal *IR*, and that the landward and seaward limits are displaced toward higher ground elevations. In macrotidal regions the submergence depth is larger, which results in

60 enhanced submergence and salinity stress for the entire marsh, causing it to shift toward higher
61 elevations. Tidal range is an important factor influencing the growth pattern of *S. alterniflora*,
62 but geomorphological factors such as topographic profiles, and the presence of cliffs and tidal
63 creeks must also be taken into account.
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70 **Keywords:** [to be added at proof stage]
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72 **1. Introduction**

73 Salt marshes are one of the most productive ecosystems in the world (Gallagher *et al.*,
74 1980), providing numerous habitats to vertebrate and invertebrate faunae, and being an
75 invaluable natural resource to coastal residents. Marsh vegetation protects the coast from storm
76 surges by dissipating wave energy, reducing tidal currents, enhancing sediment retention and
77 accelerating tidal flat expansion (Allen, 2000; Temmerman *et al.*, 2013; Gao *et al.*, 2014).
78 Because of these ecosystem services, the response of coastal marshes to sea-level rise has
79 become an important research topic. Sea-level rise leads to longer time periods over which
80 suspended sediments can deposit (Friedrichs and Perry, 2001). At the same time, longer
81 submergence increases soil anoxia, which may eventually exceed the tolerance of halophytes
82 (Bertness and Ellison, 1987; Morris *et al.*, 2002; Voss *et al.*, 2013) and the balance between
83 rates of sea-level rise and accretion rates determines whether salt marshes can survive a rise in
84 sea level (Morris *et al.*, 2002; Mudd *et al.*, 2010; Kirwan *et al.*, 2016).
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95 Both organic and inorganic deposition contributes to salt marsh accretion. The amount of
96 deposition is, amongst others, related to various properties of the vegetation, in particular
97 biomass, stem density, stem diameter and leaf area. Organic deposition is directly related to the
98 vegetation biomass. Inorganic deposition includes sediment trapping by vegetation and direct
99 settling on the salt marsh surface. Sediment trapping by vegetation is determined by leaf area
100 and the projected total area (Yang, 1998; Chen *et al.*, 2018). Sediment settling can be enhanced
101 by vegetation because it decreases flow velocity and turbulence (Shi *et al.*, 1995; Bouma *et al.*,
102 2007; Nepf, 2012; Chen *et al.*, 2016), and also dampens wave action (Wang *et al.*, 2006; Feagin
103 *et al.*, 2011; Yang *et al.*, 2012). Projected stem area and stem diameter, which are the main
104 parameters from which the damping effect of vegetation is calculated, are both related to
105 biomass (Morris and Haskin, 1990), which is thus a good proxy from which to estimate the
106 effect of vegetation on fluid and sediment. Biomass or vegetation density are therefore the most
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122 widely used parameters in bio-geomorphological modeling (Mudd *et al.*, 2004; Morris, 2006;
123 D'Alpaos *et al.*, 2007; Kirwan and Murray, 2007; Mariotti and Fagherazzi, 2010; Mudd *et al.*,
124 2010).
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127 Vegetation growth is limited by the flooding frequency and duration due to raised soil
128 salinity and anoxia (Phleger, 1971; Naidoo *et al.*, 1992; Morris, 1995; Wijte and Gallagher,
129 2013), indicating that the elevation of a marsh determines the flooding condition of the
130 vegetation. Morris *et al.* (2002) found that the above-ground biomass (B) of *Spartina*
131 *alterniflora* (*S. alterniflora*) in North Inlet, South Carolina (USA), is related to the depth below
132 mean high tide (D) by the following relationship:
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$$137 B = aD^2 + bD + c \quad (1)$$

138 where a , b and c are numerical values relating to the form of the regression.
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141 The above-ground biomass has a hump-shaped cross-shore pattern in that it increases
142 with decreasing elevation, reaches a maximum at the optimal elevation, and then decreases as
143 the elevation drops below the optimal level. There is commonly an upper and a lower elevation
144 limit between which *S. alterniflora* can survive (e.g., Gray, 1992). The seaward limit is
145 determined by soil anoxia due to excessive submergence (Naidoo *et al.*, 1992; Wijte and
146 Gallagher, 2013). Toward the landward end of the marsh, the decreasing submergence rate
147 leads to high evapotranspiration and increased soil salinity, which is ultimately fatal to
148 halophytes (Phleger, 1971; Morris, 2000). Although the data from North Inlet only covered the
149 area above optimal elevation (Morris *et al.*, 2002), eq. (1) also predicts the area below optimal
150 elevation. This predictive potential was shown to be correct by other investigations (Kirwan *et*
151 *al.*, 2012). Nevertheless, in some cases, geomorphological models have also made use of
152 parabolic equations (Morris, 2006; Kirwan and Murray, 2007; Mariotti and Fagherazzi, 2010;
153 Hagen *et al.*, 2013; Alizad *et al.*, 2016; Rodriguez *et al.*, 2017).
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165 Because the data of Morris *et al.* (2002) only cover the rising part of the hump-shaped
166 curve, a linear relationship is often used to describe the spatial pattern of the vegetation (Mudd
167 *et al.*, 2004, 2009, 2010; D'Alpaos *et al.*, 2005, 2007):
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$$170 B = \left(\frac{z_{\max} - z_b}{z_{\max} - z_{\min}} \right) B_{\max} \quad \text{for } z_{\min} \leq z_b \leq z_{\max} \quad (2)$$

171 where z_b is the local marsh elevation, B_{\max} the maximum biomass, z_{\max} and z_{\min} the growth limits
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181 of the marsh. This linear equation provides a simple and efficient prediction, and is therefore
182 particularly useful for modeling purposes, especially if the marsh is located above the optimal
183 elevation. As pointed out by Morris (2006), the choice of a biomass model and associated
184 variables should always be based on the site-specific (regional) conditions.
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188 In fact, elevation is not the only determining factor of marsh biomass distribution. Also
189 landform, tidal range and latitude can influence the vegetation pattern (e.g., Gray, 1992). Due
190 to the presence of tidal creeks, the flooding duration increases near the tidal creeks. Tidal range
191 may also influence marsh distribution by altering the growth range of the vegetation. In fact,
192 growth range was found to be proportional to tidal range (McKee and Patrick, 1988; Balke *et*
193 *al.*, 2016). Whereas the landward limit of a salt marsh is influenced by latitude and species
194 competition, the seaward (i.e. lower) limit is determined by the tolerance to submergence,
195 salinity and anoxia (McKee and Patrick, 1988). Because the tidal range differs at different
196 geographic locations, a unifying proxy is needed to identify the effect of hydrodynamic
197 condition and geomorphology on vegetation. The non-dimensional depth is calculated by the
198 ratio of the difference between mean high water level (MHW) and the bed elevation to the mean
199 tidal range. It is a useful proxy of the submergence intensity and easy to calculate (Morris *et al.*
200 2013; Alizad *et al.* 2016). The rising or lowering rate of water level is not constant during the
201 tidal cycle. The rate is maximum at the middle of flood and ebb, while the rate is minimum at
202 high or low water. Therefore, the actual submergence duration is not linear to non-dimensional
203 depth. The non-dimensional depth may generate deviations from the actual submergence
204 duration.
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218 The inundation ratio (IR) is based on the actual submergence duration and thus has the
219 direct physical meaning. *IR*, which is the ratio between inundation duration and the whole time
220 span of the associated tidal cycles, is here proposed for that purpose. In practice, and assuming
221 the relevant time span covers *n* tidal cycles and is long enough to remove the spring-neap
222 variation, *IR* can be defined as:
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$$227 \quad IR = \frac{\sum_{i=1}^n t_i}{T} \quad (3)$$

228 where t_i is the inundation duration in the *i*th tidal cycle and *T* is the duration of total *n* tidal
229 cycles. By this definition, the effects of tidal range and bed elevation are merged into a single
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240 predictive parameter (cf. also Bockelmann et al., 2002; Mudd et al., 2004).

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242 The variables need to be determined regionally by using the biomass model to predict the
243 marsh pattern. Morris *et al.* (2002) obtained the variables by performing long-term monitoring
244 of the salt marsh in the North Inlet estuary, South Carolina, USA. Interestingly, Kirwan *et al.*
245 (2012) derived the same equation on the basis of different variables derived from observations
246 in the Virginia Coast Reserve, USA. This suggests that, due to regional differences in
247 environmental conditions, more *in situ* investigations are required in geographically different
248 regions in order to explore the comparability of the interaction between vegetation and
249 geomorphology on a global scale.
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256 Although *S. alterniflora* is a native species to the east coast of America, it has been
257 introduced to China in 1979. Since then it has spread widely, especially along the coast of
258 Jiangsu Province. The reason for its introduction to the Jiangsu coast was for the purpose of
259 coastal protection and the claim of new land (Chung and Zhuo, 1985; Chen *et al.*, 2004; Chen
260 *et al.*, 2005; Zhang *et al.*, 2004). The broad and flat expanses of the tidal flats along the Jiangsu
261 coast provide excellent habitats for *S. alterniflora* and it is thus not surprising that research on
262 the evolution of *S. alterniflora* salt marshes from originally bare tidal flats has a high priority
263 in China (Zhang *et al.*, 2004; Zuo *et al.*, 2013; Gao *et al.*, 2014). Within this context, our
264 research has the following three purposes: (a) to generate the local salt marsh variables for
265 geomorphological modeling in order to assess the effects of future sea-level rise and land claims;
266 (b) to explore the effects of geomorphology and tidal range on salt marsh vegetation growth;
267 and (c) to contribute to the worldwide *S. alterniflora* salt marsh data base with the aim of
268 establishing a universal salt marsh model.
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281 **2. Methods**

282 **2.1. Study area**

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284 As study two *S. alterniflora* marshes were chosen, one located in Dafeng, the other in
285 Rudong, both located in the middle sector of the Jiangsu coast, China (Fig. 1). Due to the
286 sediment supply of the Subei Coastal Current and nearshore residual currents influenced by the
287 abandoned Yellow River Delta, the coast-normal profile is characterized by a wide and gentle
288 slope, the tidal flat being composed of fine-grained sediment. The tidal regimes in Dafeng and
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299 Rudong are irregular semidiurnal with average tidal ranges of 3 m and 4.5 m respectively (Ren,
300 1986; Wang *et al.*, 2012). The Dafeng coast is relatively more exposed compared to Rudong,
301 the longer fetch and more open environment leading to stronger wind-wave influence in the
302 former case, where the annual mean significant wave height is 0.48 m (measured at the B1
303 buoy; Fig. 1a). The Rudong coast, by contrast, while being exposed to stronger tidal currents,
304 is shielded from wave action by the radial sand ridges which emerge during low tide.
305 Correspondingly, the annual mean significant wave height measured at the B2 buoy (Fig. 1a),
306 which is located in a similar morphological environment close to Rudong, is 0.27 m.
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313 After its introduction to China, *S. alterniflora* rapidly expanded along the Jiangsu coast,
314 landward up to the local native marsh communities and seaward across the bare tidal flat. By
315 2007 the *S. alterniflora* salt marsh occupied an area of 187.1 km² (Zuo *et al.*, 2012). It showed
316 excellent ecological engineering qualities with respect to sediment capture, shoreline protection
317 and biological treatment of wastewater (Ding *et al.*, 2008; Li *et al.*, 2009; Zhang *et al.*, 2012;
318 Zuo *et al.*, 2012). Because of its expansion in the course of land claims, the *S. alterniflora*
319 marshes in Dafeng and Rudong can be regarded as representing single species marshes. Their
320 landward edges are determined by dikes, whereas their seaward edges are lined by bare tidal
321 flats.
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331 **2.2. Field surveys**

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333 Field surveys were carried out in Dafeng from 11–19 November 2016 and in Rudong from
334 24 September to 8 October 2015 and 24–25 October 2016. The two research sites represent
335 typical *S. alterniflora* salt marshes along the Jiangsu coast. In Dafeng the marsh is lined by
336 retreating rise in an upper mesotidal environment, whereas in Rudong the marsh thrives in a
337 lower macrotidal environment. The cross-shore profiles and vegetation patterns, however,
338 differ between Dafeng and Rudong. As a consequence, elevation measurements and vegetation
339 sampling were adapted to the local bed elevation profiles.
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348 **2.2.1. Bed elevation measurements**

349 A Magellan Z-MAX GPS RTK (a differential, real-time kinematic GPS system) was used
350 to measure bed elevations and positions. The instrument has a vertical accuracy of 20 mm. In
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358 each case, the GPS was allowed to stabilize for 3 seconds in order to optimize the elevation
359 accuracy. The two bed leveling profiles at Dafeng were measured in November 2016 (Fig. 1b,
360 transects DF-n and DF-s). The interval between two successive sampling points was in general
361 25 m. Vertical elevation changes were in all cases smaller than 5 cm. Only at rise and along
362 tidal creeks were the sampling intervals reduced. A short profile was measured across the
363 seaward edge of the marsh at Rudong in September 2015 (Fig.1c, transect Rd2015). Because
364 of the steeper slope beyond the seaward edge of the marsh, the interval between successive
365 elevation measurements was decreased to 5 m, corresponding elevation changes being smaller
366 than 3 cm. A second, supplementary profile with larger sampling intervals (50 m) was surveyed
367 in October 2016 (Fig.1c, transect Rd2016), the vertical elevation changes between points being
368 smaller than 5 cm.
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379 **2.2.2. Vegetation sampling**

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381 According to Gao et al. (2016), the peak season of biomass is October in Jiangsu Coast.
382 The biomass obtained at this peak season is able to represent the annual biomass. At Rudong
383 the above-ground vegetation samples were collected in October 2015 and at Dafeng in
384 November 2016. Both transects were sampled at Dafeng (Fig. 1b). In each case 12 quadrats
385 (50*50 cm) spaced 100 m apart were collected. All above-ground plants in a quadrat were
386 harvested. In addition, 3 quadrats at 0, 50, 100 m distance were collected along 8 transects
387 perpendicular to a tidal creek at Rudong (Fig. 1c). The elevation and position of each quadrat
388 was measured by the RTK-GPS. The stem heights of all plants were measured in the lab before
389 they were dried and weighed.
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399 **2.3. Laboratory analysis and data processing**

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401 The inundation ratio (*IR*) was calculated on the basis of the water level time series and the
402 elevations. The water surface was assumed to be horizontal over the whole salt marsh
403 (Friedrichs and Aubrey, 1996). The time series were obtained from the tidal gauges at Yangkou
404 Harbor, 15 km from the Rudong site, and at Dafeng Harbor, 12 km from the Dafeng site.
405 Inundation was defined as the case where the water surface elevation at a particular point was
406 higher than the ground elevation. For all those cases the inundation ratio was calculated by eq.
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420 **3. Results**

421 **3.1. Elevation**

422 The actual accuracy of the elevation measurements was on average 43 mm. According to
423 these, a low rise occurs between the marsh and the bare tidal flat at Dafeng. The height of the
424 rise was 10 cm along transect DF-n and 65 cm along transect DF-s (Fig. 2a, b) and thus increases
425 from north to south (Fig. 1b). Ground elevations across the marsh were almost at the same level
426 at Dafeng (Fig. 2a, b), the marsh platform being slightly higher than MHW (1.50 m above MSL).
427 According to our observations, the seaward edge of the salt marsh was eroding and hence
428 retreating landward at Dafeng.
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436 A rise was not observed at Rudong during the two field campaigns in 2015 and 2016. Here,
437 the salt marsh was located below the MHW level (2.23 m above MSL). The slope of the seaward
438 part of the marsh was 0.6%, that of the landward part and the bare tidal flat about 0.1% (Fig.
439 2c). The variations in ground elevation obviously imply different inundation ratios along the
440 marsh profile. Furthermore, the elevations of vegetation quadrats near the tidal creek were
441 found to be lower than those within the marsh (Fig. 2c).
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449 **3.2. Vegetation**

450 **3.2.1. Stem density and height**

451 The marshes of Dafeng and Rudong are single species marshes. Only *S. alterniflora* was
452 observed on the marsh during the field surveys. Stem density at Dafeng has two peaks, one at
453 the seaward edge, the other 1000 m from the seaward edge of the marsh (Fig. 3b). Vegetation
454 is dense (420 plants/m²) at the seaward edge of marsh, which corresponds to a high inundation
455 ratio. The second peak (550 plants/m²) results from the gentle slope and concave-up shape of
456 cross-shore elevation profile, which causes the middle part of marsh to be poorly drained and
457 the upper marsh to be inundated for a longer period of time (Fig. 2a & 2b). At Rudong the stem
458 density shows different pattern to Dafeng. The maximal stem density at the seaward edge of
459 the marsh at Rudong is 540 plants/m², from where it decreases with increasing elevation toward
460 the shore (Fig. 3a, b).
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476 Stem height shows a parabolic relationship to elevation and cross-shore distance at both
477 Rudong and Dafeng. The regression equation of stem height (h_s , m) versus elevation relative to
478 MSL (h , m) is (Fig. 3c):
479

$$480 \quad h_s = -41.41h^2 + 87.79h + 69.77 = -41.41*(h - 1.06)^2 + 116.3 \quad (4)$$

481
482 with a correlation coefficient of $R = 0.47$, whereas the regression equations of stem height (h_s ,
483 m) versus cross-shore landward distance from the seaward edge of the marsh (L , m) is (Fig.
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487 3d):

$$488 \quad h_s = -1*10^{-4}L^2 + 0.11L + 86.45 = -1*10^{-4}*(L - 550)^2 + 116.7 \quad (5)$$

489
490 with a correlations coefficient of $R=0.48$. The hump-shaped curve reaches its highest elevation
491 (1.1 m above MSL) at a distance of 550 m from the seaward edge (Fig. 3c, d). The maximal
492 stem height is 159 cm. *S. alterniflora* is short at the seaward edge because short plants survive
493 more easily under strong wave action and higher flow velocities. The plants on the landward
494 side, in turn, are short due to the limiting effects of high salinity and drought. The most
495 significant difference between the marshes at Dafeng and Rudong is their vertical growth range.
496 While the marsh at Dafeng occupies a narrow elevation range from 1.24 m to 1.85 m above
497 MSL, the marsh at Rudong ranges from mean sea level up to 2.2 m above MSL (Fig. 3a, c).
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507 **3.2.2. Biomass and Inundation ratio**

508 The minimum and maximum biomasses at Dafeng were 1160 g/m² and 2650 g/m²
509 respectively (Fig. 4a). The narrow vertical growth range of the *S. alterniflora* marsh at Dafeng
510 (1.24–1.85 m above MSL) corresponds to *IRs* ranging from 0.32–0.091. The maximum biomass
511 occurred at 1.5 m above MSL and had an *IR* of 0.18 (Figs. 4a, 5a). The minimum and maximum
512 biomasses at Rudong, by contrast, were 350 g/m² and 2850 g/m² respectively (Fig. 4b). The
513 wider vertical growth range of the marsh at Rudong (2.1–0.3 m above MSL) corresponds to *IRs*
514 ranging from 0.08–0.4. The maximum biomass occurred at 1.0 m above MSL and had an *IR* of
515 0.25 (Figs. 4b, 5b).
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522 The relationship between biomass (g/m²) and elevation (h) as well as inundation ratio (*IR*)
523 follows a parabolic trend at both Dafeng and Rudong (Figs. 4, 5). However, the corresponding
524 equations differ with respect to the values of the variables (Fig.5). Thus, the equation of biomass
525 vs. elevation for Dafeng is (Fig. 4a):
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$$B = -8392.8 h^2 + 2.58 \cdot 10^4 h - 1.79 \cdot 10^4 = -8392.8 (h - 1.54)^2 + 2002.0 \quad (6)$$

536 and for Rudong is (Fig. 4b):

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$$B = -947.4 h^2 + 1743.2 h - 1048.3 = -947.4 (h - 0.92)^2 + 1850.2 \quad (7)$$

540 According to these equations, the optimal elevation at Dafeng (1.54 m) is much higher than at
541 Rudong (0.92 m). This reflects the wider growth range of the marsh at Rudong as compared to
542 Dafeng.
543

545 In contrast to the biomass vs. elevation relationships, those of biomass vs. *IR* are quite
546 similar at the two sites. Thus, the equation for Dafeng is (Fig. 5a):
547

549
$$B = -57796 IR^2 + 2.38 \cdot 10^4 IR - 437.3 = -57796 (IR - 0.206)^2 + 2015.3 \quad (8)$$

551 and that for Rudong is (Fig. 5b):

552
$$B = -43264 IR^2 + 2.25 \cdot 10^4 IR - 1044.5 = -43264 (IR - 0.26)^2 + 1880.1 \quad (9)$$

554 According to these equations, the optimal inundation ratio at Rudong (0.26) is slightly larger
555 than that at Dafeng (0.206). Furthermore, the seaward *IR* limit at Dafeng (0.32) is smaller than
556 that at Rudong (0.4).
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561 4. Discussion

562 4.1. Tidal effect on vegetation growth

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567 *S. alterniflora* is capable of tolerating stronger environmental stress than some other
568 halophytes such as *Scirpus robustus*, *Scirpus mariqueter*, and *Spartina anglica* (Naidoo *et al.*,
569 1992; Lewis *et al.*, 2002; Chen *et al.*, 2004; Wijte and Gallagher, 2013). This enables *S.*
570 *alterniflora* to occupy elevation levels even below mean sea level (Wiggins and Binney, 1987;
571 Landin, 1991; Bulthuis and Scott, 1993), although the precise seaward limits differ in different
572 geographic regions (McKee and Patrick, 1988).
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578 Parabolic relationships between biomass and elevation were reported from North Inlet
579 (South Carolina, USA) and the Virginia Coast Reserve (Virginia, USA) (Morris *et al.*, 2002;
580 Kirwan *et al.*, 2012). In order to compare the data between different study areas, all the data
581 extracted from the literature need to be unified under a common standard. Firstly, all reported
582 elevations were related to mean sea level: $h = Z_{MHW} - D$, where h is the elevation relative to
583 MSL, Z_{MHW} is the height between mean sea level and mean high water (mean tidal amplitude)
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591 and D is the depth of occurrence below mean high water. Second, time series of water level
592 oscillations were obtained from regional tide–gauge records stored in the data base of NOAA
593 (<https://tidesandcurrents.noaa.gov/datums.html?units=1&epoch=0&id=8632200&name=Kipt>
594 [opeke&state=VA](https://tidesandcurrents.noaa.gov/datums.html?units=1&epoch=0&id=8632200&name=Kipt)). Thereafter, the inundation ratios can be calculated from the known water
595 levels and elevations. The regression parameters from four area are listed in Table 1. The results
596 from North Inlet and the Virginia Coast Reserve are displayed in Figs. 4d and 5d, and Table 2.
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604 As can be seen, the growth ranges and optimal positions are very different between the
605 marshes of Dafeng, Rudong, North Inlet and the Virginia Coast Reserve (Figs. 4d, 5d, Table
606 1). Whereas the biomass of *S. alterniflora* is similar in North Inlet and along the Jiangsu coast
607 (maximal 2000 g/m³), it is much smaller in the Virginia Coast Reserve (maximal 800 g/m³).
608 Thus, the respective equations of biomass vs. elevation for North Inlet and the Virginia Coast
609 Reserve are
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$$614 B = -18486 * (h - 0.28)^2 + 1861.6 \quad (10)$$

$$615 B = -32000 * (h - 0.10)^2 + 876.1 \quad (11)$$

616 and of biomass vs. inundation ratio:

$$617 B = -69161 * (IR - 0.324)^2 + 1861.7 \quad (12)$$

$$618 B = -74676 * (IR - 0.401)^2 + 875.5 \quad (13)$$

619 The seaward edges of the marsh in North Inlet and the Virginia Coast Reserve
620 approximates mean sea level and the inundation ratio is about 0.5. Along the Jiangsu coast the
621 seaward limit of the marsh is located slightly lower than in North Inlet and the Virginia Coast
622 Reserve, but the submergence duration is smaller, being reversed due to the larger tidal ranges
623 (Figs. 4d, 5d). The landward edge of the marsh along the Jiangsu coast, on the other hand, is
624 significantly higher than in North Inlet and the Virginia Coast Reserve (Figs. 4d, 5d), while the
625 IR value of the landward and seaward limits decrease with tidal range (Table 2). The optimal
626 IR values at Dafeng, Rudong, North Inlet and the Virginia Coast Reserve are 0.206, 0.26, 0.35
627 and 0.41, respectively (Fig. 5d, Table 2). This demonstrates that the optimal IR value also tends
628 to decrease with tidal range.
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642 The elevation of the seaward limit along the Jiangsu coast is the lowest, and that in the
643 Virginia Coast Reserve (Kirwan at al., 2012) the highest (Table 2). Introduced and hybrid plants
644 may change the tolerance of *S. alterniflora* (Strong and Ayres, 2013), but differences in tidal
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652 range provide another explanation to this phenomenon. The growth range increase with
653 increasing tidal range, whereas the landward and seaward limits decrease with increasing tidal
654 range (McKee and Patrick, 1988). Biomass of *S. alterniflora* can be influenced by latitude (Liu
655 *et al.*, 2016; Crosby *et al.*, 2017), but no significant difference was observed between 32 and
656 38 degrees North (Liu *et al.*, 2016). We assume that the submergence period and salinity
657 tolerance is similar in these areas, which eliminates the effect of hybrids and latitude. While the
658 inundation ratio in different geographic regions can be identical, the submergence depth will
659 differ if the tidal range is different. Deeper submergence due to larger tidal ranges leads to
660 stronger soil anoxia, which is unfavorable for the vegetation of the lower marsh. On the
661 landward side, however, deeper submergence enhances inundation which is otherwise lacking
662 in the higher marsh. Thus, submergence depth explains why both landward and seaward limits
663 decrease with increasing tidal range (Fig. 5d, Table 2). Likewise, the inundation depth can
664 explain the optimal *IR* value of vegetation growth. Submergence depth in microtidal
665 environments will be shallower, and vegetation growth thus needs longer inundation durations
666 to achieve higher inundation ratios.
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680 Another remarkable phenomenon is that, with increasing tidal range, the landward limit
681 decreases much more rapidly than the seaward limit (Fig. 5d, Table 2). Because the seaward
682 edge of a marsh is regularly submerged, soil anoxia is mainly controlled by inundation duration
683 not submergence depth. That explains why the seaward edge of a marsh varies much less
684 between different areas than the landward edge, where the high marsh is irregularly submerged
685 and evapotranspiration and hyper-salinity become severe. The effect of inundation duration, by
686 contrast, is small because of its short duration and submergence depth now becomes important.
687 In effect, the response of the landward limit is much greater than that of the seaward limit if the
688 tidal range changes. The same phenomenon, namely that the optimal *IR* decreases with tidal
689 range, is also valid for the optimal *IR* of *S. alterniflora* growth.
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700 **4.2 Geomorphological effect on vegetation growth**

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702 Considering the observations at Dafeng and Rudong, the situation is more complicated
703 than outlined above. The relationship of biomass and inundation frequency is similar at the two
704 locations. The seaward *IR* limits are both smaller than 0.5, which concerns the elevation of the
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709 seaward edges of the marsh above mean sea level. It is determined by salinity and submergence
710 tolerance of *S. alterniflora*. Although the tidal range at Dafeng is smaller than at Rudong, the
711 seaward limit and the optimal *IR* value is smaller at Dafeng than at Rudong (Figs. 6, 7).
712 Hydrodynamics and geomorphology play important roles in this case. Firstly, at Dafeng the
713 marsh edge retreats landward due to rise erosion. Secondly, due to the presence of the cliff,
714 wave and current action are more intense (Tonelli *et al.*, 2010; Francalanci *et al.*, 2013; Zhao
715 *et al.*, 2017), which is a disadvantage for the vegetation. In response, the optimal *IR* position
716 retreats to a higher elevation and therefore has a lower value.
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719 By the same token, the cross-shore profile of a salt marsh may also alter the inundation
720 characteristics. First of all, the marsh platform at Dafeng is located around MHW, which is
721 much higher than the marsh at Rudong (Fig. 2). As mentioned above, the gentle slope and
722 concave-up shape of the marsh at Dafeng (Fig. 2a & 2b) leads to poor drainage of the higher
723 marsh. Because of the longer inundation duration, the soil salinity is lower, which favors
724 vegetation growth of the higher marsh plants.
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727 Tidal creeks are another landform influencing the vegetation pattern. Biomass and stem
728 height of *S. alterniflora* located near the tidal creek (Figs. 3c, 4b, 5b) are clearly higher than on
729 the inner marsh. The lower elevation near tidal creeks leads to higher inundation durations.
730 While tidal creeks play an important role as drainage tunnels in salt marshes (Allen, 2000), the
731 longer water residence times in their vicinity favor vegetation growth.
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734 **4.3 Salt marsh evolution and model application**

735 As outlined above, the biomass model is clearly an important module in the
736 geomorphological evolution model (Mudd *et al.*, 2004, 2010; D'Alpaos *et al.*, 2005, 2007;
737 Morris, 2006; Kirwan and Murray, 2007; Mariotti and Fagherazzi, 2010). In the case of some
738 *S. alterniflora* (Mudd *et al.*, 2004, 2010; D'Alpaos *et al.*, 2005, 2007) and multi-species
739 marshes (Belliard *et al.*, 2017) a linear equation can be used in the biomass model. The marshes
740 at Dafeng and Rudong represent two kinds of typical marsh, being characterized by erosion
741 along the cliff and a gentle slope with little or no surface deposition in the former case, but by
742 seaward progression and a steep slope of the seaward edge in the latter case. As such, the
743 marshes of Dafeng and Rudong can be regarded as representing two different evolutionary
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772 Submergence has a positive effect on vegetation growth above the optimal *IR* elevation.
773 The linear equation covers this part of the marsh up to the landward limit and provides an
774 efficient predictor of biomass which, in this region, increases with decreasing elevation (Mudd
775 *et al.*, 2004, 2010; D'Alpaos *et al.*, 2005, 2007). With seaward spreading of the vegetation, the
776 frequency of submergence begins to inhibit the growth of *S. alterniflora*. The biomass decreases
777 with decreasing elevation from the optimal elevation to the seaward limit. Here, the vegetation
778 pattern follows a parabolic relationship between biomass and elevation. Because of decreased
779 hydrodynamics and the sediment trapping effect of the salt marsh vegetation, the elevation of
780 the entire marsh increases, whereas the slope of the inner marsh decreases and that of the
781 seaward edge increases. As time goes on, the slope of the seaward edge becomes progressively
782 steeper until a cliff is formed. The period of cliff formation is significantly affected by sediment
783 supply, biomass and overall evolution time (Mariotti and Fagherazzi, 2010; Zhao *et al.*, 2017).
784 The marshes of both the Dafeng and Rudong coasts are associated with high sediment
785 concentrations (SSCs) and large biomass (Figs. 5, 6, 7). The different variables in the biomass
786 versus *IR* relationship (e.g., optimal *IR*, landward and seaward *IR* limits, maximum biomass)
787 can thus substantially influence morphodynamic processes, and are hence extremely important
788 for morphological modeling and the development of management strategies for coastal marsh
789 protection.

800 801 802 803 804 805 806 807 **4.4. Salt marsh evolution under sea-level rise**

808 According to the IPCC prediction of sea-level rise (SLR), the eustatic contribution will be
809 0.3 to 0.8 m over the next century (Church, 2013). In general terms, coastal land loss will occur
810 if the local rate of SLR exceeds the local accretion rate (Reed, 1995). However, marsh survival
811 may be different because of biogeomorphic feedbacks resulting in increased rates of both
812 organic and inorganic accumulation (Morris *et al.*, 2002; Kirwan and Guntenspergen, 2012).
813 Thus, the spatial vegetation pattern is crucial in determining accumulation in the marsh, a dense
814 plant canopy and associated high biomass greatly reducing the vulnerability of a marsh (Kirwan
815 *et al.*, 2016). A maximal biomass and optimal marsh elevation would have the best protection
816 effect. For example, at Dafeng and Rudong, and in North Inlet and the Virginia Coast Reserve,
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829 the respective maximal biomasses are 2002, 1850, 1861 and 875 g/m². The corresponding
831 optimal elevations are 1.54, 0.92, 0.28, and 0.10 m above MSL, and the optimal *IRs* are 0.206,
832 0.260, 0.324 and 0.401.
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835 The remarkable differences between different marshes will result in different responses to
836 SLR. Because the *IR* of seaward edges are close to 0.5 in different regions, the associated lower
837 optimal *IR* means that the marshes at higher elevations and with wider elevation ranges have a
838 better chance to survive. The above-mentioned advantage of a marsh results in a stronger buffer
839 to the impact of future SLR. Therefore, a maximal biomass and optimal *IR* are useful proxies
840 in evaluating the ability of marsh adaptation to SLR. It is noteworthy, however, that the spatial
841 pattern of a marsh is not the only determining factor, sediment supply being also a significant
842 variable in the accretion of a marsh.
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851 **5. Conclusions**

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853 The biomass pattern of *S. alterniflora* in coastal marshes can be predicted by the inundation
854 ratio. According to our field surveys, the relationships between above-ground biomass and
855 inundation ratios can be described by quadratic regression equations. The optimal inundation
856 ratio for *S. alterniflora* along the Jiangsu coast ranges from 0.21~0.26, but are much lower for
857 the marsh in North Inlet (0.35) and the Virginia Coast Reserve (0.41). Similar differences apply
858 to the landward and seaward limits of *S. alterniflora*. Tidal range plays a significant role in that
859 larger tidal ranges lead to smaller optimal *IRs* and higher ground elevations at the landward and
860 seaward limits of the marsh.
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867 In addition, the landform of a salt marsh can also influence the growth pattern of *S.*
868 *alterniflora*, while geomorphological factors such the elevation profile, as well as the presence
869 of cliffs and tidal creeks, should also be taken into account. Thus, the erosion of cliffs at Dafeng
870 results in a higher seaward limit of the marsh. The gentle slope and concave-up shape of the
871 Dafeng marsh, in turn, results in poor drainage, which makes the higher marsh more suitable
872 for *S. alterniflora* than the better drained lower ground.
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Table 1 Regression parameters of $B = a * (IR - b)^2 + c$, B (g/m²) is the biomass per unit area, IR is dimensionless inundation ratio, a, b and c are regression parameters.

Location	a	b	c	R	Significance
Dafeng	-57796	-0.206	2015.3	0.54	p<0.001
Rudong	-43264	-0.260	1880.1	0.68	P<0.001
North Inlet ¹	-69161	-0.324	1861.7	0.67	P<0.001
Virginia Coast Reserve ²	-74676	-0.401	875.5	0.65	P<0.001

¹Data extracted from Morris *et al.* (2002); ²Data extracted from Kirwan *et al.* (2012).

Table 2 Inundation ratios of different geographic regions

	Rudong	Dafeng	North Inlet ¹	Virginia Coast Reserve ²
Predicted seaward limit	0.47	0.39	0.49	0.54
Measured seaward limit	0.4	0.32	0.43	0.51
Predicted landward limit	0.04	0.02	0.16	0.28
Measured landward limit	0.08	0.1	0.19	0.34
Optimal <i>IR</i> of equation	0.26	0.206	0.324	0.401
Predicted growth range	0.43	0.37	0.33	0.23
Measured growth range	0.32	0.22	0.24	0.17
Tidal range (m)	4.5	3.0	1.4	0.8
Salt marsh slope	0.1%	~0%	/	3%
Latitude	32.5	33.3	33.3	37.5

Predicted values refer to those calculated by means of the corresponding equations relating biomass and *IR* to each other (eq. 8, 9, 12, 13). ¹Data extracted from Morris *et al.* (2002); ²Data extracted from Kirwan *et al.* (2012).

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1423 Fig. 1. (a): Map of the Dafeng and Rudong study areas, Jiangsu Province, China; B1 and B2
1424 are buoy stations monitoring the wave climate. (b): The Dafeng salt marsh; DF-n and DF-s
1425 mark the two cross-shore profiles. (c): The Rudong salt marsh; Rd2015 and Rd2016 are the two
1426 transects along which elevation measurements were carried out in 2015 and 2016 respectively.
1427 DFA and RDA mark the locations of hydrodynamic measuring stations.
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1433 Fig. 2. Cross-shore elevation profiles at Dafeng and Rudong. MHW, MHWS, MHWN are mean
1434 high water, mean high water springs and mean high water neaps respectively. Elevation is
1435 relative to MSL. (a) & (b) The cross-shore elevation profiles at Dafeng. MHWS, MHW,
1436 MHWN are 1.91 m, 1.50 m and 1.31 m above MSL respectively. (c) The cross-shore elevation
1437 profile at Rudong. MHWS, MHW, MHWN are 2.84 m, 2.23 m and 1.75 m above MSL
1438 respectively. Red solid circles mark the vegetation sampling quadrats located within the marsh,
1439 the blue solid circles the quadrats near the tidal creek.
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1447 Fig. 3. Stem density and height versus elevation and cross-shore distance at Dafeng and Rudong.
1448 The cross-shore distance is landward from the seaward edge of the marsh. (a) & (b) Stem
1449 density versus Elevation and Cross-shore distance. Note the lack of correlation. (c) Stem height
1450 vs. Elevation, and. (d) Stem height vs. Cross-shore distance. For the corresponding equations
1451 and correlation coefficients of the latter two see text (eq. 4, 5). Df-n (blue solid triangles) and
1452 DF-s (red solid circles) mark samples from Dafeng; RD-c (purple open diamonds) mark
1453 samples near the tidal creek at Rudong; RD-i (green open squares) mark samples from the inner
1454 marsh at Rudong.
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1463 Fig. 4. Biomass versus elevation. Note the parabolic relationships for Dafeng (a), Rudong (b)
1464 and both together (c). For equations see text (eq. 6, 7). (d) The parabolic regressions of biomass
1465 vs. elevation at Dafeng and Rudong compared with those of North Inlet (South Carolina, USA)
1466 and the Virginia Coast Reserve (Virginia, USA). The latter data are from Morris *et al.* (2002)
1467 and Kirwan *et al.* (2012). For the equations of the latter two see text (eq. 10, 11).
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1479 Fig. 5. Biomass versus inundation ratio. Note the parabolic relationships for Dafeng (a), Rudong
1480 (b) and both together (c). For equations see text (eq. 8, 9). (d) The parabolic regressions of
1481 biomass vs. inundation ratio at Dafeng and Rudong compared with those of North Inlet (South
1482 Carolina, USA) and the Virginia Coast Reserve (Virginia, USA). The latter data are from
1483 Morris *et al.* (2002) and Kirwan *et al.* (2012). For the equations of the latter two see text (eq.
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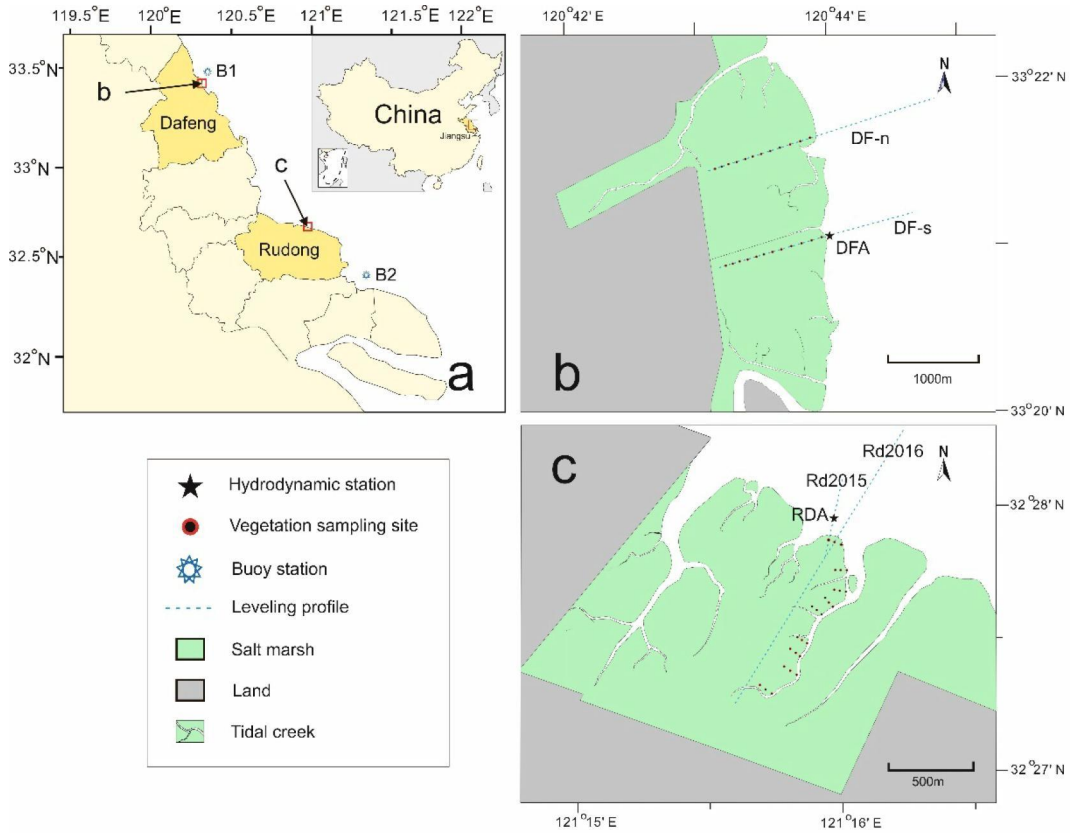


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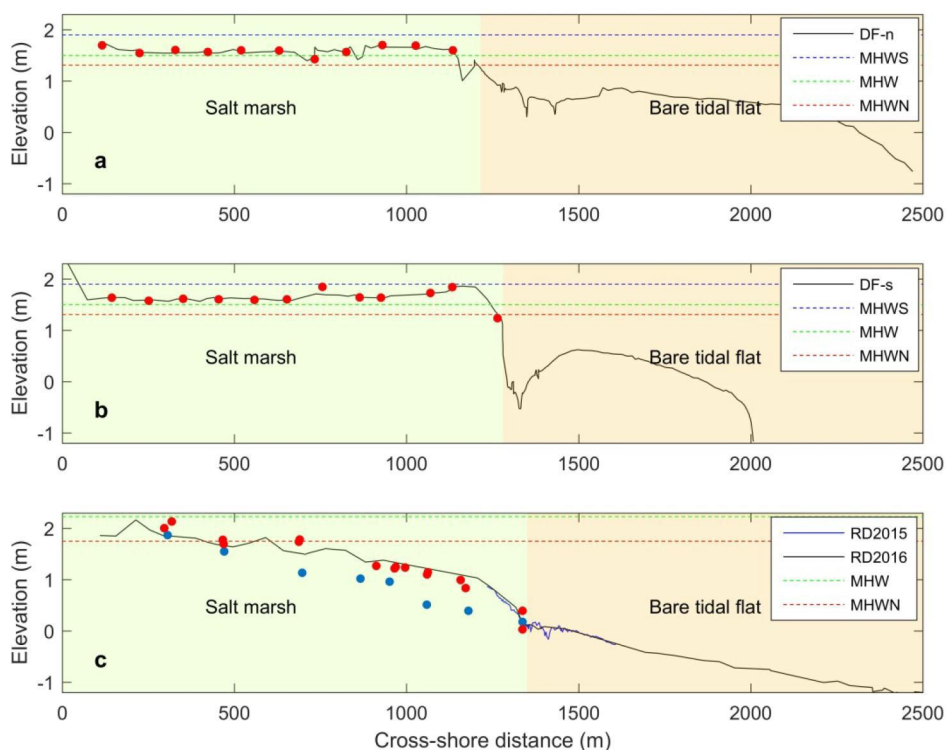


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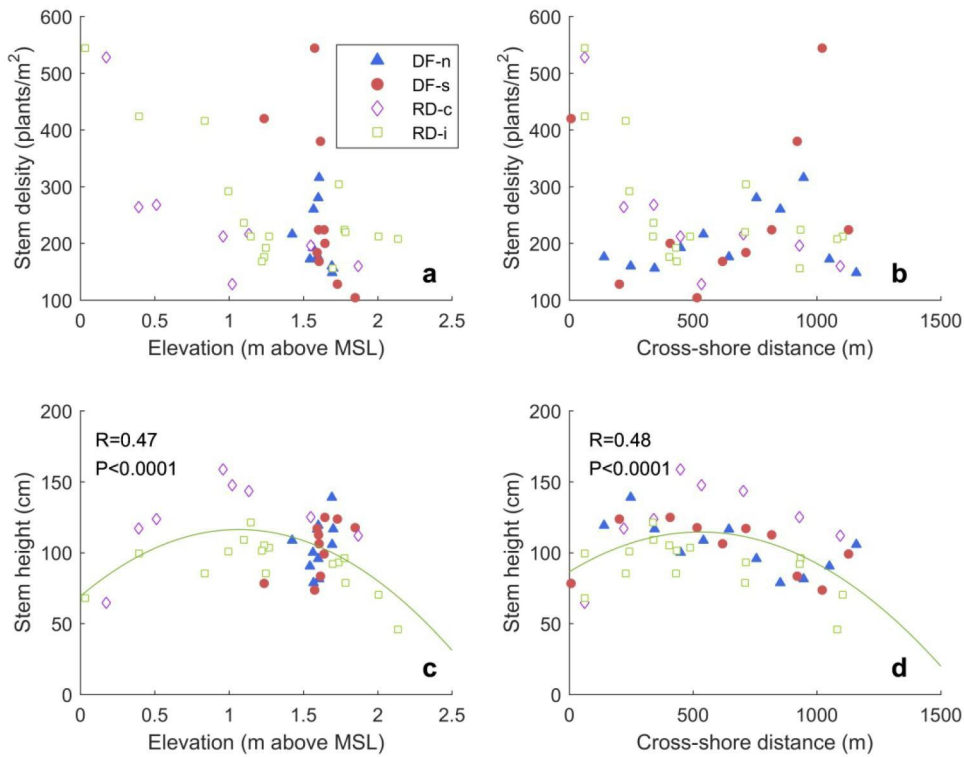


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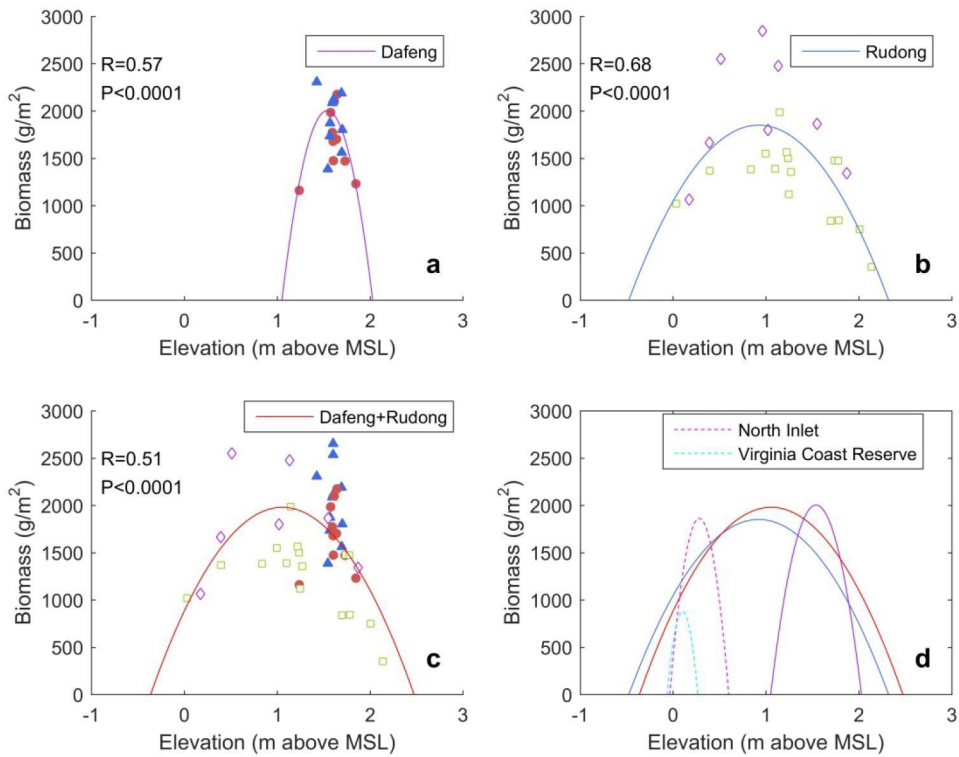


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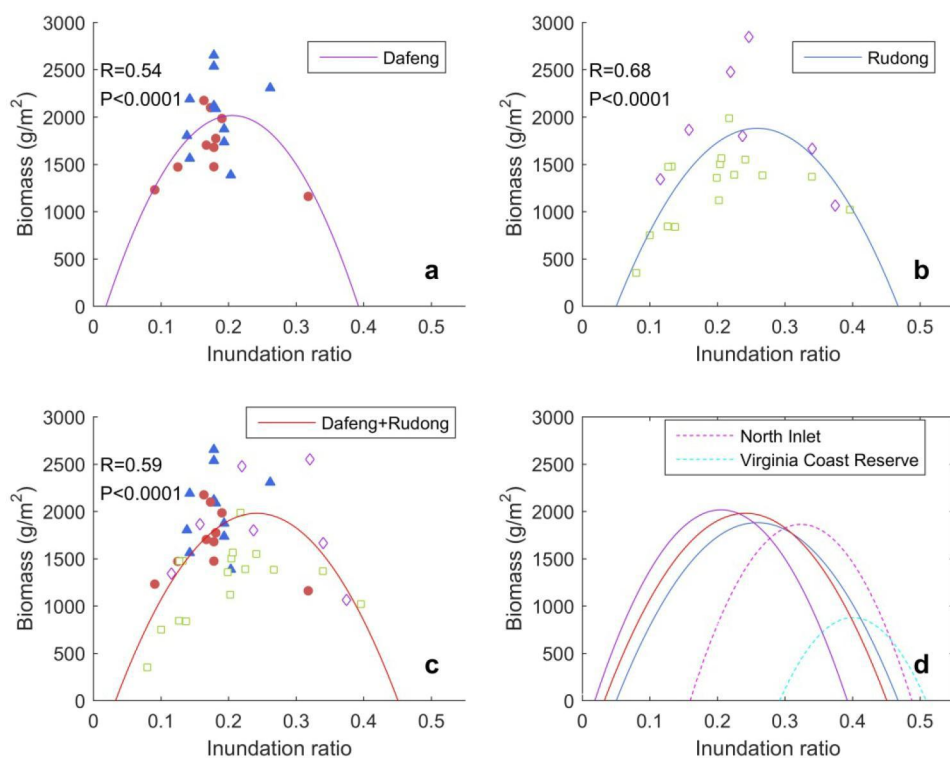


Fig. 5. Biomass versus inundation ratio. Note the parabolic relationships for Dafeng (a), Rudong (b) and both together (c). For equations see text (eq. 8, 9). (d) The parabolic regressions of biomass vs. inundation ratio at Dafeng and Rudong compared with those of North Inlet (South Carolina, USA) and the Virginia Coast Reserve (Virginia, USA). The latter data are from Morris *et al.* (2002) and Kirwan *et al.* (2012). For the equations of the latter two see text (eq. 12, 13).