RESEARCH ARTICLE

Unraveling plant strategies in tidal marshes by investigating plant traits and environmental conditions

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Abstract

Aims: Tidal marsh vegetation along estuaries is exposed to strong environmental gradients that determine which species — enabled through specific traits — can establish and persist. With these ecosystems under anthropogenic pressure, in-depth knowledge on the conservation of remaining tidal wetlands and restoration potentials is needed. In this study we elaborate the habitat conditions in the natural vegetation of the Elbe estuary and analyze: (a) which abiotic factors drive species composition; and (b) which species traits are key to the plants' strategies in this specific ecotone.

Location: Three sites in the Elbe estuary (river kilometer 671–703).

Methods: We collected data on soil nutrients, inundation period and wave height and sampled traits of the 17 most abundant plant species, which we analyzed by RLQ (three-table analysis, including environment variables [R], species abundance [L] and a species traits table [Q]).

Results: We detected a strong 'wave–disturbance–inundation gradient', which separated sparsely vegetated low-lying plots receiving high wave impact and exposed to long inundation periods, from high-lying plots showing dense vegetation and aerated soils. Close to the shore, plants showed low organ density and high investment into rhizomes, with a correlation of 0.72 between mass fraction of rhizome and phosphorus content of rhizome tissue. On higher elevations, plants strongly expressed traits relating to competition, like high allocation to stem biomass. Further, we found species with high leaf chlorophyll content showing low specific leaf area values and a negative correlation with the nutrient gradient.

Conclusion: The results of our study are particularly relevant for restoration measures in order to re-establish healthy marsh vegetation. However, changes in the environmental conditions, for instance stronger wave energies by a higher shipping frequency in the river channel and sea level rise may trigger changes in species composition through plant trait adaptations, for example by demanding a stem flexibility beyond what would be structurally feasible.

KEYWORDS
estuarine gradients, plant traits, RLQ, tidal marshes, trait response

1 | INTRODUCTION

Plants are affected by their abiotic and biotic environment and plant trait expressions mirror specific adaptations toward these environments, displaying a set of traits with strong response to the environmental constraints of a specific site (assembly rules, Keddy, 1992). Following the assembly rules, the environmental filters only allow for species that are able to cope with the environmental conditions and the interspecific competition (Weiher & Keddy, 1999). For example, as an adaptation to abiotic stress such as drought or soil salinity, plants produce scleromorphic plant tissue or grow succulent (Khan et al., 2000; Read & Sanson, 2003). With an increase of biotic stress such as competition for light, traits responsible for light capture become essential. These can include high allocation of biomass to stems and leaves and high canopy height (Poorter et al., 2012). Competition between species is another driver for different trait expressions and species composition (Weiher et al., 1998).

Across ecotones, the interface of two contrasting environments (Yarrow & Marín, 2007), trait expressions can vary strongly, depending on the extent of differences between the two adjacent systems. One such ecotone can be found in tidal marshes, which are situated along coasts and estuaries. Nowadays, tidal marshes are of high conservational value, as for instance they are home to many breeding birds, and at the same time, they face strong anthropogenic pressure as they are often alongside highly altered waterways (Eertman et al., 2002). For nature-based shoreline protection measures and the restoration of natural tidal bank vegetation (removal of stone fillings, plantation with suitable species), understanding the environmental conditions which filter for specific traits is essential. Whereas the specific trait responses of marsh plants toward the most important environmental gradients have been studied on the low elevations near the shore (Heuner et al., 2015; Carus et al., 2017a; Schoutens et al., 2019), research on the entire bank remains scarce.

Vegetation along the tidal bank is exposed to various environmental gradients: a disturbance gradient caused by wave energy is found along the elevation gradient, which decreases from the shore of the estuary to the high bank (Stiller, 2005). Perpendicular to the shore, the elevation gradient separates sites exposed to the tides with long inundation periods to less inundated, more elevated sites on the landward side. Nutrient availability is determined by dissolved nutrients from the water body, mineralized material within the vegetation and washed-in nutrients from landward sites. Depending on the extent of nutrient distribution in each of these areas, this creates a nutrient availability gradient. For salt marshes, nitrogen for example is known to be a limiting factor (Hopkinson & Giblin, 2008). Where the environmental factors create less stress (less salinity and inundation time) competition for both nutrients and light can be the driving factor. This concept was elaborated for salt marshes by Scholten et al. (1987) and also by Pennings and Callaway (1992).

Lastly, as a defining feature for marshes close to river mouths, a salt gradient runs parallel to the shore with higher salt concentrations at the river mouth and lower salt concentrations at the upstream sites (Cloern et al., 2017). Salinity also varies depending on the elevation and inundation frequency.

The trait-based approach offers many possibilities to study plant strategies and adaptations in the field (Kleyer et al., 2008) and various studies identified plant trait responses to abiotic conditions in coastal habitats (Coops et al., 1994; Silinski et al., 2016; Carus et al., 2017a; Rupprecht et al., 2017). In a coastal salt marsh for example, plant responses include traits relating to salt excretion or salt dilution by succulent growth (Flowers & Colmer, 2008). The specific impact of waves or flow velocities is also a frequent research subject: Brewer and Parker (1990) studied tensile properties of stems in moving water and found them to be an important factor for plant zonation (see Coops et al., 1994 for lakeshore zonation). Plants exposed to strong wave forces often show a high flexural stiffness (Rupprecht et al., 2015; Vuik et al., 2018). Bouma et al. (2005) have reported trade-offs between plant stiffness (withstanding waves) and experienced drag force. Adaptations to surviving long inundation periods include traits like aerenchymatic tissues or high oxygen content in rhizomes (Takahashi et al., 2014; Faußer et al., 2016). The advantage of being photosynthetically active under water is an ability found in some species like *Schoenoplectus tabernaemontani* and *Agrostis stolonifera* (Ellenberg & Leuschner, 2010).

Using the Elbe estuary in North Germany as a model system, our research questions are: (a) which are the most important environmental factors asserting the highest effect on plant distribution and traits; (b) are there trait differences between the vegetation at low and high elevations; and (c) which key traits can be identified in order to comprehend the underlying plant strategies? To address these questions, we quantified a range of important abiotic parameters, such as wave height, inundation period, salt concentration in the soil and soil nutrients (nitrogen, potassium and phosphorus content, soil carbon content). Furthermore, we identified plant traits responsive to the environmental conditions in this tidal marsh as highlighted by other studies (such as bending stiffness, biomass allocation and organ stoichiometry; Poorter et al., 2012; Minden & Kleyer, 2014; Silinski et al., 2015; Carus et al., 2016). Our hypotheses are: (a) plant species growing near the marsh edge are adapted to wave strength by a low bending stiffness (thereby reducing the risk of flower and fruit destruction by shear forces); (b) the inundation triggers a high investment in rhizomes and the ability to reproduce vegetatively; (c) plant species at higher elevations will show traits related to competition for nutrients and light, as they are exposed to higher competition from neighboring species; and (d) species sort into clusters based on similar adaptation patterns in this stressful environment and their resource usage. Through its effect on species composition, soil salinity has an impact on the clustering of plant strategies.

2 | METHODS AND MATERIALS

2.1 | Study sites

In the Elbe estuary in the northwest of Germany, three sites were chosen (Figure 1): Balje (53°51′30″ N, 9°4′30″ E), Krautsand (53°46′30″ N, 9°22′0″ E) and Hollerwettern (53°50′00″ N,

9°22′30″ E). Each site has a gradual sloped topography and relatively straight marsh edge. The climate is oceanic with an average temperature of 9.6°C, an annual precipitation of 831 mm and 1672 hrs of sunshine throughout the year (Cuxhaven, Wetterdienst, 2019). The soils are sandy–silty and in the Hollerwettern site they are influenced by deposition of sandy dredging material at higher elevations (Kappenberg & Fanger, 2007). There is no agricultural use on the sites, but the adjacent fields are used for grazing and fodder production. The elevations of the sites relative to the tidal range ($Znorm = \frac{Plot\ elevation\ -\ Mean\ Low\ Water}{(Mean\ High\ Water\ -\ Mean\ Low\ Water)}$; Heuner et al., 2019) are between 0.54 and 1.35 (Mean Low Water, MLW = 0; Mean High Water, MHW = 1). Soil salinity varies between on average 0.2 and 4 PSU (own measurements; Practical Salinity Unit as a measure of salinity based on water conductivity).

2.2 | Plot selection and vegetation zones

We selected 84 non-contiguous plots (4 m × 4 m) across the three sites, with 28 plots per site. Sampling was conducted between March 2016 and September 2017. Plots were selected by random stratified sampling at a minimum distance of 20 m from each other to avoid interferences, with the strata being elevation relative to the tidal range and vegetation zonation. The elevation was measured for each plot with a real-time kinematic global positioning system (GPS). Within the strata, the natural vegetation zonation consisted of three dominant species occurring in four different zones, which in the following text will be named after their dominant species. Each zone contained seven plots per site, species accompanying the dominant species varied between sites. The *Schoenoplectus tabernaemontani* zone is closest to the marsh edge (Pott, 1995). *Schoenoplectus tabernaemontani* can occur up to 2 m under the mean high tide level (MHW; Kötter, 1961) and is often the only species growing on the marsh edge in the study sites. *Bolboschoenus maritimus* can be found at higher elevations

(*Bolboschoenus maritimus* zone, also often the only species present) and is followed higher up the bank by *Phragmites australis* (Ellenberg & Leuschner, 2010). In this latter zone from about 0.5 m below MHW, *Phragmites australis* grows in monotypic stands (*Phragmites australis* zone), away from turbulent hydrodynamics, as it is sensitive to mechanical stress (Coops et al., 1994; Ellenberg & Leuschner, 2010). From 1 m above the MHW, *Phragmites australis* is less competitive and other species, such as *Juncus gerardii* or *Mentha aquatica* are able to establish; this zone has been defined as *Phragmites australis*/mixed community.

2.3 | Abiotic parameters

Inundation was recorded at 24 plots (two in each vegetation zone for each of the three study sites). We installed 80-cm long drainage pipes (8 cm diameter), covered with a coconut layer to prevent sediment intrusion from the sides and covered with a cap to prevent penetration of sediment from the top. The pipes were oriented vertically in the ground and were equipped with pressure loggers (SENSUS ULTRA by Reefnet, ON, Canada). The sensors recorded hydrostatic and atmospheric pressure hourly between March and October 2016. To record the corresponding air pressure, three additional loggers were attached to buildings nearby (Minden & Kleyer, 2014). The measurements were used to correct for atmospheric pressure and to calculate the water depth in the submerged pipes. To extrapolate the water depths onto the other plots, a regression was made for each site separately between the elevation and the water depth. In this way inundation period was determined as the time when the water level was above or equal to ground level and expressed as hours per day.

Wave heights were recorded on one transect per site between December 2015 and April 2017 (Schoutens et al., 2019) with nine pressure sensors (P-Log3021-MMC, Driesen & Kern, Bad Bramstedt, Germany). This transect spanned an elevation gradient from the

FIGURE 1 Position of study sites in the Elbe estuary with 28 plots each distributed over four different vegetation zones ranging from the edge of the mudflat to the high bank. The vegetation zones are illustrated for Hollerwettern, with *Schoenoplectus tabernaemontani* zone (white circle), *Bolboschoenus maritimus* zone (white triangle), *Phragmites australis* zone (white square), *Phragmites australis*/mixed community zone (white x). ATKIS® Base-DLM (left);©OpenStreetMap contributors (middle). © 2016 WSV, BfG, BAW (right)

shore to the high bank with measurement points (three per transect) between the different vegetation zones. The measurements (frequency of 8 Hz) were referenced to water surface elevation by correction of atmospheric pressure. The tidal signal was separated from the wave signal, but it was not distinguished if the waves were caused by wind or passing ships. A detailed description of the recording method for wave data can be found in Schoutens et al. (2019).

The mean wave height was used in this analysis (Heuner et al., 2015), extrapolated for all plots and calculated for each plot for three different water depth categories: <0.5 m, 0.5–1.0 m and >1.5 m. This was done because the wave height typically depends on the water depth (Schoutens et al., 2019), and the water depth varies over time (due to the tides) and spatially between the plot locations (due to different soil surface elevations). The value for wave impact in the water depth category <0.5 m for instance denotes the mean wave height in shallow water up to 0.5 m depth (description of extrapolation see Appendix S1).

Soil salinity was measured in the top soil following Schlichting et al. (1995) by determination of the conductivity: 10 g fresh soil was diluted with 25 ml H_2O, left for 30 min and conductivity measured in the excess water (WTW ph/Cond340i/SET, Tetracon 325 electrode, Weilheim, Germany). Then salinity was calculated using the UNESCO equation (UNESCO, 1981; Grasshoff et al., 1983). On each plot, the soil was sampled up to a depth of 60 cm and bulk density (g cm^{-3}) was determined for 200 cm^3 for each characteristic soil horizon by weighing a fresh and dried sample (48 hr at 105°C; Schlichting et al., 1995). Bulk density results were used to relate the analyzed soil parameters to volume and area at plot level, by multiplying the nutrient content with the mass per m^2 (derived from soil density multiplied by m^3 for each soil horizon). From the soil samples, grain size distribution (%) was determined with a Laser Particle Sizer (Analysette 22, Idar-Oberstein, Germany), using H_2O_2 to remove organic substances and subsequently related to soil horizon depth and volume and expressed as kg m^{-2}. The phosphorus (P) and potassium (K) contents (g m^{-2}) were determined following the method of Egnér et al. (1960) and measured in a continuous flow analyzer (CFA for phosphorus) or in an Atomic Adsorption Spectroscope (AAS for potassium). Calcium carbonate ($CaCO_3$) content (kg m^{-2}) was measured following Scheibler´s gasometric method (Schlichting et al. 1995). Ammonium (NH_4^+) and nitrate (NO_3^-) contents were determined using the incubation method following Gerlach (1973). The measurements were done with a continuous flow analyzer (CFA) at 660 nm (ammonium) and 540 nm (nitrate). Mineral nitrogen (N_{min}) is the sum of ammonium and nitrate, expressed in g m^{-2}. Soil carbon (C) and total nitrogen (N) contents were analyzed employing a C:N-Analyzer (Flash 2000, Thermo Scientific, WA, USA) following Allen (1989).

As a measure of vegetation density, photosynthetically active radiation (PAR) reaching the ground was recorded with a SunScan (Canopy Analysis System SS1, Cambridge, UK; see Maier et al., 2010), using the mean of at least five measurements at each plot 5 cm above the ground. One additional measurement was done near the plot in full light (i.e., above the vegetation). PAR was expressed as the percentage of the total radiation (Maier et al., 2010).

2.4 | Frequency analysis of plant species

The composition of plant species was determined with a frequency frame (50 cm × 50 cm), which contained 25 cells (each 10 cm × 10 cm) and was used four times per plot to cover an area of 1 m^2 (Tremp, 2005; Minden et al., 2012; Cebrián-Piqueras, 2017). In each cell, presence and absence of each species was recorded. Species were determined using by literature (Schmeil & Fitschen, 2003; Rothmaler, 2007). From the resulting species list, we selected a total of 17 species for which plant trait information was then collected. These species were selected so that they were present in at least 95% of frequencies recorded (Cornelissen et al., 2003). Information on species names and their occurrence in the specific zones is provided in the supporting information, Appendix S2.

2.5 | Trait measurements

Trait information was based on a total of 175 plant individuals (at least 10 individuals per species). The individuals were selected following Pérez-Harguindeguy et al. (2013): mature, healthy-looking and randomly picked from all suitable individuals of that plot. Sampling was conducted across the three sites, covering the largest range of elevations possible, i.e., the highest and lowest-lying plot on which the species appeared, see Appendix S3 for details on species numbers collected. Plants were collected at the peak of their generative stage, i.e., when seeds were ripe but not yet shed (Minden et al., 2012). Individuals were dug out with a 20 cm × 20 cm soil volume; roots and rhizomes were cleaned with water and separated from roots belonging to other individuals with tweezers. Then plants were dissected into stems, leaves, roots and rhizomes. For the grass species, the leaf area was determined from the leaf blades, whereas the sheaths were assigned to the stems (following Yan et al., 2016). For *Schoenoplectus tabernaemontani*, a species that does not produce leaves, the stem was treated as equivalent to a leaf, and only the below-ground part that did not produce chlorophyll was considered as stem. For species producing petioles, they were excluded from specific leaf area (SLA) measurements (Pérez-Harguindeguy et al., 2013).

Traits measured for all plant samples include: canopy height (cm) in the field (highest point on highest fully developed leaf; Weiher et al., 1999), specific leaf area measured on two leaves per individual (SLA, [mm^2 mg^{-1}]) using a flatbed scanner (300 dpi) and ImageJ-Software (Schneider et al., 2012). The chlorophyll content was measured in the field for each plant individual with a SPAD 502Plus (Konica Minolta, Tokyo, Japan), creating a mean of 10 measurements in "SPAD" units, which are derived from the absorbance at 650 nm and 940 nm ($\pm$61 SPAD; Süß et al., 2015). To relate this to the actual chlorophyll content of trait individuals at harvest time, SPAD values of additional leaf samples of the same species were determined (at least eight leaves per species with 20 measurements for each leaf). Of each of those leaves the area of 250 mg fresh leaf was determined

(flatbed scanner 300 dpi, ImageJ-Software), plant material was ground with acetone (80%, 10 ml) and silica sand (Lichtentaler, 1987) and filtered. The filtrate was diluted with acetone to 25 ml of total volume (Uddling et al., 2007) and chlorophyll content was analyzed in a spectrophotometer (Genesys 10 UV, Thermo Spectronic, Braunschweig, Germany) at 646 nm and 663 nm (Lichtenthaler & Buschmann, 2001). Total content of chlorophyll was calculated for the dry mass of the analyzed leaf area through the establishment of a calibration curve for each species, predicting the chlorophyll content ($\mu g\ mg^{-1}$) for each trait plant individual and its mean SPAD value, and related to the content per leaf area ($\mu g\ mm^{-2}$).

The bending properties of fresh stem samples were tested by sampling at least 20 stems per species across the three sites, harvested separately from the other trait measurements. Samples were kept cool and moist and bending tests completed within a few days at the Royal Netherlands Institute for Sea Research (NIOZ Yerseke, NL) with the Instron 5942 (Canton, MA, USA; Heuner et al., 2015; Rupprecht et al., 2015). The measurement depends on the architecture of the stem and different equations were used to calculate the flexural stiffness, which is the product of the resistance of the stems to bending (Young´s modulus [MPa]) and their cross-sectional area, expressed in N mm^2 (Coops & Van der Velde, 1996; Hamann & Puijalon, 2013; Heuner et al., 2015; Rupprecht et al., 2015; Vuik et al., 2018; for a detailed description of the calculations and a summary table of the equations used, see Appendix S4).

The mass per volume (g fresh mass cm^{-3}) and specific density (g dry mass cm^{-3}) of stems, roots, and rhizomes was determined using volumetric flasks. Root and rhizome samples (two samples of 2 cm length each) of each trait plant were weighed fresh and measured in length and all material was finally dried (72 hr at 70°C) and weighed. Specific root and rhizome length was expressed as mm per g dry mass; the dry matter content of each organ was the ratio of its dry mass to its fresh mass (mg dry mass per g fresh mass). Plant investment into each organ was expressed as mass fraction for leaves, stem (MF_{stem}), roots (MF_{roots}) and rhizome ($MF_{rhizome}$; g organ dry mass per g total dry mass). For each individual and plant organ, carbon (C), nitrogen (N) and phosphorus (P) content (g kg^{-1}) were determined. C and N content was analyzed by grinding the material in a mill ("pulverisette 7," Fritsch, Idar-Oberstein, Germany) and using the C:N-Analyzer analogous to the soil sample treatment. P content was extracted from the milled material (7–8 mg, precision balance CP 225 D, Sartorius, Goettingen, Germany) by heating the sample with nitric acid (95°C, 6 hr) and adding hydrogen peroxide (30%, 95°C, 4 hr). Finally, the volume was raised to 1 ml by addition of water (bidest) and measured in the CFA, following Murphy and Riley (1962). Mean trait values of all species can be found in Appendix S5.

2.6 | Statistical analysis

All maps were visualized with ArcGIS (ESRI, version 10.2.1), and the statistical analyses were performed with the open-source software

R version 3.4.3 (R Core Team, 2017) and RStudio (RStudio Team, 2016).

To test the effects of the study sites and the different vegetation zones on the environmental variables, we applied linear models for each environmental variable with vegetation zone (four levels) and study site (three levels) as explanatory variables. As we were only interested in the effects of vegetation zones on the measured variables, we treated the study sites as random effects (lmer[environment~zone+{1|site}], R-package *lme4*; Bates et al., 2015). To test for significant differences between the vegetation zones, we applied a post-hoc test (least-squares means) to each model (R-package *emmeans*; Lenth, 2020). The degrees of freedom are based on the Kenward–Roger method; test results are shown in Appendix S6.

To elaborate the relations between variables, a three-table analysis (RLQ) was performed, using the *ade4* package (Delédec et al., 1996; Dray & Legendre, 2008). One table contained the environmental parameters (R table), one table the species' abundances (L table) and one table the species' traits (Q table), for which the mean trait values for each species were used.

All environmental parameters were tested for normal distribution (Royston, 1982; R-Package *stats*), wave impact at water levels >1.5 m was transformed using Box–Cox, and by using logit on PAR (both with the R package *car*; Fox & Weisberg, 2019), wave impact at water levels >0.5 m was transformed to the power of 3, while log10 was used for salinity, N_{min}, clay, soil P and soil K (Becker et al., 1988; R package *base*). For the trait variables, stem flexural stiffness and total above-ground mass were log-transformed, total below-ground mass was Box–Cox-transformed and below-ground biomass specific density was transformed using log10.

Variables were aggregated if they were highly correlated and could be assigned to known concepts like allometric scaling of plant organ size (Garnier et al., 2016). Highly correlated variables showed $r > 0.3$ (environmental variables) and $r > 0.5$ (trait variables), as well as $p < 0.05$. Hereby the aggregate values were the scores of the first axis of a principal components analysis (PCA) performed on the variables. Environmental variables aggregated were: sand and clay which run reciprocally (silt was only weakly correlated) as "Grain size." P and K correlated negatively (−soil P, +soil K). Wave impact at water levels >0.5 m was aggregated with wave height at water levels >1.5 m (see Table 1). The measured soil C and N content were excluded from the actual analysis, as nitrogen availability was represented by soil N_{min}. However, as soil C and N delivered valuable background information for interpreting our results, they remained part of our data set and are presented in Appendix S7. Plot elevation was not included in the RLQ either, as the elevation was represented in the variables for inundation and wave impact (see Table 1 for summary of aggregated variables and Table 2 for all variables. For information on elevation and soil C:N ratio, see Appendix S7).

The plant traits canopy height, total below-ground and above-ground biomass and total leaf area were aggregated as "size." Stem specific density and stem mass per volume, the specific density of below-ground biomass and its volume were aggregated as "low density and high volume." Specific leaf area (Noble & Slatyr, 1980) and

TABLE 1 Variables aggregated with Principal Components Analysis (PCA) with their explained variance of the first two PCA axes and correlation coefficients with the first two axes

Aggregated variables	Aggregated variables with their positive or negative associations	Cumulative proportion explained		Correlation coefficients	
		Axis 1	Axis2	Axis 1	Axis 2
"Grain size"	+ Sand	0.87	1.00	−0.71	0.71
	− Clay			0.71	0.71
Soil P, K	− Soil P	0.68	1.00	−0.71	0.71
	+ Soil K			0.71	0.71
Wave impact at water level >0.5 m	+ Wave impact 0.5–1 m water level	0.88	1.00	0.71	0.71
	+ Wave impact >1.5 m water level			0.71	−0.71
"Size"	+ Canopy height	0.75	0.94	0.47	0.59
	+ Below-ground biomass			0.55	0.11
	+ Above-ground biomass			0.56	−0.04
	+ Total leaf area			0.39	−0.80
"Low density and high volume"	− Stem specific density	0.59	0.83	−0.52	0.45
	− Fresh mass/volume stem			−0.58	0.19
	− Specific density below-ground biomass			−0.55	−0.15
	− Fresh mass/vol. below-ground biomass			−0.31	−0.86
− SLA + chlorophyll	− SLA (specific leaf area)	0.81	1.00	−0.71	−0.71
	+ Chlorophyll content			0.71	−0.71

Note: Correlation coefficients between the variables were >0.36.

chlorophyll content were aggregated because of the relationship between SLA and photosynthesis (Leaf Economics Spectrum; Wright et al., 2004). A standard major axis regression was performed to highlight their relationship (SMA, R package *smatr*; Warton et al., 2006, 2012). This analysis can be used when similar measurement errors are associated with both variables (Cui et al., 2020). Below-ground biomass was represented in rhizome and root mass fraction (MF), to mirror nutrient storage and anchorage requirements. Similar to the nutrient status of the soil, the nutrient content of plant rhizome tissue was represented by phosphorus content alone, as adding plant tissue N and C did not add to the explained variance.

The aim of this study was to analyze the three tables that contain the data on species frequencies, plant traits and environmental data. For this purpose, a three-table analysis (RLQ) was performed, which follows a step-wise process. In order to analyze the R, L and Q tables together, a PCA was performed on both the R and Q tables and a Canonical Correspondence Analysis (CCA) on the species table (Legendre & Legendre, 2012; R package *vegan*). Then the PCAs and CCA were analyzed simultaneously. Significance of the RLQ was tested with randtest (Dray & Dufour, 2007, R package *ade4*). Based on the resulting species scores, the species were clustered into functional groups (Ward´s method; Wang et al., 2015), establishing the optimal grouping with the Caliński criterion (Caliński & Harabasz, 1974) and the *stats* package (R Core Team, 2017). The clusters highlight sets of traits that species growing under similar environmental conditions might have in common.

3 | RESULTS

3.1 | Environmental conditions

The four zones that were categorized using species' distributions differed in their environmental conditions. The relative elevation significantly increased from the *Schoenoplectus tabernaemontani* zone, to the *Bolboschoenus maritimus*, to the *Phragmites australis*, to the *Phragmites australis*/mixed community zone (see Figure 2 and Appendices S2 and S7). Accordingly, the inundation period was the longest at low elevations and differences existed between the *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus* and *Phragmites australis* zones. For the wave heights at all water levels, significant differences existed between all the zones. Soil salinity varied most strongly between the sites in the *Schoenoplectus tabernaemontani* zone; the highest values were around 3 (PSU), but were mostly below 1. The results yielded significant differences for soil salinity between the *Bolboschoenus maritimus* zone and the *Phragmites australis*/mixed zone, and for $CaCO_3$, only the *Bolboschoenus maritimus and Schoenoplectus tabernaemontani* zones were without significant differences. For sand content, significant differences existed between the *Schoenoplectus tabernaemontani* zone and the *Phragmites australis* and *Phragmites australis*/mixed zones; for soil P and K there were no differences (K content showed high variances, which, like the salinity, was strongly influenced by proximity to the sea). For N_{min} there were significand differences between *Phragmites australis*/

TABLE 2 Variables used in the RLQ, variables aggregated and correlations with the first and second RLQ axis

Variables	Positive or negative associations of aggregated variables	Unit	Correlation coefficients	
Environment			**Axis 1**	**Axis 2**
Inundation		hr day^{-1}	0.87	−0.36
Soil salinity		PSU	−0.13	0.86
"Grain size"	+ Sand	kg m^{-2}	−0.10	−0.06
	− Clay	kg m^{-2}		
CaCO$_3$		kg m^{-2}	0.53	0.18
Soil P, K	− Soil P	g m^{-2}	−0.29	0.67
	+ Soil K	g m^{-2}		
N$_{min}$		g kg^{-1}	−0.53	0.26
Wave impact at water level <0.5 m		m	0.90	0.24
Wave impact at water level >0.5 m	+ Wave impact 0.5–1 m water level	m	−0.97	−0.10
	+ Wave impact >1.5 m water level			
PAR		%	0.77	0.07
Traits				
"Size"	+ Canopy height	cm	0.12	−0.88
	+ Below-ground biomass	g		
	+ Above-ground biomass	g		
	+ Total leaf area	mm^2		
"Low density and high volume"	− Stem specific density	mg dry mass cm^{-3}	0.91	−0.18
	− Fresh mass/volume stem	g fresh mass cm^{-3}		
	− Specific density below-ground biomass	mg dry mass cm^{-3}		
	− Fresh mass/vol. below-ground biomass	g fresh mass cm^{-3}		
− SLA	− SLA (specific leaf area)	mm^2 mg^{-1}	0.84	−0.73
+ Chlorophyll	+ Chlorophyll content	µg mm^{-2}		
Flexural stiffness		N mm^2	0.50	−0.80
P in rhizome		g kg^{-1}	0.98	−0.37
MF stem		g$_{(stem)}$ g$_{(all)}^{-1}$	−0.10	0.68
MF rhizome		g$_{(stem)}$ g$_{(all)}^{-1}$	0.87	−0.65
MF root		g$_{(stem)}$ g$_{(all)}^{-1}$	−0.09	0.01

Abbreviations: PAR, photosynthetically active radiation; SLA, specific leaf area; MF, mass fraction; PSU, practical salinity unit.

mixed and all other zones. For PAR, the *Schoenoplectus tabernae-montani* zone was significantly different from all other zones. For details on test results, see Appendix S6.

3.2 | Explained variances for environmental and trait Principal Components Analysis

For the environmental variables, the PCA (significant at $p < 0.005$) explained 42.04% of the variance in the data set on the first axis and 18.43% on the second axis. The first axis was driven by hydrodynamics, with waves at low water levels and inundation duration positively connected to it. Soil salinity and nutrients were connected to the second axis. For the trait data, the explained variance in the data set through the PCA (significant at $p < 0.05$) was 50.84% on the first axis (associated with specific density and belowground MF) and

22.75% on the second axis (connected to canopy height and stem stiffness). For correlation coefficients between the original variables, see Appendix S8.
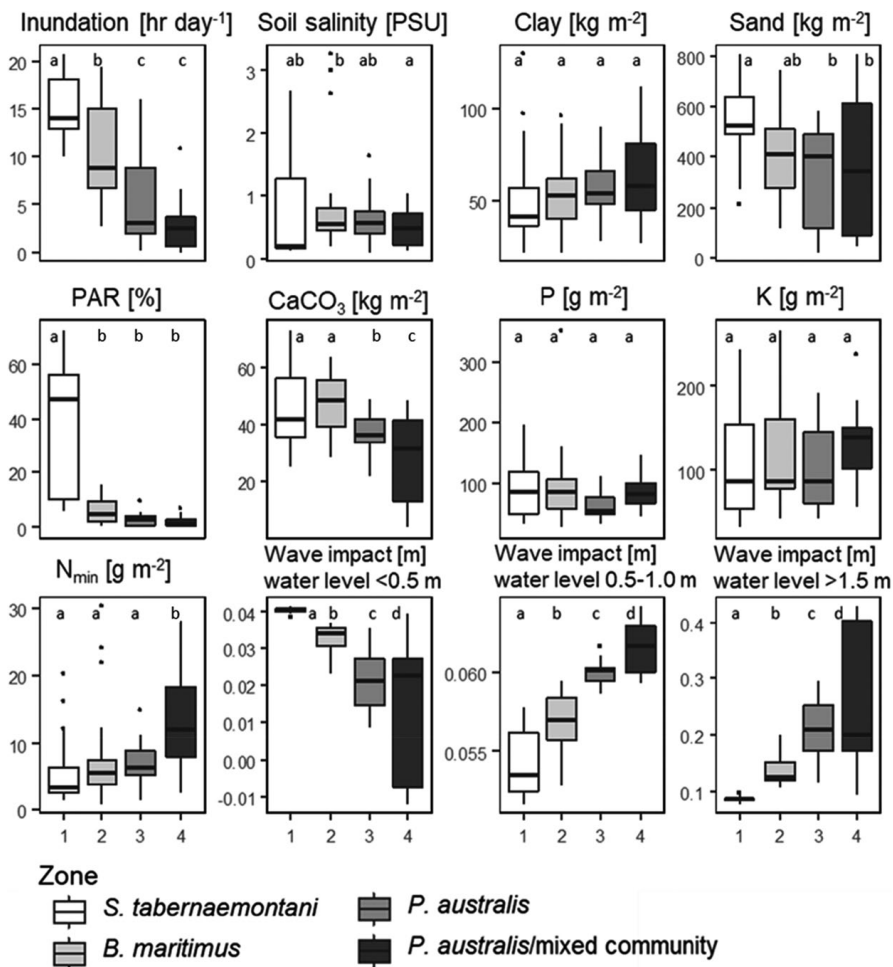
3.3 | Links between environment and plant traits — RLQ Analysis

The first RLQ axis (Figure 3, Table 2) explained 95.7% of the total variance. The second axis explained 3.35%. The analysis was significant with $p < 0.005$. The variance of the environmental scores was preserved with 91%, and of traits scores with 93% of the original PCA scores.

The strongest environmental gradients along the first axis were wave impact at water levels > 0.5 m (correlation coefficient with the first axis −0.97); a positive correlation existed for wave impact at

FIGURE 2 Environmental conditions per vegetation zone across the three study sites. *Schoenoplectus tabernaemontani* occurs at the lowest elevations, followed by dominant *Bolboschoenus maritimus*, then *Phragmites australis* and at the highest elevations *Phragmites australis/* mixed community occurs with a mixture of species. Significant differences between the zones are indicated with different letters, $p < 0.05$; for details on the significance test, see Appendix S6. For information on species zonation, plot elevation and soil C:N ratios, see Appendix S7. PSU, practical salinity unit; PAR, photosynthetically active radiation; N_{min}, plant-available nitrogen
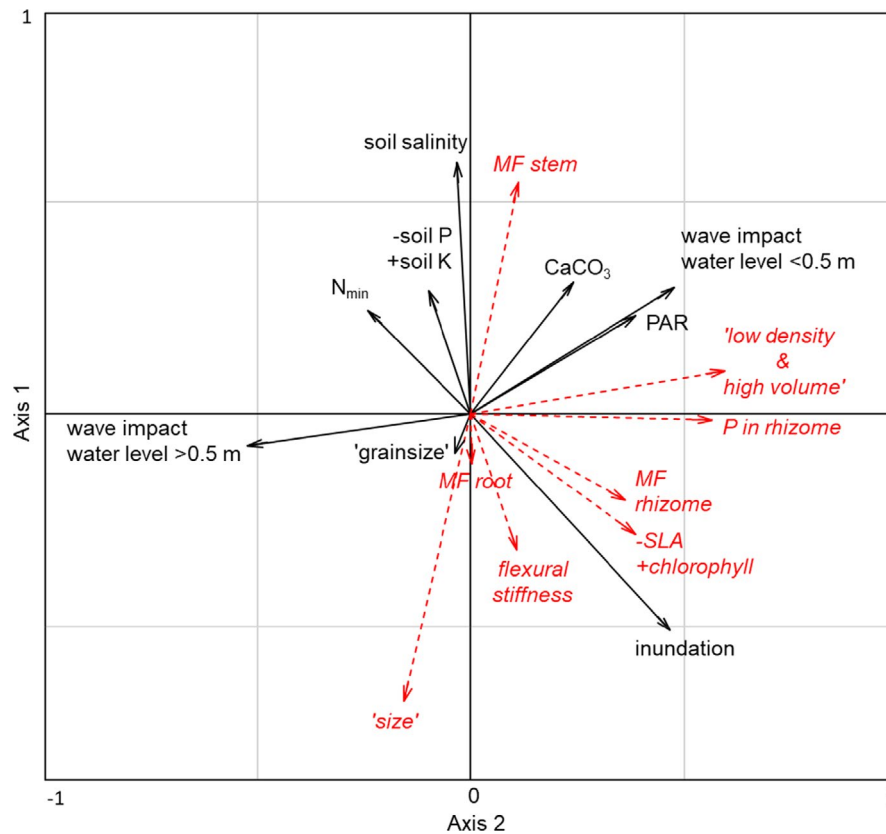
water levels <0.5 m with the first axis (0.90), inundation (0.87) and photosynthetically active radiation at ground level (PAR, 0.77). As such, this set of variables spanned a "wave disturbance–inundation gradient" along the first axis with low-lying sites receiving high wave impact and being exposed to long inundation periods. Additionally, these low-lying sites were characterized by sparse vegetation, where radiation at the soil surface was high. Opposite to this, the high-lying sites showed dense vegetation and aerated soils — here, the highest wave impact was at water levels > 0.5 m.

Further, $CaCO_3$ was positively correlated with the first axis (0.53) and higher on lower-lying sites. N_{min} was significantly lower in the *Schoenoplectus tabernaemontani zone* and highest at high elevations with short inundation durations (Figure 2).
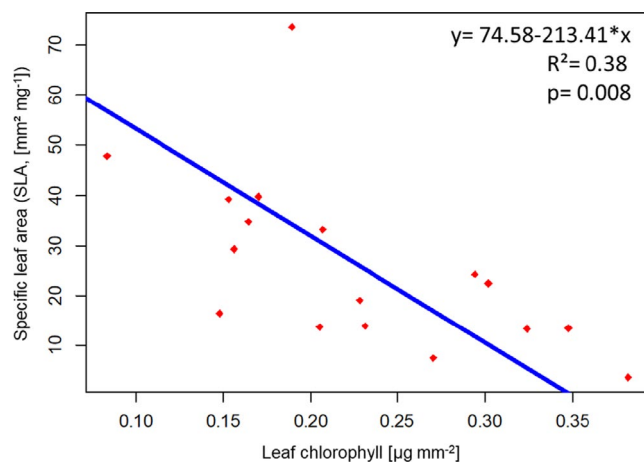
The second RLQ axis revealed a "salinity–nutrient" gradient, with phosphorus running reciprocally to potassium and soil salinity (0.86, Table 2). Plots with high influence of sea water also contained higher potassium levels whereas the less saline sites had more soil phosphorus, which was likely due to riverine input. Grain size showed very weak correlations with both the first two axes (−0.10, −0.06). The accounted variance of the second axis was very small (3.35%), which suggests that the effects of nutrient availability and salt are by far of lesser importance in the studied tidal marshes than the effects of inundation and wave impact.

Connected with the "wave disturbance–inundation" gradient, traits associated with lightweight material ("low density and high volume") were found at low-lying sites with long inundation durations (Figure 3). This aggregate only showed a high correlation with the first axis (0.91), highlighting the strong influence of the wave impact and inundation on it: plant tissue was voluminous and relatively light and plants showed a high content of phosphorus in the rhizomes, indicated by a positive correlation with the first axis (0.98). Additionally, the aggregate containing SLA and chlorophyll content showed a positive correlation with this axis ("wave disturbance\–inundation," 0.84), and a negative with the second axis (−0.73, Table 2): Plots with long inundation periods were characterized by plant species with a small SLA and high chlorophyll content per area (Figure 3). The bivariate relationship of chlorophyll content and SLA is highlighted in Figure 4 and the orientation of the SLA–chlorophyll aggregate within the RLQ to plots with long inundation duration is visible in Figure 3. The "size" gradient, on the other hand, is strongly negatively correlated with the "salinity–nutrient" gradient (i.e., with the second axis, −0.88), as is flexural stiffness (−0.80): tall species with a high biomass in below-ground and above-ground organs showed a large total leaf area and stiff stems; the flexural stiffness increased with plant size. Stem MF was highest where soil potassium was highest and

FIGURE 3 Ordination diagram of the RLQ analysis displaying the environmental variables (black solid lines) and the plant traits (red dashed lines). Inundation, water ≥ ground level; soil salinity, salinity in topsoil; "Grain size," aggregate −clay and +sand, $CaCO_3$ = carbonate; −soil P, +soil K, aggregate phosphorus and potassium; N_{min}, plant-available nitrogen; wave impact at water level <0.5 m, wave height at all water levels <0.5 m; wave impact at water levels >0.5 m, aggregate of variables for wave height >0.5 m; PAR = photosynthetically active radiation; "size," aggregate of canopy height and above- and below-ground biomass and total leaf area; "low density and high volume," aggregate of stem and below-ground biomass density and fresh mass per cm^{-3}; −SLA, +chlorophyll, aggregate of specific leaf area and leaf chlorophyll; flexural stiffness, flexural bending stiffness of stem; P in rhizome, phosphorus content in rhizome; MF stem, mass fraction stem; MF rhizome, mass fraction rhizome; MF root, mass fraction root. Correlation coefficients with the RLQ axes are given in Table 2

FIGURE 4 Standard major axis regression (SMA) of specific leaf area (SLA) and leaf chlorophyll content. Single data points are means of all trait measurements for each species

inundation was lowest and showed strong correlations with the second axis ("salinity–nutrient," 0.68). On the other hand, the

rhizome MF showed strong correlations with both axes (0.87, −0.65). The root MF was only weakly correlated to any of the gradients.
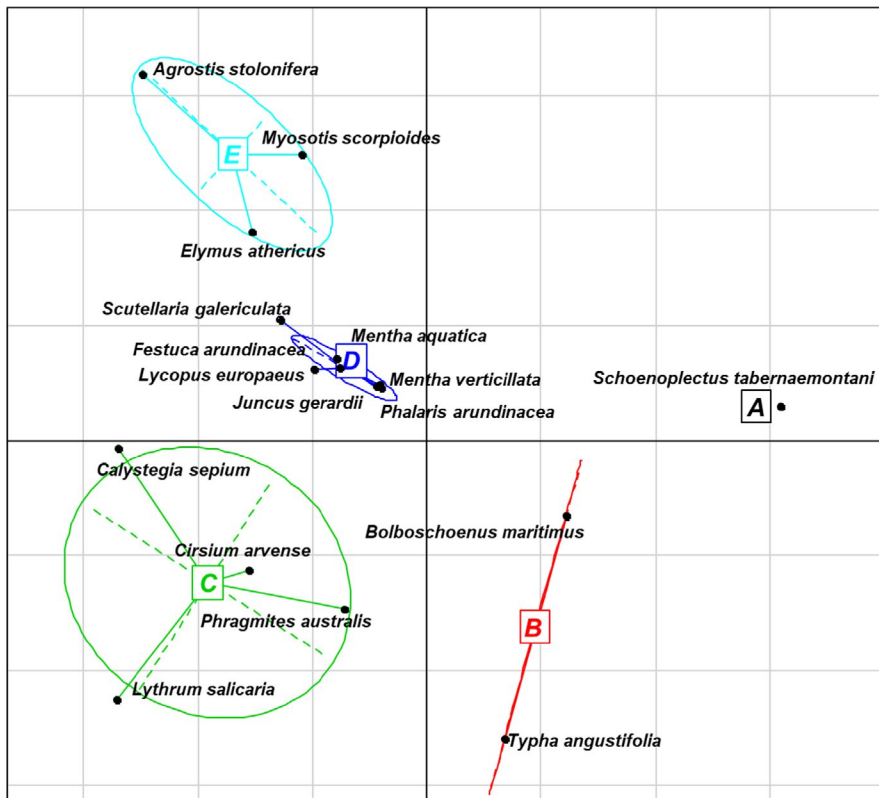
3.4 | Species cluster analysis

The cluster analysis yielded five stable functional groups for the trait species sampled (Figures 5 and 6, clusters A to E). Cluster A encompasses one species, *Schoenoplectus tabernaemontani*. Characteristic for this species is its low tissue density and high volume of stems, rhizomes and roots, high chlorophyll content and phosphate in the rhizomes (i.e., high scores for the −SLA, +chlorophyll aggregate, Figure 6c, e) associated with the detected gradients of Figure 3. The species strongly responds to the "wave disturbance–inundation" gradient along the first RLQ axis (Figures 3, 5, 6b). *Schoenoplectus tabernaemontani* grows where the wave impact in shallow water is highest and inundation durations are long. Cluster B contains two species, *Bolboschoenus maritimus* and *Typha angustifolia*, both producing high above- and

below-ground biomass ("size"), with a very stiff stem. Those trait variables are connected to the second RLQ axis, the "salinity–nutrient" gradient. Further, these species have a high rhizome MF which responds to the "wave disturbance–inundation" gradient as well (Figure 6a, d, g). The species of cluster C, *Cirsium arvense*, *Lythrum salicaria*, *Calystegia sepium* and *Phragmites australis* are grouped through the same traits as *Bolboschoenus maritimus* and *Typha angustifolia*. They too are similar in relation to their large size, low SLA, high chlorophyll and high flexural stiffness traits, with substantial investment into below- and above-ground biomass and a large total leaf area ("size," "salinity–nutrient" gradient). Their biomass is more dense than those of the species of cluster B (responding to the "wave disturbance–inundation" gradient) and they show a high root MF (Figure 6a, b, h). This cluster is found at intermediate elevations, where wave impact is highest only at deep water levels (when water levels exceed vegetation height). Cluster D contains species that have intermediate trait values regarding all of the sampled traits, with species growing on the less disturbed side of the gradient compared to clusters A–C; it includes *Mentha aquatica*, *Mentha verticillata*, *Juncus gerardii*, *Phalaris arundinacea*, *Lycopus europaeus*, *Festuca arundinacea* and *Scutellaria galericulata*. Cluster E is determined through the small size of its plants, high tissue density, high SLA and low chlorophyll per area, located on the other end of the "wave disturbance–inundation" and "salinity–nutrient" gradient compared to cluster A (Figure 6a, b, c). In our hypothesis, we expected traits typical for light and nutrient competition under these less stressful growing conditions. The cluster contains *Agrostis stolonifera*, *Myosotis scorpioides*, and *Elymus athericus* — those species are growing on higher elevations with

high stem mass fractions and a relatively small investment into below-ground organs (Figure 6).

4 | DISCUSSION

Unraveling the effects of abiotic parameters on plant traits and plant zonation in tidal marshes allows predictions of the changes in environmental conditions on plant performance and the development of conservation measures to protect them. The main findings in this study are that wave impact (height) and inundation period are by far the most important factors that determine species presence and trait expressions in the study sites. Trait responses of plants growing at low elevations to those parameters include lightweight material, strong investment into rhizomes and high leaf chlorophyll content. Contrary, at higher elevations, plants are stiffer and show a high SLA. The sampling design and the selection of individuals of a trait-species growing at different elevations, might have neglected to account for their possible plastic response within the stand; therefore, the findings of the present study have to be carefully discussed, with this issue in mind. The species' plasticity as a response to environmental factors is an important aspect in this context (Carus et al., 2016; Zhu et al., 2018), but was not the focus of this study, which was based on the mean trait values of all sampled individuals per species. The results of our RLQ analysis confirm findings of previous studies that found stem flexural stiffness and investment into rhizomes connected to hydrological gradients (wave height and inundation period). The results from our study indicate that soil nutrients and salinity only play a minor role, gaining more importance at higher

FIGURE 5 Species clusters (A–E) in the environment–trait space with respective species names. Cluster were based on trait scores, see boxplots in Figure 6. Ward´s method and the Caliński criterion were used to establish the clusters
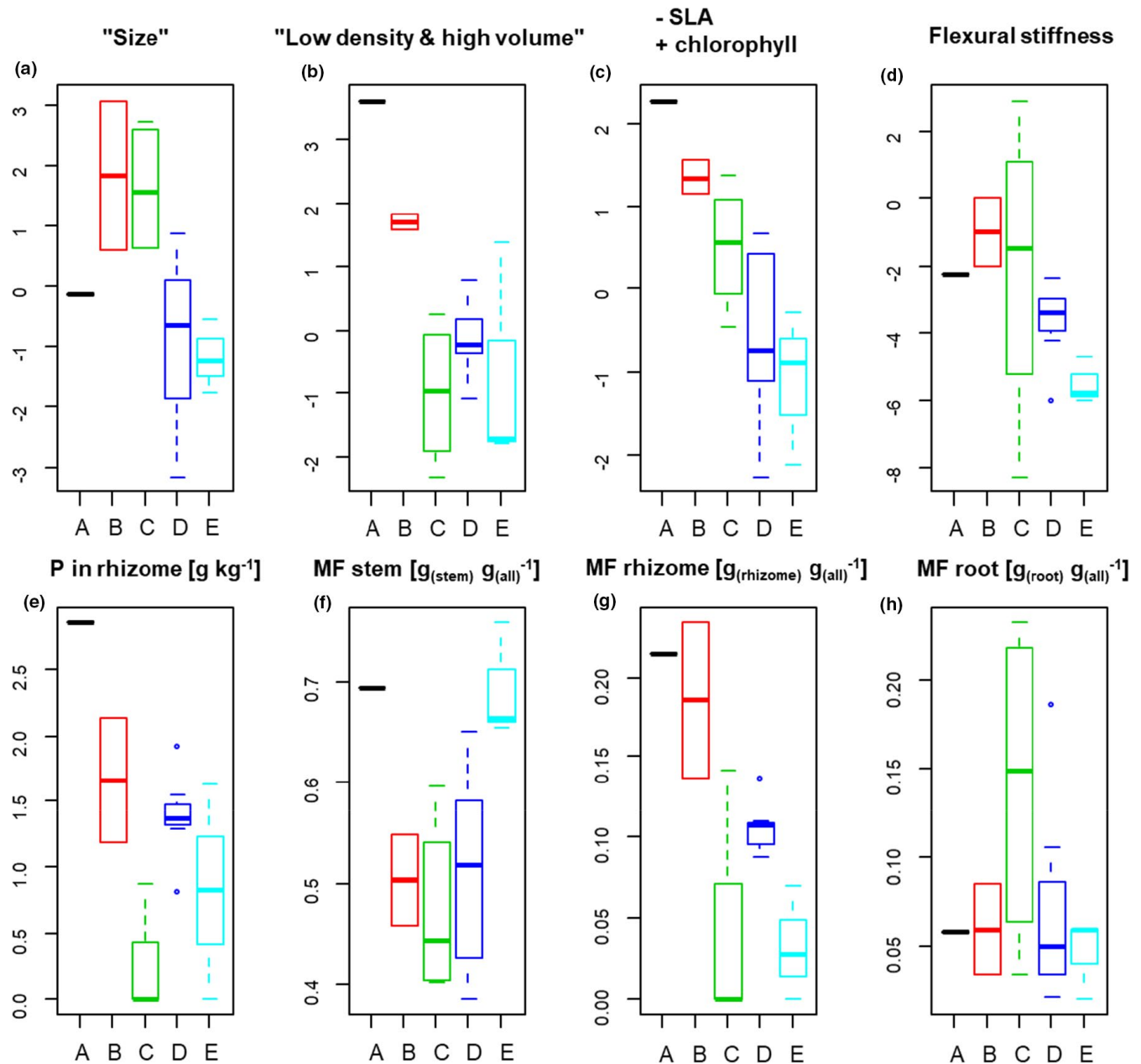
elevations that are less frequently inundated, with competition for light as a driver for species. However, in other ecosystems with a higher nutrient load of the river, nutrients may play a more important role also for plants at lower elevations (Sarneel et al., 2010).

4.1 | The impact of wave height on species distribution and plant trait expressions

As a response to waves, vegetation stands at the shore show flexible stems, a reduced competitive strength and reproduction and produce less biomass (Azza et al., 2007). Wave forces acting on plants are typically highest near the water front, as waves are attenuated when propagating inside the vegetation (Koch et al., 2009) and vegetation with less dense and more flexible stems has been shown to feel less drag force from waves (Bouma et al., 2005; Heuner et al., 2015; Heuner, 2016). Flow velocities or wave height might have a different intensity and impact on the vegetation, depending on site conditions, slope and exposure to wind and ship passages.

Many studies focus on wave impact and flow velocities: Coops et al. (1994) analyzed the effect of significant wave height (i.e., the mean wave height of the highest third of waves) and found reduced

FIGURE 6 Boxplots a–h for trait value ranges defining the species clusters of Figure 5 within the environment–trait space of the RLQ, Figure 3. The mean trait values for each species within a cluster are shown. The species clusters are named A–E, for names encompassed in the clusters see Figure 5 and Appendix S2. For aggregated variables, the y-axis shows scores of the first axis of the principal components analysis. Flexural stiffness shows the log-transformed data. For abbreviations and variables included in aggregates, see Table 2

tiller numbers and total biomass on exposed sites. Vuik et al. (2018) assumed in their model that the mean of the highest one-tenth of waves was breaking the plant stems, and in this was a significant factor controlling species distribution. This is related to stem flexural stiffness as pointed out by Rupprecht et al. (2015), who worked on biophysical properties of saltmarsh species: stems with smaller flexural stiffness can bend more easily and move along with the wave while stems that are more rigid (i.e., show higher flexural stiffness) are less able to bend (Bouma et al., 2005; Heuner et al., 2015). Often bending stiffness is determined as a key trait for species withstanding or avoiding waves (Puijalon et al., 2011; Silinski et al., 2015; Schoutens et al., 2020).

Our results also detect this as an important trait, but the density of the tissue and the nutrient storage function of the plant organs (high rhizome P) showed stronger correlations with the environmental gradients. The tissue density though was highly correlated with the flexural stiffness. Those findings confirm our first and second hypothesis that plants growing close to the shore show a high investment into below-ground organs and a low bending stiffness.

The stem stiffness can vary within species, depending on site conditions, elevation, plant height and the position within the stand (Carus et al., 2016; Zhu et al., 2019); it also varies depending on the part of the stem tested (Rupprecht et al., 2015) and the season (Coops & Van der Velde, 1996; Zhu et al., 2019). For instance, Vuik et al. (2018) found *Bolboschoenus maritimus* to have a flexural rigidity of $52,000 \pm 35,000$ N mm^2. In our study, bending stiffness of *Bolboschoenus maritimus* was found to be 136,000 N mm^2, which is similar to findings from Carus et al. (2016). The geometry of the stems has to be taken into account too: the stem shape of *Bolboschoenus maritimus*, which is triquetrous, would lead to a smaller resistance against the currents (Kötter, 1961) and withstand higher flow velocities (Carus et al., 2017a). Regarding the wave impact at higher elevations, our results show that the wave impact for water levels <0.5 m and >0.5 m are opposite to each other, meaning that higher waves occur at the higher elevated plots only at deeper water levels. The waves are being dampened by the vegetation and are therefore usually small at higher elevations at water levels <1.5 m depth. Above this water level, dissipation effects of the vegetation could not be detected for the study sites (Schoutens et al., 2019). When the tide has reached a certain height, the waves are above the *Schoenoplectus tabernaemonani* zone, with the effect that its wave-dampening effect diminishes and higher waves are able to reach higher elevations.

4.2 | The impact of inundation period on plant trait expressions

The other major impact on the species growing on the lower elevations in the Elbe estuary is long inundation periods: inundation causes stress, such as oxygen scarcity in waterlogged soil (Colmer & Voesenek, 2009) and higher levels of toxins in the soil, such as sulfide (Adam, 1990; Lamers et al., 2013). Additional to adaptations to wave impact, plants at those low elevations allocate large amounts of chlorophyll to their photosynthetic active tissue, aiding to maintain photosynthesis during times of submergence. The
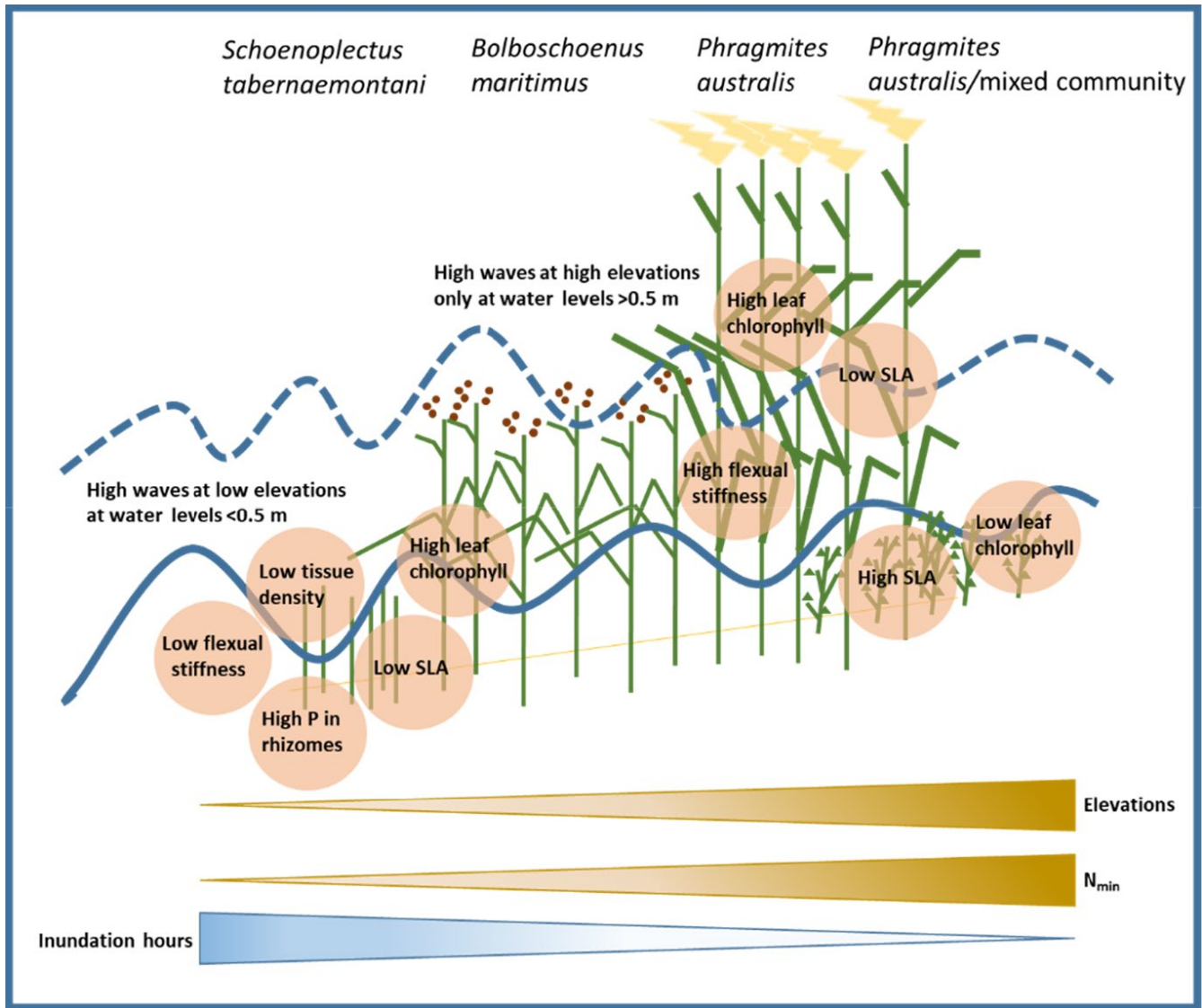
SLA was negatively related to chlorophyll (per area), which means plants with large, thin leaves had relatively little chlorophyll per area. When calculated in relation to mass, the findings are in accordance with the leaf economic spectrum (LES): a high SLA with high nutrient and chlorophyll content *per mass* (Wright et al., 2004). An inverse relationship of SLA and environmental variables as expected from the LES was found in saltmarshes (Minden & Kleyer, 2015). There, the leaf traits SLA and LDMC (leaf dry matter content) were more strongly constrained by salt, waterlogging and inundation than by soil nutrient availability. In our brackish tidal marsh habitats, the results revealed a similar pattern, but due to different plant strategies. For example, in the leafless species *Schoenoplectus tabernaemontani*, which allocates its photosynthetic active area to its stem, a high chlorophyll content allows for effective photosynthesis on a small surface. Some species are able to photosynthesize while being submerged under water and *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus* are examples of species with this ability (Clevering et al., 1996; Clevering et al., 1995).

These results point out trait–environment patterns in tidal marsh plants (see Figure 7): the traits of the species enable them to pass strong environmental filters, such as inundation duration or wave energy.

Furthermore, we found vegetation near the marsh edge has a strong rhizome system (see also Carus et al., 2017b) to ensure nutrient storage, anchorage and growth through suckers. This relationship is in accordance with our second hypothesis and supported in our results (high biomass allocation into below-ground organs and high tissue P content with a correlation of 0.72 between rhizome MF and P content, see Appendix S8). Relatively high investment into below-ground organs is known to be connected to inundation stress (Minden et al., 2012). The importance of reproduction through rhizomes and their role in energy storage is of major importance in this context (Granéli et al., 1992). Especially clonal integration could possibly enable species to extend their spatial range in less favorable conditions while still being connected with the parent individual (Burdick & Konisky, 2003; Silinski et al., 2016). Silinski et al., (2016) highlighted clonal integration as a major factor for successful expansion of *Bolboschoenus maritimus* stands. Vegetative reproduction holds many advantages over sexual reproduction in aquatic habitats — some species are combining both for short- and long-distance propagation too, like *Typha angustifolia* and *Phragmites australis* (Wetzel, 2001). As our study provides some insight into the reproductive strategies of plants from river marshes, more research is needed to further elucidate plant strategies related to reproduction in this habitat.

4.3 | The impact of soil nutrients and salinity on trait expressions and plant stoichiometry

Our results show that bending stiffness is strongly connected to the size aspect of a plant, as also shown by Zhu et al. (2019),

FIGURE 7 Schematic illustration of plant strategies in relation to the position in the tidal frame, with elevation, N_{min} (mineralized nitrogen), inundation period and wave impact in different water levels displayed as gradients. Traits shown: flexural stiffness (stem), tissue density (below- and above-ground organs), SLA (specific leaf area), P in rhizome (phosphorus content in rhizomes), leaf chlorophyll (chlorophyll content per mm^2 leaf). The soil salinity is a gradient from the mouth of the river upstream, shaping species inventory that ranges from species with adaptations regarding salt excretion or dilution downstream to species that can merely tolerate low salinity levels upstream

this being strongly connected to the "salinity–nutrient" gradient, which only has a very small explanatory value in the present RLQ analysis.

The soil nutrient contents of the study sites with phosphorus (62–92 g m^{-2}) and potassium (99–127 g m^{-2}) are sufficient for growth in every zone (Schachtschnabel et al., 1987) while N_{min} (6 and 7 g m^{-2}) is low for the *Schoenoplectus tabernaemontani* and the *Bolboschoenus maritimus* zones. For the *Schoenoplectus tabernaemontani* zone, the sand content in the soil is significantly higher than in the other zones, which explains the reduced potential to retain N_{min} here and in turn could have a size-reducing effect on the growth of *Schoenoplectus tabernaemontani*. Producing slender stems in this hydrodynamically turbulent zone is not a disadvantage though, as this helps avoiding drag forces (Puijalon et al., 2011; Heuner et al., 2015).

Following the rules of allometric scaling (Enquist & Niklas, 2002), the taller plants in this study with a large leaf area also showed a strong biomass investment into their stem (absolute, not relative). The allometric scaling model highlights the fundamental biomass partitioning rules.

Further from the shore at higher elevations with high N_{min} availability, plants show a high biomass production and a particularly large allocation to stem biomass, resulting in a dense canopy and low PAR values. In our third hypothesis, we expected values of traits related to competition such as SLA or canopy height would be higher at higher elevations compared to lower elevations. The "salinity–nutrient" (mainly P and N_{min}) gradient across the three study sites might become apparent because of the decline of the "wave disturbance–inundation" gradient: at those higher elevations,

waves are not a significant environmental factor anymore and longer inundation is rare. Species that cannot tolerate long inundation or wave activity are present here, but they still have to be salt-tolerant, due to infrequent inundation with saline water.

Competition for light is probably guiding the species traits on high-lying plots. Light becomes a limiting factor when shoots are big enough to shade out one another; the factors that influence their growth up to that point are environmental stresses and nutrient availability (Scholten et al., 1987). Taking the plant organ analysis into account (Appendix S9), there is a significant difference between plant above- and below-ground N:P ratios and organ N:P ratios for each species. This is due to different organ functions regarding the acquisition and storage of nutrients and also environmental factors like light impacting on the plants, which can affect plant N and P similarly (Güsewell, 2004). The N:P ratios for above-ground biomass are <10 for most trait species (Appendix S9), which are categorized by Güsewell (2004) as limited by N (see also Koerselman & Meuleman, 1996). The effect of competition for light at the higher elevations could be the cause for these ratios: *Scutellaria galericulata* for instance, growing beneath *Phragmites australis* at high elevations with very high N_{min} content (N:P ratio above-ground: 16.18), has an above-ground biomass N:P ratio of 8.16 — similar effects could be causing low ratios for *Myosotis scorpioides* (N:P 7.61) and *Mentha aquatica* (N:P 4.31) too, which also differed significantly from values for *Phragmites australis*.

5 | DISCUSSION

We could detect important plant traits which are connected to plant species' distributions in the tidal marshes of the three study sites in the Elbe estuary. The hypothesis was confirmed that plants growing near the estuarine shore show stiff stems and a high investment into below-ground biomass. Where waves create disturbance and plants face stress by long inundation periods, traits regarding avoiding wave energy (low flexural stiffness) and maximizing below-ground storage (for vegetative reproduction) are essential. Further, as expected in hypothesis four, traits regarding competition have higher values at higher elevations and species could be grouped based on their trait scores. Regarding the spatial distribution of the three dominant species, *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis*, the intensity of the wave impact in low water, and possibly also the low N_{min} content of the soil, may create the opportunity for *Schoenoplectus tabernaemontani* to grow in front of *Bolboschoenus maritimus* (Figure 7). Thus, *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus*, two species growing close to the shore, show a low SLA and high chlorophyll content per area, though not per mass.

From the mean high tide level upwards, wave action is reduced enough to allow *Phragmites australis* to thrive.

At those higher elevations, where inundation stress and wave disturbance are less, traits concerning competition gain more momentum. While the low-lying plots contain extreme specialist species that passed the strong filters, the high bank is home to a mixture of species that

compete for light. *Caltha palustris* for instance uses a temporal niche, having her cycle completed before the surrounding *Phragmites australis* closes the light gap (Ellenberg & Leuschner, 2010). Other species, like *Scutellaria galericulata* do not have their optimal growing conditions within the *Phragmites australis*/mixed community zone but are able to survive through a high investment into their stems and very slight material investment into leaves — with a large leaf area showing a quick turn-over rate. *Myosotis scorpioides* shows a similar ecology and, like *Mentha verticillata*, is able to fill gaps appearing in the canopy (due to wind and wave activity) with rapidly developing biomass.

The findings of this study are particularly relevant regarding projects to restore tidal marsh vegetation, as they highlight relationships between the different gradients that act on plants and their traits in an estuarine setting. Further research is needed to elaborate the role of the entire bank vegetation in ecosystem services such as wave attenuation and carbon sequestration. Changes in the environmental conditions, for example higher wave frequencies by more ships passing by in the river channel and sea level rise may trigger changes in species composition or influence the expansion of the tidal bank vegetation because higher wave frequencies may demand an even higher flexibility of the species near the shore. Another threat is caused by sea level rise, with longer times of inundation for the vegetation at low elevations and a reduction of time for photosynthesis under aerated conditions.

AUTHOR CONTRIBUTIONS

TSO: conceptualization, methodology, sampling, analysis, validation, writing initial manuscript, editing. MH: conceptualization, methodology, analysis, validation, review, editing, funding acquisition, supervision. EF: conceptualization, methodology, validation, review, editing. ST: conceptualization, methodology, validation, review, editing. KS: conceptualization, methodology, sampling, analysis, validation, review, editing. TJB: validation, resources, review, editing. VM: conceptualization, methodology, validation, review, editing, funding acquisition, supervision.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Description of extrapolation of wave measurements

Appendix S2. Species recorded in their respective zones

Appendix S3. Information on numbers of trait plant individuals and the zone of collection

Appendix S4. Equations used to calculate flexural stiffness and Young´s modulus

Appendix S5. Species mean trait values with SD and unit

Appendix S6. Details of significance test for mixed linear models

Appendix S7. Boxplots for elevations and soil C:N of the different zones

Appendix S8. Correlations of (a) trait variables, (b) environmental variables

Appendix S9. N:P ratios of the different organs of all species