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Biomechanical properties of marsh vegetation in space and time: effects of salinity, inundation and seasonality

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- **Background and Aims** Over the last decade, the importance of plant biomechanical properties in shaping wave dissipation efficiency of marsh vegetation has gained growing attention. Here we provide the first analyses of how biomechanical stem properties vary with seasons and along environmental gradients in coastal and estuarine marshes, which is essential to enable accurate assessments of flood defence value of marsh vegetation.
- **Methods** We quantified both spatial and seasonal variation in stem flexibility and breakability for a variety of common marsh vegetation (*Spartina anglica*, *Scirpus maritimus*, *Phragmites australis*, *Elymus athericus*, *Suaeda maritima*, *Aster tripolium*, *Saliconia procumbens*) distributed along both salinity and inundation gradients.
- **Key Results** Increasing salinity tends to induce a shift from species with tall shoots, high flexural stiffness (stem resistance to bending; N mm^2) towards species with shorter and more flexible stems. The same trend was found with increasing inundation stress (i.e. decreasing elevation) from the higher part of the low marsh towards the pioneer zone. Stem breakability (the force required to break or fold a stem, N) followed the same pattern of stem stiffness due to the positive relationship between flexural strength (material resistance to flexure, N mm^{-2}) and Young's bending modulus (material resistance to bending; N mm^{-2}). Shifts in stem stiffness and breakability at the community level were found to relate positively to the variation in canopy height between species, highlighting the concurrence of changes in morphological and biomechanical traits under environmental changes. Compared to the differences between species, within-species variability between sampling locations and between seasons is generally minor.
- **Conclusions** Our findings imply that environmental changes may significantly modify wave attenuation capacity of coastal vegetation by inducing species shifts. This emphasizes the need to understand the response of community composition to climate change and human disturbances, when using nature-based flood protection by coastal vegetation as an adaptive response to global change.

Keywords: Biomechanical properties, wave attenuation, coastal defence, salinity, inundation, season, stem stiffness, stem breakability.

INTRODUCTION

Increasing flood risks due to climate change and rising sea levels are challenging conventional engineered defences (Temmerman *et al.*, 2013; Bouma *et al.*, 2014; Wahl *et al.*, 2017). This provokes a paradigm shift towards innovative, nature-based solutions by harnessing the coastal defence properties of vegetated coastal ecosystems such as salt marshes (Gedan *et al.*, 2011; Shepard *et al.*, 2011; Temmerman *et al.*, 2013; Bouma *et al.*, 2014). Salt marsh canopies can attenuate waves even under extreme storm conditions (e.g. Moller *et al.*, 2014; Vuik *et al.*, 2016). The capacity for wave attenuation by vegetation depends not only on hydrodynamic conditions such as wave height and water depth (e.g. Ysebaert *et al.*, 2011; Anderson and Smith, 2014; Vuik *et al.*, 2016), but also on properties of the vegetation including standing biomass (e.g. Bouma *et al.*, 2010; Marsooli and Wu, 2014; Vuik *et al.*, 2016) and biomechanical properties such as stem stiffness (e.g. Bouma *et al.*, 2010; Feagin *et al.*, 2011; Lara *et al.*, 2016; Rupprecht *et al.*, 2017) and stem breakability (e.g. Vuik *et al.*, 2018).

Over the last decade, the importance of plant biomechanical properties in shaping wave dissipation efficiency of coastal vegetation has gained increasing attention (e.g. Bouma *et al.*, 2005; Paul *et al.*, 2012; Rupprecht *et al.*, 2015, 2017). Recent studies have shown that plant flexibility plays an important role in determining how salt marsh vegetation interacts with the orbital flows under waves (Rupprecht *et al.*, 2017; Silinski *et al.*, 2018). Plants with different stiffness and flexural strength can differ greatly in their resilience to physical damage under extreme waves (Vuik *et al.*, 2018). Flexible plant species can minimize the risk of folding and breakage through reconfiguration (Bouma *et al.*, 2005; Puijalon *et al.*, 2011). By contrast, stiff plants are more efficient in damping waves by maximizing their resistance to stress (Paul *et al.*, 2016), but may break more easily, resulting in lower wave attenuation capacity (Vuik *et al.*, 2018). Both plant flexibility and resistance to breakage can be expected to be location-specific due to trait differences in species that dominate a habitat along inundation and salinity gradients (Crain *et al.*, 2004, 2008; Pennings *et al.*, 2005). For the same species, these biomechanical properties may differ in space due to changing growing conditions (Silinski *et al.*, 2018) and vary over time because of seasonal cycles of plant growth (Liffen *et al.*, 2011; Miler *et al.*, 2014; Łoboda *et al.*, 2018).

TABLE 1. *Detailed information on sampling sites (Fig. 1) and time.*

Salinity (p.p.t.)	Site	Sampling location	Elevation (m NAP)	Species	Sampling season
0	De Zaag (DZ)	Near marsh edge	0.5	*Phragmites australis*	Dec 2014, Apr 2015, Jul 2016, Sept 2015
9	Groot Buitenschoor (GB)	Near marsh edge (GB_{Low})	1.9	*Scirpus maritimus*	Dec 2014, Apr 2015, Jul 2016, Sept 2015
		25 m from the marsh edge (GB_{High})	2.3	*Scirpus maritimus*	
11	Rilland (RL)	Nearby marsh edge	1.7	*Spartina anglica*	Dec 2014, Apr 2015, Jul 2016, Sept 2015
		Near marsh edge (RL_{Low})	1.9	*Scirpus maritimus*	
		50 m to the marsh edge (RL_{High})	2.4	*Scirpus maritimus*	
		100 m to the marsh edge	2.6	*Phragmites australis*	
20	Hellaget Polder (HG)	Near marsh edge (HG_{Low})	1.0	*Spartina anglica*	Dec 2014, Apr 2015, Jul 2016, Sept 2015
		50 m to the marsh edge (HG_{High})	1.9	*Spartina anglica*	
24	Zuidgors (ZG)	Near marsh edge	1.9	*Spartina anglica*	Dec 2014, Apr 2015, Jul 2016, Sept 2015
30	Noord-Friesland Buitendijks (NFB)	Pioneer zone	1.1	*Saliconia procumbens*	Mar 2016, Jun 2016, Aug 2016, Nov 2016
		Low marsh	1.5	*Suaeda maritima*	
		Low marsh	1.5	*Aster tripolium*	
		High marsh	1.9	*Elymus athericus*	

NAP, refers to Dutch Ordnance Datum which is close to mean sea level.

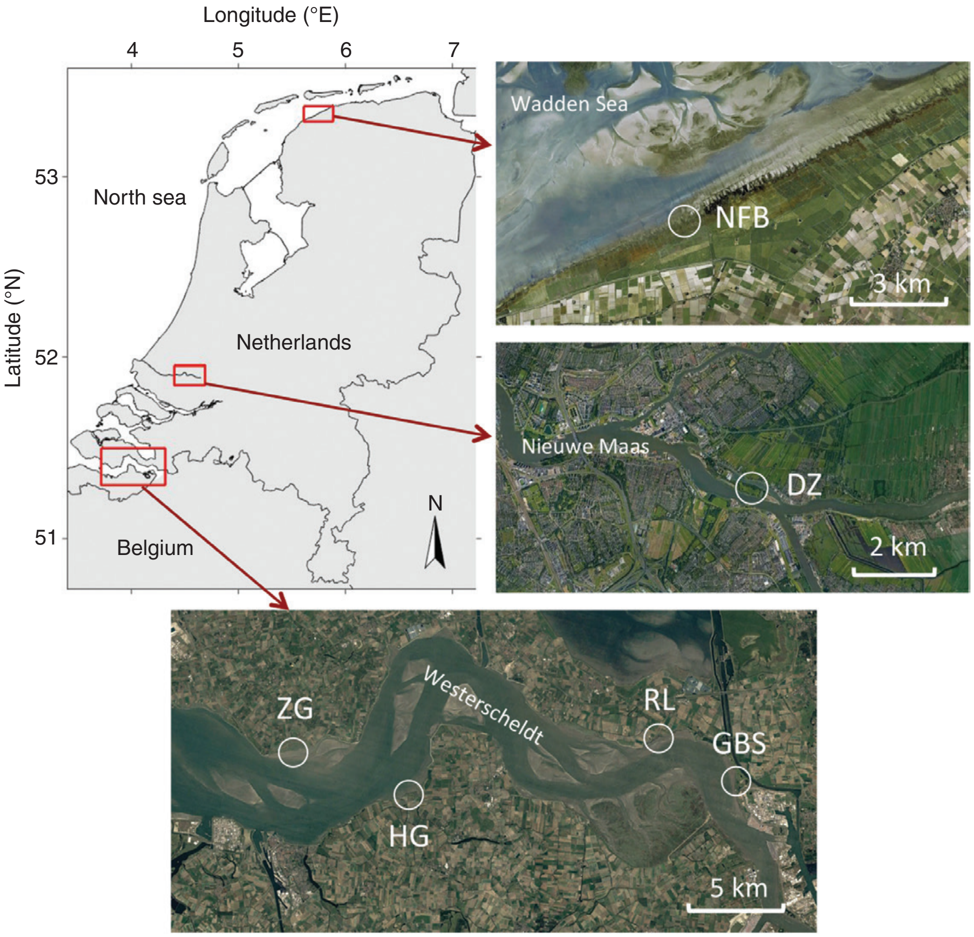

FIG. 1. Study sites. Detailed information on sampling time, sampling locations and species types at each site are given in Table 1.

However, there is a lack of understanding on how biomechanical properties vary with seasons and along environmental gradients in coastal and estuarine marshes. This knowledge gap hampers accurate assessments of the wave attenuation value of marsh vegetation.

In this study, we quantified spatial and seasonal variation for a range of plant biomechanical characteristics (i.e. flexural stiffness and breaking force of the stem, Young's bending modulus and flexural strength of the tissue) for a variety of dominant marsh species distributed along both salinity and inundation gradients. Salinity and elevation are known to be key environmental factors that govern both spatial species distribution and plant growth (canopy height, stem diameter, biomass, etc.) in estuarine and coastal marshes (e.g. Pennings *et al.*, 2005; Crain *et al.*, 2008; Ury *et al.*, 2019). Increased salinity stress has been shown to enhance rigidity of leaf tissue (e.g. Touchette *et al.*, 2009, 2014). However, it is still poorly understood how mechanical stem characteristics of marsh plants may vary seasonally and along salinity and inundation gradients. To bridge this knowledge gap, we conducted case studies in six marshes in the Netherlands, where we collected stem samples of plants growing at different elevations and at marshes with different salinity levels. In the lab, we determined stem stiffness and breakability of these samples through three-point bending tests.

MATERIALS AND METHODS

Plant species and sampling sites

We sampled seven common marsh plant species that occur in contrasting environmental conditions (Table 1). To study the effect of salinity, we compared three dominant species that inhabit the lower marsh zone in areas with different salinities: *Spartina anglica* (*Spartina*) for salt areas, *Scirpus maritimus* (*Scirpus*) for brackish areas and *Phragmites australis* (*Phragmites*) for fresh areas. To study the effect of inundation time, we compared species that are characteristic of the different marsh zones along the elevation gradient: *Elymus athericus* (*Elymus*) for the high marsh, *Suaeda maritima* (*Suaeda*) and *Aster tripolium* (*Aster*) for the low marsh, and *Saliconia procumbens* (*Saliconia*) for the pioneer zone.

To examine the impacts of salinity, we selected five Dutch marshes with contrasting salinity levels that range from 0 to 30 p.p.t. This included four salt to brackish marshes in the Westerschelde, Groot Buitenschoor (GB), Rilland (RL), Hellaget Polder (HG) and Zuidgors(ZG), and one freshwater marsh De Zaag (DZ) in the river Nieuwe Maas (Fig. 1, Table 1). In these marshes, the three dominant (pioneer) species that we sampled along the salinity gradient were *Spartina*, *Scirpus*

TABLE 2. *Details of the methods used to determine biomechanical properties.*

Variable	Units	Equation	Description	Reference
Flexural stifness (EI)	N*mm^2	$EI = (s^3F)/(48D)$	s is the distance between the two support bars; F/D describes the slope of the linear part of the force–deflection curve. D is the vertical deflection of the stem and F is the corresponding bending force.	Usherwood *et al.* (1997)
Second moment of area (I)	mm^4	$I = \pi\ (d_{out}^4 - d_{in}^4)/64$	d_{out} is the outer diameter and d_{in} (if present) is the inner diameter of the stem.	Usherwood *et al.* (1997)
Young's bending modulus (E)	N*mm^{-2}	$E = EI/I$	E is calculated by dividing flexural stiffness (EI) by the second moment of area (I)	Usherwood *et al.* (1997)
Breaking force (F_{max})	N		Directly recorded by the INSTRON machine	
Flexural strength (σ_{max})	N*mm^{-2}	$\sigma_{max} = s\ d_{out} F_{max}\ /8I$	σ_{max} is calculated based on the horizontal span of the stem between the two support bars (s), outer diameter (d_{out}), second moment of area (I) and breaking force (F_{max})	Vuik *et al.* (2018)

TABLE 3. *ANOVA table of the effects of species type and season on biomechanical properties and stem thickness of the three sampled species along the salinity gradient.*

Response variable	Source	d.f.	F value	$Pr(>F)$
Flexural stiffness	Species	2	169.320	<0.001
	Month	3	0.747	0.525
	Species:Month	6	4.135	<0.001
Breaking force	Species	2	346.106	<0.001
	Month	3	21.706	<0.001
	Species:Month	6	8.246	<0.001
Young's modulus	Species	2	48.957	<0.001
	Month	3	3.641	0.013
	Species:Month	6	4.290	<0.001
Flexural strength	Species	2	115.670	<0.001
	Month	3	1.443	0.230
	Species:Month	6	17.801	<0.001
Stem thickness	Species	2	460.809	<0.001
	Month	3	14.305	<0.001
	Species:Month	6	10.438	<0.001

and *Phragmites*. *Spartina* can be found in both salt (ZG) and brackish marshes (RL and HG), while *Scirpus* is abundant in brackish marshes (RL and GB). *Phragmites* dominates the fresh water marsh (DZ), but can also be found at higher elevations in the brackish marsh (RL). We sampled all the three species at the brackish site RL, whereas only one species was sampled for the other sites. Where *Spartina* (HG) or *Scirpus* (RL) occurred at different elevations within the same marsh, we sampled two locations: one of relatively higher elevation and the other of relatively lower elevation. This was to detect how local elevation differences may influence plant biomechanical properties for the same species (Table 1).

Coastal marshes typically display a zonation of plant species along the elevation gradient, which is also an inundation gradient. Plants growing in the high marsh can differ greatly with those growing in the low marsh (van Loon-Steensma *et al.*, 2016). To investigate how the biomechanical properties may vary between species types along the zonation (elevation) gradient, we conducted a case study in the marsh of Noord-Friesland Buitendijks, located in the Dutch Wadden sea coast (Fig. 1, Table 1), which displays a clear zonation of plant species along the elevation gradient: *Elymus* in the high marsh, *Suaeda* and *Aster* in the low marsh, and *Saliconia* in the pioneer zone.

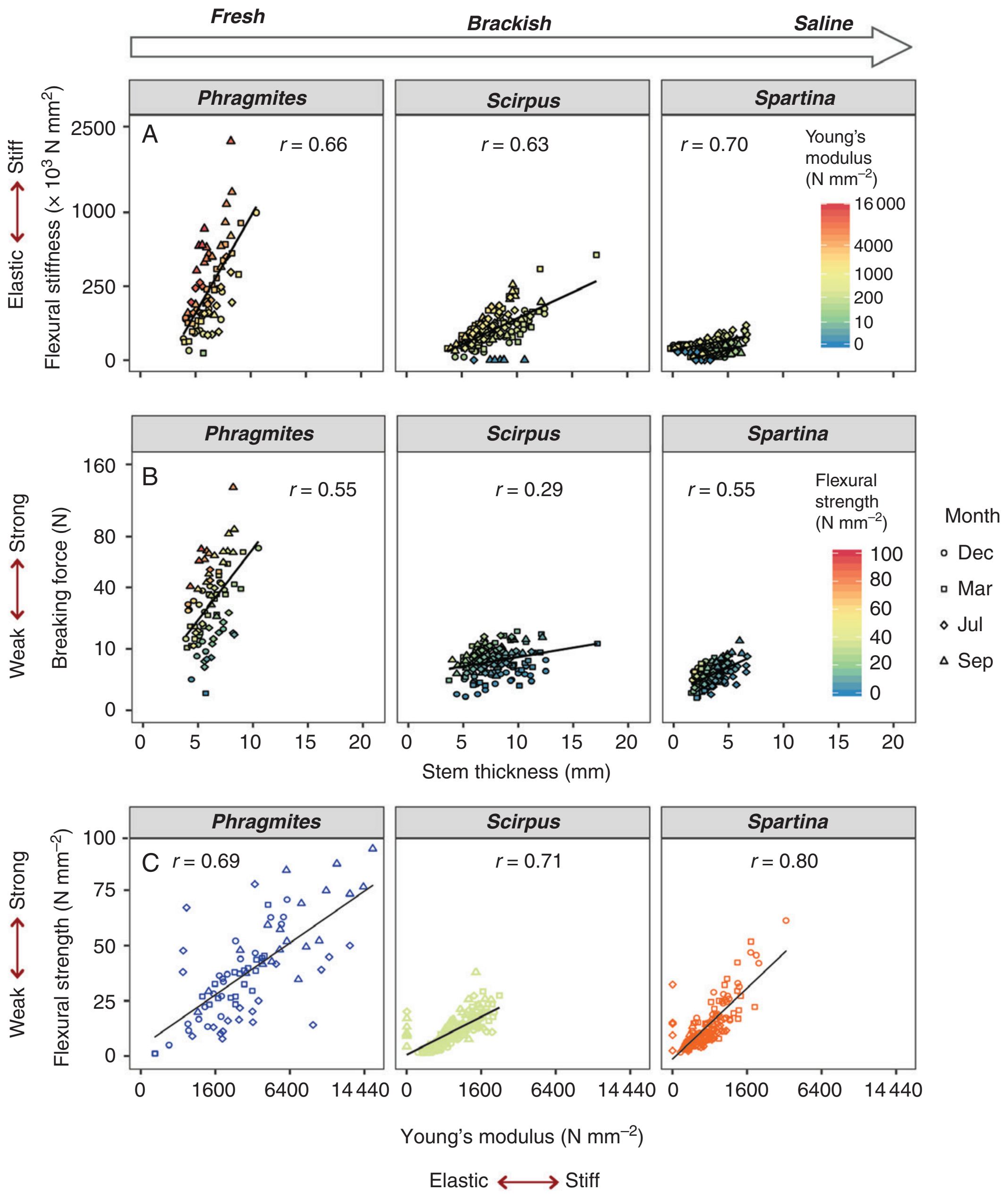

FIG. 2. Pearson's correlations between (A) flexural stiffness and stem thickness, (B) breaking force and stem thickness, and (C) flexural strength and Young's modulus for *Phragmites*, *Scirpus* and *Spartina*, respectively. The values of flexural stiffness, breaking force and Young's modulus were square root transformed to improve linearity.

For every studied plant species, we sampled four times over the seasonal cycle: spring, summer, autumn and winter (more details see Table 1). Ten stems per species per sampling location were collected on each occasion. At each sampling location, the stems were randomly chosen and cut from the bottom. Once collected, all the samples were taken back to the lab and tested within 48 h to keep the stems as fresh as possible. We also measured canopy height (measured as the distance from the highest point of the plant to the ground) for 30 random individual plants and stem density (determined in five random 50 × 50-cm quadrats) at each sampling location. This was done at the end of the growing season (September–October) when plants reach peak above-ground biomass.

Relevant biomechanical properties

Two groups of parameters can be used to describe the mechanical properties of plants: parameters describing tissue properties versus absolute parameters. Tissue properties are normalized for the dimensions of a tissue, so can be similar, for example, for a thick and a thin stem. They thus describe how tissues differ between species and may adjust to growing conditions. In contrast, absolute parameters integrate tissue properties with tissue dimensions, to describe the tissue properties that belong to a tissue of specific dimensions. The absolute parameters will thus differ between thick and thin stems made from same materials, and can be used to describe when tissue actually fails.

The key normalized parameters to describe the mechanical properties of a plant are (see Table 2 for details on calculation methods):

- Young's bending modulus (E; N mm^{-2}) describing how much force has to be applied to bend the material to a given displacement (i.e. a high value of E means lower flexibility of the stem).
- Flexural strength, also called modulus of rupture or bending strength (σ_{max}; N mm^{-2}), which is a measure of the resistance of the material to flexure.

The key absolute parameters to describe the mechanical properties of a plant are (see Table 2 for details on calculation methods):

- Breaking force or maximum bending force (F_{max}; N), describing the absolute force needed for a stem to break or fold.
- Second moment of area (I; mm^4) describing the stem morphology, which is calculated based on stem diameter.
- Flexural stiffness (EI; N mm^2), which is the product of Young's bending modulus (E; N mm^{-2}) and the second moment of area (I; mm^4). Flexural stiffness, also called stem flexibility, describes the resistance of a stem against bending (i.e. high values of EI indicate high bending resistance or stiffness, which equals the inverse of flexibility).

Three-point bending tests

We conducted three-point bending tests to determine stem flexibility and flexural strength. This was performed at the lab of the Royal Netherlands Institute for Sea Research (NIOZ) using a universal testing machine (precision ±0.5 %) with a 0.5-kN load cell (Instron 5942, Canton, MA, USA), following the same method as used by Silinski *et al.* (2018). For each sampling season and sampling location, 10 stems per species were used for bending tests. Stem flexibility and flexural strength were determined for the bottom 5–10 cm of each stem, as this is the section where the stems often break (Vuik *et al.*, 2018). For every stem, we first measured the stem diameter at ~5 cm from the bottom with an electronic caliper (precision ±0.5 mm). For hollow stems, both outer and inner diameters were determined. For *Scirpus maritimus*, which has solid but triangular stems, the mean length of the three sides of the triangular cross-section multiplied by $\sqrt{3}/2$ was determined as an equivalent measure of (outer) diameter (Vuik *et al.*, 2018). Span length of the testing section was then determined based on stem thickness (outer diameter), applying a maximum stem diameter/span length ratio of 1: 15 to

TABLE 4. *ANOVA table of the effects of sampling site and season on flexural stiffness and breaking force for the stems of the three sampled species along the salinity gradient*

Species	Response variable	Source	d.f.	*F* value	*Pr*(>*F*)
Phragmites	Flexural stiffness	Site	1	18.843	<0.001
		Month	3	13.766	<0.001
		Site:Month	3	4.738	0.005
Phragmites	Breaking force	Site	1	1.760	0.189
		Month	3	13.499	<0.001
		Site:Month	3	7.165	<0.001
Scirpus	Flexural stiffness	Site	3	8.561	<0.001
		Month	3	6.769	<0.001
		Site:Month	9	3.781	<0.001
Scirpus	Breaking force	Site	3	1.982	0.119
		Month	3	23.822	<0.001
		Site:Month	9	5.028	<0.001
Spartina	Flexural stiffness	Site	3	3.607	0.015
		Month	3	0.441	0.724
		Site:Month	9	2.671	0.007
Spartina	Breaking force	Site	3	33.9781	<0.001
		Month	3	13.7365	<0.001
		Site:Month	9	6.6817	<0.001

minimize the shear stress (Usherwood *et al.*, 1997). When the span length was fixed, the stem section for the bending test was then placed centrally onto two support bars and a metal bar was lowered from above at a displacement rate of 10 mm min^{-1} (Supplementary Data Fig. S1A). The vertical deflection of the stem (D) and the corresponding bending force (F) were recorded (Fig. S1B). Table 2 details how we used these measurements to calculate all absolute and normalized biomechanical properties.

Data analysis

We used two-way ANOVAs to analyse the effects of season and species type on stem thickness and biomechanical properties, i.e. flexural stiffness (EI), Young's modulus (E), breaking force (F_{max}) and flexural strength (σ_{max}). This was first done for the three species along the salinity gradient and later for the four species along the elevation gradient. *Post hoc* pairwise comparisons were achieved through Tukey honest significant differences (HSD) tests. For each species, we applied Pearson's correlations

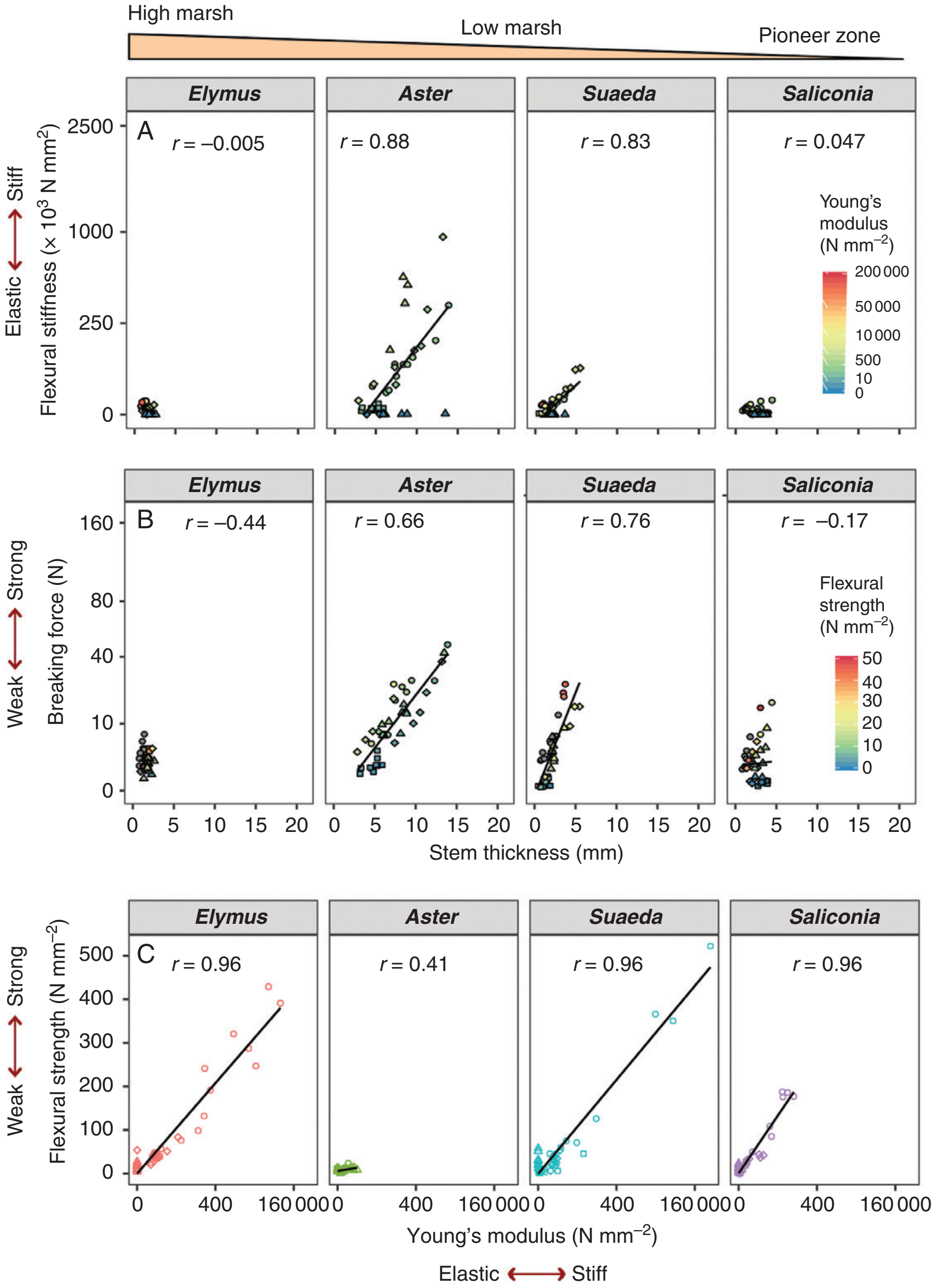

FIG. 3. Pearson's correlations between (A) flexural stiffness and stem thickness, (B) breaking force and stem thickness, and (C) flexural strength and Young's modulus for *Elymus*, *Aster*, *Suaeda* and *Saliconia*, respectively. The values of flexural stiffness, breaking force and Young's modulus were square root transformed to improve linearity.

to examine the relationships between (1) flexural stiffness and stem thickness, (2) breaking force and stem thickness, and (3) Young's modulus and flexural strength. Pearson's correlation was also applied to detect the relationship between biomechanical properties (both flexural stiffness and breaking force of the stem) and canopy height at the community level. Where necessary, the data were square root transformed to improve data normality. All statistical analyses were done in R (https://www.r-project.org), applying a significance level of α = 0.05.

RESULTS

Variation of biomechanical properties along the salinity gradient

There were significant differences of biomechanical properties between the species types along the salinity gradient (Table 3). Increasing salinity was found to induce a shift from species with stiff stems towards more flexible stems (Fig. 2A). As expected, flexural stiffness (*EI*; N mm^2) increased positively with stem thickness and Young's modulus (*E*; N mm^{-2}), i.e. with flexibility of the tissue (Fig. 2A). Due to a higher Young's modulus, *Phragmites*, which dominates in freshwater and brackish habitats, had much stiffer stems than the brackish species *Scirpus* (Fig. 2A). With shorter stems and lower Young's modulus than the other two species, the salt-tolerant species *Spartina* had the lowest stem stiffness among the three species (Fig. 2A). Similar to results for flexural stiffness, breaking force (F_{max}; N) also showed a decreasing trend for the three species along the salinity gradient (Fig. 2B), which can be explained by the positive relationship between flexural strength (σ_{max}; N mm^{-2}) and Young's bending modulus of the tissue (Fig. 2C).

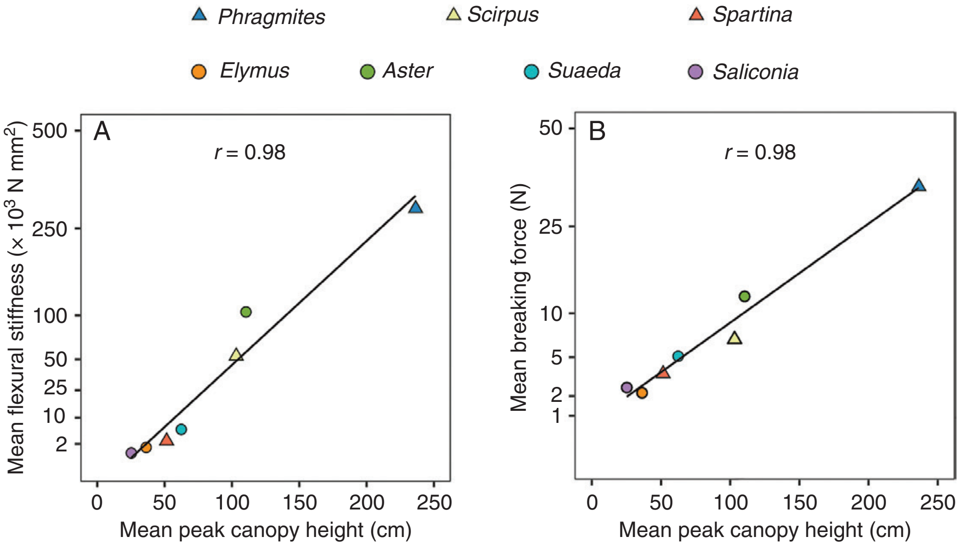

FIG. 4. Across all the sampled species in this study, there were significant positive relationships (Pearson's correlation) between mean flexural stiffness and mean peak canopy height (A), as well as mean breaking force and mean peak canopy height (B). Prior to the analysis, the values of mean flexural stiffness and mean breaking force were square root transformed to improve linearity.

TABLE 5. *ANOVA table of the effects of species type and season on biomechanical properties and stem thickness of the four sampled species along the inundation gradient*

Response variable	Source	d.f.	*F* value	*Pr*(>*F*)
Flexural stiffness	Species	3	30.767	<0.001
	Month	3	114.612	<0.001
	Species:Month	9	7.237	<0.001
Breaking force	Species	3	44.114	<0.001
	Month	3	74.767	<0.001
	Species:Month	9	11.893	<0.001
Young's modulus	Species	3	8.614	<0.001
	Month	3	152.638	<0.001
	Species:Month	9	6.732	<0.001
Flexural strength	Species	3	61.385	<0.001
	Month	3	90.673	<0.001
	Species:Month	9	12.490	<0.001
Stem thickness	Species	3	145.545	<0.001
	Month	3	6.501	<0.001
	Species:Month	9	6.927	<0.001

Variation of biomechanical properties along the elevation gradient

Our case study in the marsh NFB showed that biomechanical properties can vary drastically with changing species along the inundation gradient (Table 4). With species shifts along the elevation gradient, stem stiffness and stem breakability first increased and then decreased. The high marsh was dominated by the thin and flexible species *Elymus*, whereas the vegetation then shifted from thicker and stiffer species (i.e. *Aster* and *Suaeda*) in the higher low marsh towards the thinner and more flexible species *Saliconia* in the pioneer zone (Fig. 3). Whereas flexural stiffness of the two stiffer species *Aster* and *Suaeda* showed a clear increasing trend with growing stem thickness, the two more flexible species *Elymus* and *Saliconia* displayed no such trend (Fig. 3A). Breaking force of the four species (Fig. 3B) followed the same pattern of stem stiffness due to the positive relationship between flexural strength and Young's bending modulus of the tissue (Fig. 3C).

General trends

Across-species analysis showed that shifts in absolute values of stem stiffness and breaking force at the community level were related positively to the variation in canopy height between species (Fig. 4). The tallest species *Phragmites* had the highest flexural strength and breaking force. The two taller low marsh plants, *Aster* and *Suaeda*, had higher stem stiffness and breaking force than the two shorter species *Spartina* and *Saliconia* that dominate the pioneer zone of saline wetlands (Fig. 4). For all the sampled species, there were significant differences between seasons in biomechanical stem properties (Tables 4 and 5). However, the seasonal variability was species-specific and location-specific without any common trends (Figs 5–7). For instance, there was a significant decline in flexural strength for *Scirpus* and *Phragmites* from autumn (September–October) to winter (December) when plants turn brown, whereas the opposite was found for *Spartina* (Fig. 6B). For the same species, there were also significant differences (Table 4) in stem stiffness (Fig. 5) and stem breakability (Fig.

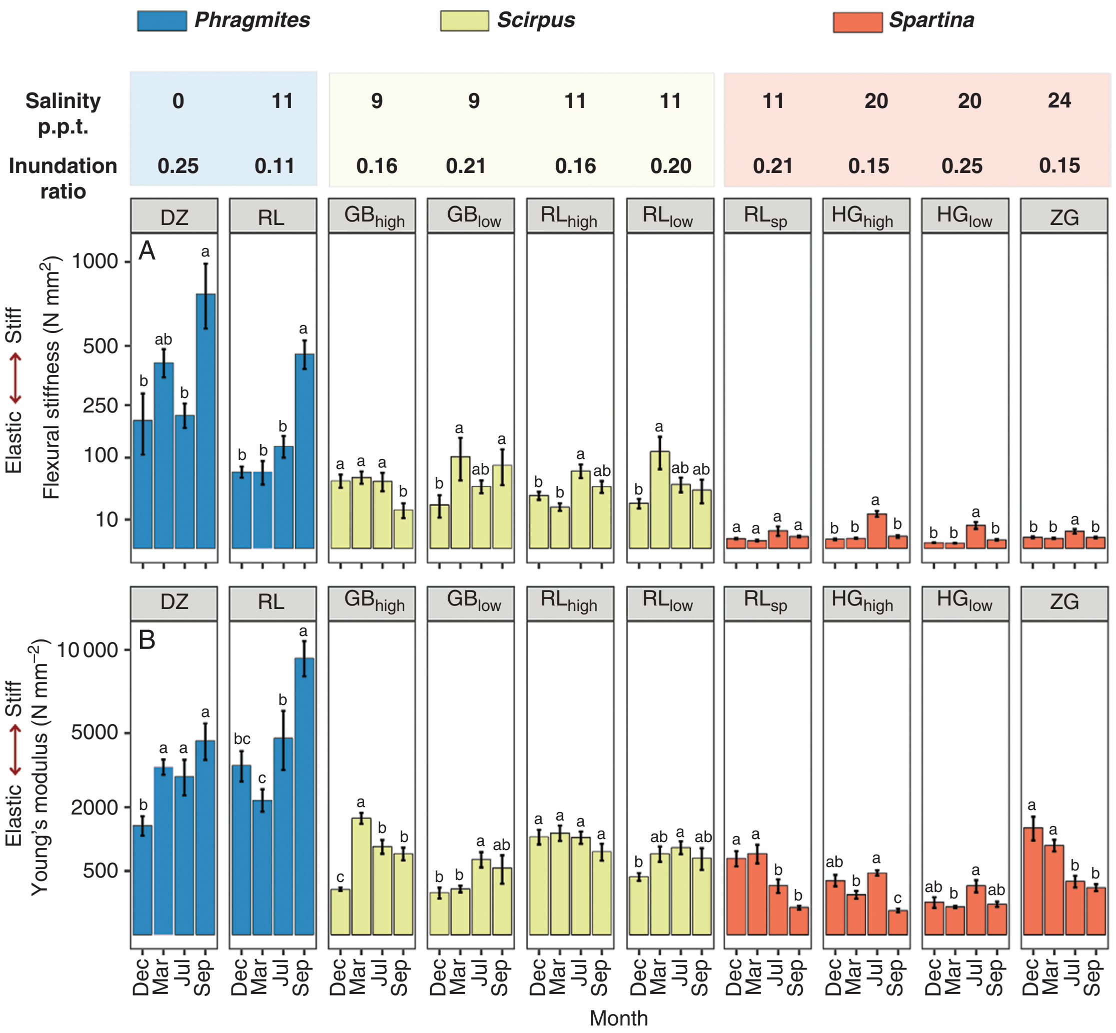

FIG. 5. Seasonal changes (mean ± s.e.) of flexural stiffness (A) and Young's modulus (B) of *Phragmites*, *Scirpus* and *Spartina* at different sampling sites. Different letters indicate significant differences ($P < 0.05$, Tukey's HSD test). Inundation ratio refers to the averaged percentage of inundation time per day.

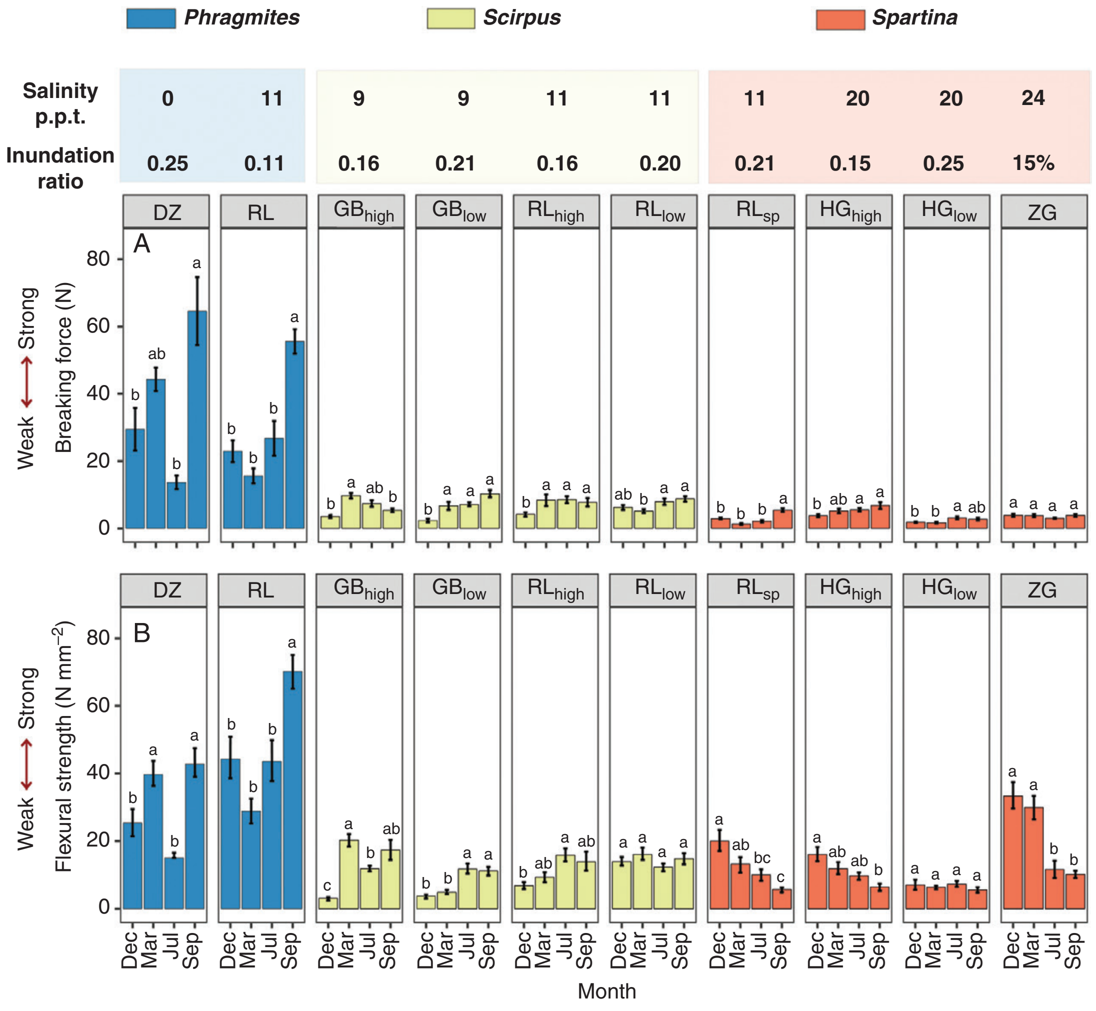

FIG. 6. Seasonal changes (mean ± s.e.) of breaking force (A) and flexural strength (B) of *Phragmites*, *Scirpus* and *Spartina* at different sampling sites. Different letters indicate significant differences ($P < 0.05$, Tukey's HSD test). Inundation ratio refers to the averaged percentage of inundation time per day.

6) between sampling locations. Within-species variations between seasons and between sampling locations, however, were generally minor compared to the differences between species (Figs 5–7).

DISCUSSION

A number of studies have assessed the biomechanical stem properties of specific marsh species, including *Atriplex* (*Halimione*) *portulacoides* (Feagin *et al.*, 2011), *Scirpus* spp. (Coops and Van der Velde, 1996; Heuner *et al.*, 2015; Carus *et al.*, 2016; Silinski *et al.*, 2018; Vuik *et al.*, 2018), *Spartina* spp. (Feagin *et al.*, 2011; Rupprecht *et al.*, 2015; Lara *et al.*, 2016; Vuik *et al.*, 2018), *Phragmitis australis* (Coops and Van der Velde, 1996), *Elymus athericus* (Moller *et al.*, 2014; Rupprecht *et al.*, 2015) and *Puccinellia maritima* (Moller *et al.*, 2014; Rupprecht *et al.*, 2015; Lara *et al.*, 2016). This study for the first time provides analyses on the spatial (i.e. along salinity and inundation gradients) and temporal (i.e. seasonal) variations in biomechanical stem properties of marsh vegetation. Our case studies in Dutch marshes on the seven dominant species clearly demonstrate that variation in plant morphology (stem thickness) and material properties (i.e. Young's modulus and flexural strength) between species can cause large differences in the absolute values for stem stiffness and breakability along environmental gradients and over seasons. Given the critical role of these biomechanical properties in determining wave attenuation efficiency of coastal vegetation (Bouma *et al.*, 2005; Paul *et al.*, 2012; Rupprecht *et al.*, 2015, 2017), such spatial and temporal variation may induce considerable variation in the wave attenuation capacity of marsh vegetation, which should be taken into account when modelling the biogeomorphic development or efficiency of nature-based flood defences with marsh vegetation.

Effects of phenotypic plasticity vs. shifts in species

Studies have shown that both terrestrial and aquatic plants display plasticity in biomechanical properties as adaptive responses to changing environmental stresses (Read and Stokes, 2006; Carmen *et al.*, 2016; Silinski *et al.*, 2018). A recent study on a single marsh plant, *Scirpus maritimus*, found that stems become more flexible with increasing wave

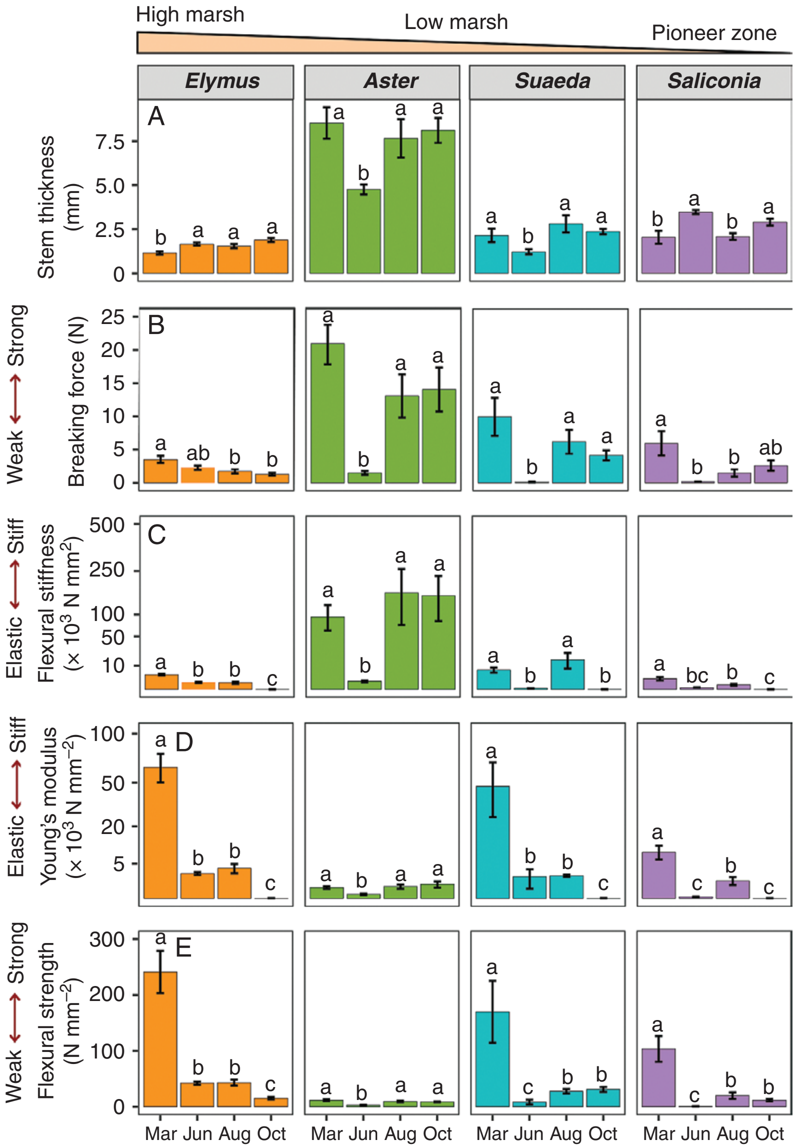

FIG. 7. Seasonal changes (mean ± s.e.) in stem thickness (A) and biomechanical properties (B–E) of *Elymus*, *Aster*, *Suaeda* and *Saliconia* along the elevation gradient. Different letters indicate significant differences ($P < 0.05$, Tukey's HSD test).

stress (Silinski *et al.*, 2018). The current study on multiple species along the salinity gradient and inundation gradient demonstrate that variation of biomechanical properties as a response to changing stress levels can even be bigger when inducing changes at the community level. Our results reveal that raised salinity levels in the low marsh can induce a shift from stiffer species such as *Phragmites* towards more flexible species such as the brackish marsh pioneer *Scirpus* and the salt-water pioneer *Spartina* (Fig. 2). Increased inundation may cause a shift in the low marsh from stiffer plants such as *Aster* to the more flexible species *Saliconia* or *Spartina* (Figs 3 and 4). This means that species shifts resulting from environmental changes such as salt water intrusion and alteration of freshwater discharge (Neubauer and Craft, 2009) may cause considerable changes in plant biomechanical properties and thus wave attenuation values.

Shoot length as a key driver of species differences in biomechanics

The current study highlights in particular that variation in biomechanical properties at the community level is closely related to differences in plant canopy height between species. Taller species tend to have stiffer and stronger stems than shorter ones (Fig. 4), which may result from the fact that taller plants generally need stronger shoots to support the higher biomass (Jagels *et al.*, 2018). A positive relationship between plant morphology and biomechanical properties has been similarly seen in other plant communities. A comprehensive analysis of the mechanical and morphological traits of seagrasses showed that larger leaves typically had higher leaf breaking force, to tolerate the greater drag forces due to the larger leaf area (Carmen *et al.*, 2016). The positive link between stem biomechanical properties and canopy height could explain the variation in stem

TABLE 6. *Stem density (mean ± s.d.) and canopy height (mean ± s.d.) of all the sampled species at the end of the growing season (September–October)*

Species	Stem density (no. m^{-2})	Sample size	Canopy height (cm)	Sample size
Phragmites	309 ± 103	10	236 ± 62	60
Scirpus	352 ± 75	20	103 ± 25	120
Spartina	1092 ± 269	20	51 ± 13	120
Saliconia	520 ± 49	5	25 ± 6	30
Suaeda	201 ± 69	5	62 ± 8	30
Aster	67 ± 38	5	110 ± 30	30
Elymus	1098 ± 143	5	36 ± 9	30

stiffness and breakability along salinity and inundation gradients. Increased salinity and inundation can induce a change of vegetation from taller plants towards shorter ones. As a consequence, plant stems shift from being stiffer and stronger towards being more flexible and weaker. In addition, while taller species tend to have higher thresholds for stem breakage, they may still break more easily than shorter ones due to the higher contact area with water (Vuik *et al.*, 2018).

Species-specific differences in seasonality may explain differences in stem breakage

Seasonality is a key environmental factor that governs plant functional traits such as canopy height (e.g. Liu *et al.*, 2004), stem diameter (e.g. this study, Singh *et al.*, 1990) and shoot density (e.g. Orth and Moore, 1986), yet its effects on plant biomechanical properties are generally overlooked in previous studies (but see Łoboda *et al.*, 2018). In this study, all examined species show seasonal variability in biomechanical properties, while the variation trend is species-specific. For instance, flexural strength of *Spartina* was highest in winter (December), whereas it was lowest for *Scirpus* in the same season (Fig. 6B). Such difference may explain the observed difference in stem breakage between these two species. *Spartina* can preserve most of its above-ground biomass until the end of winter, whereas most *Scirpus* stems break from autumn onwards (Vuik *et al.*, 2018). Information on seasonal variation in stem breakability is essential to enable accurate assessments of the flood protection value of coastal vegetation, as the timing of storms varies with geographical locations, and coinciding seasonal variations in storm intensity and vegetation characteristics determine to what extent vegetation may contribute to flood protection during storms (Moller *et al.*, 2014; Vuik *et al.*, 2016, 2018).

Effect of global change on the biomechanics of marsh vegetation

For the same species, biomechanical properties can differ between sampling locations as a response to variations in growing conditions such as salinity level and water depth. Yet such differences are negligible compared to the differences between species. These results suggest that environmental changes such as increased inundation period due to sea level rise or enhanced salinity because of salt intrusion would not result in major changes in plant biomechanical properties, unless they induce shifts in species. In addition to biomechanical properties, shifts in species also alter other properties in relation to wave attenuation such as stem density (Table 6), canopy height (Fig. 4, Table 6) and stem thickness (Figs 2 and 3). For instance, increased drought has shifted the dominant vegetation type in a Mediterranean salt marsh from the tall, dense and stiff *Spartina* to the short, sparse and more flexible *Saliconia* (Strain *et al.*, 2017). The changes in plant morphological traits and biomechanical properties will inevitably result in significant changes in wave attenuation values of the salt marsh (Bouma *et al.*, 2005, 2014; Ysebaert *et al.*, 2011; Vuik *et al.*, 2016).

Implications for modelling wave attenuation by coastal vegetation

The presented seasonal and species-specific data on stem bending strength (σ_{max}) can feed the stem breakage model that predicts storm wave-induced vegetation loss, based on physical conditions and vegetation properties including σ_{max} (Vuik *et al.*, 2018). This is crucial for enabling accurate calculation of wave attenuation during extreme conditions that remove weak plants (e.g. Moller *et al.*, 2014; Rupprecht *et al.*, 2017; Vuik *et al.*, 2018). Another essential input for calculating wave dissipation by coastal vegetation is bulk drag coefficient (Mendez and Losada, 2004), which is largely determined by stem flexibility (e.g. Bouma *et al.*, 2010; Vuik *et al.*, 2016; Rupprecht *et al.*, 2017). Yet, bulk drag coefficient (C_D) is determined usually by calibration of this parameter with respect to the Reynolds number (*Re*), based on experiments (Mendez and Losada, 2004; Moller *et al.*, 2014; Vuik *et al.*, 2016). Here, we advocate that data on stem flexibility (*EI*) of different species and seasons should be combined with measurements of flow regime and wave dissipation, to explore the possibility of establishing quantitative relationships between *EI* and C_D. Once such relationships are established, one can derive C_D of a certain species for a given season based on the corresponding *EI*. This would mean models for computing wave attenuation by different vegetation type at different seasons could be applied without experimental calibration of drag against observed dissipation.

CONCLUSIONS

Overall, the current study highlights the importance of season and environmental gradients in determining the biomechanical properties of coastal vegetation, which are key determinants for its wave attenuation capacity and thus its value as nature-based coastal defence. While previous studies underline the role of variability in plant mechanical traits as adaptation strategies to biotic (e.g. herbivory: Lucas *et al.*, 2000; Sanson *et al.*, 2001) and abiotic mechanical forces, such as wind (Cordero, 1999; Pigliucci, 2002) or hydrodynamics (Bouma *et al.*, 2005; Puijalon *et al.*, 2011; Silinski *et al.*, 2018), our study indicates that shifted biomechanical properties as a result of self-adaptation to changed environmental conditions can have cascading effects on the role of plants in climate adaptation. Detailed information on the biomechanical properties of the seven common salt marsh vegetation types can provide useful inputs for numerical models that seek to assess the spatial and temporal variation of wave attenuation by coastal vegetation, which is a vital but often ignored step in the design and implementation of nature-based flood protection. Our findings also suggest that climate change may cause major changes in coastal protection functions of salt marshes by inducing shifts in dominant species types, imposing long-term uncertainties over nature-based flood protection.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Fig. S1: (A) Set-up of the Instron three-point bending test; (B) a typical force–displacement curve.

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