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Conquering New Frontiers: The Effect of Vegetation Establishment and Environmental Interactions on the Expansion of Tidal Marsh Systems

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Abstract

Tidal marshes are dynamic systems whose lateral expansion depends on various biologically, physically, and geomorphologically controlled small- and large-scale feedback networks. Due to the bimodal existence of two landscape states at the tidal marsh edge (vegetated tidal marsh flat and bare tidal flat), and the high wave energy affecting the foremost seaward (pioneer) zone of tidal marshes, plant seedlings face two challenges: 1) successful seed settling and germination or clonal expansion and establishment under non-optimal conditions, and 2) a variety of abiotic stresses after establishment. Modelling and laboratory studies have addressed the reciprocal relationship especially between hydrodynamic and sedimentary forces and vegetation traits and have revealed fundamental mechanisms and feedbacks. Nevertheless, validations of the findings from artificial environments in natural ecosystems are still lacking. In this review, we present the current state of literature to vegetation-abiotic interactions, focusing on the establishment and adaptation of seedlings and propagules and what effect they may have on the prospective evolution of tidal marshes.

Keywords Tidal marshes · Marsh evolution · Edge configuration · Vegetation-abiotic interactions · Traits · Seedlings

Introduction

Tidal marshes are widely distributed in sheltered areas such as estuaries or tidal bays and provide a complex of habitats (Allen 2000; Adam 2002; Townend et al. 2011). Colonized by mostly halophytic herbs, grasses, and low shrubs, they are frequently inundated by tides and exposed to steady changes in their physical, geomorphological, and ecological environment (Allen 2000; Bakker et al. 2005). Future sea level rise and the increase of extreme events such as storms and floods as well as other anthropogenic pressures (e.g. urban settlement, dyke construction) may compromise the evolution of coastal wetlands and their future development (van der Wal and Pye 2004; Gedan et al. 2009; Valiela et al. 2009). As a result, a loss of coastal wetlands worldwide has been detected and may increase in the future (Valiela et al. 2009; Deegan et al. 2012; Mariotti and Carr 2014; Balke et al. 2016; Donatelli et al. 2018).

Of particular ecological and morphological importance for the lateral fate of a tidal marsh are the marsh-tidal flat transitions, which – on a centimeter scale – are often characterized by a coexistence of low-lying, bare, unvegetated areas and higher parts covered by vegetation (Fagherazzi et al. 2006; Evans et al. 2019). Evans et al. (2019) specified the tidal marsh edge as a transition between a tidal flat, which falls below the critical height for vegetation development, and an area which is sufficiently elevated for survival of perennial vegetation to persist. However, elevation is a function of local environmental parameters and landscape geometry, which makes a uniform definition difficult and

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requires local adaptations (Adam 2002; Balke et al. 2016). Nonetheless, the foremost seaward edge region is involved in lateral expansion or retreat of tidal marshes due to intense exposure to environmental forces, such as hydrodynamics and wave regime, and associated sediment deposition or erosion. Bio-geomorphological feedback from interactions in local hydrodynamic (tides and waves) and sedimentary regimes as well as vegetation growth result in large-scale self-organizing systems and possible nonlinear responses to changes in the climatic system (van de Koppel et al. 2012; Balke et al. 2016; Schwarz et al. 2018; Dai et al. 2021). Although the effect of establishing vegetation and its interaction with the environment on the fate of tidal marshes are recognized as a fundamental parameter in models as well as in laboratory and field experiments, the natural complexity and diversity of tidal marsh vegetation complicate an adequate integration into modelling studies or an appropriate depiction in laboratory studies. Moreover, the biological process of how vegetation disperses and establishes itself in tidal marshes due to species- specific traits both at the intra- and interspecific levels is still only fragmentarily understood.

In this review, we analyze and discuss the requirements for the establishment of tidal marsh plants at the exposed fringe of the marsh towards the unvegetated bare tidal flats. We primarily focused on peer-reviewed publications between 2000 and 2022, but also consulted older fundamental research. In addition, we included experimental as well as modelling studies in our research, but focused on the former. First, we addressed the morphological lateral development of tidal marshes. Subsequently, the requirements for vegetative and generative propagation, as well as germination were examined in more detail. In this regard, we addressed (1) the "Windows of Opportunity" framework (Balke et al. 2011), (2) adaptive strategies of plants, and (3) their bio-physical and bio-geomorphological interactions with environmental parameters such as wave and sediment dynamics, which are highly relevant to the development of tidal marshes. Resulting ecosystem modifications, critical thresholds, and potential tipping points are discussed in the last section.

Tidal Marshes vs. Mangroves–Common Characteristics

Since tidal marshes occur globally (Mcowen et al. 2017; Fig. 1), the forms, patterns, and processes of this ecosystem are diverse. Willard and Darnell (1982) previously identified six primary environmental factors including substrate, salinity, temperature, degree of protection from waves and water,

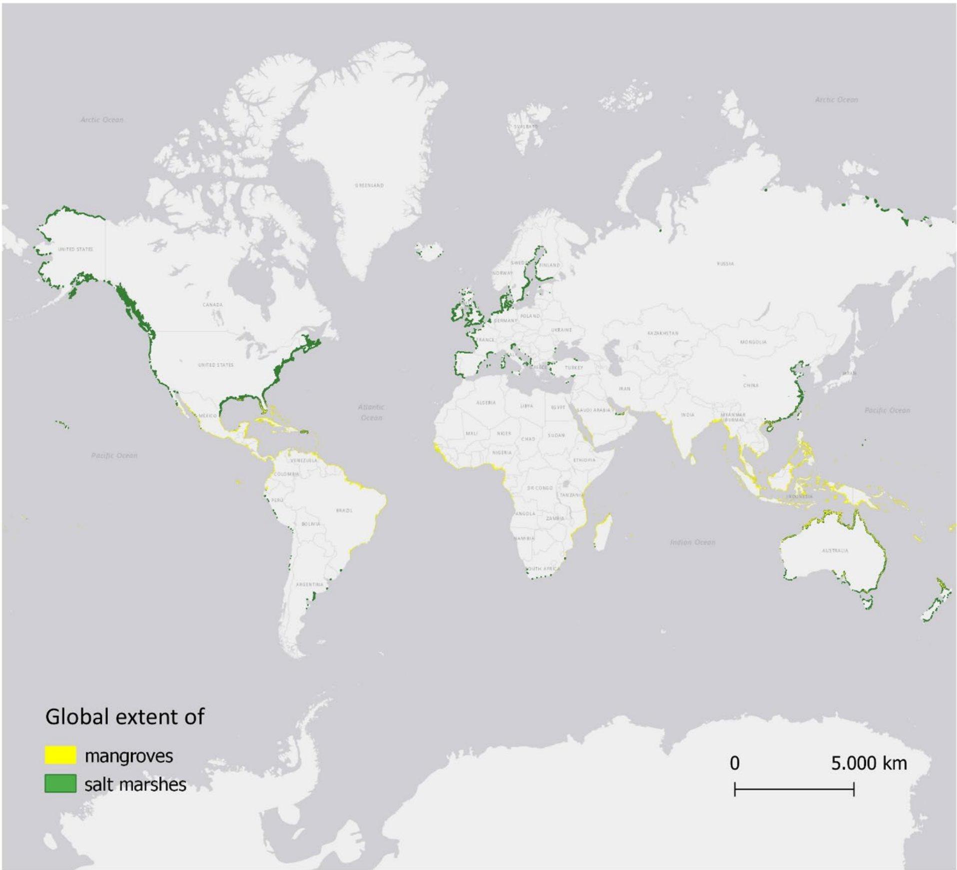

Fig. 1 Overview on the global distribution of salt marsh (green; Mcowen et al. 2017) and mangrove (yellow; Bunting et al. 2018) ecosystems

degree of inundation as well as desiccation, and water depth, which in different combinations provide habitat conditions for various ecological coastal systems. Assuming these factors as determining the limit for marsh plant occurrence, they found ten coastal ecological systems for the United States only and separated coastal marshes in freshwater marshes (inland or tide-influenced), intermediate and tide-influenced marshes with low to moderate salinity, as well as seaward and tide-influenced salt marshes (cf. Willard and Darnell 1982). The idea of macroclimate-controlled vegetation communities and functional groups in coastal wetland was represented by Gabler et al. (2017). They observed that mangrove forests occur in warm and wet zones, graminoid-dominated marshes in cool, wet zones, succulent-dominated marshes in more arid zones and unvegetated salt flats in hypersaline regions depending on certain macroclimate conditions.

This review focuses on graminoid-dominated tidal marshes and also includes succulent vegetation. In tropical and subtropical zones, mangroves are considered the tropical equivalent of tidal marshes (Fig. 1). Ecological theories—such as the Windows of Opportunity framework (see Chapter 4.2.1), the physiological-ecological-amplitude-concept (see Chapter 4.2) or the stress-gradient hypothesis (see Chapter 5.2.1)—may be applied to both ecosystems (see Friess et al. 2012). Furthermore, the habitat overlapping and adaptations of both community types to their environments may be of importance when climate change-induced habitat migration is considered (e.g. Chen et al. 2020). The mangrove's geographical extent is limited by a low tolerance of some species to extreme freezing or chilling events (e.g. Cook-Patton et al. 2015; Lu et al. 2021) and hypersaline conditions (e.g. Gordon 1988). In zones characterized by high saline conditions, mangroves are typically replaced by tidal marshes or unvegetated salt flats (Adam 1990). However, in both tidal marshes and mangroves, similar abiotic factors play a critical role in vegetation development, such as regular inundation, salinity, anoxic soil conditions, waterlogging, drag forces by waves and wind, as well as erosion or sedimentation (reviewed for mangroves: Lugo and Snedaker 1974; Kathiresan and Bingham 2001; Krauss and Ball 2013, reviewed for tidal marshes: Townend et al. 2011; Vernberg 1993; Boorman 2003; Fig. 2). In addition, the colonization of bare tidal flats by vegetative (e.g. rhizomes fragments or vivipary) and generative (seedling establishment through seeds) dispersal of mangrove or tidal marsh vegetation appears to follow similar rules of abiotic-plant-interactions (see Krauss et al. 2008) with high susceptibility of young plants to disturbance by wave energy and sedimentation or erosion (Balke et al. 2011, 2013; Fig. 4) as well as changes in the microhabitat (Devaney et al. 2017). While the ecological interactions of seedlings with their environment at the mangrove edge and their effect on mangrove spread has been

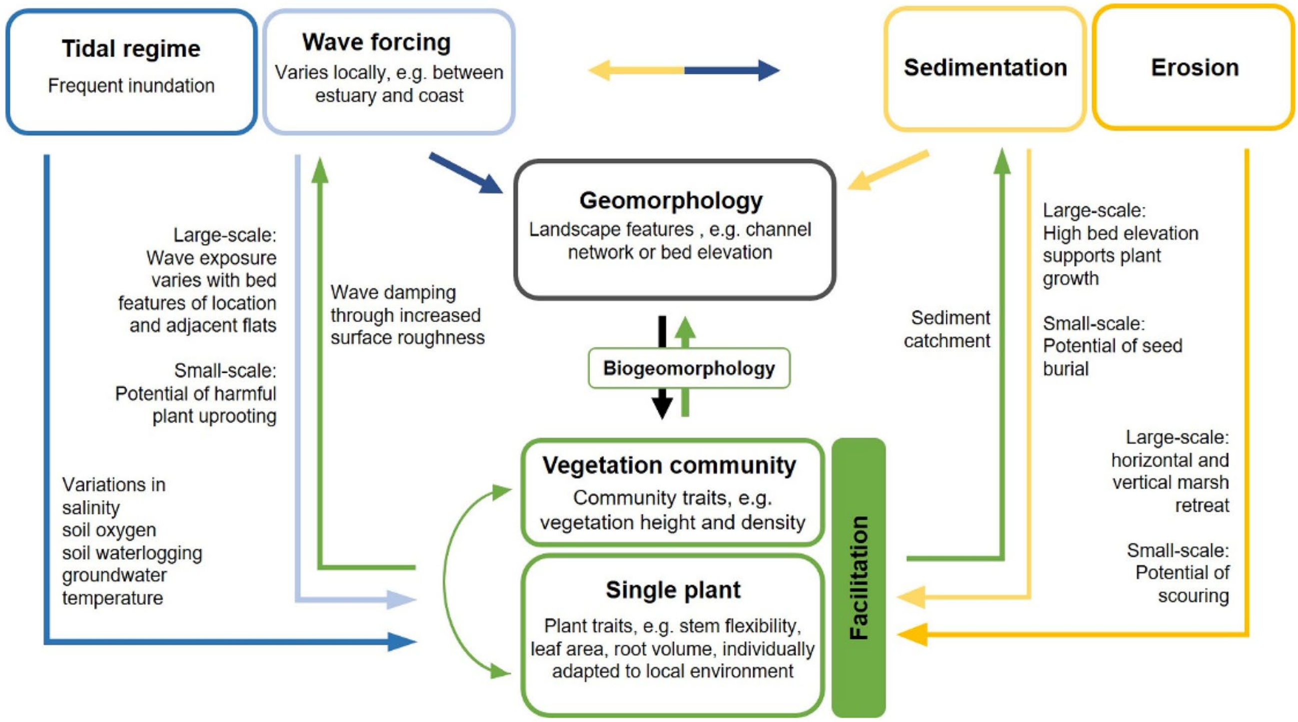

Fig. 2 Simplified interactions between the main abiotic drivers of hydrodynamic (blue) and sedimentary regimes (yellow), geomorphology (black), and vegetation (green) in tidal marshes. Vegetation is capable of responding to its environment and, conversely, engineering it as well, resulting in diverse ecosystem services such as wave attenuation, erosion mitigation as well as habitat and nutrient provision

broadly studied and summarized in the literature (Austin and Tomlinson 1987; Krauss et al. 2008; Friess et al. 2012; Schwarz et al. 2022), this ecological view on colonization processes of unvegetated flats and open patches by seedlings in tidal marshes is still lacking.

Lateral Marsh Development and Alternating Processes in Tidal Marshes

In many cases, tidal marshes emerge from the infilling of tidal basins by sediment, when the local sediment infilling rate exceeds the rate of relative sea level rise (Redfield 1965; Gunnell et al. 2013). Accretion of tidal marshes depends on the availability of sediment, the hydroperiod, the flow field over the marsh, and coupled settlement and trapping processes through the presence of vegetation (Reed 1990; Marani et al. 2011; Townend et al. 2011). The origin of sediments can be diverse, varying from external sources due to erosion of adjacent coasts and flats or riverine sediment inputs from the catchment, to internal sources by resuspension on intertidal mudflats or erosion of edges and channel creeks (Temmerman et al. 2005, 2007; Townend et al. 2011; Leonardi et al. 2018). A sufficient sediment supply (continuous or pulse) and the related increased concentration of suspended sediment can enhance the marsh progradation and may imply a number of positive feedbacks, such as an increased bed elevation resulting in a decrease of wave heights and energies at the marsh edge (Marani et al. 2010; Mariotti and Fagherazzi 2010; Mudd 2011; Figs. 2 and 3A1-3). Otherwise, when sediment supply is insufficient, subtle changes in the flat elevation decide over the marsh state due to the control of bed elevation by the erosive power of waves (Mudd 2011; Fig. 3B 2–4). Gourgue et al. (2022) recently demonstrated that the resilience of a restored tidal marsh system was even more sensitive to sediment suspension than to rates of SLR and that restoration design options can steer bio-geomorphic developments (tested for tidal inlets) which is in agreement with the findings of Liu et al. (2021).

Once formed, many tidal marshes can persist even at lower sediment supply (Kirwan et al. 2011) and are often capable of achieving a relatively constant equilibrium in the vertical direction (Kirwan et al. 2010). However, they can alternate between advancing and retreating phases (Fagherazzi et al. 2013). A model describing the evolution of tidal marshes in the Rehoboth Bay, Delaware, indicated three probable different marsh evolutional states: (i) retreat through erosion, (ii) marsh progradation, and (iii) marsh drowning due to relative sea level rise (Schwimmer and Pizzuto 2000).

The establishment of tidal marshes on previously unvegetated tidal flats (or vice versa, i.e. its regression to unvegetated tidal flats) can be simplified into four successive states (Fig. 3). While in the first developmental state sedimentation and hydrodynamic processes are the primary driving factors (Fig. 3A1-3), vegetation encroachment drives the formation process in the last developmental state (Fagherazzi 2013; Gunnell et al. 2013; Fig. 3A4) by contributing to increased sediment deposition and adding belowground biomass, e.g. roots and rhizomes, that strengthen and protect the accumulated sediment of the newly developed flat.

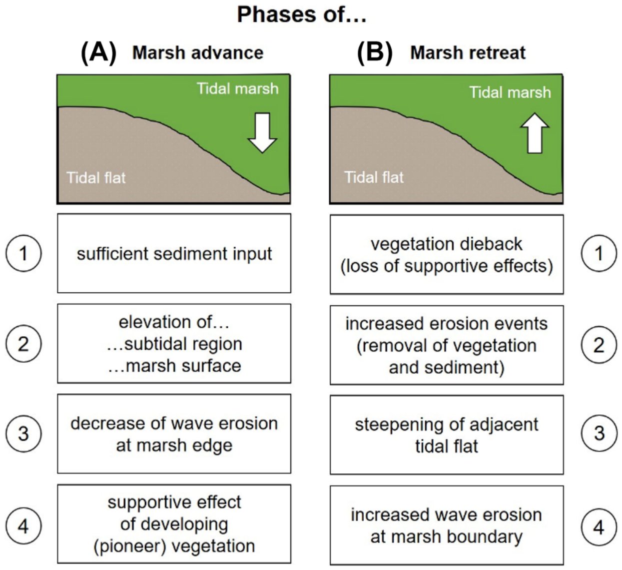

Fig. 3 Simplified illustration of developmental steps in the pioneer zone of tidally influenced tidal marshes during establishment of a new tidal marsh area on a previously bare tidal flat (left) or during retreat under unfavorable conditions (right). Although the establishment of vegetation occurs only in the last step of development (No. 4, left), it plays a crucial role in the future stability and persistence of the new tidal marsh areas. Loss of vegetation (No. 1, right) often results in loss of extensive areas of the ecosystem

Colonization of Bare Flats – Abiotic Filters for Vegetation Establishment

Settling Requirements – Vegetation Distribution

Dispersal Ability of Tidal Plants by Seeds

To successfully establish from seeds, plants have to pass two consecutive phases: 1) the release of viable seeds from the parent plant, and 2) the movement of released seeds (Chambers and MacMahon 1994; Fig. 4). The first phase involves mainly gravity. The seed is detached from the parent plant and falls beneath it, unless seed appendages such as wings, pappus or hooks in conjunction with a vector (e.g. wind, water or animals) favor a deposition farther

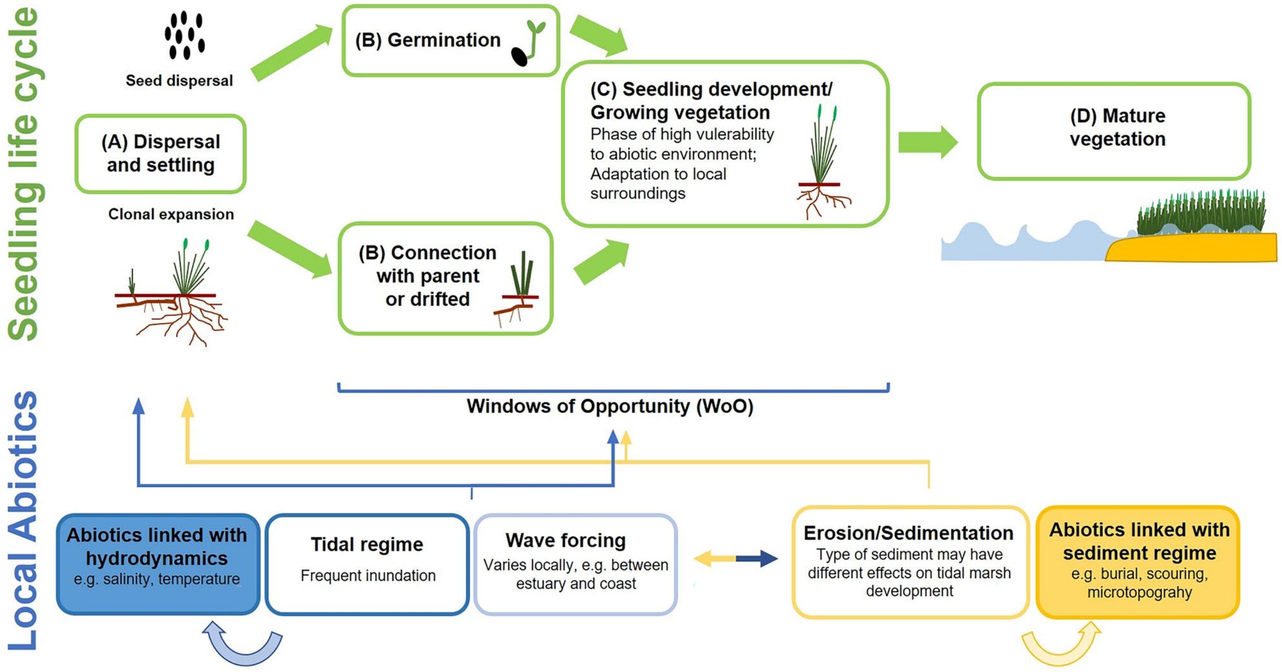

Fig. 4 In the life cycle (green) of a tidal marsh plant the propagation (**A**) is followed by the germination (**B**) and seedling establishment (**C**) until the vegetation is mature (**D**). The developmental path of a plant depends on whether its propagation is generative (seeds) or vegetative (clonal), also varying in the prerequisite (e.g. connection with parental plant vs. solitary growth). However, at both paths, seedlings are vulnerable for disturbances, particularly by hydrodynamics (blue) and sedimentation (yellow), and have similar requirements for their survival. During the propagation (**A**), seed and propagule transport is particularly driven by currents and waves. Subsequently, germination and seedling establishment (**B** and **C**) need a disturbance-free time (Windows of Opportunity; WoO) from strong abiotic factors such as high wave energy (e.g. inducing drag and scouring) or excessive sedimentation (e.g. potential burial of seeds) to grow and develop sufficient above- and belowground biomass

away from the parent plant (Chambers and MacMahon 1994; Tackenberg et al. 2003).

The second phase appears to be more complex for tidal marshes, since it involves physical drivers, i.e. tides, waves, sedimentation, and wind, as well as species- and plant-specific characteristics. Whether a seed lands within dense vegetation, on sites covered with plant debris, on exposed soils and free patches, or even on neighboring plants, affects its dispersal distances and establishment success (short and lower for dense vegetation; Chambers and MacMahon 1994). The proximity of mature marshes facilitates seedling establishment (Wolters et al. 2005; Mossman et al. 2012a; b; Zhu et al. 2014), since an increased abundance of adults entails greater seed input (Rand 2000). Investigating spatial and seasonal patterns of seedling establishment in the Tijuana River National Estuarine Research Reserve, California, Morzaria-Luna and Zedler (2007) recorded only seedlings of *Sacocornia pacifica* as highly abundant, which were already dominant in the mature canopy. In contrast, in a study on the spread of vegetation on restoration sites in the Yzer estuary, Belgium, Erfanzadeh et al. (2010) did not find any correlation between the abundance of species on the restoration site and their abundance on the reference site, suggesting that seed production rates of single species are more important than a standing cover of mature vegetation. Seed production and seed settling can differ across tidal marsh species, as shown for *Salicornia europaea*, *Limonium vulgare*, *Elytrigia atherica*, and *Atriplex prostata* (Chang et al. 2007). While *S. europaea* and *L. vulgare* displayed an exponential decrease of seed production and seed settling with increasing age of the community, both parameters increased linearly for *E. atherica* and logistically for *A. prostata.* Seeds of tidal marsh species typically disperse either immersed or buoyant in a species-specific manner (Erfanzadeh et al. 2010). Moreover, seed traits such as mass, length, width, and depth affect the dispersal and a subsequent establishment (Chambers and MacMahon 1994; see also heteromorphism, Chapter 5.1.1), e.g. by affecting the depth of burial (Chambers and MacMahon 1994) or increasing the buoyancy as shown for first colonizers with high seed production rates (Leck and Simpson 1995; Erfanzadeh et al. 2010).

Apart from surface slope and wind, waves (Zhu et al. 2021) and tides (Huiskes et al. 1995; Chang et al. 2007) are physical drivers to disperse seeds of tidal marsh plants, but are admittedly also involved in seed loss. In the Westerschelde, Netherlands, seed numbers visibly decreased with distance from the tidal marsh edge and much of the seed was washed away (retention < 20%; Zhu et al. 2014). Burial can prevent the seed from washing away, but the success of germination of seeds decreases with increasing burial depth (Bouma et al. 2016), and a highly dynamic bed level as well as fluctuations in frequent inundation can increase the seed mortality even before settling (van Regteren et al. 2020). Therefore, intensified sediment disturbances result in lower persistence of seeds and probably threaten the seed bank in combination with hydrodynamic disturbances, such as increased wave forces and storm events under climate change (Zhu et al. 2021).

Distribution of seeds is usually described in a rather local pattern (Rand 2000; Morzaria-Luna and Zedler 2007) based on a higher probability of transportation to higher marsh zones, rather than seaward (Huiskes et al. 1995). Retention of seeds and propagules by increasing vegetation density as well as features of the local microtopography (e.g. increased seed trapping by crab burrowing and stem basal sediment hollows, Qiu et al. 2021) may have a supportive effect on seeds distribution. In sheltered regions, such as densely vegetated patches, both seeds and propagules may not disperse at all (Hutchings and Russell 1989; Huiskes et al. 1995). In a connectivity experiment on a German Barrier Island, Lõhmus et al. (2020) found that long-distance dispersal resulted from a link between sufficient habitat connectivity and suitable seed traits. The process may allow colonization of more distant areas and bare tidal flats in front of a tidal marsh edge, which may be a bottleneck for marsh resilience, when facing sea level rise (Zhu et al. 2020). However, studies about long-distance dispersal are scarce.

Dispersal Ability of Tidal Plants by Clonal Expansion

While mangrove systems often expand in episodic events in a homogenous vegetation band by often viviparous germination (seeds germinate at parent plant and are released already in seedling state; Balke et al. 2011; Austin and Tomlinson 1987), perennial tidal marsh plants expand more continuously through clonal growth (Proffitt et al. 2003; van Wesenbeeck et al. 2008b; Schwarz et al. 2022; Fig. 4) or rhizome tearing and drifting to new habitats with re-rooting (Boedeltje et al. 2007; Fig. 4). Commonly, clonal growth means the ability of mature plants to produce vegetative offspring which typically are genetically identical to the parent plant (Price and Marshall 1999; Dong et al. 2014). The forms of clonal growth are diverse, including, for instance, stolons and rhizomes, bulbils, tubers, tillers or plant fragmentation (summarized in Price and Marshall 1999) and can be advantageous for local colonization and competition. Sharing environmental resources, i.e. by increased resource uptake and distributing the assimilated resource among the affiliated ramets from resource-rich patches to patches with low resources, can control the ramet's survival, development, and physiological and morphological structure, making clonal plants to strong competitors (Price and Marshall 1999; Jaafry et al. 2016).

In his conceptual framework, Grace (1993) identified six functions of clonal reproduction in aquatic environments as a basic set that supports vegetation persistence: l) numerical increase, 2) dispersal, 3) resource acquisition, 4) storage, 5) protection, and 6) anchorage. The forms of clonal reproduction such as rhizomes, tillers, bulbills (see Chapter 4.1.2), and their related functional traits (e.g. spreading distance, the time of the connection between parental plant and offspring, number of clonal offspring) presumably serve to accomplish these six functions. Due to both the variety of habitat characteristics and the clonal growth forms, the capacity for clonal growth and the functional traits vary among individual community types (Grace 1993; Klimeš 2008; Sosnová et al. 2010; Klimešová and Herben 2015). Therefore, studies on clonal dispersal rates in tidal marshes are scarce. While some studies examine the distribution of clonal growth forms and clonal traits across habitats (e.g. wetlands: Sosnová et al. 2010; temperate plant communities: Klimešová and Herben 2015), clonal dispersal and clonal growth rates for tidal marshes depend on the environment and are modeled in a species-specifical way (e.g. *Spartina alterniflora*: Dennis et al. 2011; clonal expansion rate of *Bolboschoenus maritimus* with 0.018 compared to *Phragmites australis* with 0.01: Carus et al. 2017b). Clonal growth forms and functional traits such as the lateral expansion (m yr^{-1}) can be retrieved genus- or species-specific in the CLO-PLA database (Klimešová J. and Klimeš L. 2019), but need to be related to environmental parameters.

After Settling – Requirements for Germination and Establishment

The germination and establishment of tidal marsh seedlings usually depend on post-dispersal environmental conditions of hydrodynamics (Casanova and Brock 2000; Bockelmann et al. 2002; Cao et al. 2018; French 2018), sedimentation/erosion (Bouma et al. 2009b; Cao et al. 2018), and sediment stability (Cao et al. 2018), which are potentially the bottlenecks to seedling establishment on tidal flats (Temmerman et al. 2007; Bouma et al. 2009b; Schwarz et al. 2011; Friess et al. 2012; Hu et al. 2015; Fig. 4). The physiological-ecological-amplitude-concept of Scholten et al. (1987) states that the occurrence of organisms along an environmental gradient depends on the species-specific stress tolerance on the more stressful side of the gradient and on competitive ability on the more benign side. Applied to tidal marshes, this means that the seaward side of the gradient would have species that show high tolerance to e.g. flooding, salinity, and wave breaking, and the landward species would be more tolerant to competitive pressure (Carus et al. 2016).

Flooding of tidal marsh land influences the surface and groundwater (Xin et al. 2022), flux rates (e.g. of nutrients or gases, Nahrawi et al. 2020), salt input, soil water logging, as well as light and desiccation stress for tidal marsh plants (e.g. Derksen-Hooijberg et al. 2019). For newly establishing plants at the tidal marsh edge, frequent inundation means additional disturbance, even in sheltered areas when wave forcing and scouring are low. Vegetation recovery can critically slow down with increased inundation, as shown for a macrotidal, polyhaline marsh system dominated by *Spartina anglica* and a microtidal, mesohaline marsh system, dominated by *Schoenoplectus americanus* (van Belzen et al. 2017).

Besides inundation, salinity also conttibutes to the characteristic zonation of tidal marshes due to a higher sensitivity of high marsh plants to both (Bertness and Ellison 1987; Janousek and Mayo 2013). Especially, seedlings are exposed to increased salinity levels during germination and root formation resulting from accumulated salt in the upper centimeters of the soil—regardless of whether they are growing in the lower or upper tidal marsh (Ungar 1991). Exceptions comprise some halophytes that grow better in saline conditions (e.g. genera *Salicornia*, *Suaeda*, *Sarcocornia*, *Batis*, Shumway and Bertness 1992; Guo and Pennings 2012; Lõhmus et al. 2020).

This appears to be consistent with the ecological rachet model (see Fagherazzi et al. 2020 for tidal marshes, and Kearney et al. 2019 for flooded coastal pine forests) that assumes each plant community to have a flood tolerance threshold as a function of the complex interaction of abiotic and biotic factors. This flood tolerance is species-, but also age-dependent. In general, young plants show a lower tolerance to disturbed environmental conditions (i.e. regular immersion as well as hydrodynamic and sedimentary stresses) at the boundary between tidal flat and tidal marsh than mature plants (Bouma et al. 2016; Fagherazzi et al. 2019, 2020; Poppema et al. 2019; Fig. 4) since they may be longer submerged due to lower plant heights and thereby reduced photosynthetic rates. Thus, a successful development of initial foreshore vegetation requires suitable conditions.

Windows of Opportunity (WoO) Framework

To avoid seed loss and support germination, seeds and propagules must be trapped and deposited in suitable microhabitats with comparatively mild environmental conditions (Bouma et al. 2009a; b; Cao et al. 2018; 2020a) and open patches (Metcalfe et al. 1986; Shumway and Bertness 1992). Harper et al. (1961) have shown that 'safe sites', i.e. microsites in the colonized habitat that provide an opportunity for escape from stressful conditions, control the plant population (for experimental evidence, see Harper et al. 1965). Accordingly, the size of a population of seedlings is a function of the seed number reaching suitable habitats and the rate of successful germination there (Harper et al. 1961; 1965; Eriksson and Ehrlén 1992). However, due to increasing stress towards the pioneer zone and potentially decreasing vegetation densities, such 'safe sites' are not necessarily provided.

The WoO framework introduced by Balke et al. (2011, 2014) complements the plant ecological idea of the 'safe sites' with the requirement of a disturbance-free period, which allows the seedling to develop a sufficient, individual-specific protection from becoming uprooted due to wave action and erosion (e.g. increased investment in the root system). It is hypothesized that physical processes limit the establishment of seedlings on bare tidal flats (see also Friess et al. 2012). By using flume studies with buoyant propagules of *Avicennia alba*, three critical thresholds were identified that had to be passed to ensure establishment (Balke et al. 2011). The first WoO includes a disturbance-free period for sufficient rooting of propagules, while the second and third WoO require calm hydrodynamics for plant strengthening and limited high-energy events to avoid uprooting (Fig. 4). Subsequent model studies extended the framework to seedling establishment in tidal marshes and continuously refined it by adding additional determining factors, such as bed shear stress or bed level change (Hu et al. 2015; Poppema et al. 2019), showing that even small variations in environmental conditions affect plant development in the pioneer zone. Cao et al. (2020a) assumed a critical threshold of wave action, hampering both seedling establishment and growth of the species *Spartina anglica*, *Bolboschoenus maritimus* and *Phragmites australis*. The authors further found that after only seven weeks of wave exposure, seedling survival and growth were significantly limited. Generally, too strong hydrodynamic forces may result in the removal of seedlings by drag forces or uprooting by scouring and long-term erosion (Bouma et al. 2009b; Schoutens et al. 2021). A period of time with little or no disturbance, thus, appears to be crucial for seedlings to grow sufficient roots to withstand environmental pressures (Boorman 2003).

Response vs. Effect—How Pioneer Vegetation Interacts with Surroundings

The main determinants for tidal marsh plants in their early life stages are disturbances by tides, waves, and sediment regime as well as resource limitations. This corresponds to the assumption that plant communities are a result of abiotic (e.g. climate, resources, disturbances) and biotic (e.g. predation, competition) filters that confine which species and traits can occur (Lavorel and Garnier 2002, consistent with Scholten et al. 1987; Fig. 5). According to the response-effect-framework of Lavorel and Garnier (2002), 'response traits' are associated with the response of plants to environmental conditions (see below), while 'effect traits' determine how plants affect their environment and ecosystem function. Moreover, some traits can be effect and response trait at the same time (Suding et al. 2008), as for example Minden and Kleyer (2011) have shown for stem biomass, specific leaf area, and C:N ratios in salt marsh systems. By affecting abiotic processes and structures of the surrounding environment, e.g. by intensifying water flow and associated erosion between patches (van Wesenbeeck et al. 2008a), tidal marsh plants can create scale-dependent feedbacks and, therefore, result in self-organized landscapes (Temmerman et al. 2005, 2007; van de Koppel et al. 2005, 2012; van Hulzen et al. 2007; van Wesenbeeck et al. 2008b; Bouma et al. 2013; Marani et al. 2013). Especially in the seaward pioneer zone characterized by a bi-stability between unvegetated tidal flats and vegetated marsh surface, effects of vegetation can thus be critical – making its consideration worthwhile (see below Chapter 5, especially 5.2.3).

Tidal Marsh Plant's Responses to Environment

Reproduction Traits From Parental Plants

Heteromorphism, i.e. the production of two or more distinct seed types, which may differ in their traits, e.g. in morphology, ripening, dormancy, seed size, dispersal, or germination time (Venable 1985; Hughes 2018; Fig. 6), is known for some halophytic species of the genera *Salicornia* and *Suaeda* as an evolutionary strategy to adapt to heterogenous and disturbed habitats (reviewed in Liu et al. 2018). *Salicornia europaea* produces a large number of light seeds associated with water dispersal (Lõhmus et al. 2020) with two seed types, differing but complementing each other in the mechanism of salt tolerance which improves the germination even at high salinities (Orlovsky et al. 2016; Calone et al. 2020). Variability of germination as well as the mean daily and final germination of the dimorphic seeds increased with salinity also for *Salicornia ramosissima* (Ameixa et al. 2016). Similar behavior was identified for *Suaeda* species. Cao et al. (2020b) observed three types of seeds for *Suaeda aralocaspica* – brown, large black, and small black – with varying traits in color, size, mass and germination and, thus, assumed variations in seed heteromorphism to likely be associated with environmental conditions (annual precipitation, temperature, daylight and their monthly distribution in different calendar years). The germination percentage of brown seeds of *S. aralocaspica* were higher than those of black seeds (Wang et al. 2012). Moreover, the germination percentage increased from high-salinity maternal plants, suggesting also a maternal effect before seed release. Also, the germination success of black and brown seeds of *Suaeda salsa* was affected by abiotic conditions (Zhang et al. 2021). While brown seeds reached a high germination percentage over a wide temperature range, germination of black seeds gradually increased with rising temperature.

For tidal marsh plants, the clonal reproduction ability can be a survival warranty. *Phragmites australis*, for instance, can occur in different patterns, such as the colonization of open patches, linear clonal expansion (along a preferred axis) as well as non-directional, circular clonal expansion. Therefore, it is able to colonize many landscape positions along the brackish tidal marshes at the mid-Atlantic coast (Lathrop et al. 2003). Similar results were shown in tidal marshes of New England, western Atlantic coast, whereby

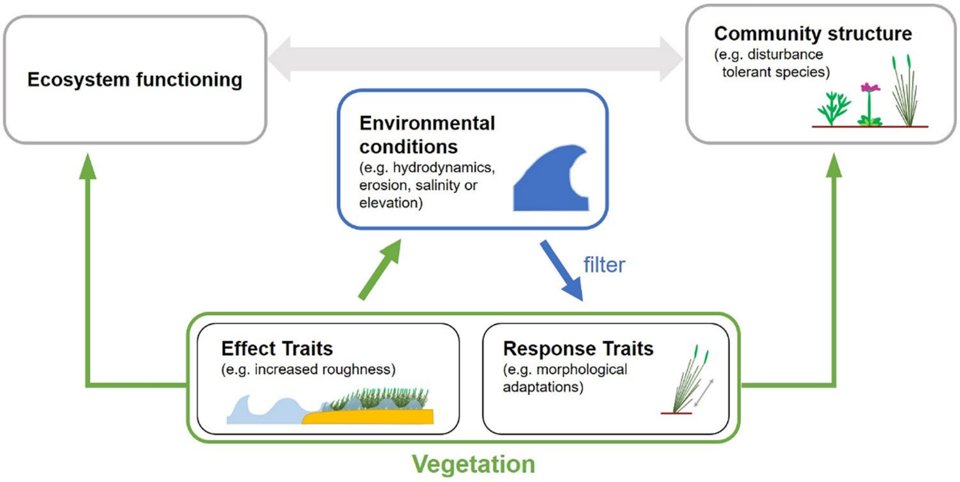

Fig. 5 The local environment such as wave and sedimentation can act as a filter on vegetation, only allowing for plant traits that can cope with the conditions (response traits) and, therefore, affecting the community structure. Traits that, in turn, show an effect on the local environment (effect traits) are important for the whole ecosystem functioning. Some plant traits can be both response and effect traits at the same time and, thus, are highly important for the ecosystem

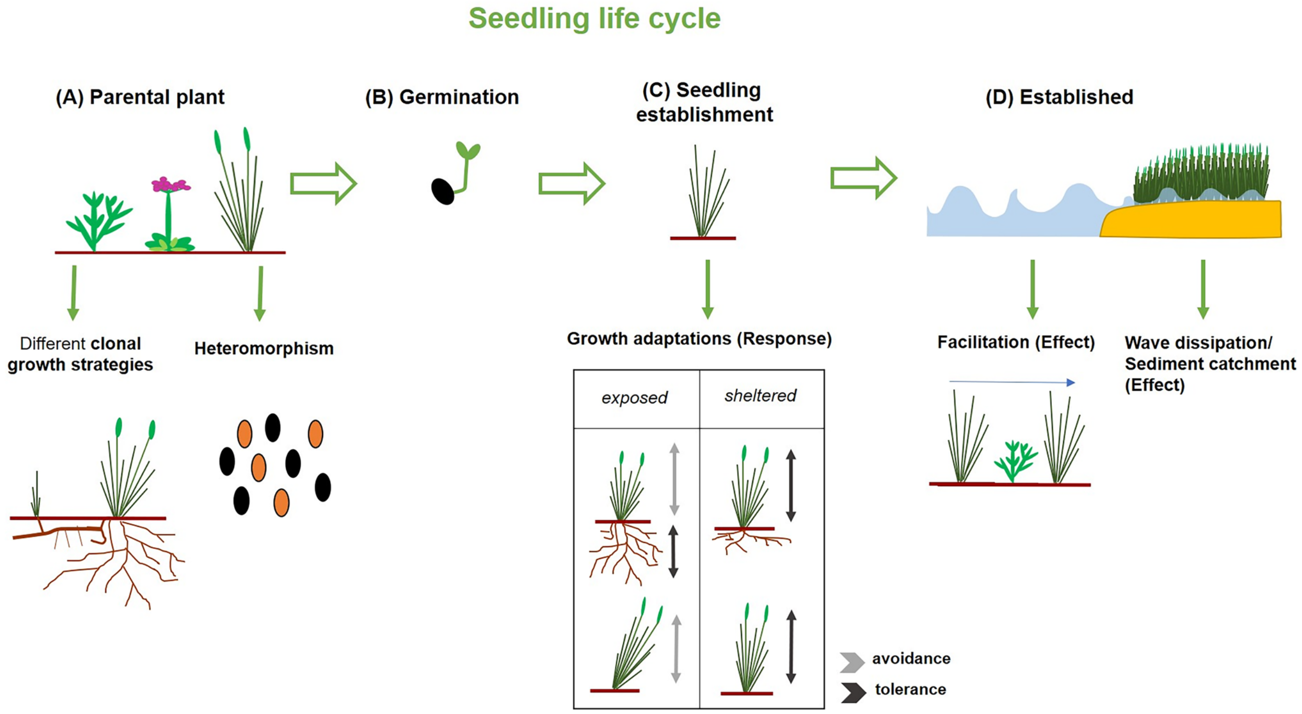

Fig. 6 Examples for adaptations of tidal marsh plants depending on seedling life cycle (**A**-**D**). Already traits of parental plants may have an impact on the survival and establishment of future seedlings (**A**). After germination (**B**), the seedlings themselves begin to interact with their environment and adapt to local conditions, e.g. following the avoidance or tolerance strategy when exposed to drag forces and associated erosion (**C**). However, traits can not only be a resonse to the environment but also affect it. Facilitation, wave dissipation and sediment catchment are examples for effect traits that may affect the ecosystem functioning after the establishment (**D**)

the growth of *P. australis* was diminished by reduced oxygen levels in the water-logged soils in the lower marsh and neighboring vegetation (Amsberry et al. 2000). Also for *Spartina densiflora*, four different clonal adaptations linked to the environmental conditions of high and low marshes were recognized, including dense colonization of open patches in tussocks, the lack of dormant periods and high tiller production rates and growth, the physiological integration between ramets, and also high rates of sexual reproduction (Nieva et al. 2005). The different reproductive strategies enable the species to invade uncolonized patches by clonal expansion as well as new sites with calm conditions by sexual dispersal, conferring resistance even to catastrophic events.

Adaptation Strategies After Germination – Avoidance and Tolerance

External mechanical forces, such as wind and wave movements, can cause great disturbance in marsh ecosystems (Ennos 1997; Read and Stokes 2006) and necessitate adaptation strategies of plants to avoid mechanical failure. Commonly, there are two plant growth strategies to minimize the negative external impact: either avoidance or tolerance (Puijalon et al. 2011). While the *avoidance strategy* involves traits that prevent the plants from failure, e.g. by minimizing the effect of drag forces, the *tolerance strategy* comprises traits enabling the plant to cope with unfavorable conditions, e.g. maximizing the plant resistance to breakage (Fitter and Hay 2002; Puijalon et al. 2008, 2011). Adaptations of morphological traits, such as reduced aboveground biomass und increased belowground biomass in wind-, wave- and sediment-exposed areas (avoidance; Silinski et al. 2018; Fig. 6), or higher rigidity of plant tissues (tolerance; Coops et al. 1996; Puijalon et al. 2011; Silinski et al. 2018; Fig. 6), are needed to survive the challenging or stressful environment.

Studies in the Elbe Estuary, Germany, found that abiotic factors such as tidal flooding duration, inundation and elevation height, as well as biotic interspecific competition affect not only the growth pattern and zonation, but also the species-specific tolerance to local hydrodynamics (Heuner et al. 2016, 2019; Carus et al. 2017a; Schoutens et al. 2020; Schulte Ostermann et al. 2021a). Species growth forms, e.g. by investing in their tissue construction and adapted anchoring (Bouma et al. 2005a; van Hulzen et al. 2007; Schwarz et al. 2015) as well as growth patterns interact directly with sediment and hydrodynamic conditions (Schwarz et al. 2015; Heuner et al. 2019). Responses to both were shown for seedlings of *Spartina anglica*, *Phragmites australis* and *Scirpus* *maritimus* (Cao et al. 2020a). After long-time exposure to waves, all three were found to invest more in their belowground biomass (increased root-shoot ratio) and to be more flexible as well as smaller after adaptation time. Schoutens et al. (2020) observed that the more seaward growing brackish pioneer species *Schoenoplectus tabernaemontani* exhibits lower flexural stiffness and less standing aboveground biomass due to leafless stems in order to reduce experienced drag forces by waves than the stiffer species *Bolboschoenus maritimus*, showing simultaneously a trade-off between wave attenuation and the expressed avoidance strategy.

Response to Salt Stress

Salinity is known to be a limiting factor for plant species in saline environments (Adam 1990). It affects the biogeochemical nutrient cycling processes such as N and P sorption, denitrification, and nitrification (Megonigal and Neubauer 2018) as well as carbon sequestration (Luo et al. 2019). First, salt stress is osmotic due to NaCl-induced reduction of hydraulic conductance in soil solutions which lessen water and solute uptake by plants (Assaha et al. 2017). Second, ion toxicity by the accumulation of Na^+ in plant cells and tissues interfere with plant growth and development, including, e.g. reduced leaf expansion, closed stomata, and thereby decreased photosynthesis (Rahnama et al. 2010). Increased levels of Na^+ potentially induce cytosolic K^+ effluxes with harmful imbalances in cellular homeostasis, increased oxidative stress, and interferences with Ca^{2+} and K^+ functions (reviewed in Assaha et al. 2017).

Plants growing under saline conditions have, therefore developed, various adaptations to cope with high salinities (reviewed in Yan et al. 2013; Zhang and Shi 2013). Salt resistance varies with soil and microclimatic conditions as well as with the halophyte type (genetic variability for each species), plant's life form and during developmental phases (Breckle 2002). To grow on a favorable site or to limit root growth to distinct soil horizons is a possible strategy to avoid salt stresses. Inversely, evasion and adaptation processes (e.g. selectivity against Na and Cl, compartmentation of salt within plant/tissues/cells, accumulation of salt in xylem parenchyma of roots and shoots) up to salt tolerance by succulent growth allow for plants to actively deal with salt (summarized in Breckle 1990, 2002).

For tidal marsh plants, Minden and Kleyer (2011) identified three general strategies to withstand salt stresses: 1) the exclusion of salt ions, 2) the dilution of cell sap, and 3) morphological and biochemical adaptations to osmotic pressures. Moreover, some tidal marsh species can combine several adaptations (cf. Minden 2010), improving their response to salinity and conditioning local plant communities and zonation (Watson and Byrne 2009). Simplified, halophytes cannot compete in more terrestrial areas, due to the high energy demand for salt stress coping mechanisms. In contrast, non-halophytes cannot survive in saline conditions (Davy 2002), creating a zonation through different niches. Thus, salt-tolerant tidal marsh species can be found more downstream in estuaries than upstream (Perry and Atkinson 2009). In response to future sea level rise, variations in the salt input, therefore, may result in a changed species composition, especially for fresh and mixed marshes, where salt-tolerant species replace those with higher susceptibility and thus modifying trait structure with potentially critical changes in trait-mediated ecosystem processes.

Tidal Marsh Plant's Effect on Environmental Conditions

Facilitation – Mutual Support within a Plant Community

Facilitation suggests that some plants are able to support others (e.g. less tolerant plants) exposed to disturbance and immersion (Fig. 2). Callaway (1995) reviewed facilitation processes in general plant communities and the mechanisms by which they pursue. Especially resource and habitat modifications and buffering of external forces by plants result in beneficial conditions for other species. The form of support is manifold and system-dependent. For tidal marshes this may imply that individuals or species following the tolerance strategy are able to protect and strengthen other plants with a lower capacity by buffering wave forces by increased surface roughness and resulting in milder conditions for landward marsh areas (Schulte Ostermann et al. 2021b).

However, facilitation is not limited to plant-plant interaction. In the stress-gradient-hypothesis framework, positive interactions such as facilitation are assumed to be positively correlated with increasing physical and biological stress (Bertness and Callaway 1994; He et al. 2013; He and Bertness 2014, cf. the previously mentioned physiological-ecological-amplitude-concept of Scholten et al. 1987), which have been investigated over different trophic levels for coastal systems (seagrass: Williams 1990, dunes: Fischman et al. 2019, marshes: Bertness and Shumway 1993; Bertness and Leonard 1997; Daleo and Iribarne 2009). Qiu et al. (2021) showed, for example, a relationship between microtopographic structures generated by crabs and enhanced seed trapping of *Suaeda salsa* in tidal marshes. A similar facilitation was found for the growth of mussels and the pioneer species *Spartina alterniflora* (Crotty and Angelini 2020). Mussel aggregations enhance patch-scale ecosystem functions, such as primary production of *Spartina*, presence and abundance of mobile macroinvertebrates, and metrics of species diversity. Furthermore, Castellanos et al. (1994) demonstrated in a field experiment the potentially important effect of facilitation between *Spartina maritima* and *Arthrocnemum perenne* for tidal marsh succession. Nevertheless, studies on the contribution of facilitation in tidal marsh succession during pioneer zone expansion or recolonization are scarce – even though the high disturbance regime of abiotics at the seaward edge of tidal marsh suggests mutual support of ecosystem compartments when applying the stress-gradient-hypothesis.

Effects of Tidal Marsh Plants on Waves – Wave Dissipation

Hydrodynamic disturbances typically arise from drag forces by waves and currents that exert mechanical stress on tidal marsh plants. As soon as their resistance threshold is exceeded, plants experience uprooting and breakage (Denny 1994). In response, they can either avoid drag forces, e.g. by reconfiguration (Bouma et al. 2005b), or increase their resistance (see Chapter 5.1.2; Fig. 6), causing different species-dependent wave dissipation capacities (Bouma et al. 2005a, 2005b, 2010). Depending on the vegetation density, canopy height, vegetation structure, and plant spacing (Leonard et al. 1995; Möller 2006; Bradley and Houser 2009; Bouma et al. 2010; Ysebaert et al. 2011; Yang et al. 2012), the flow field is generally changed and the energy regime is reduced when entering the vegetated marsh area (Leonard and Luther 1995; Nepf and Koch 1999; Leonard and Croft 2006; Neumeier and Amos 2006). Möller and Spencer (2002) showed that the most rapid reduction in wave heights takes place in the first 10 m of constantly vegetated tidal marsh areas, starting from the seaward edge, and was significantly higher than wave height reductions over tidal flats and the entire marsh area. In contrast, Yang et al. (2012) observed a wave elimination over a longer distance of ~ 80 m in the Yangtze Estuary, China.

Thereby, the effect of vegetation on the impinging forces can be species dependent as reviewed by Denny (2021), and plant trait dependent as demonstrated in experimental studies, where phenotypical and biomechanical traits, such as stiffness/flexibility and frontal area for species of different ecosystems, affect hydrodynamic forcing (Paul et al. 2012; Aberle and Järvelä 2013; Paul and Gillis 2015), and vice versa (Boller and Carrington 2006). In a flume experiment with canopies of the two tidal marsh grasses *Elymus athericus* and *Puccinellia maritima*, for instance, the effect of both species on the wave orbital velocities varied with water depth and wave period under intermediate hydrodynamic conditions (42 – 62 cm s^{-1}; Rupprecht et al. 2017). While under high water levels and long wave periods *Elymus athericus* showed stem folding and the flexible *Puccinellia* canopy contributed significantly more to wave dissipation, *Elymus* canopies reduced near-bed velocity more under low levels and short periods. Mentioned stem folding and breakage of *Elymus athericus* had a threshold orbital velocity of $\leq$ 42 cm s^{-1}. In contrast, *Puccinellia maritima* survived simulated extreme events without damage. Furthermore, a greater motion of *Puccinellia maritima* appeared under larger waves and stronger currents without any correlation between increasing wave energy and wave dissipation (Möller et al. 2014). Vegetation in the foremost tidal marsh zone, thus, favors conditions for vegetation in higher elevated marsh areas (see Facilitation). Nevertheless, it implies that wave energy in the seaward pioneer zone and the forces acting on establishing seedlings are particularly high, making safe sites rare and the seedling's development more difficult.

Effects of Tidal Marsh Plants on Sedimentary Processes

During the initial developmental phase of tidal marshes, low sediment stability and high wave forcing inhibit the colonization by higher plants and dense vegetation in the tidal marsh pioneer zones. Increased sediment accretion and induced higher bed elevations, in turn, reduce wave forcing and sediment remobilization, enabling fast vegetation colonization and enhance long-term persistence for young plants (Li et al. 2021b; Fig. 3 and 4). Therefore, plant-induced deposition of entrained sediment, for example by increased canopy structures (Krone 1985; Leonard and Luther 1995), can be particularly relevant for the establishment of seedlings and when considering vertical and lateral expansion of the tidal marsh. Typically, fast colonizers establish at first in tidal marsh pioneer zones, reducing the flow and, thus, supporting sediment accretion, improving the environmental conditions and facilitating intermediate and slow colonizers (Prach and Pyšek 1999; Bouma et al. 2007; Schwarz et al. 2018; Brückner et al. 2019). However, transplantation experiments of van Wesenbeeck (2007) suggested that surpassing a biomass or density threshold results in a clearly increased survival of seedlings, e.g. through self-facilitation by increased wave damping and enhanced sedimentation. Since the disturbance regimes in the lower zones of tidal marshes lead to increased plant mortality, density steadily decreases towards the seaward side (field observation: Zheng et al. 2016; modelling: Schwarz et al. 2018; Brückner et al. 2019), and colonization can be impeded.

Apart from aboveground characteristics, belowground biomass likely contributes to sediment stability. Feagin et al. (2009) assumed that plants modify soil parameters, e.g. by incorporation of detritus and fine-grained sediments into the soil matrix and making the soil less dense, less coarse and more cohesive. Likewise, in recent field studies improved soil resistance by plant-mediated soil structures (Li et al. 2021a), species-dependent effects on sediment shear strength (Evans et al. 2022), and intraspecific variability in root densities that positively affected sediment stability (Battisti et al. 2019) were observed. Furthermore, in a present biogeomorphological study, plant species-dependent variations (e.g. *Spartina* and *Puccinellia* root structures), plant colonization events, and bioturbation activity controlled the morphology of macropores and sediment cohesiveness, as well as the structural stability, and the persistence of these pores (Chirol et al. 2021). They considered vegetation cover particularly in fine silt/clay-sediments to be beneficial for water circulation, erosion mitigation and marsh functioning. It needs to be investigated experimentally under laboratory and field conditions, how root structure and interactions of aboveground and belowground plant biomass may affect future erosion events due to increased storm surge rates.

Plant-Mediated Landscape Forming—Self-Organization and Critical State Shifts

By combining the bifurcated effect of vegetation on hydrodynamic events and sedimentary processes, implications of both can be expanded to levels of landscape forming processes. In a study based on aerial photography and LiDAR of the Western Scheldt Estuary, SW Netherlands, Wang et al. (2020) found that tidal currents and wind wave abruptly change at the transition zone between low-elevated bare mudflats and high-elevated marsh areas, suggesting biogeomorphic feedbacks between vegetation growth, hydrodynamics, and sedimentary processes to cause state shifts. Inversely, vegetation die-off decrease platform sedimentation rates and filling of existing channels (Temmerman et al. 2012), or support formation of new or expansion of existing bare open water pools ("ponds"; Schepers et al. 2017, 2020; reviewed in Leonardi et al. 2018).

Even on a smaller scale, this correlation was observed by Schwarz et al. (2015). They detected a strong relationship between species-specific and plant-specific traits, physical stressors (waves, sediment), and the magnitude of those large-scale feedbacks. The strength and spatial extent of scale-dependent feedbacks can, thereby, be species-dependent, as shown in a flume experiment for three generic tidal marsh pioneer species (*Puccinellia* spp., *Spartina* spp. and *Salicornia* spp.) and their effect on flow deviations (Bouma et al. 2013). Species with fast and spatially extensive colonization strategies, for example, produce more homogenous geomorphic patterns than species with slow and patchy colonization strategies (Temmerman et al. 2007; Corenblit et al. 2015; Schwarz et al. 2018). In a recent laboratory study, clonal expansion traits of the marsh species *Spartina anglica*, *Phragmites australis*, and *Scirpus maritimus* seemed to be responsible for different configurations of the seaward edge (Cao et al. 2021). Even if the colonization of an area is initially carried out by only a small number of fast colonizers, they may contribute significantly to the stabilization of pre-existing channels and the consolidation of the landscape configuration (Schwarz et al. 2018). This idea was explicitly investigated for the species *Spartina anglica*, *Puccinellia maritima*, and *Salicornia procumbens* (Bij de Vaate et al. 2020). While the first two species favored channel development, the initial colonizer *Salicornia procumbens* did not induce significant topographic change. This circumstance is probably due to the species-dependent growth habit and can result in self-organizing spatial structures in tidal marsh ecosystems (van de Koppel et al. 2005; Weerman et al. 2010; Schwarz et al. 2018; Dai et al. 2021).

Positive bio-geomorphic feedbacks, as previously shown, can also reverse into a critical state, as it is known e.g. for *Spartina anglica*. The typical centrifugally expanding tussocks are able to accrete due to increased sediment trapping (Castellanos et al. 1994; Sánchez et al. 2001; van Hulzen et al. 2007), which enhances plant growth by reducing the inundation period and improving nutrient availability (Hemminga et al. 1998). This positive feedback can be reversed when the pronounced tussocks promote higher flow velocities between adjacent patches (van de Koppel et al. 2005; van Wesenbeeck et al. 2008a) reducing particle settling and promoting edge retreat (Temmerman et al. 2005; 2007). Thus, Widdows et al. (2008) observed wave attenuation of *Spartina anglica* to be accompanied by increased turbulent kinetic energy and bed shear stress. In field measurements, bed shear stress values exceeded the critical erosion threshold at the tidal marsh edge, but not over the bare mudflat during the inundation period. Hence, the impact of wind-induced waves and related edge erosion was increased by the interaction with *Spartina anglica* stems, questioning the role of *Spartina anglica* as a 'biostabilizer' of fine muddy sediment.

Those critical feedback loops are conceivable for a wide range of growth forms of vegetation or landscape configurations in tidal marshes. On a larger scale, a state of self-organized criticality can establish, a process where large-scale ordered spatial patterns result from disordered initial conditions due to local interactions (Rietkerk and van de Koppel 2008; Bouma et al. 2009a; van Belzen et al. 2017). For other ecosystems, such as savanna and peatlands, it is known that catastrophic shifts may be indicated by self-organized spatial patchiness (Rietkerk et al. 2004). In a theoretical and empirical study on clay accumulation and plant growth feedbacks in tidal marshes, van de Koppel et al. (2005) found such a possible critical state at the tidal marsh edge, when tidal flats deepen and become more vulnerable for wave attack and erosion, while the marsh area remains at a constant height or even increases in elevation. The coexistence of a state of bi-stability as mentioned e.g. for the transition between vegetated areas and unvegetated bare flats (Fagherazzi et al. 2006; Wang et al. 2020) provides a point of attack for rapid, potentially severe changes to the system.

The effects of vegetation on smaller scales (wave action and sedimentary processes) and larger scales (landscape forming) are critical to the persistence and stability of existing tidal marshes, as well as their expansion. Changing conditions, such as increased storm events, rising sea levels, and thus increased salinity in brackish and also freshwater areas (estuaries), may cause critical variations in plant community and the expressed trait composition. Trait-mediated processes may, therefore, turn non-beneficial, shifting formerly stable tidal marshes into unstable conditions. Counteracting such state shifts requires a fundamental system knowledge of vegetation-abiotic interactions with respect to certain community, species and plant effects.

Conclusion

1. The expansion of many tidal marsh areas is driven by reduced hydrodynamic forcing and, therefore, reduced erosive processes as well as infilling of bays with sediments. When the elevation exceeds a critical threshold, vegetation is able to establish. Subsequently, reciprocal relationships between abiotic forces and establishing vegetation decide over stability and persistence of the colonized areas.
2. For successful settling and development, specific habitat requirements must be met. 'Safe sites' that protect seedlings from disturbances and a disturbance-free period during the developmental phase (WoO) are crucial, especially in exposed areas, such as the pioneer zone of tidal marshes. However, the susceptibility of plants to hydrodynamic as well as sedimentary regimes and disturbances is species- and life stage-dependent and may vary locally.
3. After initial establishment, vegetation begins to interact with their environment, following different strategies and adaptation mechanisms. Mediated by their life history and biomechanical traits, plants respond to environmental conditions (i.e. flooding stress by tides, drag forces by waves and currents as well as linked scouring events, erosion or sediment burial) and affect ecosystem functioning (e.g. influencing the species composition by faciliation, and increasing the surface roughness with following sediment deposition and wave propagation).
4. Vegetation-abiotic-interactions are coupled to landscape configuration and can impact the formation processes in both ways – positively or negatively. Thus, they significantly contribute to the sensitive equilibrium in dynamic tidal marsh systems and may affect the function of critical shifts between alternative stable states.

In this review, we presented an ecological view on tidal marsh development, highlighting the pathway from seeds/propagules to developed plants and reveal important habitat requirements. We have shown that marsh vegetation can respond to and, in turn, affect its environment as well as landscape formation processes and persistence, e.g. by generating self-organized patterns. It was pointed out that young plants are more vulnerable to their environment than already established vegetation. Sea level rise and stronger and more frequent storm surges can, thus, either inhibit seed and propagule dispersal (e.g. washing away to unsuitable habitats) or a successful establishment (e.g. reduced WoO). This may adversely affect tidal marsh expansion and makes benign conditions for seedlings increasingly important for future restoration projects. When addressing biodiversity conservation goals, a sediment supply is required which is sufficiently high to ensure an appropriate bed height for vegetation growth and low enough to enable habitat diversity (channel systems, vegetation development without climax species dominance). Such thresholds are responsible for critical transitions when an ecosystem passes a bifurcation point due to variability of environmental conditions (e.g. unvegetated/vegetated; Balke et al. 2014). Since stressors mediating the establishment are not necessarily the same as the stressors responsible for the collapse, van Belzen et al. (2022) expand the WoO concept by complex noise-induced critical transitions, showing that timescales of the tolerance development by the organism as well as the environmental variability have to be proportional, i.e. shorter periods may result in a collapse of establishment opportunities to a much smaller range of parameter space. Thus, in addition to creating suitable conditions to exceed critical thresholds, sufficient time for ecosystem recovery appropriate to the species' tolerance period is necessary for future restoration projects.

Although it has long been recognized that interactions between vegetation and abiotics play a decisive role in the landscape formation processes of salt marshes, investigating these reciprocal interactions is still challenging. Various laboratory studies attempt to artificially display natural interactions between abiotics, such as waves and sediment, and vegetation, providing substantial insights and revealing fundamental mechanisms and feedbacks. However, the locality, variability, and complexity of a natural marsh system is difficult to reproduce, and validation of laboratory results under natural conditions often still lacks, which impedes the development of adequate restoration measures. Hence, especially transplantation experiments, large scale mesocosms, and more extensive long-term monitoring focusing on individual, species, and community scales are required to complete discoveries of laboratory and modelling studies and offering protection for tidal marsh ecosystems as well as integration ecosystem services in nature-based coastal protection.

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contributed sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Declarations

Conflict of Interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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