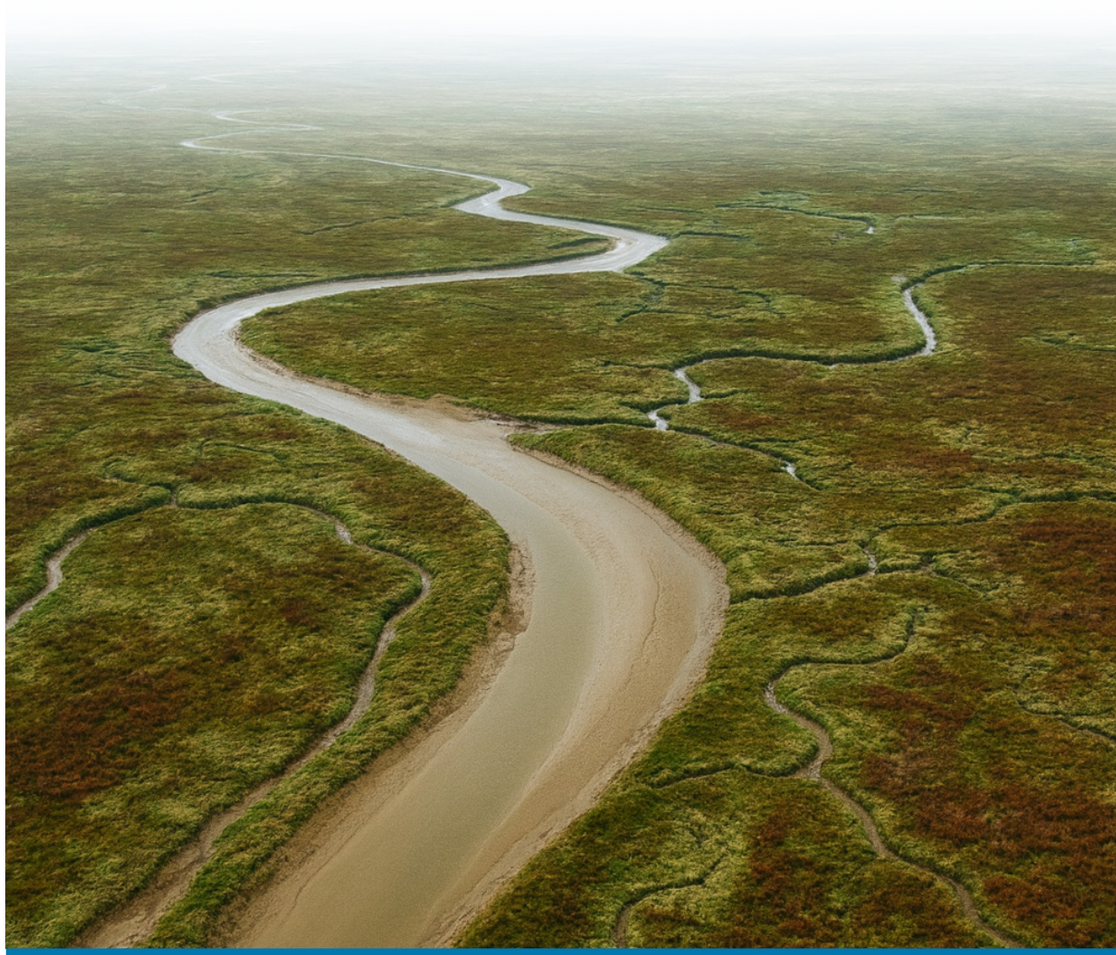
Biotic and abiotic interactions affecting early development of tidal marsh ecosystems

Sarah Hautekiet

Biotic and abiotic interactions affecting early development of tidal marsh ecosystems

Sarah Hautekiet



Supervisors **Prof. Dr. Stijn Temmerman | Prof. Dr. Maarten G. Kleinhans**

Thesis submitted for the degree of Doctor of Science: Biology
Faculty of Science | Antwerp, 2026

University of Antwerp

Biotic and abiotic interactions affecting early development of tidal marsh ecosystems

Biotische en abiotische interacties tijdens de ontwikkeling van jonge schor-ecosystemen

Thesis submitted for the degree of Doctor in Science: Biology at the University of Antwerp to be defended by

Sarah Hautekiet

Promotor: Prof. dr. Stijn Temmerman

Co-promotor: Prof. dr. Maarten G. Kleinhans

Faculty of Science
Department of Biology
Antwerp, 2026

University of Antwerp

Jury members

Internal

Prof. dr. ir. Filip Meysman
Prof. dr. Ivan Nijs
Prof. dr. Els Prinsen
Prof. dr. Sara Vicca

External

Prof. dr. Thorsten Balke (Carl von Ossietzky University of Oldenburg, Germany)
Prof. dr. Hannah Mossman (Manchester Metropolitan University, UK)

De doctoraatsonderzoeker en promotor(en) verklaren dat het doctoraatsonderzoek werd uitgevoerd volgens de principes van de wetenschappelijke integriteit, zoals vermeld in het Algemeen Doctoraatsreglement en Algemeen Charter van de Doctorandus van UAntwerpen en het Integriteitscharter voor Doctorandi en Promotoren verbonden aan de Universiteit Antwerpen.

Summary

Tidal marshes are dynamic coastal ecosystems located along sheltered coastlines (such as estuaries) that are frequently subjected to flooding from tides. They belong among the most valuable ecosystems on our planet since they provide crucial ecosystem services such as shoreline protection and carbon sequestration. A key feature of these ecosystems is the creek network dissecting the marsh platform. These creeks control the exchange of water, sediment, and nutrients between the marsh and the adjacent estuary. This exchange can be further influenced by the geometric properties of the creeks (e.g. channel width and depth), which vary widely between tidal marshes. Tidal creeks thus play an important role in the ecosystem functioning and its geomorphological development.

Over the past centuries, tidal marshes have been put under increasing pressure due to anthropogenic disturbance (e.g. land reclamation, embankment and industrial expansion) and are now further threatened by climate change related stressors (e.g. sea level rise). As such, these ecosystems are subjected to continuous degradation, leading to the loss of ecosystem services. This has created a growing interest for tidal marsh restoration. An increasingly used restoration strategy is the reintroduction of tides in formerly embanked areas by the landward construction of new dikes, followed by the partial/total removal of old, existing dikes. The aim of such practices is to create an intertidal ecosystem that displays equivalent characteristics and ecosystem functions as natural reference systems. However, restored tidal marshes often differ from their natural counterparts in this regard. Several studies have shown that they exhibit a lack of species richness and topographic diversity, a lower creek network density, and hindered groundwater dynamics. Furthermore, vegetation colonization is often delayed in restoration sites, but the mechanisms behind this delay are still poorly understood. Hence, we need a thorough understanding of the mechanisms driving tidal marsh development to improve outcomes in future restoration projects.

In this thesis, we aimed to advance our understanding of the abiotic and biotic mechanisms affecting tidal marsh development. Specifically, we had two main objectives: 1) investigating the relative roles of abiotic and biotic processes in tidal creek network development, and 2) investigating the mechanisms restricting or promoting pioneer vegetation establishment. In order to achieve this, we conducted scaled laboratory experiments in the Metronome tidal flume facility (Utrecht University), field monitoring, field experiments and a field mesocosm experiment in the brackish part of the Scheldt estuary, a mesocosm experiment in the lab (NIOZ, the Netherlands), and geospatial analyses of marsh development in restoration sites along the Scheldt estuary.

It is well established that both abiotic and biotic processes shape tidal creek network development. Previous studies have shown that vegetation generally promotes creek

network density through vegetation-flow-landform feedbacks. Plant recruitment strategies can further affect this process: patchy colonization by slow-establishing pioneers create higher creek network densities than spatially homogenous colonization by fast-establishing pioneers. Our flume experiments confirmed that vegetation colonization of an initially bare tidal landscape affects creek network formation. However, it revealed that the temporal rate of colonization (fast versus slows) exerts a stronger control on network density than the spatial colonization pattern (patchy versus homogenous). Vegetation colonization primarily affected tidal creek network development during the transition from a bare intertidal mudflat to a vegetated marsh. Furthermore, we found that abiotic processes are the dominant driver of creek incision. The strength of hydrodynamic forcing determines whether biotic processes can modify the creek network, indicating that their role is secondary to physical drivers.

Next, we investigated the mechanisms that control pioneer vegetation establishment on initially non-vegetated tidal mudflats, which are typically the first stages of ecosystem development in tidal marsh restoration projects. Field and mesocosm studies, complemented by geospatial analyses, revealed that vegetation colonization is strongly constrained by low intertidal elevation, rapid sediment accretion, and poor sediment drainage. Such conditions can typically be found in recently de-embanked areas and create issues such as the maintenance of waterlogged, unconsolidated sediments. The presence of historically compacted subsoil layers (resulting from years of agricultural activities) might further exacerbate these conditions. This strongly limits the development of erosion-resistant sediment beds and negatively affects seedling survival. Our geospatial analysis and field mesocosm experiment showed that well-drained sediment beds, such as tidal creek edges, promote plant establishment even in lower parts of the tidal frame. These well-drained areas exhibit increased sediment stability, which could be attributed to efficient lateral porewater drainage, prolonged surface drying, and evaporation. Such processes of sediment drying during low tides can rapidly increase the erosion resistance of initially waterlogged sediment surfaces, improving conditions for seed retention and seedling survival. Our results therefore emphasize that sediment drainage, air exposure, and evaporation-induced development of sediment erosion resistance are critical abiotic processes determining whether vegetation can establish successfully.

Aside from these abiotic processes, our findings suggest that three-way interactions between benthic algae, macrobenthos and pioneer plants affect pioneer plant establishment on initially non-vegetated tidal mudflats. Previous studies have already shown that plant seedling predation by macrobenthos can strongly limit plant colonization. Field transplantation of seedlings and mesocosm experiments, complemented by field monitoring showed that this top-down control of macrobenthos on plant seedling establishment can be mitigated by the presence of

filamentous mat-forming algae (e.g. *Vaucheria*). *Vaucheria* is mainly known for its biostabilizing abilities, creating elevated hummocks and locally increasing sediment stability. Here, we showed that the algae can also suppress polychaete densities by (1) creating less favorable conditions for the predator or by (2) offering an alternative, more digestible food source (i.e. lack of lignin). The former could be attributed to the dense algal mat, which might restrict polychaete burrowing activity and induce anoxic conditions in the sediment below the algal mat. As such, filamentous algae act as ecosystem engineers that create refuges from environmental stressors such as sediment erosion and seedling predation, thereby facilitating the establishment of pioneer vegetation.

Integrating these insights, the thesis demonstrates that abiotic and biotic processes are closely intertwined in shaping tidal marsh development. Abiotic factors (i.e. sediment drainage, intertidal elevation, and evaporation) can create well-drained, erosion-resistant surfaces that provide the physical foundation for facilitative biotic interactions. Poor drainage, low sediment shear strength, and seedling predation emerged as key bottlenecks that can delay the transition from bare mudflat to vegetated marsh. Improving drainage through creek excavation, reworking compacted subsoil layers, or enhancing topographic diversity may accelerate this transition. Similarly, promoting algal colonization could serve as a cost-effective measure to facilitate plant establishment.

Samenvatting

Schorren zijn dynamische kustecosystemen die voorkomen langs beschutte kustlijnen (zoals estuaria) en regelmatig overstromen door getijden. Ze behoren tot de meest waardevolle ecosystemen, omdat ze essentiële ecosysteemdiensten leveren zoals kustbescherming en koolstofvastlegging. Een belangrijk kenmerk van deze ecosystemen is het netwerk van kreken dat het platform doorsnijdt. De kreken regelen de uitwisseling van water, sediment en voedingsstoffen tussen het systeem en het aangrenzende estuarium. Deze uitwisseling kan verder worden beïnvloed door de geometrische eigenschappen van de geulen (zoals breedte en diepte), die sterk kunnen variëren tussen verschillende schorsystemen. Kreken spelen dus een belangrijke rol in het functioneren van het ecosysteem en in de geomorfologische ontwikkeling ervan.

In de afgelopen eeuwen zijn schorren onder toenemende druk komen te staan door menselijke verstoringen (zoals landaanwinning, bedijking en industriële uitbreiding). Daarnaast worden ze nu verder bedreigd door klimaatgerelateerde stressfactoren (zoals zeespiegelstijging). Hierdoor ondergaan deze ecosystemen een voortdurende degradatie, wat leidt tot verlies van ecosysteemdiensten. Dit heeft gezorgd voor een toenemende interesse in het herstel van schorren. Een steeds vaker toegepaste herstelstrategie is het herintroduceren van getijden in voorheen ingedijkte gebieden door het landinwaarts aanleggen van nieuwe dijken, gevolgd door gedeeltelijke of volledige verwijdering van oude dijken. Het doel van dergelijke maatregelen is om een intergetijdengebied te creëren dat vergelijkbare kenmerken en functies vertoont als natuurlijke referentiesystemen. Herstelde schorren verschillen echter vaak van hun natuurlijke tegenhangers. Verschillende studies hebben aangetoond dat ze een lagere soortenrijkdom en topografische variatie vertonen, een lagere dichtheid aan kreken hebben, en dat de grondwaterdynamiek wordt belemmerd. Bovendien verloopt de vestiging van vegetatie vaak traag in de herstelgebieden, maar de mechanismen achter deze vertraging zijn nog slecht begrepen. Daarom is een grondig inzicht in de processen die de ontwikkeling van schorren beïnvloeden noodzakelijk om toekomstige herstelprojecten te verbeteren.

In dit proefschrift hebben we geprobeerd onze kennis te vergroten van de abiotische en biotische mechanismen die de ontwikkeling van schorren beïnvloeden. We hadden hierbij twee hoofdobjectieven: 1) het onderzoeken van de relatieve rol van abiotische en biotische processen bij de ontwikkeling van getijdengeulnetwerken, en 2) het bestuderen van de mechanismen die de vestiging van pioniervegetatie beperken of bevorderen. Om dit te bereiken voerden we geschaalde lab-experimenten uit in de Metronome-getijdensimulator (Universiteit Utrecht), veldmonitoring, veldexperimenten en een veld-mesocosmosexperiment in het brakwatergedeelte van het Schelde-estuarium, een lab-mesocosmosexperiment

(NIOZ, Nederland) en geospatiale analyses van schorre ontwikkeling op herstelsites langs het Schelde-estuarium.

Het is algemeen bekend dat zowel abiotische als biotische processen de ontwikkeling van kreeknetwerken vormgeven. Eerdere studies hebben aangetoond dat vegetatie over het algemeen de dichtheid van kreeknetwerken verhoogt via terugkoppelingsmechanismen tussen vegetatie, stroming en sediment. Ook de vestigingsstrategie van planten kan dit proces beïnvloeden: “patchy” kolonisatie door langzaam vestigende pioniers leidt tot dichtere kreeknetwerken dan homogene kolonisatie door snel vestigende pioniers. Onze stroomgootexperimenten bevestigden dat vegetatiekolonisatie van een aanvankelijk kale getijdenvlakte de vorming van geulnetwerken beïnvloedt. Ze toonden echter aan dat de snelheid van kolonisatie (snel versus langzaam) een sterkere invloed heeft op de netwerkdichtheid dan het ruimtelijke patroon (“patchy” versus homogeen). Vegetatie beïnvloedde vooral de ontwikkeling van geulnetwerken tijdens de overgang van een onbegroeide slik naar een begroeide schorre. Daarnaast bleek dat abiotische processen de belangrijkste drijfveer zijn voor kreekinsnijding. Biotische processen kunnen enkel het kreeknetwerk wijzigen indien de hydrodynamische kracht dit toelaat en spelen dus een secundaire rol.

Vervolgens onderzochten we de mechanismen die de vestiging van pioniervegetatie bepalen op aanvankelijk onbegroeide modderplaten. Dit is typisch de eerste fase in de ontwikkeling van schorren binnen herstelprojecten. Veld- en mesocosmosexperimenten, aangevuld met geospatiale analyses, toonden aan dat vegetatiekolonisatie sterk wordt beperkt door lage intergetijdenhoogtes, snelle sedimentatie en slechte drainage van het sediment. Dergelijke omstandigheden komen vaak voor in recent ontpolderde gebieden en leiden tot problemen zoals het behoud van waterverzadigde, niet-geconsolideerde sedimenten. De aanwezigheid van gecompacteerde bodems (door langdurige landbouwactiviteiten) kan deze omstandigheden nog verergeren. Dit beperkt sterk de ontwikkeling van erosiebestendige sedimentlagen en heeft een negatief effect op het overleven van zaailingen. Onze geospatiale analyse en veld-mesocosmosexperimenten toonden aan dat goed drainerende sedimentoppervlakken, zoals de randen van kreken, de vestiging van planten bevorderen, zelfs in lagere delen van het getijdengebied. Deze goed drainerende zones vertonen een grotere sedimentstabiliteit, wat mogelijk te danken is aan efficiënte laterale drainage van poriewater, langdurige oppervlaktedroging en evaporatie. Zulke droogprocessen tijdens laagwater kunnen de erosiebestendigheid van aanvankelijk waterverzadigde sedimenten snel verhogen, wat de omstandigheden voor zaadretentie en kiemplantoverleving verbetert. Onze resultaten benadrukken dus dat sedimentdrainage, luchtblootstelling en evaporatiegestuurde ontwikkeling van erosiebestendigheid cruciale abiotische processen zijn die bepalen of vegetatie zich succesvol kan vestigen

Naast deze abiotische processen suggereren onze bevindingen dat drieweginteracties tussen benthische algen, macrofauna en pionierplanten de vestiging van pioniervegetatie beïnvloeden op aanvankelijk kale moddervlakten. Eerdere studies hebben al aangetoond dat predatie op plantenzaailingen door macrofauna de kolonisatie sterk kan beperken. Veldtransplantaties van zaailingen en mesocosmosexperimenten, aangevuld met veldmonitoring, lieten zien dat deze 'top-down'-controle van macrofauna op zaailingvestiging kan worden verminderd door de aanwezigheid van draadvormige matvormende algen (zoals *Vaucheria*). *Vaucheria* staat vooral bekend om zijn biostabiliserende eigenschappen: het vormt verhoogde bulten en verhoogt lokaal de sedimentstabiliteit. Hier toonden we aan dat de alg ook de dichtheid van borstelwormen kan onderdrukken door (1) minder gunstige omstandigheden voor de predator te creëren of (2) een alternatief, beter verteerbaar voedselaanbod te bieden (door het ontbreken van lignine). Het eerste effect kan worden toegeschreven aan de dichte algenmat, die de graafactiviteit van de wormen beperkt en een anoxische omgeving creëert in het sediment onder de mat. Draadvormige algen fungeren dus als ecosysteemingenieurs die toevluchtsoorden creëren tegen omgevingsstressoren zoals erosie en zaailingpredatie. Op deze manier bevorderen ze de vestiging van pioniervegetatie.

Wanneer we deze inzichten samenbrengen, laat dit proefschrift zien dat abiotische en biotische processen nauw met elkaar verweven zijn in het vormgeven van schorre-ontwikkeling. Abiotische factoren (zoals drainage, intergetijdenhoogte en evaporatie) kunnen goed gedraineerde, erosiebestendige oppervlakken creëren die de fysieke basis vormen voor gunstige biotische interacties. Slechte drainage, lage erosiebestendigheid en zaailingpredatie kwamen naar voren als belangrijke knelpunten die de overgang van kale slikke naar begroeide schorre vertragen. Het verbeteren van drainage via uitgraven van kreken, het bewerken van gecompacteerde bodems of het vergroten van de topografische variatie kan deze overgang versnellen. Daarnaast kan het stimuleren van algenkolonisatie een kosteneffectieve maatregel zijn om plantvestiging te bevorderen.

Acknowledgments

At long last, I get to write my acknowledgments. A moment I have been both dreading and longing for. It feels almost impossible to put the emotions I am currently feeling into words. But I will give it a try!

I would like to start by thanking my promoters, Stijn and Maarten, for taking a chance on me. Quite simply, I would not be writing this thesis if it were not for you. I am deeply grateful for your guidance and support throughout my PhD. Stijn, thank you for your constructive feedback, your encouragement, and for sharing your enthusiasm, not only for intertidal wetlands. One of the first things I learned about you was your fondness for Gouden Carolus Tripel, a beer you (wrongly, if you ask me) claim to be the best in the world. But hey, to each their own! Maarten, thank you for being your passionate self. Your speed of thinking and ability to make connections never cease to amaze me. You often reminded me of a modern-day Homo universalis, with your broad interests and curiosity. What connects you both is your remarkable ability to convey passion to others and that is truly inspiring.

Next, I would like to thank the jury members for giving insightful feedback and the stimulating discussion during the internal defense. Your comments offered new perspectives and undoubtedly improved this thesis.

I now turn to my dear colleagues from the Ecosphere research group. My first day in the office felt a bit surreal. It was the middle of the covid pandemic and, as such, many people were not present on campus. Entering the office, feeling a bit unsure of myself, I was welcomed by a Westmalle Tripel banner on one wall and an impressive collection of plastic bottle photos taken by Bert on the other. I remember thinking: "What did I sign myself up for?" Luckily, life soon returned to normal, and as I got to know my colleagues, I quickly realized that starting this PhD had been a good decision. As we would say in Dunglish: "I landed with my bum in the butter". I was incredibly fortunate to be surrounded by people who look out for one another, celebrate successes together, share frustrations, and offer support through difficult moments. If there is one key lesson I take from this PhD, it is the importance of community.

Within that community, I would first like to thank the biogeomorphology subgroup. Your constructive feedback on presentations and manuscripts, your help during fieldwork, and the positive atmosphere you created made a real difference throughout my PhD. Thanks to you, I could leave the office almost every day with a big smile, regardless of the circumstances.

Ken and Ignace, my dear "Boergondiërs", you have been a constant source of support throughout this PhD journey. I am deeply grateful for your help during field campaigns and for your patience in answering my many (many) questions. Beyond

being wonderful colleagues, you introduced me to the simple joys of sharing a glass of beer or wine and a piece of cheese in good company. My stomach and liver may not always have agreed (especially after that week in Austria), but I certainly did. And for this, I should probably also thank you, JP, for introducing them to this lifestyle in the first place.

Among the many colleagues who made this experience so enjoyable, I especially want to mention Mona. Whether it is building marsh organs in the field, sewing a kitchen apron or baking pancakes in the office, you approach everything with 100% enthusiasm. Your hands-on mindset and your ability to cheer up the people around you made my time (and undoubtedly that of many others) in Wilrijk brighter and a lot more fun.

Besides spending time in the office next door, I particularly cherished the many chats in my own office with Laura, Greg, and Julio. I can honestly say that "office day" was the highlight of my week, and I could not have wished for better office mates. Laura, I truly enjoyed our countless coffee, chai latte, and ice-cream breaks, as well as our padel outings (during which we may or may not have crushed the post-docs). Those padel matches naturally bring me to you, Greg. Your boundless enthusiasm on court, including the occasional unnecessary jump or stealing balls from your doubles partner, never failed to make me laugh. That same energy and dedication carried over into your unofficial role as my pseudo-supervisor. I am incredibly grateful for the time you took to read my work and provide feedback, and I learned a great deal from our discussions. Beyond being an excellent post-doc (and hopefully soon professor!), your cheerful presence and our chats about your furry and non-furry kids never failed to lift my spirits.

I would also like to thank Maria-Esther and Faras for the chats in the break room and in the office. You offered a welcome distraction from work, especially during those final months on campus!

Aside from the people in my subgroup, there are many others who left a lasting mark on me.

Maede, you were the very first colleague in Antwerp I could truly call a friend. I believe fate brought us together during that biology BBQ in 2021. There is no greater joy than finding someone who you can talk to about absolutely everything, going from tv-shows to politics. Thank you for sharing your Persian heritage with me. I hope our friendship continues, even across longer distances.

Furthermore, a very special thank you goes to my number one Survivor Alliance: Harvey and AJ. Harvey, from the very beginning, we clicked on so many levels. You

were the person I could always turn to, whether I needed to vent, reflect, or simply talk things through. Our conversations, on just about any topic, are something I will always cherish. Without a doubt, my experience in Antwerp would not have been the same without you. Thanks to you, I found my tribe in Wilrijk, and a fellow delusional soul always willing to sign up for ambitious plans such as the Dodentocht.

One essential member of that tribe is AJ. Between tennis matches, shared runs, after-work drinks, and parties (with excellent games organized by you), we collected many memorable moments. Our shared love for reality TV and games eventually led to the recurring joke that we might one day attempt The Amazing Race as a duo. Although, whether we would get anywhere with my "great" sense of direction, remains highly questionable.

I may have not explicitly included you in my Survivor Alliance, Mathilde, but you absolutely belong there. You are my ride or die and secret top-two. Over the past year, you were the person with whom I could say things out loud, unfiltered and without fear of judgment. Your kindness, honesty, and open-heartedness meant the world to me, and your friendship made a truly significant contribution to this thesis. Thank you for being your wonderful, French, and sassy self. I hope we will share many more tv-show viewing parties, complete with our very necessary uncensored commentary, along with many more dinners and drinks.

I would also like to thank those who brought warmth and positive energy to everyday moments, whether in the break room, at after-work drinks, parties, conferences, or during frolleague weekends. Dorian and Heleen, you never failed to brighten up the room with your sunny personalities, and Dorian, amai, your baked treats were always a delight. I genuinely think it might be time to open a pastry shop! Speaking of pastries, I also have fond memories (despite quite a bit of bickering) of making Apfelstrudel in Austria together with you, Niels. Sparks, laughter, and overall good vibes were guaranteed at any gathering thanks to April, Iris, Jayson, Jodie, and Moses. And finally, I certainly cannot forget about one of my favorite couples, Royna. Roy, I loved our conversations about metal music and your many other passions, stretching from beer to gastropods. Rina, from the moment you shared your love for cheesy fairy tales such as "Drei Haselnüsse für Aschenbrödel", I knew in my heart we were going to be friends.

Lauren, supervising you as my first master's thesis student was a real pleasure. I am immensely grateful for your help and enjoyed our chats, as well as the many hours spent walking (sometimes crawling) through the mud together. I would also like to thank the rest of the field and lab technicians, whose hard work keeps everything running smoothly.

Lotte, you are a logistical mastermind. I am endlessly impressed by your problem-solving skills and drive. Thanks for your support and the engaging conversations!

Beyond my colleagues, I would like to thank my friends. Anne-Lynn, Fien, Lize, and Silke, your friendship has been a constant throughout my life, even when we did not see each other as often as we would like. Board game nights, coffee stops, city trips, museum visits, and walks provided much-needed breaks and moments of joy during these past years.

Dieu, we supported each other throughout our PhD journeys, and I am so proud of you and in awe of your mindset. Thank you for saying the right things at the right time. I hope we will get to see each other more frequently in the future.

My fellow biologists Ines, Inge, Heleen, Lize, Manon, and Nele (I still regard you as a biologist, Nele), our catch-ups over a nice cup of coffee or tea and pastries were always a treat. I am already looking forward to test new pastry shops with you!

Last but not least, I would like to thank my parents for their unwavering support and for being my safe haven. Mamulda, you have always supported me in anything I tried and sometimes gently pushed me out of my comfort zone (which, frankly, I sometimes need). You taught me several invaluable lessons I will carry forward: (1) failure is not the end, learn from your mistakes and try again, (2) reach out to people when you need help, and (3) always look at things from a positive perspective.

Ráda bych také poděkovala tebe, babičko, za tvou podporu a za snahu porozumět mému tématu, i když bylo obtížné vysvětlit.

I would like to end my acknowledgments with one final statement for all of you who have stuck with me. "**You need a healthy dose of delulu, to make things come trululu**." Cheers, everyone!

Table of contents

Chapter 1 Introduction 1

Chapter 2 On the relative role of abiotic and biotic controls in channel network development: insights from scaled tidal flume experiments 23

Chapter 3 Competing biotic interactions between fibrous algae and macrobenthos shape pioneer vegetation establishment in tidal marshes 59

Chapter 4 Edges of opportunity: Tidal creek edge processes drive pioneer marsh vegetation establishment 85

Chapter 5 Bottlenecks for pioneer plant establishment in restored tidal marshes: effect of subsoil, sediment drainage, and elevation 111

Chapter 6 General discussion 139

Chapter 7 Supplementary information 161

1

Introduction

1.1 Tidal marshes: valuable ecosystems under pressure

Tidal mudflats and marshes are dynamic ecosystems located at the interface between land and sea. They are typically found in temperate climate zones at mid to high latitudes along the intertidal zone of sheltered coastlines (such as estuaries, deltas, and tidal inlets). Their distribution can span across the full salinity gradient, ranging from freshwater to brackish to saline zones (Townend et al., 2011; Worthington et al., 2024). These ecosystems are frequently flooded, with inundation patterns driven by daily (ebb-flood) and monthly (spring-neap) tidal cycles, which strongly influence the characteristics of these habitats. Lower-lying tidal mudflats are flooded at every high tide and are typically unvegetated, whereas higher-lying tidal marshes are only flooded during higher tides. This reduced flooding allows tidal marshes to host vegetation and animal communities that have adapted to these challenging conditions.

Despite only making up a small portion of our terrestrial landscape, with global estimates varying from about 52,880 km^2 (Worthington et al., 2024) to 90,800 km^2 (Murray et al., 2022), tidal marshes belong among the most productive ecosystems, providing a wide array of ecosystem services (Barbier et al., 2011; Mitsch et al., 2013). They provide habitats for specialized fauna and flora, nursery grounds for fish, and feeding grounds for migratory birds (Greenberg et al., 2014; Mcowen et al., 2017). Apart from their significance for estuarine biodiversity, they play an essential role in nutrient cycling and water filtration as they trap sediments and filter pollutants (Barbier et al., 2011; Friess et al., 2020; Spencer & Harvey, 2012). Furthermore, tidal marshes are globally recognized for being hotspots of carbon sequestration. When expressed per surface area, their capacity to sequester and store organic carbon in their sediments exceeds that of many terrestrial and marine ecosystems and is as such of high relevance for climate change mitigation (Temmink et al., 2022). Additionally, they act as a natural barrier against coastal hazards (e.g., floods and storms) by attenuating waves, storm surges and shoreline erosion (Schoutens et al., 2019; Temmerman et al., 2023).

Despite their importance, tidal wetlands are among the most threatened ecosystems worldwide due to centuries of anthropogenic disturbance (Barbier et al., 2011; Kirwan & Megonigal, 2013). Human societies have long been drawn to coastal and estuarine environments due to their fertile soils and reliable access to water, conditions that facilitated agriculture, settlement and trade. In efforts to mitigate flooding and storm surges, communities constructed embankments (also called seawalls, dikes, or levees), thereby altering natural hydrological and sedimentary regimes (Knottnerus, 2005; Meier, 2004). With population growth and industrial expansion, demands for maritime transport, agricultural land, and secure living space intensified. These increasing demands prompted interventions such as dredging to maintain navigable waterways and constructing embankments to

reclaim land and reduce flood risk. Land reclamation often involves the conversion of tidal marshes into human land use by constructing dikes. These structures disconnect the systems from adjacent estuaries, thereby stopping tidal inundation. This is followed by drainage of the former marsh soil through excavating drainage ditches, sometimes combined with pumping drainage water towards adjacent estuaries. The conversion to embanked land, often for agricultural activities, is referred to as "polders" in the Low Countries (Bakker et al., 2002; Wolters et al., 2005b). Such interventions left lasting imprints on the coastal landscape and altered hydrological and geomorphological processes (Lee et al., 2006; Temmerman & Kirwan, 2015). Alongside these anthropogenic pressures, climate change introduced additional stressors (e.g. sea-level rise, increased storm intensity, and altered sediment dynamics). Sea-level rise (SLR) can pose a threat to tidal marshes by resulting in increased duration and frequency of tidal inundation. If the rate of SLR exceeds the ability of the marsh to accrete vertically through sediment deposition and organic matter accumulation, the ecosystems may degrade and eventually drown (Fagherazzi et al., 2020; Reed, 1995). Increased storm intensity and the associated storm surge may further exacerbate tidal marsh loss through shoreline erosion and flooding (Cahoon, 2006; Schuerch et al., 2013; Temmerman et al., 2023), while reduced sediment supply (e.g. by river damming) can limit marsh accretion (Cahoon et al., 2019; Kirwan & Megonigal, 2013; Syvitski et al., 2005; Yang et al., 2005). As a result of these stressors, tidal wetlands are experiencing continued degradation and declining ecosystem functionality, which raises concerns for biodiversity conservation and coastal protection (Fluet-Chouinard et al., 2023; van Dijk et al., 2021).

1.2 The benefits and challenges of tidal marsh restoration

Recognizing both the risks of wetland degradation and the ecological and economic benefits of wetlands, tidal marsh conservation and restoration have received increasing attention. One widely applied restoration strategy is managed realignment. This restoration strategy entails the landward construction of dikes, followed by partial or complete removal of the pre-existing dikes along the estuarine shoreline, to reintroduce tidal exchange between formerly diked (embanked) land and the adjacent estuary (Airoldi et al., 2021; French, 2006; Morris, 2013). The term "managed realignment" is commonly used in the UK, whereas further in this thesis we also refer to it as "de-embankment". These measures aim to reinstate hydrodynamic and sedimentary processes, with the objective that once these processes are restored, the development of a tidal marsh ecosystem (with characteristic sediment properties, benthic communities, and vegetation) will naturally follow.

Restoring these processes not only supports ecological recovery but also reinstates its valuable nature-based coastal storm buffer function. During extreme high (storm)

tides, storm surges can be attenuated by friction created from marsh vegetation and by the tidal marsh acting as a temporal water storage (e.g. Smolders et al., 2015; Stark et al., 2015). Hence, the associated flood risk is dampened. Furthermore, marsh vegetation reduces shoreline erosion aboveground (i.e. vegetation canopy) by attenuating wind waves and tidal currents, and belowground (i.e. root network) by stabilizing the sediment bed (Brooks et al., 2021; Garzon et al., 2019; Möller et al., 2014).

Tidal marsh restoration can be considered successful if the system presents equivalent ecosystem functions like adjacent natural marshes. However, restored tidal marshes often differ from natural reference systems. They can display reduced species richness (Lawrence et al., 2022; Mossman et al., 2012), lack of topographic heterogeneity and lower creek network density (Lawrence et al., 2018; Vandenbruwaene et al., 2012), impaired groundwater fluxes (Spencer et al., 2017; Van Putte et al., 2020), and delayed vegetation establishment (Cao et al., 2021; Wolters et al., 2005a). Understanding the processes driving tidal marsh development is therefore essential to improve restoration outcomes and guide management strategies. Popular restoration strategies include de-embankment to restore tidal exchange, creek excavation, raising the landscape, adding microtopography and planting vegetation (He et al., 2025).

1.3 Tidal creek networks: essential features in tidal marshes

A defining feature of tidal marshes is the presence of tidal creek networks that dissect the marsh platform. These creeks (also referred to as channels) function as the primary conduits of intertidal wetlands by transporting water, sediment, nutrients and biota (e.g. seeds, larvae, fish, etc.) in and out of the system (Fagherazzi et al., 2012; Vandenbruwaene et al., 2012). The geometric features of these creek networks, which vary across tidal marsh systems, can further influence this exchange. These features are typically quantified using metrics such as channel width and depth, as well as proxies for the density of the channel network like drainage density (i.e. the ratio between the total channelized network length and watershed surface area) (Kearney & Fagherazzi, 2016; Marani et al., 2003). As such, tidal creek networks play a central role in the ecosystem functioning of tidal marshes, shaping their geomorphological and ecological development. Consequently, effective tidal marsh restoration necessitates a comprehensive understanding of tidal creek network formation and evolution.

Tidal creeks start to form during the early stages of tidal marsh development. On initially unvegetated tidal mudflats, typically, tidal flow concentrates in topographic depressions, initiating a feedback in which increased flow velocity enhances scouring of the depressions (D'Alpaos et al., 2006; Stefanon et al., 2010). As a result, higher bottom shear stresses are created that promote erosion and further deepening of the initial depressions. The latter feeds back to further concentration

of tidal flow until initial channel features are formed. Subsequent creek development is mainly driven by headward erosion and connection of channels (D'Alpaos et al., 2005). Once pioneer marsh vegetation starts to establish on initially unvegetated tidal mudflats, an additional vegetation-flow-landform feedback emerges that actively modifies creek geomorphology, resulting in self-organization of the tidal marsh landscape (Schwarz et al., 2018; Temmerman et al., 2007; Vandenbruwaene et al., 2013). Specifically, vegetation can affect creek network complexity by stabilizing the existing creek banks, which enables the development of meandering channels (Tal & Paola, 2010). Furthermore, creek development is influenced by vegetation-induced friction. The vegetation canopy slows down tidal currents within vegetation patches, promoting sedimentation and further vegetation establishment (Bouma et al., 2007; Vandenbruwaene et al., 2011). Meanwhile, the tidal flow follows the path of least resistance and therefore accelerates around and between vegetation patches, which can initiate creek formation (Temmerman et al., 2007; Vandenbruwaene et al., 2015). In general, findings have suggested that these processes lead to higher channel drainage efficiencies (e.g. higher drainage density) in vegetated marshes compared to unvegetated mudflats (Kearney & Fagherazzi, 2016). Additionally, plant recruitment strategies can affect creek network formation. Previous studies have indicated that different spatio-temporal colonization patterns lead to differences in creek network densities and drainage efficiency (Bij de Vaate et al., 2020; Schwarz et al., 2018). For instance, patchy colonization by slow-establishing pioneers (e.g. *Spartina* spp. – Fig. 1.1 on the left) results in more extensive creek networks than the more spatially homogeneous colonization patterns by fast-establishing pioneer species such as *Salicornia* spp. (Fig 1.1 on the right) (Schwarz et al., 2018, 2022). Thus, differences in recruitment strategies could have consequences on the functioning of the tidal marsh.



Figure 1.1: *Spartina anglica* patches (left) and *Salicornia europeae* isolated plants (right) during the early colonization of a tidal flat (Schiermonnikoog, the Netherlands).

Overall, it is well-established that tidal creek network development in marshes arises from the interaction between hydrodynamic forces (tidal currents), geomorphic features of the landscape (e.g. mean marsh elevation and slope), and vegetation traits

(e.g. colonization pattern, stem density and height) (Bij de Vaate et al., 2020; Li et al., 2019). Multiple studies suggested that vegetation may enhance creek network formation during the transition from bare mudflat to a vegetated marsh (Bij de Vaate et al., 2020; Schwarz et al., 2014), whereas its influence may diminish once the marsh is densely vegetated (Liu et al., 2022). In contrast, abiotic processes could exert a more dominant control on the overall structure and complexity of tidal networks (Liu et al., 2022). The relative importance of abiotic versus biotic processes in tidal creek network development, however, remains an open question.

Clarifying the contribution of these processes is essential to explain how tidal creek networks are shaped and how they will evolve. Achieving this requires an adequate research approach. Previous research has largely relied on numerical models or empirical analyses (e.g. Kirwan & Murray, 2007; Schwarz et al., 2018; Vandenbruwaene et al., 2013). However, these approaches often have drawbacks such as oversimplifying real-life processes in models or issues with site-specific conditions in empirical studies.

Scaled laboratory experiments, which are typically used to study the landscape-scale morphodynamics of fluvial and tidal systems, can be used as an alternative approach (e.g. Kleinhans et al., 2015; Stefanon et al., 2010; Tal & Paola, 2010; Zhou et al., 2014). Such experiments are conducted in flume facilities, specialized labs that can mimic natural stream conditions and enable the study of interactive effects between water flow and ecosystems. The setup generally consists of a channel with water flow, a sediment bed and the presence or absence of live vegetation. These experiments offer multiple advantages: the materials and processes are real, initial and boundary conditions can be controlled, the systems can develop much faster than in nature, and large spatial (~km) and temporal (~decadal) scale processes can be scaled down. The majority of scaled laboratory experiments have been conducted in a fluvial and estuarine context and indicated that vegetation can steer the development and evolution of such systems (Kleinhans et al., 2022; Tal & Paola, 2010; van Dijk et al., 2013; Weisscher et al., 2022). However, we are lacking such flume experiments (including and excluding plant effects) in an intertidal basin context. This could be attributed to issues with scale effects, such as unrealistic scouring (e.g. Stefanon et al., 2010; Vlaswinkel & Cantelli, 2011). Recent advances have demonstrated that the most limiting scale effects can be mitigated by using a flume with a tilting bed consisting of poorly sorted sand (Kleinhans et al., 2012, 2015, 2017). Such a unique flume setup is available in the Metronome tidal flume facility at the University of Utrecht (Fig. 1.2), and is mainly used to study the morphodynamics of rivers. In this thesis, we will use the facility to investigate creek network development in an intertidal basin context with and without inclusion of living vegetation.



Figure 1.2: The Metronome tidal flume facility (left), and a close up of a scaled flume experiment including living vegetation (right). Photo on the left taken by Merel Tuk and on the right by Maarten Kleinhans.

1.4 Pioneer vegetation establishment: abiotic and biotic controls

The transition from bare mudflat to vegetated tidal marsh represents a pivotal stage in ecosystem development. This process is typically initiated by the establishment of pioneer vegetation in the bare intertidal flat. However, many restoration sites experience issues with a delayed pioneer vegetation establishment in (parts of) the system, which could limit the ecosystem services they are providing. Ensuring the successful establishment of pioneer species is therefore one of the key challenges for intertidal marsh restoration.

Successful establishment of pioneer vegetation depends on two broad conditions: (1) the arrival of propagules through dispersal from neighboring mature marshes or clonal expansion through lateral outgrowth of root systems, and (2) the suitability of the environmental conditions (abiotic and biotic) for seed retention, germination, and seedling establishment (Erfanzadeh et al., 2010; Steinigeweg et al., 2023; van Regteren et al., 2019). Soil surface elevation within the intertidal zone (relative to the high and low tide levels) is one of the most critical abiotic factors, delineating the zones where plant communities can establish (Dale & Arnall, 2024; Wang & Temmerman, 2013). At low elevations, seed retention and seedling anchorage are hindered by frequent and prolonged tidal inundation, anoxic and waterlogged soils, intense hydrodynamics (i.e. drag from currents and waves) and sediment dynamics (i.e. erosion and accretion), which can bury or wash away seeds/seedlings (Cao et al., 2018, 2021; van Regteren et al., 2020). Above an elevation threshold, which typically depends on the physiological limits of marsh plants, vegetation establishment becomes theoretically possible (Wang & Temmerman, 2013). This elevation threshold seems to depend on inundation frequency, rather than inundation duration (Balke et al., 2016).

The moment of successful recruitment relies on sufficiently long disturbance-free periods (i.e. periods without tidal inundation, limited bed level changes, and limited tidal currents and waves) after propagule dispersal, also referred to as "Windows of Opportunity" (Balke et al., 2014; Hu et al., 2015, 2021; van Belzen et al., 2022). This temporary absence of physical disturbance allows seedling germination and establishment. Once their roots have grown sufficiently in depth, plants become more resilient to external forcing (Redelstein et al., 2018). Importantly, elevation is closely linked to the occurrence and required duration of disturbance-free periods. As these periods generally become more frequent and longer with increasing elevation in the intertidal zone, plant recruitment can take place more frequently (Balke et al., 2014).

Effective sediment drainage represents another key abiotic factor influencing pioneer vegetation establishment. Drainage refers to the movement of water toward tidal creeks during ebb, which occurs both at the surface (flow of water over the sediment surface) and subsurface (porewater flow through the sediment pores). Both drainage processes are typically enhanced on slightly elevated microtopographic surfaces (Fivash et al., 2019) and along tidal creek edges (Ursino et al., 2004; Xin et al., 2010). Restored tidal marshes, however, often deal with poor drainage conditions which might be related to the presence of a historically compacted soil layer (due to years of soil drainage and agricultural practices before the marsh restoration). Previous studies indicated that a compacted subsoil impedes porewater fluxes (Spencer et al., 2017; Van Putte et al., 2020) and tidal creek network (Lawrence et al., 2018; Vandenbruwaene et al., 2012). Poor drainage of sediment deposited on top of the compact subsoil may not only create anoxic conditions in the root zone, negatively affecting seedling growth (Ursino et al., 2004), but may also lead to the persistence of fluid, unconsolidated sediment beds (Grabowski et al., 2011; Oosterlee et al., 2020). Such sediments typically exhibit low sediment shear strength (i.e. low resistance to erosion) (Cao et al., 2021, 2022), which in turn makes seedlings, with limited root anchorage, vulnerable to erosion (Cao et al., 2018, 2022; Redelstein et al., 2018). Despite these insights, the mechanisms by which environmental parameters such as sediment surface elevation, sediment drainage, and their interactions govern pioneer vegetation establishment in restored systems remain poorly understood.

Biotic interactions add another layer of complexity. In this thesis, we focus on the interactions among three species belonging to key groups of organisms commonly found in brackish tidal marshes in NW Europe: the polychaete *Hediste diversicolor*, the benthic filamentous algal genus *Vaucheria* sp. and the pioneer marsh plant *Aster tripolium*.

The polychaete worm *Hediste diversicolor* is one of the most prevalent benthic invertebrate species found in brackish water zones of estuaries. This omnivore can

negatively affect seedling survival through seed and seedling predation and/or bioturbation (Hughes et al., 2000; Hughes & Paramor, 2004; Paramor & Hughes, 2004, 2007; van Regteren et al., 2017; Zhu et al., 2016). Since *Hediste* belongs among the first colonizers of low-lying tidal marsh restoration sites, it could actively hinder vegetation establishment (Paramor & Hughes, 2005; Van den Neucker et al., 2007).

The widespread yellow-green algae *Vaucheria* sp. can be frequently found in intertidal environments. *Vaucheria* algae are able to tolerate desiccation and typically form dense algal mats consisting of filaments penetrating the sediment bed. These mats trap sediment particles, thereby developing elevated microtopography, and creating more erosion-resistant sediments, which could facilitate pioneer plant establishment (Gallagher & Humm, 1981; van de Vijsel,et al., 2020; 2021; Wilcox, 2012).

Observations suggest a potential three-way interaction between polychaetes, algae and pioneer marsh plants: algal mats have been hypothesized to counteract the top-down control of polychaetes on plant establishment, but experimental evidence is lacking (van de Vijsel et al., 2021). Unraveling how these interactions function is crucial for understanding early tidal marsh development and to realize more effective restoration strategies.

1.5 Aims and outline of this thesis

In recent decades, estuaries in NW Europe have become a focal region for tidal marsh restoration on formerly embanked land, motivated by both ecological objectives and the growing need for nature-based shoreline protection. However, these restoration sites often display slow or limited development of tidal marsh landscapes compared to natural tidal marsh systems. A better understanding of mechanisms driving tidal marsh development is needed to design effective measures for future restoration projects (see Fig. 1.3). In this thesis, our aim is to provide new insights on the development of two key features of tidal marsh landscapes (i.e. creek networks and marsh vegetation) by investigating: **1)** the relative role of abiotic and biotic factors in tidal creek development and evolution, and **2)** the mechanisms restricting and promoting pioneer vegetation establishment in restored tidal marshes. Based on our findings, we will propose restoration guidelines that could help create fully functioning ecosystems.

Our first main objective focuses on the short- and long-term geomorphological evolution of tidal creek networks under varying spatio-temporal vegetation colonization patterns in landscape-scaled experiments (Chapter 2). The second main objective addresses processes governing the transition from a bare intertidal mudflat to a vegetated tidal marsh in restoration sites. Specifically, we examine the mechanisms influencing pioneer vegetation establishment during the initial stages of marsh development (Chapters 3, 4 & 5). First, we investigate the effects of

competing algal–benthos–plant interactions on pioneer vegetation establishment (Chapter 3). Next, we study the effects of proximity to tidal creeks in facilitating vegetation colonization (Chapter 4). Finally, we identify mechanisms delaying and promoting vegetation establishment in restored tidal marshes (Chapter 5). The sections below provide a more detailed overview of each chapter.

To address our first objective, we apply novel flume experiments with a tilting bed to investigate the relative role of abiotic and biotic processes affecting tidal creek network development. Specifically, in **Chapter 2**, we compare creek network development under three scenarios: (1) an unvegetated intertidal basin, (2) a vegetated basin with a patchy vegetation recruitment strategy, and (3) a vegetated basin with a hydrochorous recruitment strategy. We hypothesize that vegetation positively affects creek network density and that this effect differs between plant recruitment strategies. Hydrochorous plant colonization, in which pioneer plants produce large numbers of seeds dispersed by tidal flow, is expected to generate lower creek density compared to the slower, patchy plant colonization. Furthermore, we expect recruitment strategies to influence creek development primarily during the transition from a bare to a vegetated state.

The chapters addressing our second main objective zoom in on the initial stages of tidal marsh development in restored sites, with a particular focus on the mechanisms that restrict or promote pioneer plant establishment. Early marsh development often follows a successional sequence: initial colonization by polychaetes (e.g. *Hediste diversicolor*), followed by algae (e.g. *Vaucheria* sp.), and finally pioneer plants (e.g. *Aster tripolium*). Previous studies have shown that polychaetes inhibit pioneer plant colonization, whereas filamentous algae may facilitate it. This suggests that competing biotic interactions between algae, macrobenthos, and pioneer plants play a key role. In **Chapter 3**, we investigate the nature of these interactions and their influence on pioneer vegetation establishment using monitoring surveys, field transplantation, and a mesocosm experiment. We hypothesize that filamentous algae mitigate the top-down control of polychaetes on pioneer plants by excluding them.

Field observations indicate that these filamentous algae and pioneer plants preferentially establish along tidal creek edges before expanding across the tidal marsh restoration sites. In **Chapter 4**, we explore the mechanisms underlying this distinct spatio-temporal vegetation pattern using (1) a geospatial analysis and (2) an evaluation of parameters which could depend on creek proximity (i.e. seed deposition/retention and sediment characteristics). We hypothesize that seed availability is higher alongside creeks and that sediment characteristics vary with distance from creek edge (e.g. higher shear strength near tidal creeks).

De-embanked areas often experience delayed pioneer plant colonization during the early developmental stages. We investigate to which extent this can be linked to the low initial platform elevation, which may cause too large sediment dynamics

(erosion and accretion rates), and poor sediment drainage due to the presence of a compacted subsoil. In particular we address the interactions between these two factors and the mechanistic basis of delayed vegetation colonization. **Chapter 5** investigates how these factors interact and how they can constrain/promote the transition to a vegetated marsh in a recently de-embanked site. First, we assess the relation between intertidal elevation, bed level, and vegetation, using a geospatial analysis. Three elevation zones are determined based on this analysis: (1) a bare zone where we expect that vegetation cannot establish, (2) a transition zone representing the elevation threshold for plant establishment, and (3) a vegetated level where we expect that plants can readily establish. We then test the effect of these intertidal elevation zones and sediment drainage on seedling survival using a field mesocosm experiment. The results of this mesocosm experiment are verified under field conditions using a field transplantation experiment. We hypothesize that the effect of intertidal elevation and drainage is most relevant in the transition zone.

In **Chapter 6** we summarize our findings and discuss their implications for tidal marsh restoration.

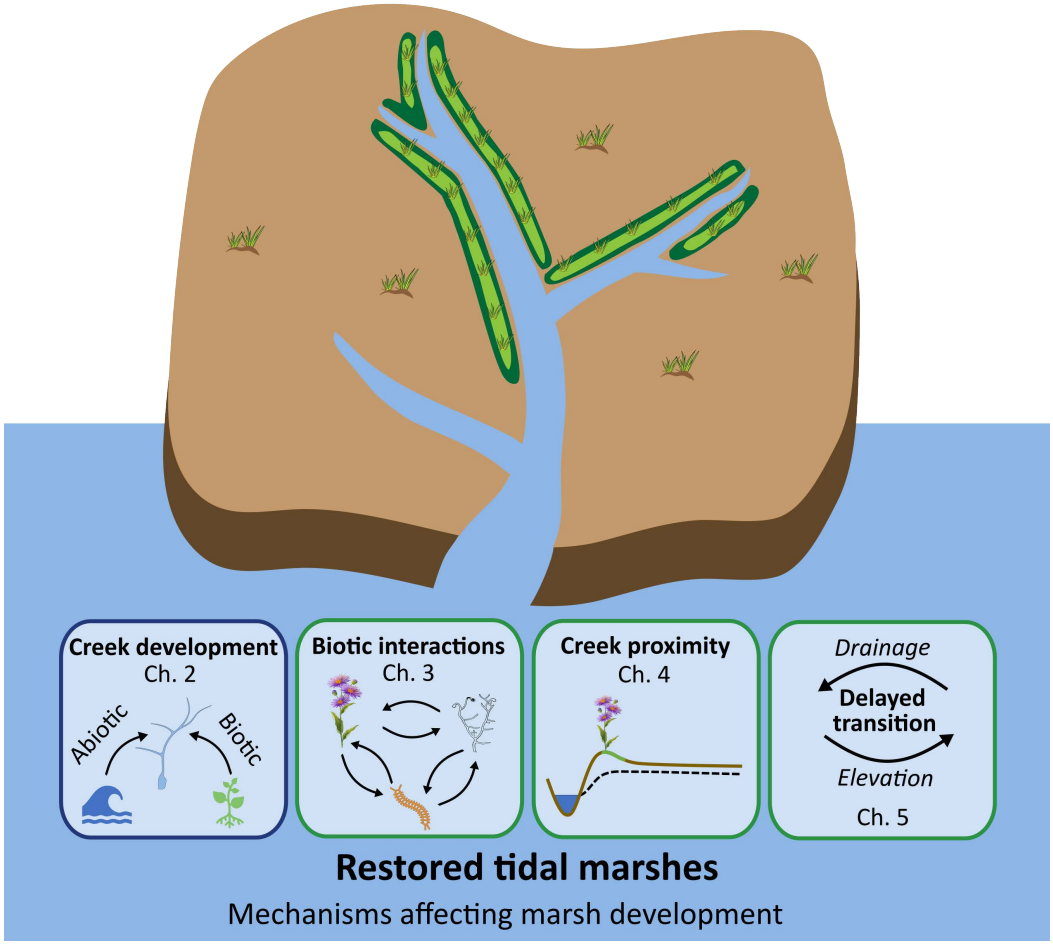


Figure 1.3: Conceptual overview of the thesis outline, with the main aim to unravel the abiotic and biotic mechanisms affecting tidal marsh development. We start by investigating the effect of these mechanisms on tidal creek network development (Chapter 2), and then focus on pioneer vegetation establishment in restored tidal marshes (Chapters 3, 4 & 5). Here, we study the effect of competing biotic interactions between algae, macrobenthos and pioneer plants (Chapter 3), followed by the processes creating favorable conditions for vegetation establishment near tidal creeks (Chapter 4), and finally the mechanisms created by local elevation and drainage causing delayed vegetation establishment in restored tidal marshes (Chapter 5).

1.6 References

Airoldi, L., Beck, M. W., Firth, L. B., Bugnot, A. B., Steinberg, P. D., & Dafforn, K. A. (2021). Emerging Solutions to Return Nature to the Urban Ocean. *Annual Review of Marine Science*, *13*(1), 445–477. https://doi.org/10.1146/annurev-marine-032020-020015

Bakker, J. P., Esselink, P., Dijkema, K. S., Van Duin, W. E., & De Jong, D. J. (2002). Restoration of salt marshes in the Netherlands. *Hydrobiologia*, *478*(1–3), 29–51. https://doi.org/10.1023/A:1021066311728

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: Identifying Windows of Opportunity for recovery. *Journal of Ecology*, *102*(3), 700–708. https://doi.org/10.1111/1365-2745.12241

Balke, T., Stock, M., Jensen, K., Bouma, T. J., & Kleyer, M. (2016). A global analysis of the seaward salt marsh extent: The importance of tidal range. *Water Resources Research*, *52*(5), 3775–3786. https://doi.org/10.1002/2015WR018318

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Bij de Vaate, I., Brückner, M. Z. M., Kleinhans, M. G., & Schwarz, C. (2020). On the Impact of Salt Marsh Pioneer Species-Assemblages on the Emergence of Intertidal Channel Networks. *Water Resources Research*, *56*(3). https://doi.org/10.1029/2019WR025942

Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T., & Herman, P. M. J. (2007). Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. *Continental Shelf Research*, *27*(8), 1020–1045. https://doi.org/10.1016/j.csr.2005.12.019

Brooks, H., Möller, I., Carr, S., Chirol, C., Christie, E., Evans, B., Spencer, K. L., Spencer, T., & Royse, K. (2021). Resistance of salt marsh substrates to near-instantaneous hydrodynamic forcing. *Earth Surface Processes and Landforms*, *46*(1), 67–88. https://doi.org/10.1002/esp.4912

Cahoon, D. R. (2006). A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts*, *29*(6), 889–898. https://doi.org/10.1007/BF02798648

Cahoon, D. R., Lynch, J. C., Roman, C. T., Schmit, J. P., & Skidds, D. E. (2019). Evaluating the Relationship Among Wetland Vertical Development, Elevation Capital, Sea-Level Rise, and Tidal Marsh Sustainability. *Estuaries and Coasts*, *42*(1), 1–15. https://doi.org/10.1007/s12237-018-0448-x

Cao, H., Zhu, Z., Balke, T., Zhang, L., & Bouma, T. J. (2018). Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration: Sediment dynamics affect seedling establishment. *Limnology and Oceanography*, *63*(2), 647–659. https://doi.org/10.1002/lno.10657

Cao, H., Zhu, Z., Hu, Z., Wang, H., & Bouma, T. J. (2022). Drainage-Improved Sediment Strength Enhances Saltmarsh Seedling Establishment Chance. *Frontiers in Marine Science*, *9*, 874680. https://doi.org/10.3389/fmars.2022.874680

Cao, H., Zhu, Z., van Belzen, J., Gourgue, O., van de Koppel, J., Temmerman, O. S., Herman, P. M. J., Zhang, L., Yuan, L., & Bouma, T. J. (2021). Salt marsh establishment in poorly consolidated muddy systems: Effects of surface drainage, elevation, and plant age. *Ecosphere*, *12*(9). https://doi.org/10.1002/ecs2.3755

Dale, J., & Arnall, A. (2024). Managed and unmanaged realignment as a nature-based solution to saltmarsh habitat loss: A sedimentary perspective. *Nature-Based Solutions*, *6*, 100166. https://doi.org/10.1016/j.nbsj.2024.100166

D'Alpaos, A., Fagherazzi, S., & Rinaldo, A. (2005). Tidal network ontogeny: Channel initiation and early development. *Journal of Geophysical Research*, *110*(F2), F02001. https://doi.org/10.1029/2004JF000182

D'Alpaos, A., Lanzoni, S., Mudd, S. M., & Fagherazzi, S. (2006). Modeling the influence of hydroperiod and vegetation on the cross-sectional formation of tidal channels. *Estuarine, Coastal and Shelf Science*, *69*(3–4), 311–324. https://doi.org/10.1016/j.ecss.2006.05.002

Erfanzadeh, R., Garbutt, A., Pétillon, J., Maelfait, J.-P., & Hoffmann, M. (2010). Factors affecting the success of early salt-marsh colonizers: Seed availability rather than site suitability and dispersal traits. *Plant Ecology*, *206*(2), 335–347. https://doi.org/10.1007/s11258-009-9646-8

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpaos, A., van de Koppel, J., Rybczyk, J. M., Reyes, E., Craft, C., & Clough, J. (2012). Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Reviews of Geophysics*, *50*(1), RG1002. https://doi.org/10.1029/2011RG000359

Fagherazzi, S., Mariotti, G., Leonardi, N., Canestrelli, A., Nardin, W., & Kearney, W. S. (2020). Salt Marsh Dynamics in a Period of Accelerated Sea Level Rise. *Journal of Geophysical Research: Earth Surface*, *125*(8). https://doi.org/10.1029/2019JF005200

Fivash, G. S., van Belzen, J., Temmink, R. J. M., Didderen, K., Lengkeek, W., Heide, T. V. D., & Bouma, T. J. (2019). Elevated micro-topography boosts growth rates in Salicornia procumbens by amplifying a tidally driven oxygen pump: Implications for natural recruitment and restoration. *Annals of Botany*, *125*, 353–364. https://doi.org/10.1093/aob/mcz137

Fluet-Chouinard, E., Stocker, B. D., Zhang, Z., Malhotra, A., Melton, J. R., Poulter, B., Kaplan, J. O., Goldewijk, K. K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A. M., Davidson, N., Finlayson, C. M., Lehner, B., … McIntyre, P. B. (2023). Extensive global wetland loss over the past three centuries. *Nature*, *614*(7947), 281–286. https://doi.org/10.1038/s41586-022-05572-6

French, P. W. (2006). Managed realignment – The developing story of a comparatively new approach to soft engineering. *Estuarine, Coastal and Shelf Science*, *67*(3), 409–423. https://doi.org/10.1016/j.ecss.2005.11.035

Friess, Daniel A., Yando, E. S., Alemu I, J. B., Wong, L.-W., Soto, S. D., & Bhatia, N. (2020). Ecosystem services and disservices of mangrove forests and salt marshes. In *Oceanography and Marine Biology*. Taylor & Francis. https://library.oapen.org/handle/20.500.12657/43146

Gallagher, S. B., & Humm, H. J. (1981). *Vaucheria* (Xanthophyceae, Vaucheriaceae) of the central Florida

gulf coast. *Bulletin of Marine Science*, *31*(1), 184–190.

Garzon, J. L., Maza, M., Ferreira, C. M., Lara, J. L., & Losada, I. J. (2019). Wave Attenuation by *Spartina* Saltmarshes in the Chesapeake Bay Under Storm Surge Conditions. *Journal of Geophysical Research: Oceans*, *124*(7), 5220–5243. https://doi.org/10.1029/2018JC014865

Grabowski, R. C., Droppo, I. G., & Wharton, G. (2011). Erodibility of cohesive sediment: The importance of sediment properties. *Earth-Science Reviews*, *105*(3–4), 101–120. https://doi.org/10.1016/j.earscirev.2011.01.008

Greenberg, R., Cardoni, A., Ens, B. J., Gan, X., Isacch, J. P., Koffijberg, K., & Loyn, R. (2014). The distribution and conservation of birds of coastal salt marshes. In B. Maslo & J. L. Lockwood (Eds.), *Coastal Conservation* (1st ed., pp. 180–242). Cambridge University Press. https://doi.org/10.1017/CBO9781139137089.008

He, Q., Li, Z., Elphick, C. S., Sun, Y., Sutherland, W. J., Taylor, N. G., & Wasson, K. (2025). Making Restoration Effective for Dynamic Coastal Wetlands. *Global Change Biology, 31*(9). https://doi.org/10.1111/gcb.70455

Hu, Z., Borsje, B. W., van Belzen, J., Willemsen, P. W. J. M., Wang, H., Peng, Y., Yuan, L., De Dominicis, M., Wolf, J., Temmerman, S., & Bouma, T. J. (2021). Mechanistic Modeling of Marsh Seedling Establishment Provides a Positive Outlook for Coastal Wetland Restoration Under Global Climate Change. *Geophysical Research Letters*, *48*(22), e2021GL095596. https://doi.org/10.1029/2021GL095596

Hu, Z., van Belzen, J., Van Der Wal, D., Balke, T., Wang, Z. B., Stive, M., & Bouma, T. J. (2015). Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: The importance of temporal and spatial variability in hydrodynamic forcing. *Journal of Geophysical Research: Biogeosciences*, *120*(7), 1450–1469. https://doi.org/10.1002/2014JG002870

Hughes, R. G., Lloyd, D., Ball, L., & Emson, D. (2000). The effects of the polychaete *Nereis diversicolor* on the distribution and transplanting success of *Zostera noltii. Helgoland Marine Research*, *54*(2–3), 129–136. https://doi.org/10.1007/s10152005011

Hughes, R. G., & Paramor, O. A. L. (2004). On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, *41*(3), 440–448. https://doi.org/10.1111/j.0021-8901.2004.00915.x

Kearney, W. S., & Fagherazzi, S. (2016). Salt marsh vegetation promotes efficient tidal channel networks. *Nature Communications*, *7*(1), 12287. https://doi.org/10.1038/ncomms12287

Kirwan, M. L., & Megonigal, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, *504*(7478), 53–60. https://doi.org/10.1038/nature12856

Kirwan, M. L., & Murray, A. B. (2007). A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences*, *104*(15), 6118–6122. https://doi.org/10.1073/pnas.0700958104

Kleinhans, M. G., Roelofs, L., Weisscher, S. A. H., Lokhorst, I. R., & Braat, L. (2022). Estuarine morphodynamics and development modified by floodplain formation. *Earth Surface Dynamics*, *10*(2), 367–381. https://doi.org/10.5194/esurf-10-367-2022

Kleinhans, M. G., van der Vegt, M., Leuven, J., Braat, L., Markies, H., Simmelink, A., Roosendaal, C., van Eijk, A., Vrijbergen, P., & van Maarseveen, M. (2017). Turning the tide: Comparison of tidal flow by periodic sea level fluctuation and by periodic bed tilting in scaled landscape experiments of estuaries. *Earth Surface Dynamics*, *5*(4), 731–756. https://doi.org/10.5194/esurf-5-731-2017

Kleinhans, M. G., van der Vegt, M., van Scheltinga, R. T., Baar, A. W., & Markies, H. (2012). Turning the tide: Experimental creation of tidal channel networks and ebb deltas. *Netherlands Journal of Geosciences - Geologie En Mijnbouw*, *91*(3), 311–323. https://doi.org/10.1017/S0016774600000469

Kleinhans, M. G., van Scheltinga, R. T., van der Vegt, M., & Markies, H. (2015). Turning the tide: Growth and dynamics of a tidal basin and inlet in experiments. *Journal of Geophysical Research: Earth Surface*, *120*(1), 95–119. https://doi.org/10.1002/2014JF003127

Knottnerus, O. S. (2005). History of human settlement, cultural change and interference with the marine environment. *Helgoland Marine Research*, *59*(1), 2–8. https://doi.org/10.1007/s10152-004-0201-7

Lawrence, P. J., Smith, G. R., Sullivan, M. J. P., & Mossman, H. L. (2018). Restored saltmarshes lack the topographic diversity found in natural habitat. *Ecological Engineering*, *115*, 58–66. https://doi.org/10.1016/j.ecoleng.2018.02.007

Lawrence, P. J., Sullivan, M. J. P., & Mossman, H. L. (2022). Restored saltmarshes have low beta diversity due to limited topographic variation, but this can be countered by management. *Journal of Applied Ecology*, *59*(7), 1709–1720. https://doi.org/10.1111/1365-2664.14179

Lee, S. Y., Dunn, R. J. K., Young, R. A., Connolly, R. M., Dale, P. E. R., Dehayr, R., Lemckert, C. J., Mckinnon, S., Powell, B., Teasdale, P. R., & Welsh, D. T. (2006). Impact of urbanization on coastal wetland structure and function. *Austral Ecology*, *31*(2), 149–163. https://doi.org/10.1111/j.1442-9993.2006.01581.x

Li, X., Leonardi, N., & Plater, A. J. (2019). A Stochastic Approach to Modeling Tidal Creek Evolution: Exploring Environmental Influences on Creek Topologies Through Ensemble Predictions. *Geophysical Research Letters*, *46*(23), 13836–13844. https://doi.org/10.1029/2019GL085214

Liu, Z., Gourgue, O., & Fagherazzi, S. (2022). Biotic and abiotic factors control the geomorphic characteristics of channel networks in salt marshes. *Limnology and Oceanography*, *67*(1), 89–101. https://doi.org/10.1002/lno.11977

Marani, M., Belluco, E., D'Alpaos, A., Defina, A., Lanzoni, S., & Rinaldo, A. (2003). On the drainage density of tidal networks. *Water Resources Research*, *39*(2). https://doi.org/10.1029/2001WR001051

Mcowen, C., Weatherdon, L., Bochove, J.-W., Sullivan, E., Blyth, S., Zockler, C., Stanwell-Smith, D., Kingston, N., Martin, C., Spalding, M., & Fletcher, S. (2017). A global map of saltmarshes. *Biodiversity Data Journal*, *5*, e11764. https://doi.org/10.3897/BDJ.5.e11764

Meier, D. (2004). Man and environment in the marsh area of Schleswig–Holstein from Roman until late Medieval times. *Quaternary International*, *112*(1), 55–69. https://doi.org/10.1016/S1040-6182(03)00065-X

Mitsch, W. J., Bernal, B., Nahlik, A. M., Mander, Ü., Zhang, L., Anderson, C. J., Jørgensen, S. E., & Brix, H. (2013). Wetlands, carbon, and climate change. *Landscape Ecology*, *28*(4), 583–597. https://doi.org/10.1007/s10980-012-9758-8

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., Van Wesenbeeck, B. K., Wolters, G., Jensen, K., Bouma, T. J., Miranda-Lange, M., & Schimmels, S. (2014). Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience*, *7*(10), 727–731. https://doi.org/10.1038/ngeo2251

Morris, R. K. A. (2013). Managed realignment as a tool for compensatory habitat creation – A re-appraisal. *Ocean & Coastal Management*, *73*, 82–91. https://doi.org/10.1016/j.ocecoaman.2012.12.013

Mossman, H. L., Davy, A. J., & Grant, A. (2012). Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites? *Journal of Applied Ecology*, *49*(6), 1446–1456. https://doi.org/10.1111/j.1365-2664.2012.02198.x

Murray, N. J., Worthington, T. A., Bunting, P., Duce, S., Hagger, V., Lovelock, C. E., Lucas, R., Saunders, M. I., Sheaves, M., Spalding, M., Waltham, N. J., & Lyons, M. B. (2022). High-resolution mapping of losses and gains of Earth's tidal wetlands. *Science*, *376*(6594), 744–749. https://doi.org/10.1126/science.abm9583

Oosterlee, L., Cox, T. J. S., Temmerman, S., & Meire, P. (2020). Effects of tidal re-introduction design on sedimentation rates in previously embanked tidal marshes. *Estuarine, Coastal and Shelf Science*, *244*, 106428. https://doi.org/10.1016/j.ecss.2019.106428

Paramor, O. A. L., & Hughes, R. G. (2004). The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on loss of saltmarsh in south-east England. *Journal of Applied Ecology*, *41*(3), 449–463. https://doi.org/10.1111/j.0021-8901.2004.00916.x

Paramor, O. A. L., & Hughes, R. G. (2005). Effects of the invertebrate infauna on early saltmarsh plant colonisation of managed realignment areas in south-east England. *Marine Ecology Progress Series*, *303*, 61–71. https://doi.org/10.3354/meps303061

Paramor, O. A. L., & Hughes, R. G. (2007). Restriction of *Spartina anglica* (C.E. Hubbard) marsh development by the infaunal polychaete *Nereis diversicolor* (O.F. Müller). *Estuarine, Coastal and Shelf Science*, *71*(1–2), 202–209. https://doi.org/10.1016/j.ecss.2006.07.012

Redelstein, R., Zotz, G., & Balke, T. (2018). Seedling stability in waterlogged sediments: An experiment with saltmarsh plants. *Marine Ecology Progress Series*, *590*, 95–108. https://doi.org/10.3354/meps12463

Reed, D. J. (1995). The response of coastal marshes to sea-level rise: Survival or submergence? *Earth Surface Processes and Landforms*, *20*(1), 39–48. https://doi.org/10.1002/esp.3290200105

Schoutens, K., Heuner, M., Minden, V., Schulte Ostermann, T., Silinski, A., Belliard, J., & Temmerman, S. (2019). How effective are tidal marshes as nature-based shoreline protection throughout seasons? *Limnology and Oceanography*, *64*(4), 1750–1762. https://doi.org/10.1002/lno.11149

Schuerch, M., Vafeidis, A., Slawig, T., & Temmerman, S. (2013). Modeling the influence of changing storm patterns

on the ability of a salt marsh to keep pace with sea level rise. *Journal of Geophysical Research: Earth Surface*, *118*(1), 84–96. https://doi.org/10.1029/2012JF002471

Schwarz, C., Gourgue, O., van Belzen, J., Zhu, Z., Bouma, T. J., van de Koppel, J., Ruessink, G., Claude, N., & Temmerman, S. (2018). Self-organization of a biogeomorphic landscape controlled by plant life-history traits. *Nature Geoscience*, *11*(9), 672–677. https://doi.org/10.1038/s41561-018-0180-y

Schwarz, C., van Rees, F., Xie, D., Kleinhans, M. G., & van Maanen, B. (2022). Salt marshes create more extensive channel networks than mangroves. *Nature Communications*, *13*(1), 2017. https://doi.org/10.1038/s41467-022-29654-1

Schwarz, C., Ye, Q. H., van der Wal, D., Zhang, L. Q., Bouma, T., Ysebaert, T., & Herman, P. M. J. (2014). Impacts of salt marsh plants on tidal channel initiation and inheritance: Salt marsh plants channel development. *Journal of Geophysical Research: Earth Surface*, *119*(2), 385–400. https://doi.org/10.1002/2013JF002900

Smolders, S., Plancke, Y., Ides, S., Meire, P., & Temmerman, S. (2015). Role of intertidal wetlands for tidal and storm tide attenuation along a confined estuary: A model study. *Natural Hazards and Earth System Sciences*, *15*(7), 1659–1675. https://doi.org/10.5194/nhess-15-1659-2015

Spencer, K. L., Carr, S. J., Diggens, L. M., Tempest, J. A., Morris, M. A., & Harvey, G. L. (2017). The impact of pre-restoration land-use and disturbance on sediment structure, hydrology and the sediment geochemical environment in restored saltmarshes. *Science of The Total Environment*, *587–588*, 47–58. https://doi.org/10.1016/j.scitotenv.2016.11.032

Spencer, K. L., & Harvey, G. L. (2012). Understanding system disturbance and ecosystem services in restored saltmarshes: Integrating physical and biogeochemical processes. *Estuarine, Coastal and Shelf Science*, *106*, 23–32. https://doi.org/10.1016/j.ecss.2012.04.020

Stark, J., Van Oyen, T., Meire, P., & Temmerman, S. (2015). Observations of tidal and storm surge attenuation in a large tidal marsh: Tidal and Storm Surge Attenuation in a Marsh. *Limnology and Oceanography*, *60*(4), 1371–1381. https://doi.org/10.1002/lno.10104

Stefanon, L., Carniello, L., D'Alpaos, A., & Lanzoni, S. (2010). Experimental analysis of tidal network growth and development. *Continental Shelf Research*, *30*(8), 950–962. https://doi.org/10.1016/j.csr.2009.08.018

Steinigeweg, C. S., Paul, M., Kleyer, M., & Schröder, B. (2023). Conquering New Frontiers: The Effect of Vegetation Establishment and Environmental Interactions on the Expansion of Tidal Marsh Systems. *Estuaries and Coasts*, *46*(6), 1515–1535. https://doi.org/10.1007/s12237-023-01220-y

Syvitski, J. P. M., Vörösmarty, C. J., Kettner, A. J., & Green, P. (2005). Impact of Humans on the Flux of Terrestrial Sediment to the Global Coastal Ocean. *Science*, *308*(5720), 376–380. https://doi.org/10.1126/science.1109454

Tal, M., & Paola, C. (2010). Effects of vegetation on channel morphodynamics: Results and insights from laboratory experiments. *Earth Surface Processes and Landforms*, *35*(9), 1014–1028. https://doi.org/10.1002/esp.1908

Temmerman, S., Bouma, T. J., Van de Koppel, J.,

Van der Wal, D., De Vries, M. B., & Herman, P. M. J. (2007). Vegetation causes channel erosion in a tidal landscape. *Geology*, *35*(7), 631. https://doi.org/10.1130/G23502A.1

Temmerman, S., Horstman, E. M., Krauss, K. W., Mullarney, J. C., Pelckmans, I., & Schoutens, K. (2023). Marshes and Mangroves as Nature-Based Coastal Storm Buffers. *Annual Review of Marine Science*, *15*(1), 95–118. https://doi.org/10.1146/annurev-marine-040422-092951

Temmerman, S., & Kirwan, M. L. (2015). Building land with a rising sea. *Science*, *349*(6248), 588–589. https://doi.org/10.1126/science.aac8312

Temmink, R. J. M., Lamers, L. P. M., Angelini, C., Bouma, T. J., Fritz, C., Van De Koppel, J., Lexmond, R., Rietkerk, M., Silliman, B. R., Joosten, H., & Van Der Heide, T. (2022). Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots. *Science*, *376*(6593). https://doi.org/10.1126/science.abn1479

Townend, I., Fletcher, C., Knappen, M., & Rossington, K. (2011). A review of salt marsh dynamics: A review of salt marsh dynamics. *Water and Environment Journal*, *25*(4), 477–488. https://doi.org/10.1111/j.1747-6593.2010.00243.x

Ursino, N., Silvestri, S., & Marani, M. (2004). Subsurface flow and vegetation patterns in tidal environments. *Water Resources Research*, *40*(5). https://doi.org/10.1029/2003WR002702

van Belzen, J., Fivash, G. S., Hu, Z., Bouma, T. J., & Herman, P. M. J. (2022). A probabilistic framework for windows of opportunity: The role of temporal variability in critical transitions. *Journal of The Royal Society Interface*, *19*(190), 20220041. https://doi.org/10.1098/rsif.2022.0041

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Cusseddu, V., Purkis, S. J., Rietkerk, M., & van de Koppel, J. (2020). Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. *Earth Surface Processes and Landforms*, *45*(5), 1141–1154. https://doi.org/10.1002/esp.4783

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., & van de Koppel, J. (2021). Algal-Induced Biogeomorphic Feedbacks Lay the Groundwork for Coastal Wetland Development. *Journal of Geophysical Research: Biogeosciences*, *126*(10). https://doi.org/10.1029/2021JG006515

Van den Neucker, T., Verbessem, I., Vandevoorde, B., Van Braeckel, A., Stevens, M., Spanoghe, G., Gyselings, R., Soors, J., De Regge, N., De Belder, W., & Van den Bergh, E. (2007). *Evaluatie van natuurontwikkelingsprojecten in het Schelde-estuarium.* Rapport van het Instituut voor Natuur-en Bosonderzoek. https://purews.inbo.be/ws/portalfiles/portal/5370095/VandenNeucker_etal_2007_EvaluatieNatuurontwikkelingsprojectenScheldeEstuarium.pdf

van Dijk, W. M., Cox, J. R., Leuven, J. R. F. W., Cleveringa, J., Taal, M., Hiatt, M. R., Sonke, W., Verbeek, K., Speckmann, B., & Kleinhans, M. G. (2021). The vulnerability of tidal flats and multi-channel estuaries to dredging and disposal. *Anthropocene Coasts*, *4*(1), 36–60. https://doi.org/10.1139/anc-2020-0006

van Dijk, W. M., Teske, R., van de Lageweg, W. I., & Kleinhans, M. G. (2013). Effects of vegetation distribution on experimental river channel dynamics: Channel dynamics and vegetation. *Water Resources*

Research, *49*(11), 7558–7574. https://doi.org/10.1002/2013WR013574

Van Putte, N., Temmerman, S., Verreydt, G., Seuntjens, P., Maris, T., Heyndrickx, M., Boone, M., Joris, I., & Meire, P. (2020). Groundwater dynamics in a restored tidal marsh are limited by historical soil compaction. *Estuarine, Coastal and Shelf Science*, *244*, 106101. https://doi.org/10.1016/j.ecss.2019.02.006

van Regteren, M., Amptmeijer, D., De Groot, A. V., Baptist, M. J., & Elschot, K. (2020). Where does the salt marsh start? Field-based evidence for the lack of a transitional area between a gradually sloping intertidal flat and salt marsh. *Estuarine, Coastal and Shelf Science*, *243*, 106909. https://doi.org/10.1016/j.ecss.2020.106909

van Regteren, M., Colosimo, I., de Vries, P., van Puijenbroek, M. E. B., Freij, V. S., Baptist, M. J., & Elschot, K. (2019). Limited seed retention during winter inhibits vegetation establishment in spring, affecting lateral marsh expansion capacity. *Ecology and Evolution*, *9*(23), 13294–13308. https://doi.org/10.1002/ece3.5781

van Regteren, M., ten Boer, R., Meesters, E. H., & de Groot, A. V. (2017). Biogeomorphic impact of oligochaetes (Annelida) on sediment properties and *Salicornia* spp. Seedling establishment. *Ecosphere*, *8*(7), e01872. https://doi.org/10.1002/ecs2.1872

Vandenbruwaene, W., Bouma, T. J., Meire, P., & Temmerman, S. (2013). Biogeomorphic effects on tidal channel evolution: Impact of vegetation establishment and tidal prism change. *Earth Surface Processes and Landforms*, *38*(2), 122–132. https://doi.org/10.1002/esp.3265

Vandenbruwaene, W., Meire, P., & Temmerman, S. (2012). Formation and evolution of a tidal channel network within a constructed tidal marsh. *Geomorphology*, *151–152*, 114–125. https://doi.org/10.1016/j.geomorph.2012.01.022

Vandenbruwaene, W., Schwarz, C., Bouma, T. J., Meire, P., & Temmerman, S. (2015). Landscape-scale flow patterns over a vegetated tidal marsh and an unvegetated tidal flat: Implications for the landform properties of the intertidal floodplain. *Geomorphology*, *231*, 40–52. https://doi.org/10.1016/j.geomorph.2014.11.020

Vandenbruwaene, W., Temmerman, S., Bouma, T. J., Klaassen, P. C., de Vries, M. B., Callaghan, D. P., van Steeg, P., Dekker, F., van Duren, L. A., Martini, E., Balke, T., Biermans, G., Schoelynck, J., & Meire, P. (2011). Flow interaction with dynamic vegetation patches: Implications for biogeomorphic evolution of a tidal landscape. *Journal of Geophysical Research: Earth Surface*, *116*(F1), F01008. https://doi.org/10.1029/2010JF001788

Vlaswinkel, B. M., & Cantelli, A. (2011). Geometric characteristics and evolution of a tidal channel network in experimental setting. *Earth Surface Processes and Landforms*, *36*(6), 739–752. https://doi.org/10.1002/esp.2099

Wang, C., & Temmerman, S. (2013). Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. *Journal of Geophysical Research: Earth Surface*, *118*(1), 229–240. https://doi.org/10.1029/2012JF002474

Weisscher, S. A. H., Van den Hoven, K., Pierik, H. J., & Kleinhans, M. G. (2022). Building and Raising Land: Mud and Vegetation Effects in Infilling Estuaries. *Journal of Geophysical Research: Earth Surface*, *127*(1). https://doi.org/10.1029/2021JF006

298

Wilcox, M. (2012). Occurrence of the marine yellow-green algae *Vaucheria velutina* C. Agardh and *Vaucheria longicaulis* Hoppaugh (Xanthophyceae: Vaucheriaceae) in Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *46*(2), 285–290. https://doi.org/10.1080/00288330.2011.622444

Wolters, M., Garbutt, A., & Bakker, J. P. (2005a). Plant colonization after managed realignment: The relative importance of diaspore dispersal: Plant colonization after managed realignment. *Journal of Applied Ecology*, *42*(4), 770–777. https://doi.org/10.1111/j.1365-2664.2005.01051.x

Wolters, M., Garbutt, A., & Bakker, J. P. (2005b). Salt-marsh restoration: Evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, *123*(2), 249–268. https://doi.org/10.1016/j.biocon.2004.11.013

Worthington, T. A., Spalding, M., Landis, E., Maxwell, T. L., Navarro, A., Smart, L. S., & Murray, N. J. (2024). The distribution of global tidal marshes from Earth observation data. *Global Ecology and Biogeography*, *33*(8). https://doi.org/10.1111/geb.13852

Xin, P., Gibbes, B., Li, L., Song, Z., & Lockington, D. (2010). Soil saturation index of salt marshes subjected to spring-neap tides: A new variable for describing marsh soil aeration condition. *Hydrological Processes*, *24*(18), 2564–2577. https://doi.org/10.1002/hyp.7670

Yang, S. L., Zhang, J., Zhu, J., Smith, J. P., Dai, S. B., Gao, A., & Li, P. (2005). Impact of dams on Yangtze River sediment supply to the sea and delta intertidal wetland response. *Journal of Geophysical Research: Earth Surface*, *110*(F3). https://doi.org/10.1029/2004JF000271

Zhou, Z., Olabarrieta, M., Stefanon, L., D'Alpaos, A., Carniello, L., & Coco, G. (2014). A comparative study of physical and numerical modeling of tidal network ontogeny. *Journal of Geophysical Research: Earth Surface*, *119*(4), 892–912. https://doi.org/10.1002/2014JF003092

Zhu, Z., van Belzen, J., Hong, T., Kunihiro, T., Ysebaert, T., Herman, P. M. J., & Bouma, T. J. (2016). Sprouting as a gardening strategy to obtain superior supplementary food: Evidence from a seed-caching marine worm. *Ecology*, *97*(12), 3278–3284. https://doi.org/10.1002/ecy.1613



2

On the relative role of abiotic and biotic controls in channel network development: insights from scaled tidal flume experiments

Sarah Hautekiet, Jan-Eike Rossius, Olivier Gourgue, Maarten G. Kleinhans & Stijn Temmerman

Based on:

Hautekiet, S., Rossius, J.-E., Gourgue, O., Kleinhans, M., and Temmerman, S.: On the relative role of abiotic and biotic controls in channel network development: insights from scaled tidal flume experiments, Earth Surf. Dynam., 12, 601–619, https://doi.org/10.5194/esurf-12-601-2024, 2024.

2.1 Abstract

Tidal marshes provide highly valued ecosystem services, which depend on variations in the geometric properties of the tidal channel networks dissecting marsh landscapes. The development and evolution of channel network properties are controlled by both abiotic (dynamic flow–landform feedbacks) and biotic processes (e.g. vegetation–flow–landform feedbacks). However, the relative role of biotic and abiotic processes, and under which condition one or the other is more dominant, remains poorly understood. In this study, we investigated the impact of spatio-temporal plant colonization patterns on tidal channel network development through flume experiments. Four scaled experiments mimicking tidal landscape development were conducted in a tidal flume facility: two control experiments without vegetation, a third experiment with hydrochorous vegetation colonization (i.e. seed dispersal via the tidal flow), and a fourth with patchy colonization (i.e. by direct seeding on the sediment bed). Our results show that more dense and efficient channel networks are found in the vegetation experiments, especially in the hydrochorous seeding experiment with slower vegetation colonization. Further, an interdependency between abiotic and biotic controls on channel development can be deduced. Whether biotic factors affect channel network development seems to depend on the force of the hydrodynamic energy and the stage of the system development. Vegetation–flow–landform feedbacks are only dominant in contributing to channel development in places where intermediate hydrodynamic energy levels occur and mainly have an impact during the transition phase from a bare to a vegetated landscape state. Overall, our findings suggest a zonal domination of abiotic processes at the seaward side of intertidal basins, while biotic processes have an additional effect on system development more towards the landward side.

2.2 Introduction

Tidal wetlands are valuable coastal ecosystems providing numerous ecosystem services such as shoreline protection and carbon sequestration (Allen, 2000; Barbier et al., 2011; Leonardi et al., 2018; Mcowen et al., 2017; Rogers et al., 2019). The landscape is dissected by tidal channel networks, which play a key role in the ecosystem functioning since channels act as major flow paths for water, nutrients, sediments, and biota (Fagherazzi et al., 1999, 2012; Huiskes et al., 1995; Kearney and Fagherazzi, 2016; Temmerman et al., 2007; Vandenbruwaene et al., 2012). The geometric properties of the channel networks (e.g. density of channelization, channel width, depth, and cross-sectional area) can widely vary within tidal marsh systems both locally and globally. Understanding these spatial variations in geometric properties is essential as they may imply variability in the ecosystem functioning and associated ecosystem services of tidal marshes. For instance, it has been shown that (1) the depth of subsurface groundwater fluctuations varies with distance from channels (Ursino et al., 2004; Van Putte et al., 2020), and hence related processes such as vegetation zonation, rates of carbon sequestration, and nutrient cycling in marsh sediments also vary as a function of distance from channels and thus channel drainage density (Krask et al., 2022; Roner et al., 2016; Xin et al., 2022); (2) marsh resilience to sea level rise depends on sediment accretion rates which also vary as a function of distance from channels (D'Alpaos et al., 2007; Fagherazzi et al., 2012; Kirwan et al., 2008; van Dobben et al., 2022); and (3) storm surge attenuation is less effective when marshes have wider, deeper, and denser channel networks (Stark et al., 2016; Temmerman et al., 2012, 2023).

Abiotic and biotic processes actively shape the tidal landscape and affect the geometric properties of channel networks. Tidal channels develop due to abiotic feedback between spatial heterogeneity in topography and/or sediment erodibility, on the one hand, and tidal flow and erosion patterns, on the other hand. Once initial depressions form by spatial heterogeneity, flow converges to these depressions, initiating channel formation (D'Alpaos et al., 2006; Kleinhans et al., 2009; Stefanon et al., 2010). The evolution of these channels is typically driven by headward erosion (Kleinhans et al., 2012; D'Alpaos et al., 2005; Stefanon et al., 2010), which is mainly induced by ebb currents (Geng et al., 2020). Such channels are ebb-dominant in the unvegetated state, meaning that the landward fluxes of sediment, nutrients, and biota remain limited (Kleinhans et al., 2009; D'Alpaos et al., 2005; Mariotti and Fagherazzi, 2011). But once vegetation has settled alongside the channels, the tides within the channels are more symmetrical, allowing sediment trapping (Kleinhans et al., 2009; Stark et al., 2017). In the past few decades, geometric features of tidal wetlands have been extensively investigated, revealing an abiotic relation between tidal prism and channel cross-sectional area, not only for tidal inlets (e.g. Byrne et al., 1980; Jarrett, 1976; Myrick and Leopold, 1963) but also explaining variations in channel cross-sectional areas within channel networks of tidal wetlands (D'Alpaos et

al., 2010; Rinaldo et al., 1999b). Furthermore, spatial variations in geometric properties of marsh channel networks were found to be related to the respective tidal watershed area (D'Alpaos et al., 2010; Marani et al., 2003; Rinaldo et al., 1999a, b).

Biotic factors affect the landscape configuration of tidal wetlands through feedback between plants, water flow, and sediment (Bouma et al., 2013; Temmerman et al., 2005, 2007; Vandenbruwaene et al., 2013). Vegetation slows down flow velocity locally within patches (Zong and Nepf, 2010, 2011, 2012; Ortiz et al., 2013; Meire et al., 2014) and triggers the initiation of channel formation by flow acceleration next to and in between vegetation patches (Schwarz et al., 2014; Temmerman et al., 2007; Vandenbruwaene et al., 2015). The resulting landscapes have a higher density of channelization (Vandenbruwaene et al., 2013) and more efficiently draining channel networks in comparison to unvegetated landscapes, as larger portions of marsh platforms are closer to a channel (Kearney and Fagherazzi, 2016). Moreover, life history traits, such as plant recruitment strategies, can influence wetland geomorphology and channel network characteristics (Bij de Vaate et al., 2020; Schwarz et al., 2018, 2022). Specifically, a slow patchy colonization pattern seems to enhance the formation of new channels. In contrast, a fast homogeneous colonization pattern tends to favor stabilization of pre-existing channels, leading to a lower density of channel networks (Schwarz et al., 2018, 2022).

Both abiotic and biotic controls on tidal channel formation and evolution have been identified, but the relative role of abiotic and biotic factors, and under which conditions one or the other is more dominant, remains poorly understood. We suspect this is partly because tidal channel networks develop over large spatial ($\sim$ km^2) and temporal scales ($\sim$ decades), while biota and their patterns have much smaller scales. Furthermore, subtle differences in gradual marsh vegetation development, caused by different life history traits, might cumulatively lead to large-scale, long-term effects on tidal channel network development. Present insights mainly come from either numerical models simulating tidal channel network development over such large spatial scales and timescales as a result of plant–flow–sediment feedbacks (D'Alpaos et al., 2007; Gourgue et al., 2022; Kirwan and Murray, 2007; Schwarz et al., 2018), which have the disadvantage that they may ignore real-life processes, or empirical analyses of tidal channel geometric properties from different wetland sites (Kearney and Fagherazzi, 2016; Kleinhans et al., 2009; Liu et al., 2022; Vandenbruwaene et al., 2013), which have the drawback that site-specific conditions that may have affected the channel development are not necessarily known and difficult to control. Experimental studies, which enable the isolation of abiotic and biotic effects (e.g. by repeated experiments with and without vegetation), are practically impossible on the relevant spatial ($\sim$ km^2) and temporal scales ($\sim$ decades) unless they are scaled.

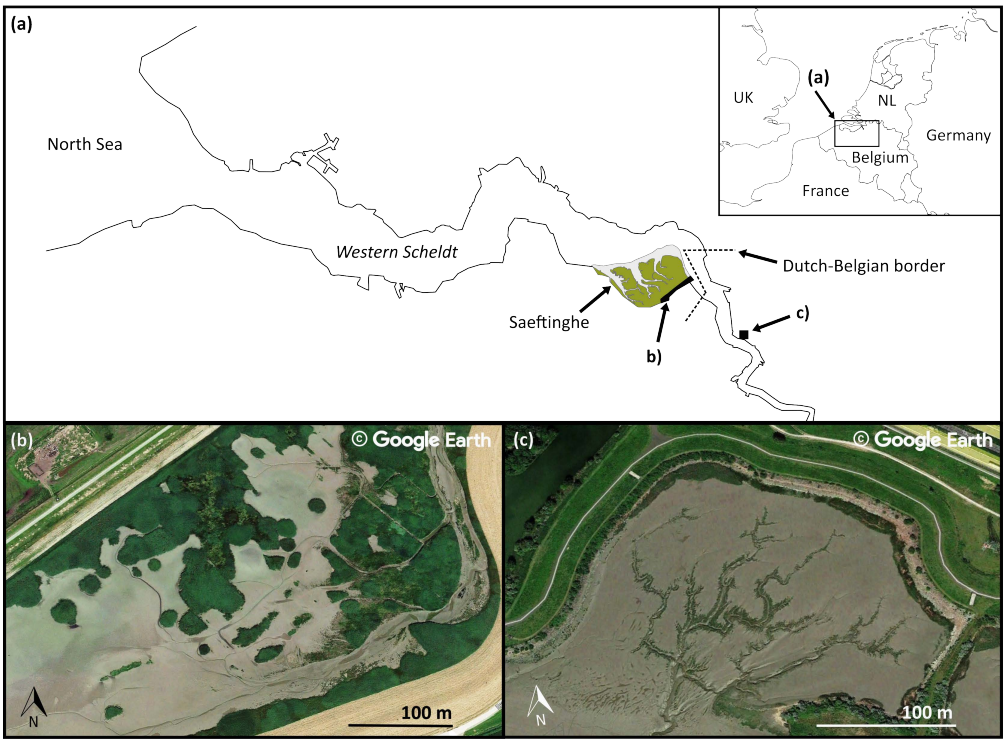


Figure 2.1: a) Overview of two example sites along the Scheldt estuary (N Belgium and SW Netherlands) where patchy and hydrochorous plant colonization patterns can be found: **b)** the Sieperda marsh (NL), showing a patchy colonization strategy, and **c)** the Lillo-Potpolder (BE), exhibiting a hydrochorous colonization strategy. The satellite imagery was extracted from © Google Earth 2013 (image of the Sieperda marsh) and © Google Earth 2021 (image of the Lillo-Potpolder).

In general, scaled laboratory experiments have been used to study the formation and evolution of fluvial and tidal landscapes with live vegetation in a simplified setting (Kleinhans et al., 2015a; Tal and Paola, 2007; Piliouras et al., 2017; Piliouras and Kim, 2019a, b; Zhou et al., 2014). Nevertheless, few morphodynamic experiments with tides have been conducted due to issues with scale effects (e.g. Stefanon et al., 2010; Tambroni et al., 2005; Vlaswinkel and Cantelli, 2011). Recent advances made in scaled tidal morphodynamic experiments, in particular using flumes with a tilting bed to generate tidal flow, allow for overcoming the most limiting scale effects and developing realistic estuarine morphologies (Kleinhans et al., 2012, 2017b, 2015b). So far, most flume experiments comparing bare and vegetated tidal systems have been carried out in an estuarine context (i.e. with a landward river discharge boundary and seaward tidal boundary) and indicate that vegetation can influence the morphological development of partially filled estuaries (Kleinhans et al., 2022; Weisscher et al., 2022). These experiments showed that vegetation confines the flow

into channels and reduces both channel mobility and local flow velocity, ultimately contributing to bar stabilization and further infilling of the estuary. To our knowledge, experiments have not been conducted yet with a focus on (1) channel network development in an intertidal basin context (i.e. only seaward tidal boundary and closed landward boundary) and (2) the role of vegetation presence or absence and colonization patterns in the resulting channel network geometric properties.

In this study, we aim to advance our understanding of the relative roles of abiotic and biotic effects in the development of landward-branching, blind-ending tidal channel networks within intertidal basins through novel flume experiments. Specifically, we investigate the impact of three different spatio-temporal plant colonization strategies on channel network formation: (1) a control without plant colonization, (2) hydrochorous colonization, and (3) patchy colonization (see Fig. 2.1). The hydrochorous colonization experiment represents certain aspects of tidal wetland systems dominated by annual (e.g. *Salicornia* spp.) and biennial (e.g. *Aster* spp.) pioneer plants producing many seeds that typically disperse hydrochorously with the tidal flow (Gray, 1971; Davy et al., 2001; Huiskes et al., 1995). The patchy colonization experiment, on the other hand, represents systems dominated by slowly colonizing perennial plants (e.g. *Scirpus* or *Spartina* spp.), which reproduce clonally, thereby developing gradually expanding vegetation patches (Bouma et al., 2007; Schwarz et al., 2018, 2022; Vandenbruwaene et al., 2011). We hypothesize that the patchy recruitment strategy will be associated with local flow deceleration within vegetation patches and flow acceleration next to expanding patches. Hence, it might enhance channel formation and result in higher channel density compared to the scenario without plant colonization. The hydrochorous recruitment strategy may show a more homogenous spatial recruitment pattern. Therefore, it might generate less local flow concentration and thus produce less dense channel networks. The effect of vegetation is hypothesized to be most relevant during the transition phase from bare to vegetated intertidal wetlands, after which the system is expected to evolve toward a morphodynamic equilibrium.

2.3 Methods

2.3.1 Experimental set-up and procedure

Four landscape-scale experiments of salt marshes were conducted in the Metronome tidal facility at Utrecht University: two control experiments without vegetation (only sand), a third experiment with hydrochorous seeding of vegetation, and a fourth with patchy seeding. Initial conditions and general settings were the same for all four experiments, and only the presence or absence of vegetation and the type of vegetation seeding were different (see Sect. 2.3.2).The Metronome is a 20 m long and 3 m wide box-shaped flume where tides are generated by periodically tilting the construction over the short central axis (Kleinhans et al., 2017b). It has been

designed to overcome scale problems observed in previous scaled morphodynamic studies of tidal landscapes (e.g. Stefanon et al., 2010). A complete overview of the design and functioning of the flume can be found in Kleinhans et al. (2017b). For the current experiments, a 7.4 m long and 2.4 m wide zone, acting as an intertidal basin, was created and filled with an 11.5 cm thick sand bed (Fig. 2.2). It was bordered by two fixed non-erodible barrier islands connecting the intertidal basin with the "sea basin", which initially had no sand bed but just the fixed flume bottom. The barrier islands (each 50 cm wide, ± 1.23 m long, and 25 cm high) were installed to create a 55 cm wide tidal inlet. We decided to use fixed barriers to avoid interference with the flume walls and to create a branching channel network similar to the results obtained by Kleinhans et al. (2012). These barriers consisted of a wooden framework with inclined sides and sandy round heads. Their entire exterior was covered in bubble wrap to have a uniform surface with increased hydraulic roughness.

Furthermore, a landward barrier along the complete width of the tidal basin was created to confine the system. The 30 cm wide borders of the tidal basin were slightly elevated at 14.5 cm (Fig. 2.2). The initial bed, including elevated borders, was levelled and consisted of poorly sorted sand with a median grain size d_{50} = 0.55 mm, d_{10} = 0.32 mm, and d_{90} = 1.2 mm.

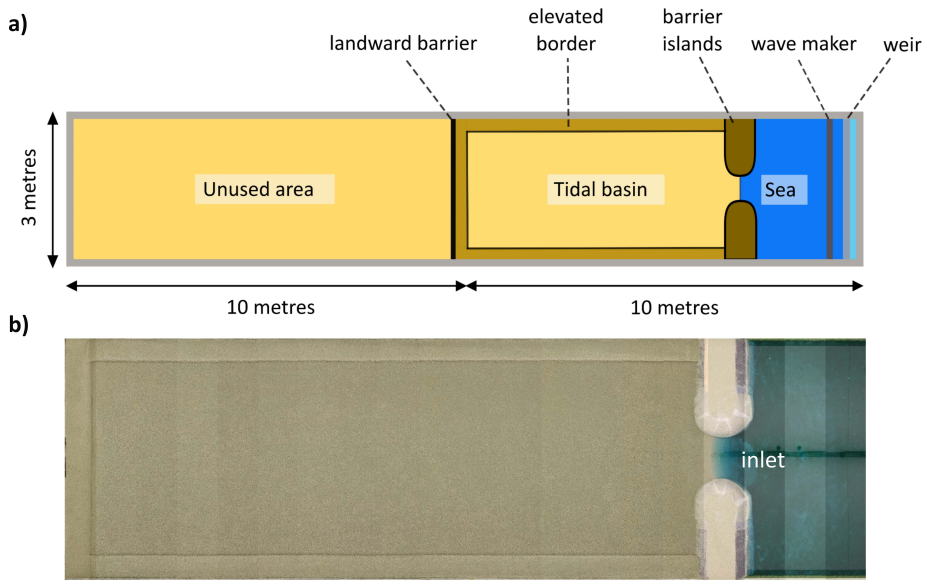


Figure 2.2: Top-view sketch **a)** and overhead photograph mosaic **b)** of the experimental set-up of the flume showing features such as the tidal basin, elevated borders along the tidal basin, the landward barrier of the tidal basin, the sea basin, and barrier islands adjacent to the tidal inlet connecting the sea and tidal basin.

The experiments were run for 5000 (first control experiment), 5500 (hydrochorous vegetation experiment), and 10 000 tidal cycles (second control and patchy vegetation experiment), respectively. These numbers correspond to about 7, 8, and 14 years of natural tidal cycles in case of a semi-diurnal tidal regime. As every tidal cycle in the Metronome takes 40 seconds, the experiments took 5 and 10 days to run for the first and second control experiment, respectively. The vegetated experiments took longer to run as we had to wait for four days between sowing events for seeds to germinate and grow sprouts. They both took around one month and a half (± 50 days) to run. The selected experimental settings were based on 12 pilot experiments (all without inclusion of vegetation) in which settings such as sea level and tidal inlet width were varied until a dendritic channel network was created while avoiding interference with the flume walls.

Tidal asymmetry was imposed on the tilting flume to create a flood-dominant system. A principal tide (M2) was generated with a period of 40 s at an amplitude of 75 mm, while the overtide (M4) had an amplitude of 15 mm (i.e. 20% of M2 component) over a period of 20 s. This resulted in a maximum slope of 0.009 m/m during flood and a maximum slope of 0.006 m/m during ebb. These conditions are similar to those in Weisscher et al. (2022), where the tidal asymmetry limited net seaward export of sediment observed in most tidal experiments in the literature. At the seaward end, waves were generated by a horizontal paddle with a frequency of 2 Hz during the flood phase. These monochromatic waves impacted initial system development and the rate of channel development as sediments were mobilized by the combined action of waves and tidal currents. Behind the wave maker, a vertically moving weir regulated the water level in the sea basin (Fig. 2.2), so that a constant horizontal water level of 9.2 cm above the flume floor was maintained within the sea basin. Due to the tilting of the flume, water was flooding in and draining out of the tidal basin part of the flume.

The main reason for driving the tidal flow by tilting rather than periodic sea-level fluctuation is that, with the latter, flow friction is larger in the flume than in the real world, leading to unrealistically low velocities and sediment mobility. By tilting the flume, sediment transport dynamics are more realistic (Kleinhans, et al., 2017b). This is important as the sediment has to be rather coarse to obtain channels and shoals and avoid the ubiquitous but unrealistic scours usually observed in scaled tidal landscape experiments (Kleinhans, et al., 2017a).

2.3.2 Vegetation protocol

A single plant species was selected for the vegetation experiments based on previous experiments (Lokhorst et al., 2019; Weisscher et al., 2022) and pilot tests (see Supporting information Section S2.1): *Lotus pedunculatus*. This species was found suitable for our scaled tidal marsh experiments as 1) it germinates and develops into

sprouts within a few days in the Metronome, 2) it does not grow too tall (~2-3 cm) in the absence of nutrients, 3) it shows eco-engineering traits similar to marsh vegetation such as increased friction and bank stabilization and 4) compared to other species, such as alfalfa (used in previous scaled flume studies on rivers such as Tal & Paola (2007)), it does not establish in unsuitable locations (i.e. in channels).

After an initial 1000 tidal cycles, allowing initial morphodynamic development without presence of vegetation, we started the first sowing event, followed by 440 or 500 tidal cycles, then sowed again, followed by another 440 or 500 tidal cycles. This procedure was repeated until we reached 4500 (patchy experiment) and 5000 (hydrochorous vegetation experiment) tidal cycles. We performed two experiments with two different sowing patterns, as explained below. More information about the sowing procedure can be found in the Supplementary information (section S2.1).

Hydrochorous sowing experiment

During this experiment, *Lotus* seeds were dropped in the water at the tidal inlet between the two barrier islands (see Fig. 2.2) and then dispersed by the flowing water (hereafter: "hydrochorously"), representing a system dominated by predominantly hydrochorous seed dispersal, such as observed in real tidal marshes formed by *Aster* spp. or *Salicornia* spp. The seeds were soaked for 24 hours prior to every sowing event to stimulate germination. Hydrochorous sowing events took place over the course of 60 tidal cycles, which were part of the 500-cycle interval between subsequent sowing events. Before every sowing event, the flume was drained, as acquiring digital surface models requires a dry sand bed. Afterwards, the first ten tidal cycles were run without adding seeds to re-establish a normal tidal flow pattern. In the subsequent 25 tidal cycles, a spoonful of *Lotus* was released per flood phase in the tidal inlet, followed by another 25 tidal cycles to spread the seeds. Finally, the flume was stopped for four consecutive days to allow germination and development of the sprouts. We maintained a water level of 9.2 cm in the sea basin to keep the sand bed in the tidal basin moist to avoid subsurface drainage and plant growth in channels and other submerged areas that eventually developed within the tidal basin. Around 160 000 seeds (i.e. 200 g) were supplied per sowing event to obtain a vegetation cover equaling about half the tidal basin at the end of the experiment. This was not achieved as many seeds either ended on the ebb-delta seaward from the tidal inlet or disappeared entirely from the system into the sea basin. The low vegetation cover could be related to the fact that *Lotus* seeds did not disperse over the whole tidal basin during sowing events since they are transported as bed load.

Patchy sowing experiment

In contrast to the hydrochorous experiment, vegetation was sown manually in circular patches while tilting of the flume was halted. As such, we aimed to mimic a

system dominated by a patchy colonization pattern typically observed in real *Spartina* or *Scirpus* spp marshes. A different sowing procedure was used as soaked seeds are difficult to handle for manual sowing. Pilot tests (see Supplementary information - Section S2.1) showed that this procedure did not substantially alter seed viability and germination rate. Before every sowing event, seeds were soaked for one day and then dried the following day. The objective was to obtain a vegetation cover of 60% over the tidal basin (i.e. ± 10.7 m^2) after 4500 tidal cycles, considering an average density of 10 seeds/cm^2 and a germination rate of 50%. For every sowing event, 13 new patches with a radius of 2.5 cm were sown and the radius of existing patches was increased by 5 cm. To resemble natural processes, we did not re-sow in areas where (part of) a patch disappeared or where a channel developed (see Fig. 2.6a). Neither were new patches sown in channels. The exact location of every patch was pre-determined using a computer algorithm that provided a random distribution of gradually expanding patches over the tidal basin (Fig. 2.3). Similar to the hydrochorous experiment, the flume was stopped for four days to allow germination and development of the sprouts.

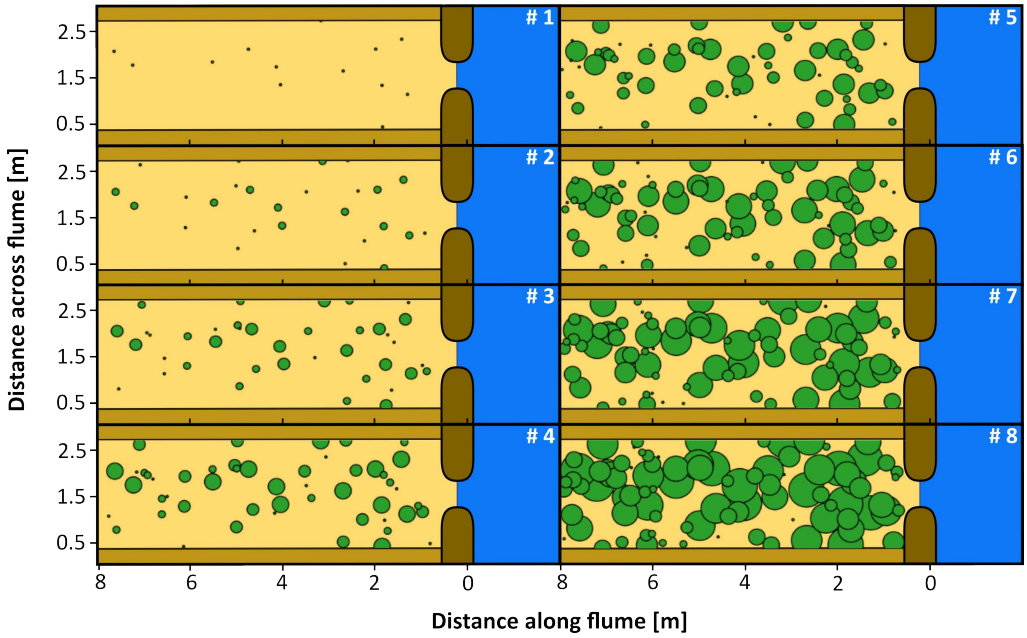


Figure 2.3: Overview of the computer-generated, random patch locations over the course of eight sowing events in the patchy vegetation experiment. The green circles represent patches; 13 new patches appear per sowing event, while the existing patches expand. The numbers indicate the order of sowing events taking place with an interval of 500 tidal cycles in between: #1 represents the start of these events (after 1000 tidal cycles) and #8 the end (after 4500 tidal cycles).

2.3.3 Data collection and analysis

Digital elevation models were acquired using laser line scanning to analyze the morphological development of all experiments. Specifically, we worked with digital surface models (DSMs) as these include the top of the vegetation canopy. The laser line scanner was installed on a gantry above the flume, which moved over the entire length of the flume. It projected a laser line covering the complete width of the flume, which was then registered by a camera, within which the laser line position was identified and filtered at subpixel resolution. The laser line scanner had a horizontal resolution of about 0.75 mm and a vertical resolution of about 0.2 mm.

DSM acquisition requires a dry bed. Therefore, the flume was drained slowly to avoid morphological perturbation. DSMs were acquired every 440 or 500 tidal cycles (i.e. in line with the sowing events) until the end of every experiment. The first control experiment ended after 5000 tidal cycles when a morphodynamic equilibrium was reached (i.e. when the rate of change of system properties, such as eroded volume and channel migration, stabilized; Fig. 2.10, 2.11 and Fig. S2.6). In the hydrochorous experiment, another DSM was captured at 5500 tidal cycles. The patchy vegetation and second control experiment ran longer, until 10 000 tidal cycles, in order to check whether a morphodynamic equilibrium was indeed reached after 5000 tidal cycles. During the second half of these experiments, DSMs were acquired with an interval of 500 or 1000 cycles.

Additional to the laser line scanner, a single-lens reflex camera was mounted on the moving gantry. Overhead photos with a resolution of 4000 by 6000 pixels were taken from the dry and wet sand bed, before and after DSMs were acquired. We took extra overhead photos during the vegetation experiments after the four-day germination period following each sowing event. The images were calibrated for internal and external parameters (i.e. lens correction, geometric rectification) before they were stitched (see Supplementary information S2.1 and Leuven et al., 2018).

DSM processing

As mentioned before, DSMs were acquired from laser line scanning. First, the raw laser line scanner data underwent a calibration and correction process for the laser-camera system. Subsequently, the corrected data were filtered to exclude the 10th and 90th percentiles to remove outliers before interpolating them to a 3 x 3 mm grid size. Erosion and sedimentation maps were computed by subtracting a DSM with a DSM from the previous time step. During the hydrochorous vegetation experiment, an external disturbance slightly changed the position of the laser-camera system between 1500 and 3500 tidal cycles. Basic corrections were applied. Specifically, a correction value was retrieved by calculating the median of the differences between two DSMs (one 'undisturbed' DSM and one DSM after the position of the laser-camera system changed). This value was then added to the elevation data.

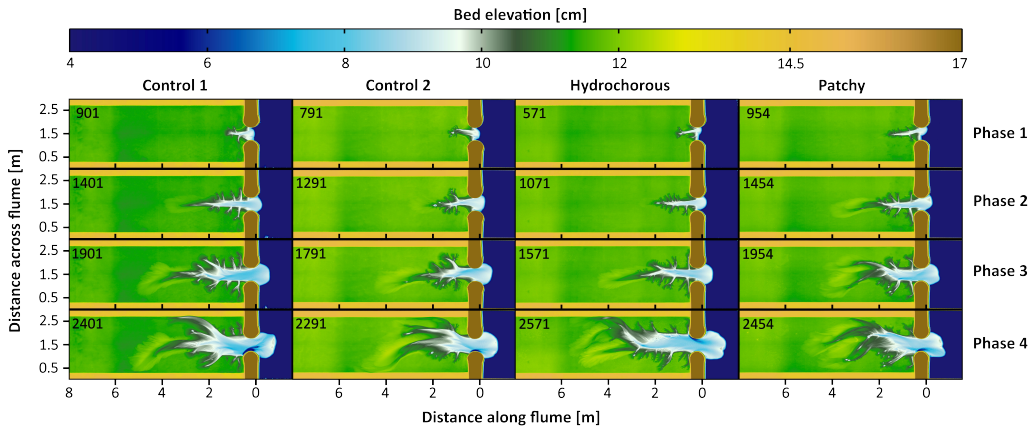


Figure 2.4: Plan view of Digital Surface Models (DSM) showing the four phases throughout the morphological development of the salt marsh experiments without vegetation but only sand (Control 1 and 2 in the two left columns), with hydrochorous seeding of vegetation and with patchy seeding (two right columns). Numbers indicate the corrected number of tidal cycles after which the DSM is shown.

Vegetation detection

The corrected and stitched overhead photos were used to detect vegetation and observe its cover development. We computed the green chromatic coordinate (GCC) as this color index has been proven to track canopy development successfully (Nijland et al., 2014; Sonnentag et al., 2012). Furthermore, Sonnentag et al. (2012) have shown that GCC suppresses changes in scene illumination more effectively than other color indices. The index was calculated using the following equation:

$$GCC = \frac{G}{R + G + B}$$

where B, R and G represent the blue, red and green bands from the images.

To explore the spatial variability in the temporal development of the vegetation cover, as a function of distance from the tidal inlet, mean vegetation cover was computed over six zones of 1 m long along the full length of the tidal basin and across the complete width of the flume (3 m).

Channel geometric properties

Various channel geometric properties were quantified to compare the channel networks obtained by the different experiments. For this purpose, the Python toolbox TidalGeoPro (see Gourgue et al., 2022) was applied. This toolbox consists of a fully automated methodology to extract channel networks and their geometric properties from an input digital elevation model. The process involves several steps. First, a median neighborhood analysis was performed on the DSMs (Liu et al., 2015).

For each pixel, the median elevation was calculated among all neighboring pixels within a window of several sizes to incorporate small-, medium- and large-sized channels (i.e. 201-by-201, 501-by-501 and 1001-by-1001 pixels). If the difference between the window median and the local pixel elevation was below a certain threshold (respectively, 0.0015, 0.005 and 0.0055 m) for at least one window size, the local pixel was identified as a channel. A raw channel network skeleton was retrieved containing some "erroneous" skeleton sections that did not connect to the channel network. This skeleton was cleaned in the next step by applying a threshold ratio (i.e. skeleton section length divided by the distance between the downstream node and the remaining skeleton). If a skeleton section length is below this threshold (1.7 in this case), it is removed. Then, a final channel network skeleton with equidistant skeleton points (3 mm) was computed as the center line of the channel network. Finally, the tidal watershed area (based on distance to channel pixels) and the total upstream channel length (i.e. combined length of all channels with the tidal watershed) were computed for every skeleton point. The channel drainage density, the mean unchanneled path length and the geometric efficiency were only computed at the inlet for the entire channel network.

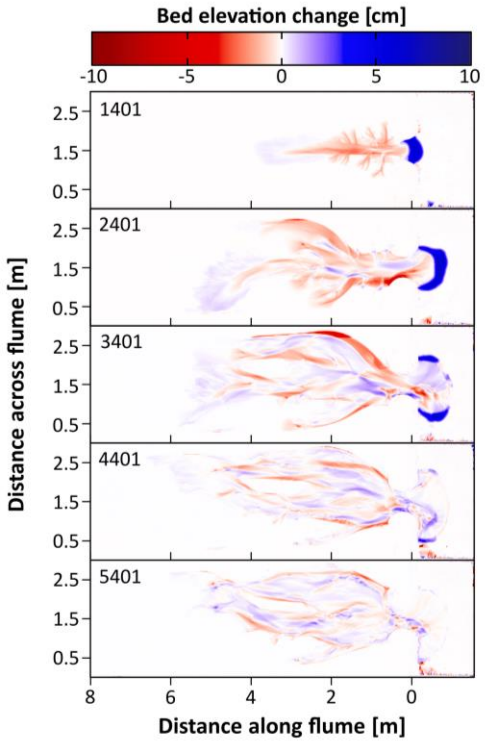


Figure 2.5: Maps of erosion (red shades) and sedimentation (blue shades) resulting from the first control experiment for different time steps showing a decline in morphological change. Erosion and sedimentation are computed with respect to the previous time step, in steps of 500 tidal cycles. For each time step, numbers indicate the corrected number of tidal cycles after which the erosion-sedimentation maps are shown. Only one experiment (control 1) is shown here as an example. Erosion and sedimentation maps for the other experiments can be found in the Supporting information (Fig. S2.5).

The drainage density (D) represents the extent of tidal channelization and is defined as the total upstream channel length divided by the watershed surface area (Horton, 1932, 1945; Marani et al., 2003). However, it fails to capture the branching and meandering characteristics of the channel network (Kirchner, 1993; Marani et al., 2003). The geometric efficiency (e_g) is a more appropriate measure to characterize these characteristics (Kearney & Fagherazzi, 2016) and is defined as the inverse of drainage density (D^{-1}) divided by the mean unchanneled path length (Marani et al., 2003). The mean unchanneled path length (mUPL) of a watershed is calculated as the mean distance to the closest channel, thus providing another proxy for the efficiency with which tidal channels drain a watershed (Marani et al., 2003; Tucker et al., 2001).

Finally, we computed a measure of local drainage densities (D_L) for six zones (mentioned in section 2.3.3 Vegetation detection) to explore spatial variability in drainage densities among zones at increasing distances from the tidal inlet. The local drainage density is the total channel length within the zone, divided by the zone surface area.

Data correction for variability in initial system development

Although we aimed to start each of the four experiments from the same initial conditions, it is unavoidable to have slight differences in the initial sediment bed slopes and sediment properties. These differences induced different rates of channel development in the initial phases of the experiments when no vegetation was sown yet, which caused the channel development to occur faster or slower and hence to appear shifted in time when compared between the four experiments. To allow comparison of the later development of the four experiments, after the sowing of vegetation started and channel branching initialized, the origin of the time axis (i.e. number of tidal cycles) of each experiment was determined at a point in time where the same volume of sediment was displaced and the development decelerated. In this case, the erosion of the tidal basins in terms of volume per unit of time decelerated around the time an eroded volume of 0.02 m^3 was reached (see Supplementary information – Fig. S2.6). The curve, describing erosion volume with time, started to flatten at that point and the effects of the variability in initial system development damped out. Therefore, the time scale in the time series plots and maps was shifted up to about 1000-2000 cycles to a corrected tidal cycle number of zero when an eroded volume of 0.02 m^3 was reached in every experiment.

2.4 Results

2.4.1 Salt marsh development and dynamics

In general, four phases could be distinguished throughout the experiments' morphological development (Fig. 2.4). During the first phase, seen after around 500-

1000 tidal cycles, one to three small channels formed around the inlet which expanded by backward erosion (see Fig. 2.5). In the next phase, around 1000-1500 tidal cycles (T = ± one and half year to two years in real-time), one of these channels developed into an elongated main channel with small side branches. The side branches were increasingly larger near the inlet, creating a Christmas tree-shaped channel system. In the third phase, around 1500-2000 tidal cycles (T = ± two to three years), the main channel became wider and the channel system continued expanding through backward erosion during the ebb phases. During the flood phases, a sediment depositional lobe developed at the landward end of the channel system (see Fig. 2.4 and 2.5b & c). In the final phase, around 2000-2500 tidal cycles (T = ± three to three and a half years), multiple channels branched off from the main channel in the landward part of the system. This led to an expansion of channels over the width of the flume and the development of channel bends cutting into the elevated borders. A dynamic channel-bar pattern emerged between these channel bends with continuous sediment redistribution. Past this point (> 4000 tidal cycles; T = over five and a half years), morphological change declined drastically (see Figs. S2.1-2.4) and a dynamic equilibrium was reached, in which channels were still able to migrate by erosion on one side and deposition on the other side of channels, but without much new channel expansion (Fig. 2.5d & e). The most landward area remained largely unaffected during the experiments.

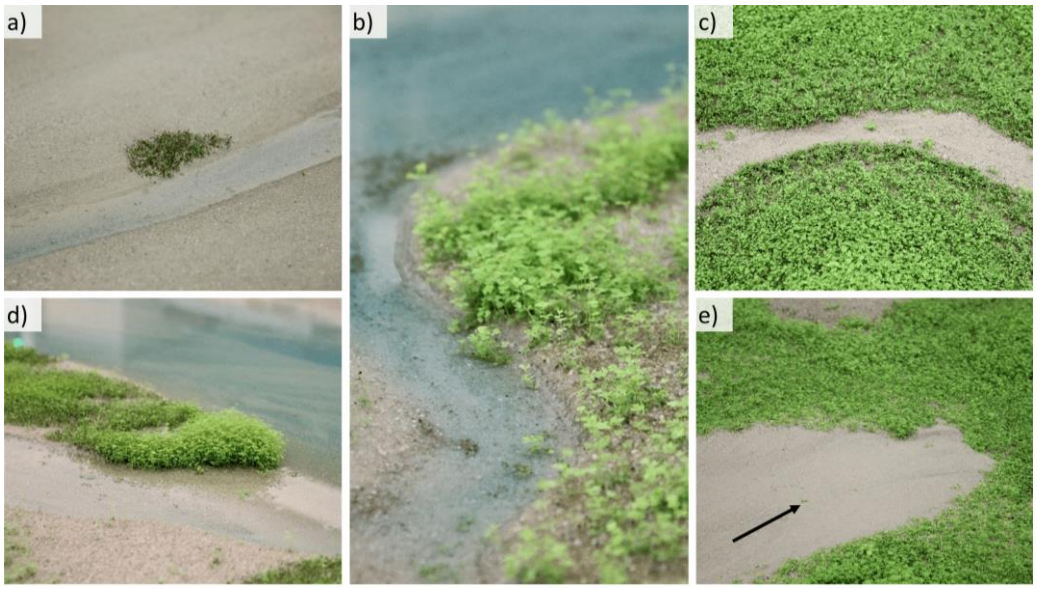


Figure 2.6: Photographs of vegetation-induced features in the experiments: **a)** a germinating patch of seeds sown next to a channel, **b)** a vegetated levee fringing along a channel, **c)** channel initiation induced by vegetation, **d)** channel bank stabilization by vegetation, **e)** sediment trapping induced by blocking of tidal flow in front of vegetation (flood flow direction indicated by arrow).

Differences in morphological development between experiments started to occur once sufficient vegetation had been established, which was observed between phases three and four (Fig. 2.4). During both control experiments without vegetation, the main channel started to branch and widen close to the inlet, as the absence of vegetation enabled channel erosion. The main channel started to branch more landward in the vegetation experiments. Furthermore, in the vegetation experiments, a more landward elongated main channel developed while the channel system widened further landward from the inlet. This pattern is most noticeable in the hydrochorous experiment, which could be caused by the establishment of vegetation fringing along the banks of the main channel. In the patchy experiment, an asymmetrical expansion of the channel system was observed as erosion of the left bank was limited by the presence of dense vegetation patches (Figs. 2.4, 2.7 & 2.8).

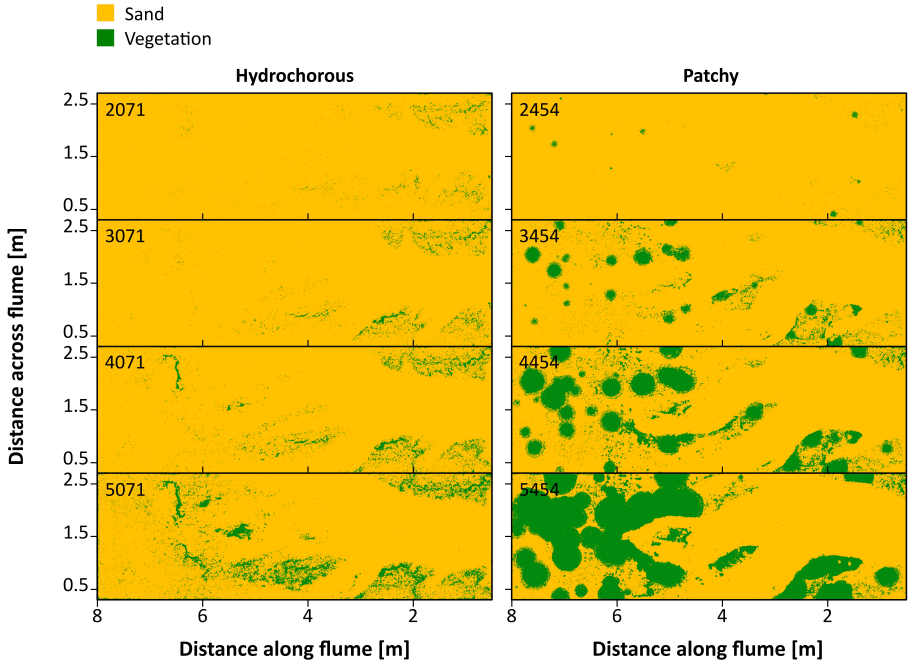


Figure 2.7: Vegetation cover development in the hydrochorous and patchy seeding experiments. Numbers indicate the corrected number of tidal cycles after which the vegetation cover is shown.

2.4.2 Vegetation establishment and disappearance

Analysis of the dynamic changes in vegetation cover depicted clear differences between the vegetation colonization patterns in the hydrochorous and patchy experiments (Fig. 2.7). In the hydrochorous experiment, vegetation first established along the channel banks close to the inlet. As the experiment progressed, vegetation settled more landward along the channel fringes (see Fig. 2.6b) and the depositional

lobe. In the patchy experiment, the emergence of new and expansion of established circular patches can be seen. Patches disappeared partly or completely in unfavorable locations where channel erosion occurred or where the force of tidal flow was too strong. For instance, after 4500–5500 cycles, we observed that the left channel bend (assuming an observer looks from the seaward inlet into the landward direction) was cutting through patches. Some of the uprooted vegetation was dispersed by the tide within the system and re-settled in different locations, such as the channel banks near the inlet. In both experiments, vegetation cover development started tentatively. Vegetation cover remained too low for visualization until 2500 tidal cycles, even though two sowing events had already occurred. Thereafter, vegetation cover started to increase. A similar vegetation cover development was observed in the most seaward zone of the tidal basin (Figs. 2.8a-c). Followed by the zone with the lowest vegetation cover (Fig. 2.8d), coinciding with the development of channel bends. In the most landward part, an exponential increase in vegetation cover took place as disturbance by tidal flow or channel erosion remained low (Figs. 2.8e-f). Besides, uprooted and secondary dispersed vegetation tended to settle in these areas. Overall, vegetation mainly grew above mean sea level, in the upper half of the intertidal zone (see Supporting information - Fig. S2.7).

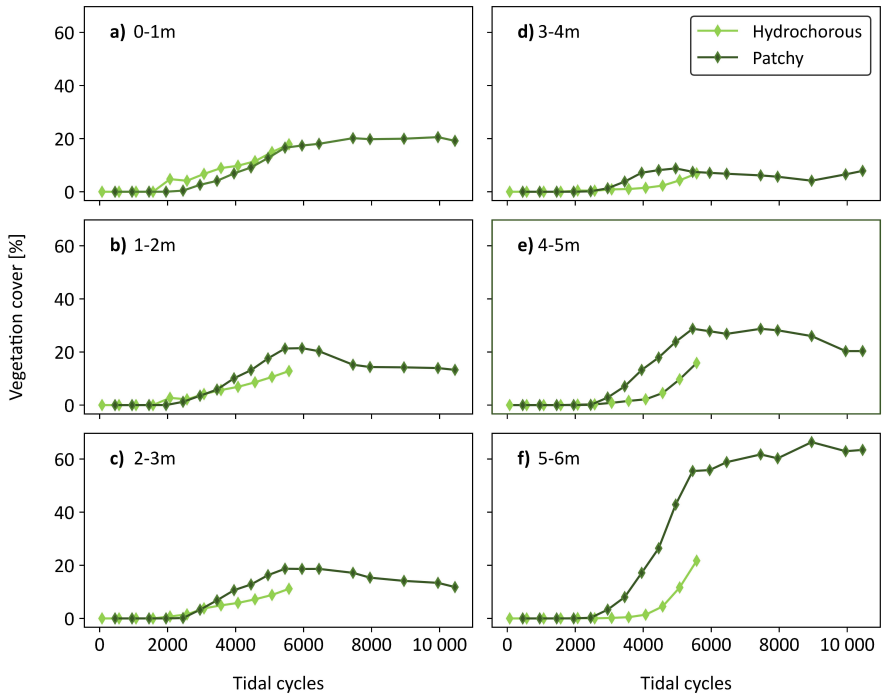


Figure 2.8: Development of vegetation cover over corrected number of tidal cycles in six zones divided along the length of the flume (i.e. at different distances from the tidal inlet): **a)** 0-1 m, **b)** 1-2 m, **c)** 2-3 m, **d)** 3-4 m, **e)** 4-5 m and **f)** 5-6 m.

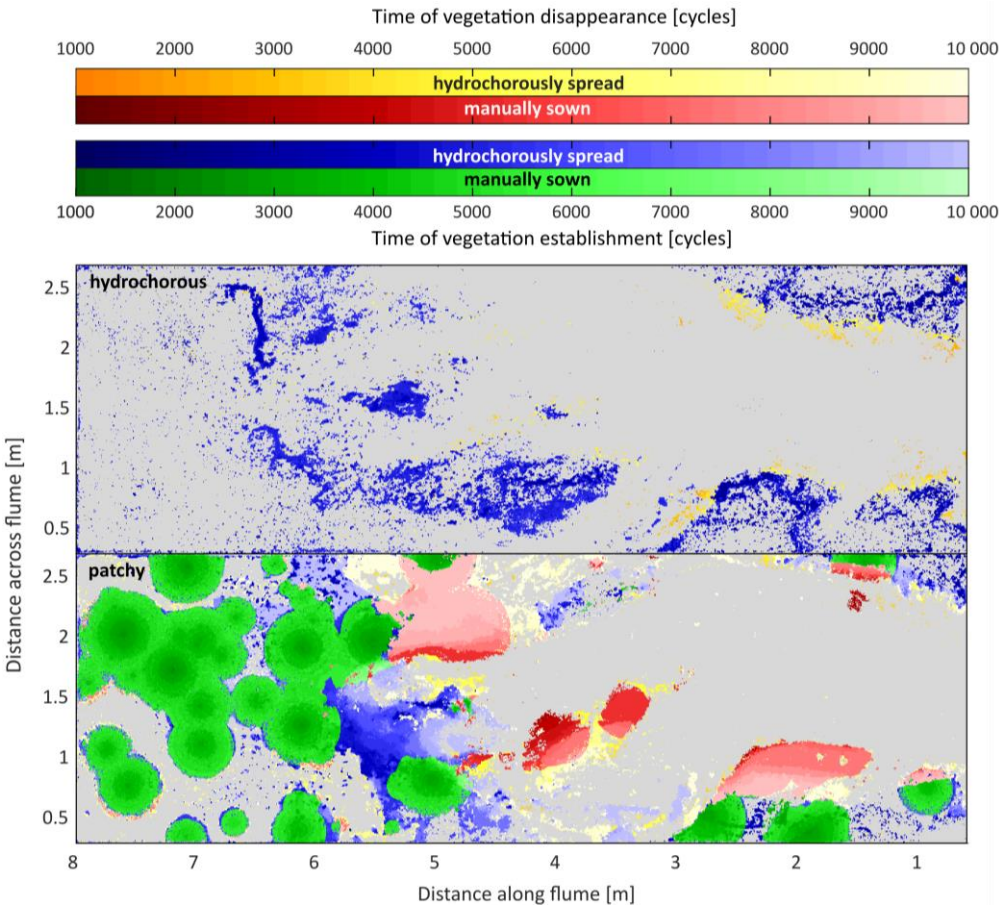


Figure 2.9: Maps showing the timing (expressed as corrected number of tidal cycles) of vegetation establishment and disappearance in the experiments with hydrochorous seeding (top) and patchy seeding (bottom). Green and blue color shades depict vegetation establishment over time; green represents manual seeding and blue hydrochorous seed dispersal. Seeds were added until the corrected time step of ± 5000 cycles. Red and yellow color palettes depict disappearance over time; red corresponds to disappearance of manually sown patches and yellow to disappearance of hydrochorously spread vegetation. Hydrochorous seed dispersal in the patchy experiment is attributed to uprooted vegetation that dispersed with the flow and settled at different locations. Darker shades indicate vegetation establishment or disappearance during earlier stages of the experiments. Grey shows areas where vegetation never settled.

To get a better understanding of the vegetation cover development, a map of vegetation establishment and disappearance over time was made (Fig. 2.9). The hydrochorous experiment mainly showed disappearance of vegetation in the seaward part of the system. Specifically, the vegetated channel banks started eroding over time as the main channel widened (see Fig. 2.6d). In the patchy experiment

disappearance mainly took place in the vegetated bar in the zone 3 to 4 m from the inlet during the intermediate stages. The uprooted vegetation of these patches then started to be redistributed and settle more landward, near other existing patches. The combination of this redistribution and settling of vegetation and continuously expanding patches around 5 to 6 m from the inlet resulted in a very dense patch of vegetation around 5500 tidal cycles (Figs. 2.8 and 2.9). During the second half of the patchy experiment (5000-10 000 tidal cycles; T = ± 7 to 14 years in real-time), the fixed vegetated bank around 1.5 to 3 m from the inlet eroded as the left channel bend (as seen from vertical top-view) expanded laterally. The dense vegetation patch had a major impact on the system development as it limited the travel distance of tidal flow. Some vegetation closest to the landward channel ends got uprooted but remained in place as sand deposition restricted movement (see Fig. 2.6e). Shortly after 9000 tidal cycles, the right side of the vegetation patch breached making space for system expansion. However, the uprooted vegetation (obtained from this breach) settled landward from the area creating a new vegetation barrier.

2.4.3 Channel geometric properties

The geometric properties of the developing channel systems were compared between all experiments after correcting the time axis and revealed certain differences. In the early stages of the experiments, from 0 to around 2000 tidal cycles, drainage density appeared to develop very similarly in all experiments but remained slightly smaller in the second control experiment (Fig. 2.10a). Around 2500 to 5000 tidal cycles, higher drainage densities were observed in the vegetation experiments. Differences became more quickly apparent in the hydrochorous experiment (2500 tidal cycles), while higher densities only started to become noticeable in the patchy experiment around 3500 tidal cycles. The higher degree of channelization is associated with vegetation establishment (Figs. 2.7, 2.8 and 2.9). Drainage density stabilized after 5000 tidal cycles (corresponds to ± seven years in real-time). Similar patterns were found in geometric efficiency (Fig. 2.10b) and mean unchanneled path length (Fig. 2.10c). However, it is apparent that mainly the hydrochorous experiment led to higher geometric efficiency around 3500 to 5000 tidal cycles, thus reflecting a more branching and meandering channel network. After 5000 tidal cycles, the patchy vegetation pattern also started to influence geometric efficiency. Geometric efficiency stabilized during the patchy and second control experiment during these final stages (> 5000 tidal cycles). The mean unchanneled path lengths also began to differ between experiments around 2500 to 3000 tidal cycles. Once again, differences first started becoming visible in the hydrochorous experiment (around 2500 tidal cycles), while the patchy experiment lagged a bit behind (around 4500 tidal cycles). We observed larger mean unchanneled path lengths in both control experiments. A comparison between the vegetation experiments revealed larger mean unchanneled path lengths in the patchy experiment. Based on these results, it

seems that the tidal channels of the hydrochorous experiment were most efficient in terms of draining a watershed.

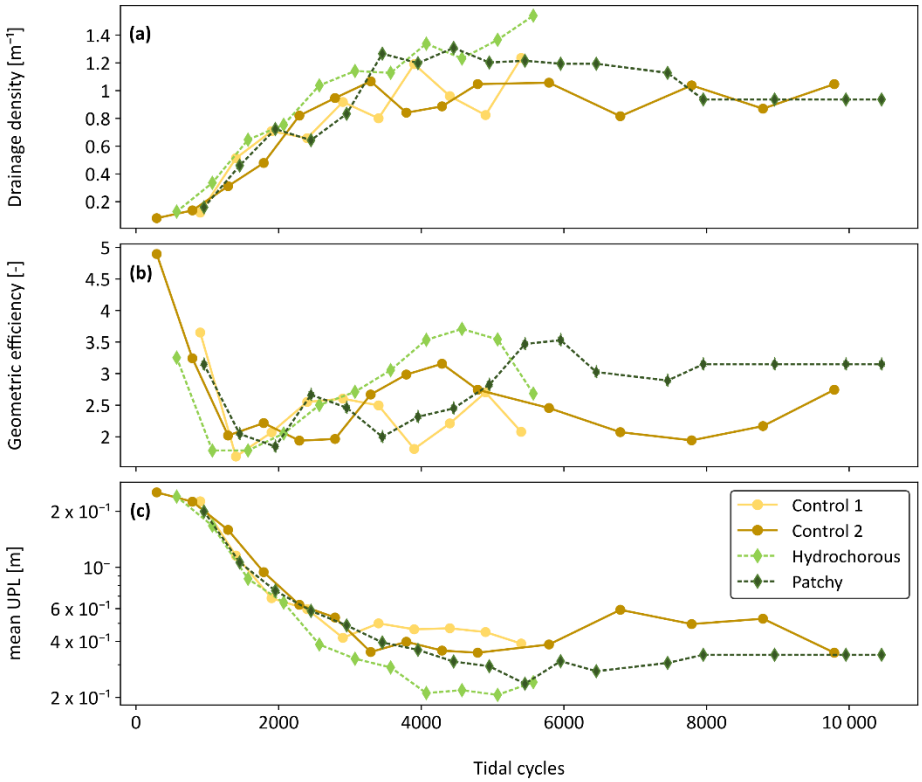


Figure 2.10: Comparison of channel network metrics between the control experiments (yellow = control 1; light-brown = control 2 and solid lines) and vegetated experiments (light-green = hydrochorous; dark-green = patchy and dashed lines). Evolution of **a)** drainage density, **b)** geometric efficiency and **c)** mean unchanneled path length (mean UPL) over time (expressed as corrected number of tidal cycles).

To have a closer look at spatial variability of the channel geometric properties within the simulated tidal basins, drainage densities were calculated for the aforementioned six zones (see section 2.3.3 - Vegetation detection). We observed a very dynamic pattern in the first two zones, starting from the inlet, without a discernible vegetation effect (Figs. 2.11 a-b). Local drainage densities increased during the early stages of the experiments. Around 1500 to 2000 tidal cycles, a sudden decrease was noticed in all experiments. This decrease was caused by the widening of the main channel at the expense of side channels. The local drainage densities recovered from this decline as side channels reconnected and channel bends started moving more seaward. After 5000 tidal cycles, the variables stabilized.

A similar trend was observed in the more landward zones (2 to 6 m – see Figs. 2.11 c-e). Here, we finally started to see flow-vegetation interaction around 2500 tidal cycles. The patchy experiment reached peak local drainage density (D_L) in zones 2 to 3 m and 3 to 4 m from the inlet, while the positive effect of vegetation on D_L decreased in the most landward zones (4 to 5 m and 5 to 6 m from the inlet). The peak, seen around 5500 to 6000 tidal cycles, in the most landward zone coincided with a late expansion of central branching channels. Afterwards, the D_L decreased since the left side branch became less active before reaching an equilibrium. In the hydrochorous experiment, peak drainage densities developed more landward. In contrast to the patchy experiment, the positive effect of vegetation on drainage density did not decrease but rather stabilized in the landward zones.

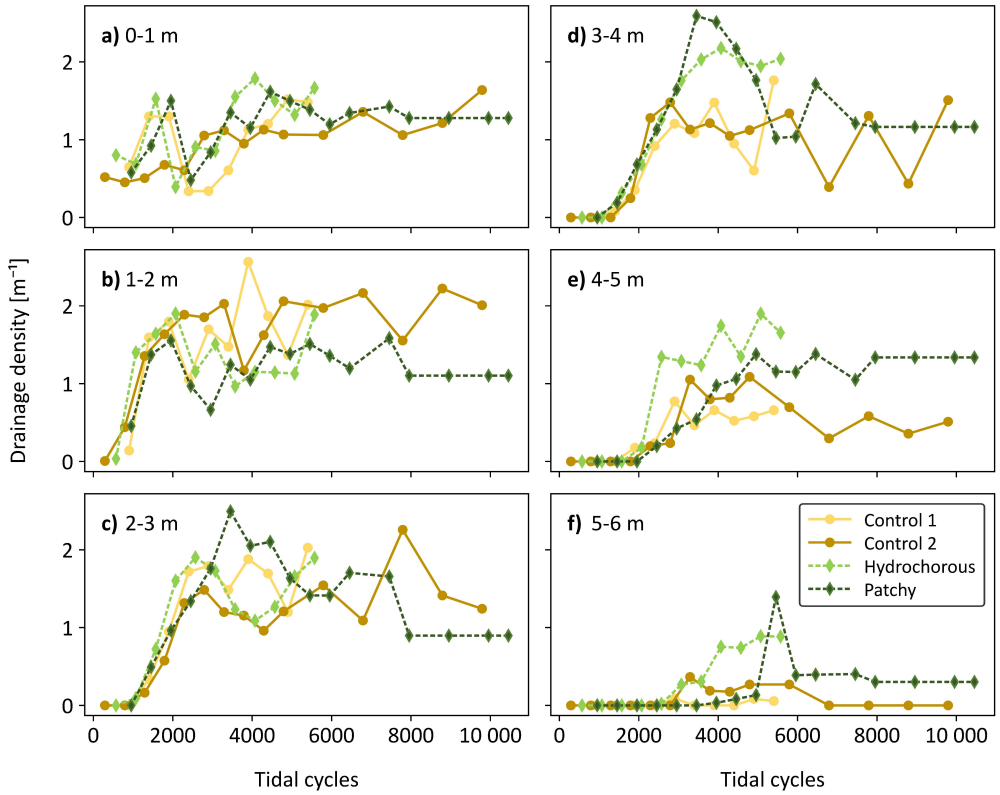


Figure 2.11: Evolution of drainage density over time (expressed as corrected number of tidal cycles) in six zones divided along the length of the flume (i.e. at different distances from the tidal inlet: **a)** 0-1 m, **b)** 1-2 m, **c)** 2-3 m, **d)** 3-4 m, **e)** 4-5 m and **f)** 5-6 m).

To get a better overview of where peak D_L was reached, the variables were plotted along the length of the flume for specific time steps (Fig. 2.12). We focused on the time steps around 3000 to 5500 tidal cycles as by then sufficient vegetation had established to affect the system development. Earlier and later stages either did not

include enough vegetation or exhibited stabilization in drainage densities. The location of local drainage density peaks differed between the unvegetated and vegetated experiments. The highest D_L in both control experiments was found in the second closest zone to the inlet (Fig. 2.12 b-c: 1 to 2 m), corresponding to the seaward system expansion seen in the morphological development (see Supplementary information - Figs. S2.1-2.4). Peak D_L was reached more landward in the vegetation experiments. During the patchy experiment a peak was depicted around 2 to 3 m before reaching a plateau around 3 to 4 m, followed by a steep decrease in D_L. A more diffused peak was observed in the hydrochorous experiment around 3 to 4 m before gradually decreasing in more landward zones. If we compare the drainage densities with the vegetation cover during the same time steps, we can notice the variables mirror each other. Vegetation cover slowly increased in seaward areas before decreasing around 3 to 4 m. In landward areas, vegetation cover rose quickly over time which is especially noticeable in the patchy experiment (Fig. 2.12 e-f).

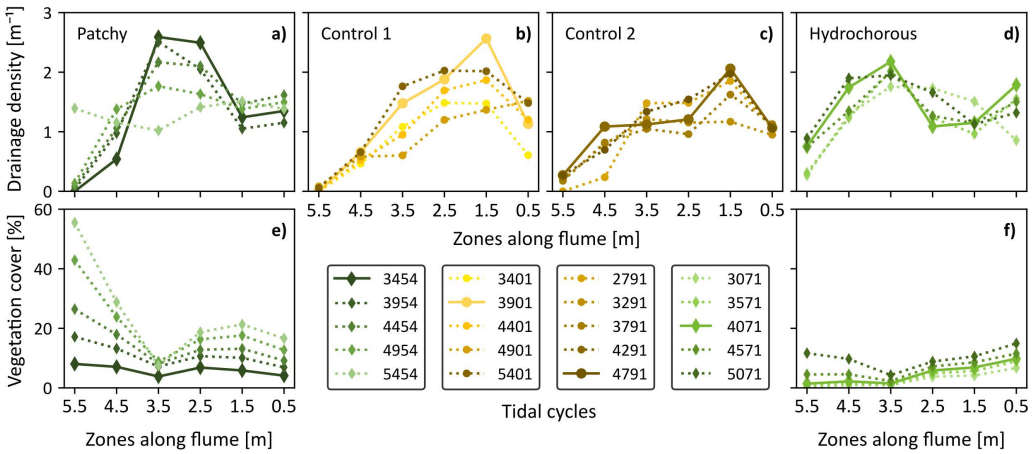


Figure 2.12: Local drainage density and vegetation cover of all experiments between approximately 3000 and 5500 corrected tidal cycles for different zones along the length of the flume (i.e. at different distances from the tidal inlet). The solid lines represent peak drainage density.

2.5 Discussion

Tidal channel networks and their geometric properties play an import role in the functioning of tidal wetlands (Fagherazzi et al., 1999; Friedrichs & Perry, 2001; Kearney & Fagherazzi, 2016; Temmerman et al., 2007). Novel scaled flume experiments, simulating a developing intertidal basin, were conducted to improve our understanding of the relative roles of abiotic and biotic processes on the development of tidal landscapes. The experiments showed that abiotic and biotic factors both affect the development and evolution of channel networks, where

abiotic factors cause a general similarity in tidal system dimensions and development, but biotic factors cause considerable differences. The vegetated experiments led to more efficient channel networks, both on a local and system-wide scale. At the same time, the contrasting recruitment strategies produced surprising differences in channel geometric properties. The hydrochorous seeding experiment resulted in a better-drained system with a higher geometric efficiency compared to the patchy seeding experiment.

2.5.1 System-wide scale

Our findings on geometric channel network properties on a system-wide scale generally align with other studies showing more efficient channel networks in vegetated intertidal marshes as compared to adjacent non-vegetated intertidal flats, based on numerical models (e.g. Schwarz et al., 2014; Temmerman et al., 2007) and remote sensing analyses (e.g. Kearney & Fagherazzi, 2016; Vandenbruwaene et al., 2013). In line with these previous studies, we can explain this as vegetation establishment slowing down the flow inside vegetated zones while at the same time concentrating and accelerating the flow in between vegetated zones (Bouma et al., 2013; Vandenbruwaene et al., 2011), thereby favoring channel development and resulting in higher channel drainage density and efficiency. However, the differences we found between the two recruitment strategies are at first sight contrasting with the findings of Schwarz et al. (2018), who showed more efficient channel networks in systems with a slow, patchy plant colonization (by *Spartina* spp.), as compared to systems with a fast, more homogenous plant colonization (by *Salicornia* spp.). The authors proposed that this can be related to local flow concentration. The resulting channel development is favored between slowly colonizing vegetation patches, while such flow concentration is limited in case of rapid, more homogeneous colonization. The different outcome of our experiments might be connected to the rate of vegetation cover development and final vegetation cover obtained. In the hydrochorous seeding experiment, the vegetation cover increased slowly over time and remained lower than in the patchy seeding experiment. Hence our hydrochorous experiment did not resemble a rapid, more homogeneous colonization pattern, as observed in marshes dominated by rapid and widespread hydrochorous seed dispersal by *Salicornia* spp. (Schwarz et al., 2018). Ultimately, in our hydrochorous experiment, the low vegetation cover and slow colonization might explain why flow concentration between the slowly developing vegetation zones favored new channel development and why we saw more efficient channel networks than in the patchy experiment with more rapid colonization. As such, our experimental results suggest that the rate of vegetation cover development plays a more dominant role than vegetation patchiness in affecting the resulting channel network development. This finding is quite similar to previous non-tidal experimental results, suggesting that rapid vegetation colonization can inhibit channel network development (Piliouras et al., 2017; Tal & Paola, 2007) and it adds new insights compared to previous studies

(Schwarz et al., 2018, 2022). An additional possibility is that the distribution of the circular patches in the patchy seeding experiment affected system development. Patches located in undisturbed areas (most landward from the inlet) could expand without inhibitions, while uprooted vegetation also tended to settle in these regions. This led to the growth of a giant patch on the landward side, which might have impeded system development and led to a lower channel network efficiency.

The observed differences between the vegetated and non-vegetated experiments (Figs. 2.10-2.12) were most noticeable during the transition from a bare to a "vegetated state" (tidal basin covered by a sufficient number of dense vegetation patches). Once a vegetated state was reached, channel geometric properties stabilized and differences between the experiments became less noticeable. The stabilization of network characteristics could be attributed to the stabilization of channel banks, slowing down of erosion and potentially the slight reduction in tidal prism (e.g. Kleinhans et al., 2022; Marani et al., 2003; Tal & Paola, 2010; Vandenbruwaene et al., 2012, 2013; Weisscher et al., 2022). This stabilization or slight reduction in tidal prism might be related to the ebb-delta, which kept growing in height and width over the course of the experiments and reduced the volume of water entering the system.

2.5.2 Local scale

Based on the results on a local scale, we introduce a conceptual diagram (Fig. 2.13) proposing an interdependency between abiotic and biotic factors in the development of tidal channel networks. Abiotic processes (ambient hydrodynamic energy determined by tidal prism) control whether biotic factors (vegetation colonization) play an additional role in channel development. This seems consistent with the findings of the remote sensing analysis of Liu et al. (2022), where the authors suggest that abiotic factors have a stronger control on channel network geometry than biotic factors. The influence of biotic factors is secondary, but it remains important during system development (most notably during the early stages).

In the most seaward zones of the intertidal basin (Fig. 2.11; 0-3 m from the tidal inlet), we could not observe systematic differences in channel drainage density between the vegetated and non-vegetated experiments, suggesting that abiotic factors predominantly affect the formation of channels in this most seaward zone. We hypothesize that the tidal prism tends to be large there (leading to strong hydrodynamic energy) and impedes interaction between vegetation and channel development as vegetation establishment is hindered by the strong flow conditions, except for the edges of the tidal basin where lower flow currents occur. Another possibility is that the existence of channels before sowing events commenced reduced the influence of plant-flow interactions (D'Alpaos et al., 2005; Schwarz et al., 2014).

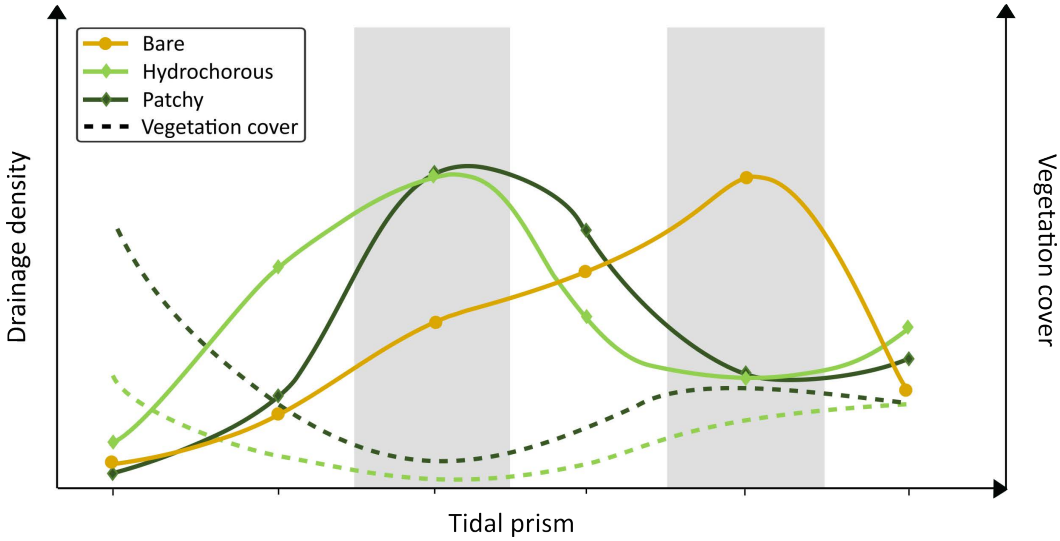


Figure 2.13: Conceptual graph of main results. The effects of tidal prism (reflecting hydrodynamic energy) and vegetation cover on drainage density are expressed. The grey shaded regions represent zones varying in levels of tidal prism in which we see the highest drainage density for bare and vegetated landscapes. Bare landscapes show peak drainage density in regions with high tidal prism. Landscapes with hydrochorous and patchy recruitment strategies reach their peak in regions with intermediate hydrodynamic energy and vegetation cover. High vegetation cover in combination with low tidal prism leads to a decrease in drainage density.

In the more landward zone (Fig. 2.11; 3-5 m from the tidal inlet), where hydrodynamic energy is supposedly weaker due to a landward reduction in tidal prism, we observed higher channel drainage densities in the vegetated experiments than in the non-vegetated control experiments. This suggests that biotic factors play a dominant role during the development of channel networks in zones with more intermediate hydrodynamic energy levels. Plant-flow interactions can take place as vegetation is not washed away, while concentrated flow around vegetation patches promotes channel development resulting in a higher degree of channelization (Schwarz et al., 2014; Temmerman et al., 2007; Vandenbruwaene et al., 2013, 2015). The more spatially homogeneous and hence weaker hydrodynamics in bare systems, on the other hand, may be responsible for the lower degree of channelization (e.g. Temmerman et al., 2005; Vandenbruwaene et al., 2013, 2015; Kearney and Fagherazzi, 2016). Field studies (such as Vandenbruwaene et al., 2015) have shown that this is related to more spatially homogenous sheet flow conditions on bare mudflats because of more spatially homogenous bed friction. In vegetated marshes, spatial heterogeneity in vegetation-induced friction promotes flow concentration towards bare channels.

Finally, in the most landward zones of the tidal basin (Fig. 2.11; 5-6 m from tidal inlet), we suggest that both biotic and abiotic factors no longer affect further channel network development. The hydrodynamic energy is too low to allow flow-topography feedback and plant-flow interactions. At the same time, dense vegetation patches impede system expansion by blocking the tidal flow leading to low drainage densities.

Our findings might have important implications for understanding the relative role of abiotic and biotic processes on channel network development in tidal systems with an overall landward gradient of decreasing tidal hydrodynamic forces (e.g. back-barrier tidal basins with a seaward tidal inlet , or tidal flats-marsh complexes with an overall seaward sloping topography). Smaller-scale individual marsh islands with more complex topographies will likely show a more complex spatial pattern in tidal hydrodynamic forces than our experiments. Further research is required to investigate the interdependencies between these processes as it could provide valuable insights for managing, conserving, and restoring tidal marsh ecosystems. Besides, examining the influence of different hydrodynamic energy levels on the role of biotic processes in channel development could potentially help predict how tidal marshes may respond to environmental changes, including sea level rise or altered hydrological regimes. Overall, these findings highlight the complexity of tidal marsh ecosystem dynamics and emphasize the need for a holistic approach to managing and restoring tidal marshes.

2.6 Conclusion

Our findings uncovered an interdependency between abiotic and biotic processes in tidal channel network development in which the abiotic processes seem to control whether biotic processes affect channel development. The relative role of these processes relies on the different hydrodynamic energy zones found over the tidal landscape and the stage of the system development. Abiotic factors (flow-topography feedback) mainly dominate channel development in seaward zones with strong hydrodynamics as vegetation gets washed away. Biotic factors (i.e. vegetation colonization) start having an additional effect in more landward zones with an intermediate level of hydrodynamic energy as they allow plant-flow interaction. The vegetation patches lead to concentrated flow around vegetation patches, promoting channel development and a higher channel network efficiency. The resulting channel networks are mainly affected by the rate of vegetation cover development instead of vegetation patchiness. Once the hydrodynamic energy level gets too low, biotic processes hardly play a role. The tidal flow is too weak to ensure plant-flow interaction and initiate further channel network development. Both processes predominantly have an impact during the transition from a bare to a vegetated landscape.

2.7 Acknowledgements

We would like to thank our Bsc thesis and Msc thesis students Tim van Meurs and Thomas Veerman for the help provided during the scaled flume experiments. Furthermore, we cordially acknowledge the technical support of the experiments by the lab technicians and help during the sowing events. The resources and services used in part of the data-analysis were provided by the VSC (Flemish Supercomputer Center), funded by the Research Foundation-Flanders (FWO) and the Flemish Government. This project has received funding from the Research Foundation-Flanders (FWO – fundamental research project – grant no. G031620N).

2.8 References

Allen, J. (2000). Morphodynamics of Holocene salt marshes: A review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quaternary Science Reviews*, *19*(12), 1155–1231. https://doi.org/10.1016/S0277-3791(99)00034-7

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Bij de Vaate, I., Brückner, M. Z. M., Kleinhans, M. G., & Schwarz, C. (2020). On the Impact of Salt Marsh Pioneer Species-Assemblages on the Emergence of Intertidal Channel Networks. *Water Resources Research*, *56*(3). https://doi.org/10.1029/2019WR025942

Bouma, T. J., Temmerman, S., van Duren, L. A., Martini, E., Vandenbruwaene, W., Callaghan, D. P., Balke, T., Biermans, G., Klaassen, P. C., van Steeg, P., Dekker, F., van de Koppel, J., de Vries, M. B., & Herman, P. M. J. (2013). Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. *Geomorphology*, *180–181*, 57–65. https://doi.org/10.1016/j.geomorph.2012.09.005

Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T., & Herman, P. M. J. (2007). Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. *Continental Shelf Research*, *27*(8), 1020–1045. https://doi.org/10.1016/j.csr.2005.12.019

Byrne, R. J., Gammisch, R. A., & Thomas, G. R. (1980). Tidal prism-inlet area relations for small tidal inlets. *Coastal Engineering Proceedings*, *1*(17), 149. https://doi.org/10.9753/icce.v17.149

D'Alpaos, A., Fagherazzi, S., & Rinaldo, A. (2005). Tidal network ontogeny: Channel initiation and early development. *Journal of Geophysical Research*, *110*(F2), F02001. https://doi.org/10.1029/2004JF000182

D'Alpaos, A., Lanzoni, S., Marani, M., & Rinaldo, A. (2007). Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. *Journal of Geophysical Research*, *112*(F1), F01008. https://doi.org/10.1029/2006JF000537

D'Alpaos, A., Lanzoni, S., Marani, M., & Rinaldo, A. (2010). On the tidal prism–channel area relations. *Journal of Geophysical Research*, *115*(F1), F01003. https://doi.org/10.1029/2008JF001243

D'Alpaos, A., Lanzoni, S., Mudd, S. M., & Fagherazzi, S. (2006). Modeling the influence of hydroperiod and vegetation on the cross-sectional formation of tidal channels. *Estuarine, Coastal and Shelf Science*, *69*(3–4), 311–324. https://doi.org/10.1016/j.ecss.2006.05.002

Davy, A. J., Bishop, G. F., & Costa, C. S. B. (2001). *Salicornia* L. (*Salicornia pusilla* J. Woods, *S. ramosissima* J. Woods, *S. europaea* L., *S. obscura* P.W. Ball & Tutin, *S. nitens* P.W. Ball & Tutin, *S. fragilis* P.W. Ball & Tutin and *S. dolichostachya* Moss). *Journal of Ecology*, *89*(4), 681–707. https://doi.org/10.1046/j.0022-0477.2001.00607.x

Fagherazzi, S., Bortoluzzi, A., Dietrich, W. E., Adami, A., Lanzoni, S., Marani, M., & Rinaldo, A. (1999). Tidal networks: 1. Automatic network extraction and preliminary scaling features from digital terrain maps. *Water Resources*

Research, *35*(12), 3891–3904. https://doi.org/10.1029/1999WR900236

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpaos, A., van de Koppel, J., Rybczyk, J. M., Reyes, E., Craft, C., & Clough, J. (2012). Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Reviews of Geophysics*, *50*(1), RG1002. https://doi.org/10.1029/2011RG000359

Friedrichs, C. T., & Perry, J. E. (2001). Tidal Salt Marsh Morphodynamics: A Synthesis. *Journal of Coastal Research*, 7–37.

Geng, L., Gong, Z., Zhou, Z., Lanzoni, S., & D'Alpaos, A. (2020). Assessing the relative contributions of the flood tide and the ebb tide to tidal channel network dynamics. *Earth Surface Processes and Landforms*, *45*(1), 237–250. https://doi.org/10.1002/esp.4727

Gourgue, O., van Belzen, J., Schwarz, C., Vandenbruwaene, W., Vanlede, J., Belliard, J.-P., Fagherazzi, S., Bouma, T. J., van de Koppel, J., & Temmerman, S. (2022). Biogeomorphic modeling to assess the resilience of tidal-marsh restoration to sea level rise and sediment supply. *Earth Surface Dynamics*, *10*(3), 531–553. https://doi.org/10.5194/esurf-10-531-2022

Gray, A. J. (1971). Variation in Aster tripolium L., with particular reference to some British populations [Ph.D. thesis, Keele University]. In *Keele University* (United Kingdom). https://eprints.keele.ac.uk/id/eprint/5892/

Hautekiet, S., Rossius, J.-E., Gourgue, O., Kleinhans, M. G., & Temmerman, S. (2023). *Data supplement to "On the relative role of abiotic and biotic controls on channel network development: Insights from scaled tidal flume experiments"* (Version 1.0) [Dataset]. Utrecht University. https://doi.org/10.24416/UU01-0MNEHQ

Horton, R. E. (1932). Drainage-basin characteristics. *Transactions, American Geophysical Union*, *13*(1), 350. https://doi.org/10.1029/TR013i001p00350

Horton, R. E. (1945). Erosional development of streams and their drainage basins: Hydrophysical approach to quantitative morphology. 56, 2 75-370. *Progress in Physical Geography: Earth and Environment*, *19*(4), 533–554. https://doi.org/10.1177/030913339501900406

Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beeftink, W. G., Markusse, M. M., & Munck, W. D. (1995). Seed Dispersal of Halophytes in Tidal Salt Marshes. *The Journal of Ecology*, *83*(4), 559. https://doi.org/10.2307/2261624

Jarrett, J. T. (1976). *Tidal Prism—Inlet Area Relationships*. Coastal Engineering Research Center (U.S.), General Investigation of Tidal Inlets Research Program Engineer Research and Development Center (U.S.). https://hdl.handle.net/11681/3226

Kearney, W. S., & Fagherazzi, S. (2016). Salt marsh vegetation promotes efficient tidal channel networks. *Nature Communications*, *7*(1), 12287. https://doi.org/10.1038/ncomms12287

Kirchner, J. W. (1993). Statistical inevitability of Horton's laws and the apparent randomness of stream channel networks. *Geology*, *21*(7), 591. https://doi.org/10.1130/0091-7613(1993)021%253C0591:SIOHSL%253E2.3.CO;2

Kirwan, M. L., & Murray, A. B. (2007). A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences*, *104*(15), 6118–6122.

https://doi.org/10.1073/pnas.0700958104

Kirwan, M. L., Murray, A. B., & Boyd, W. S. (2008). Temporary vegetation disturbance as an explanation for permanent loss of tidal wetlands. *Geophysical Research Letters*, *35*(5), L05403. https://doi.org/10.1029/2007GL032681

Kleinhans, M. G., Braudrick, C., van Dijk, W. M., van de Lageweg, W. I., Teske, R., & van Oorschot, M. (2015a). Swiftness of biomorphodynamics in Lilliput- to Giant-sized rivers and deltas. *Geomorphology*, *244*, 56–73. https://doi.org/10.1016/j.geomorph.2015.04.022

Kleinhans, M. G., Leuven, J. R. F. W., Braat, L., & Baar, A. (2017a). Scour holes and ripples occur below the hydraulic smooth to rough transition of movable beds. *Sedimentology*, *64*(5), 1381–1401. https://doi.org/10.1111/sed.12358

Kleinhans, M. G., Roelofs, L., Weisscher, S. A. H., Lokhorst, I. R., & Braat, L. (2022). Estuarine morphodynamics and development modified by floodplain formation. *Earth Surface Dynamics*, *10*(2), 367–381. https://doi.org/10.5194/esurf-10-367-2022

Kleinhans, M. G., Schuurman, F., Bakx, W., & Markies, H. (2009). Meandering channel dynamics in highly cohesive sediment on an intertidal mud flat in the Westerschelde estuary, the Netherlands. *Geomorphology*, *105*(3–4), 261–276. https://doi.org/10.1016/j.geomorph.2008.10.005

Kleinhans, M. G., van der Vegt, M., Leuven, J., Braat, L., Markies, H., Simmelink, A., Roosendaal, C., van Eijk, A., Vrijbergen, P., & van Maarseveen, M. (2017b). Turning the tide: Comparison of tidal flow by periodic sea level fluctuation and by periodic bed tilting in scaled landscape experiments of estuaries. *Earth Surface Dynamics*, *5*(4), 731–756. https://doi.org/10.5194/esurf-5-731-2017

Kleinhans, M. G., van der Vegt, M., van Scheltinga, R. T., Baar, A. W., & Markies, H. (2012). Turning the tide: Experimental creation of tidal channel networks and ebb deltas. *Netherlands Journal of Geosciences - Geologie En Mijnbouw*, *91*(3), 311–323. https://doi.org/10.1017/S0016774600000469

Kleinhans, M. G., van Scheltinga, R. T., van der Vegt, M., & Markies, H. (2015b). Turning the tide: Growth and dynamics of a tidal basin and inlet in experiments. *Journal of Geophysical Research: Earth Surface*, *120*(1), 95–119. https://doi.org/10.1002/2014JF003127

Krask, J. L., Buck, T. L., Dunn, R. P., & Smith, E. M. (2022). Increasing tidal inundation corresponds to rising porewater nutrient concentrations in a southeastern U.S. salt marsh. *PLOS ONE*, *17*(11), e0278215. https://doi.org/10.1371/journal.pone.0278215

Leonardi, N., Carnacina, I., Donatelli, C., Ganju, N. K., Plater, A. J., Schuerch, M., & Temmerman, S. (2018). Dynamic interactions between coastal storms and salt marshes: A review. *Geomorphology*, *301*, 92–107. https://doi.org/10.1016/j.geomorph.2017.11.001

Leuven, J. R. F. W., Braat, L., Dijk, W. M., Haas, T., Onselen, E. P., Ruessink, B. G., & Kleinhans, M. G. (2018). Growing Forced Bars Determine Nonideal Estuary Planform. *Journal of Geophysical Research: Earth Surface*, *123*(11), 2971–2992. https://doi.org/10.1029/2018JF004718

Liu, Y., Zhou, M., Zhao, S., Zhan, W., Yang, K., & Li, M. (2015). Automated extraction

of tidal creeks from airborne laser altimetry data. *Journal of Hydrology*, *527*, 1006–1020. https://doi.org/10.1016/j.jhydrol.2015.05.058

Liu, Z., Gourgue, O., & Fagherazzi, S. (2022). Biotic and abiotic factors control the geomorphic characteristics of channel networks in salt marshes. *Limnology and Oceanography*, *67*(1), 89–101. https://doi.org/10.1002/lno.11977

Lokhorst, I. R., Lange, S. I., Buiten, G., Selaković, S., & Kleinhans, M. G. (2019). Species selection and assessment of eco-engineering effects of seedlings for biogeomorphological landscape experiments. *Earth Surface Processes and Landforms*, *44*(14), 2922–2935. https://doi.org/10.1002/esp.4702

Marani, M., Belluco, E., D'Alpaos, A., Defina, A., Lanzoni, S., & Rinaldo, A. (2003). On the drainage density of tidal networks. *Water Resources Research*, *39*(2). https://doi.org/10.1029/2001WR001051

Mariotti, G., & Fagherazzi, S. (2011). Asymmetric fluxes of water and sediments in a mesotidal mudflat channel. *Continental Shelf Research*, *31*(1), 23–36. https://doi.org/10.1016/j.csr.2010.10.014

Mcowen, C., Weatherdon, L., Bochove, J.-W., Sullivan, E., Blyth, S., Zockler, C., Stanwell-Smith, D., Kingston, N., Martin, C., Spalding, M., & Fletcher, S. (2017). A global map of saltmarshes. *Biodiversity Data Journal*, *5*, e11764. https://doi.org/10.3897/BDJ.5.e11764

Meire, D. W. S. A., Kondziolka, J. M., & Nepf, H. M. (2014). Interaction between neighboring vegetation patches: Impact on flow and deposition. *Water Resources Research*, *50*(5), 3809–3825. https://doi.org/10.1002/2013WR015070

Myrick, R. M., & Leopold, L. B. (1963). Hydraulic geometry of a small tidal estuary. *US Geological Survey Professional Paper*, *422-B*, 18.

Nijland, W., de Jong, R., de Jong, S. M., Wulder, M. A., Bater, C. W., & Coops, N. C. (2014). Monitoring plant condition and phenology using infrared sensitive consumer grade digital cameras. *Agricultural and Forest Meteorology*, *184*, 98–106. https://doi.org/10.1016/j.agrformet.2013.09.007

Ortiz, A. C., Ashton, A., & Nepf, H. (2013). Mean and turbulent velocity fields near rigid and flexible plants and the implications for deposition: VEGETATION IMPACT ON FLOW AND DEPOSITION. *Journal of Geophysical Research: Earth Surface*, *118*(4), 2585–2599. https://doi.org/10.1002/2013JF002858

Piliouras, A., & Kim, W. (2019a). Delta size and plant patchiness as controls on channel network organization in experimental deltas. *Earth Surface Processes and Landforms*, *44*(1), 259–272. https://doi.org/10.1002/esp.4492

Piliouras, A., & Kim, W. (2019b). Upstream and Downstream Boundary Conditions Control the Physical and Biological Development of River Deltas. *Geophysical Research Letters*, *46*(20), 11188–11196. https://doi.org/10.1029/2019GL084045

Piliouras, A., Kim, W., & Carlson, B. (2017). Balancing Aggradation and Progradation on a Vegetated Delta: The Importance of Fluctuating Discharge in Depositional Systems. *Journal of Geophysical Research: Earth Surface*, *122*(10), 1882–1900. https://doi.org/10.1002/2017JF004378

Rinaldo, A., Fagherazzi, S., Lanzoni, S., Marani, M., & Dietrich, W. E. (1999a). Tidal networks: 2. Watershed delineation

and comparative network morphology. *Water Resources Research*, *35*(12), 3905–3917. https://doi.org/10.1029/1999WR900237

Rinaldo, A., Fagherazzi, S., Lanzoni, S., Marani, M., & Dietrich, W. E. (1999b). Tidal networks: 3. Landscape-forming discharges and studies in empirical geomorphic relationships. *Water Resources Research*, *35*(12), 3919–3929. https://doi.org/10.1029/1999WR900238

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91–95. https://doi.org/10.1038/s41586-019-0951-7

Roner, M., D'Alpaos, A., Ghinassi, M., Marani, M., Silvestri, S., Franceschinis, E., & Realdon, N. (2016). Spatial variation of salt-marsh organic and inorganic deposition and organic carbon accumulation: Inferences from the Venice lagoon, Italy. *Advances in Water Resources*, *93*, 276–287. https://doi.org/10.1016/j.advwatres.2015.11.011

Schwarz, C., Gourgue, O., van Belzen, J., Zhu, Z., Bouma, T. J., van de Koppel, J., Ruessink, G., Claude, N., & Temmerman, S. (2018). Self-organization of a biogeomorphic landscape controlled by plant life-history traits. *Nature Geoscience*, *11*(9), 672–677. https://doi.org/10.1038/s41561-018-0180-y

Schwarz, C., van Rees, F., Xie, D., Kleinhans, M. G., & van Maanen, B. (2022). Salt marshes create more extensive channel networks than mangroves. *Nature Communications*, *13*(1), 2017. https://doi.org/10.1038/s41467-022-29654-1

Schwarz, C., Ye, Q. H., van der Wal, D., Zhang, L. Q., Bouma, T., Ysebaert, T., & Herman, P. M. J. (2014). Impacts of salt marsh plants on tidal channel initiation and inheritance: Salt marsh plants channel development. *Journal of Geophysical Research: Earth Surface*, *119*(2), 385–400. https://doi.org/10.1002/2013JF002900

Sonnentag, O., Hufkens, K., Teshera-Sterne, C., Young, A. M., Friedl, M., Braswell, B. H., Milliman, T., O'Keefe, J., & Richardson, A. D. (2012). Digital repeat photography for phenological research in forest ecosystems. *Agricultural and Forest Meteorology*, *152*, 159–177. https://doi.org/10.1016/j.agrformet.2011.09.009

Stark, J., Meire, P., & Temmerman, S. (2017). Changing tidal hydrodynamics during different stages of eco-geomorphological development of a tidal marsh: A numerical modeling study. *Estuarine, Coastal and Shelf Science*, *188*, 56–68. https://doi.org/10.1016/j.ecss.2017.02.014

Stark, J., Plancke, Y., Ides, S., Meire, P., & Temmerman, S. (2016). Coastal flood protection by a combined nature-based and engineering approach: Modeling the effects of marsh geometry and surrounding dikes. *Estuarine, Coastal and Shelf Science*, *175*, 34–45. https://doi.org/10.1016/j.ecss.2016.03.027

Stefanon, L., Carniello, L., D'Alpaos, A., & Lanzoni, S. (2010). Experimental analysis of tidal network growth and development. *Continental Shelf Research*, *30*(8), 950–962. https://doi.org/10.1016/j.csr.2009.08.018

Tal, M., & Paola, C. (2007). Dynamic single-thread channels maintained by the

interaction of flow and vegetation. *Geology*, *35*(4), 347. https://doi.org/10.1130/G23260A.1

Tal, M., & Paola, C. (2010). Effects of vegetation on channel morphodynamics: Results and insights from laboratory experiments. *Earth Surface Processes and Landforms*, *35*(9), 1014–1028. https://doi.org/10.1002/esp.1908

Tambroni, N., Bolla Pittaluga, M., & Seminara, G. (2005). Laboratory observations of the morphodynamic evolution of tidal channels and tidal inlets: Tidal channels and tidal inlets. *Journal of Geophysical Research: Earth Surface*, *110*(F4), F04009. https://doi.org/10.1029/2004JF000243

Temmerman, S., Bouma, T. J., Govers, G., Wang, Z. B., De Vries, M. B., & Herman, P. M. J. (2005). Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh: *Journal of Geophysical Research: Earth Surface*, *110*(F4), F04019. https://doi.org/10.1029/2005JF000301

Temmerman, S., Bouma, T. J., Van de Koppel, J., Van der Wal, D., De Vries, M. B., & Herman, P. M. J. (2007). Vegetation causes channel erosion in a tidal landscape. *Geology*, *35*(7), 631. https://doi.org/10.1130/G23502A.1

Temmerman, S., De Vries, M. B., & Bouma, T. J. (2012). Coastal marsh die-off and reduced attenuation of coastal floods: A model analysis. *Global and Planetary Change*, *92–93*, 267–274. https://doi.org/10.1016/j.gloplacha.2012.06.001

Temmerman, S., Horstman, E. M., Krauss, K. W., Mullarney, J. C., Pelckmans, I., & Schoutens, K. (2023). Marshes and Mangroves as Nature-Based Coastal Storm Buffers. *Annual Review of Marine Science*, *15*(1), 95–118. https://doi.org/10.1146/annurev-marine-040422-092951

Tucker, G. E., Catani, F., Rinaldo, A., & Bras, R. L. (2001). Statistical analysis of drainage density from digital terrain data. *Geomorphology*, *36*(3–4), 187–202. https://doi.org/10.1016/S0169-555X(00)00056-8

Ursino, N., Silvestri, S., & Marani, M. (2004). Subsurface flow and vegetation patterns in tidal environments. *Water Resources Research*, *40*(5). https://doi.org/10.1029/2003WR002702

van Dobben, H. F., de Groot, A. V., & Bakker, J. P. (2022). Salt Marsh Accretion With and Without Deep Soil Subsidence as a Proxy for Sea-Level Rise. *Estuaries and Coasts*, *45*(6), 1562–1582. https://doi.org/10.1007/s12237-021-01034-w

Van Putte, N., Temmerman, S., Verreydt, G., Seuntjens, P., Maris, T., Heyndrickx, M., Boone, M., Joris, I., & Meire, P. (2020). Groundwater dynamics in a restored tidal marsh are limited by historical soil compaction. *Estuarine, Coastal and Shelf Science*, *244*, 106101. https://doi.org/10.1016/j.ecss.2019.02.006

Vandenbruwaene, W., Bouma, T. J., Meire, P., & Temmerman, S. (2013). Bio-geomorphic effects on tidal channel evolution: Impact of vegetation establishment and tidal prism change. *Earth Surface Processes and Landforms*, *38*(2), 122–132. https://doi.org/10.1002/esp.3265

Vandenbruwaene, W., Meire, P., & Temmerman, S. (2012). Formation and evolution of a tidal channel network within a constructed tidal marsh. *Geomorphology*, *151–152*, 114–125. https://doi.org/10.1016/j.geomorph.2012.01.022

Vandenbruwaene, W., Schwarz, C., Bouma, T. J., Meire, P., & Temmerman, S. (2015). Landscape-scale flow patterns over a vegetated tidal marsh and an unvegetated tidal flat: Implications

for the landform properties of the intertidal floodplain. *Geomorphology*, *231*, 40–52. https://doi.org/10.1016/j.geomorph.2014.11.020

Vandenbruwaene, W., Temmerman, S., Bouma, T. J., Klaassen, P. C., de Vries, M. B., Callaghan, D. P., van Steeg, P., Dekker, F., van Duren, L. A., Martini, E., Balke, T., Biermans, G., Schoelynck, J., & Meire, P. (2011). Flow interaction with dynamic vegetation patches: Implications for biogeomorphic evolution of a tidal landscape. *Journal of Geophysical Research: Earth Surface*, *116*(F1), F01008. https://doi.org/10.1029/2010JF001788

Vlaswinkel, B. M., & Cantelli, A. (2011). Geometric characteristics and evolution of a tidal channel network in experimental setting. *Earth Surface Processes and Landforms*, *36*(6), 739–752. https://doi.org/10.1002/esp.2099

Weisscher, S. A. H., Van den Hoven, K., Pierik, H. J., & Kleinhans, M. G. (2022). Building and Raising Land: Mud and Vegetation Effects in Infilling Estuaries. *Journal of Geophysical Research: Earth Surface*, *127*(1). https://doi.org/10.1029/2021JF006298

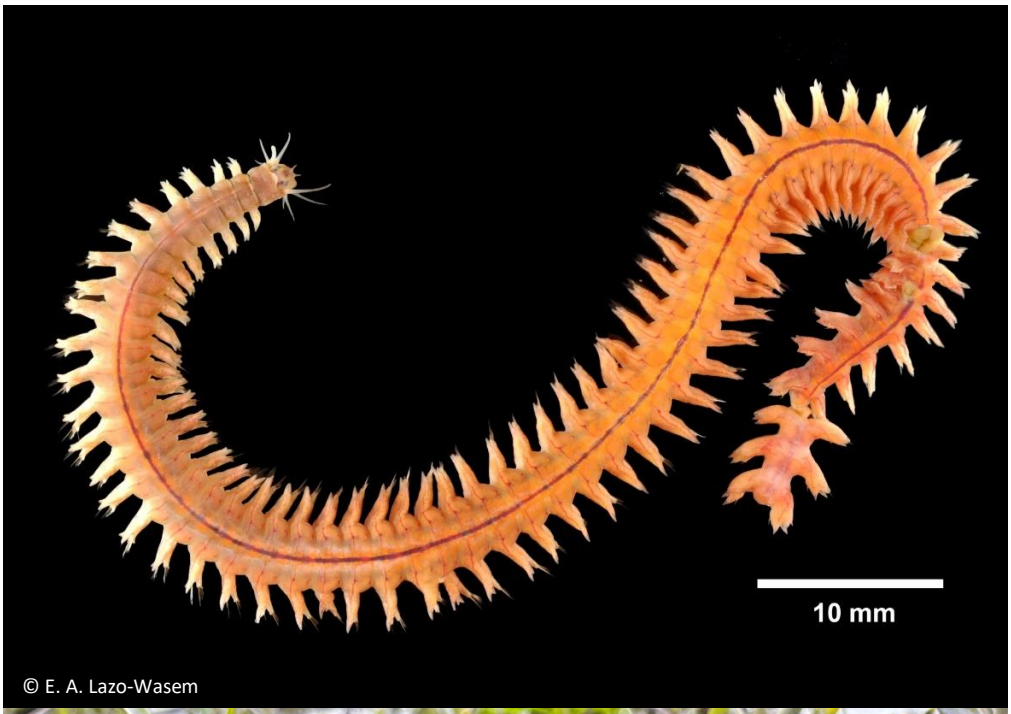
Xin, P., Wilson, A., Shen, C., Ge, Z., Moffett, K. B., Santos, I. R., Chen, X., Xu, X., Yau, Y. Y. Y., Moore, W., Li, L., & Barry, D. A. (2022). Surface Water and Groundwater Interactions in Salt Marshes and Their Impact on Plant Ecology and Coastal Biogeochemistry. *Reviews of Geophysics*, *60*(1). https://doi.org/10.1029/2021RG000740

Zhou, Z., Olabarrieta, M., Stefanon, L., D'Alpaos, A., Carniello, L., & Coco, G. (2014). A comparative study of physical and numerical modeling of tidal network ontogeny. *Journal of Geophysical Research: Earth Surface*, *119*(4), 892–912. https://doi.org/10.1002/2014JF003092

Zong, L., & Nepf, H. (2010). Flow and deposition in and around a finite patch of vegetation. *Geomorphology*, *116*(3–4), 363–372. https://doi.org/10.1016/j.geomorph.2009.11.020

Zong, L., & Nepf, H. (2011). Spatial distribution of deposition within a patch of vegetation. *Water Resources Research*, *47*(3), 2010WR009516. https://doi.org/10.1029/2010WR009516

Zong, L., & Nepf, H. (2012). Vortex development behind a finite porous obstruction in a channel. *Journal of Fluid Mechanics*, *691*, 368–391. https://doi.org/10.1017/jfm.2011.479



© E. A. Lazo-Wasem



3

Competing biotic interactions between fibrous algae and macrobenthos shape pioneer vegetation establishment in tidal marshes

Sarah Hautekiet, Jim van Belzen, Gregory S. Fivash, Ken Schoutens, Johan van de Koppel, Oberon Geunens, Wim Mertens, Bart Vandevoorde, Tjeerd J. Bouma & Stijn Temmerman

Submitted in Limnology and Oceanography

3.1 Abstract

The conservation and restoration of tidal marshes and their highly valued ecosystem services requires in-depth knowledge of the ecological processes facilitating or hindering marsh vegetation establishment on initially bare mudflats. While abiotic factors such as impact of hydrodynamics and sediment bed dynamics have been extensively studied, the role of biotic interactions in marsh establishment is less understood. Here, we investigate how interactions among three key organism groups -benthic polychaetes (*Hediste diversicolor*), benthic filamentous algae (*Vaucheria* sp.), and pioneer plant species (*Aster tripolium*)- control early successional dynamics in brackish tidal marshes in a northwestern European estuary. Combining field monitoring, field transplantation experiments and lab mesocosm experiments, we show that polychaete predation substantially reduces plant seedling survival, thereby constraining vegetation establishment. However, mat-forming filamentous algae, which preferentially establish adjacent to tidal drainage channels, play a pivotal role in mitigating these negative effects of polychaetes on plant seedlings. Algal mats had significantly lower polychaete densities and higher seedling survival compared to bare mudflats. Further, algae reduced polychaete-induced seedling mortality, likely by limiting burrowing activity and potentially offering an alternative food source. Our findings highlight the critical role of benthos-algae-plant interactions in the early stages of tidal marsh development. These insights suggest that promoting filamentous algal mat development -for instance, by creating drainage channels or topographic heterogeneity- could enhance tidal marsh restoration success by facilitating pioneer vegetation establishment.

3.2 Introduction

In recent years, tidal marsh conservation and restoration have received increasing attention due to the invaluable ecosystem services these habitats provide (Barbier et al., 2011; Gedan et al., 2009; Zhao et al., 2016), including nature-based shoreline protection (e.g. Schoutens et al., 2019; Temmerman et al., 2023) and climate mitigation through carbon sequestration (e.g. Huyzentruyt et al., 2024; Rogers et al., 2019). Tidal marsh conservation and restoration efforts are especially relevant since tidal marshes have been massively lost in previous centuries due to human-induced land use changes, such as land reclamation for agriculture, industry, or urbanization. To halt and reverse this loss, a thorough understanding of the processes and mechanisms governing tidal marsh ecosystem development is essential to enable successful restoration efforts. However, our knowledge of the initial establishment phase -critical for the restoration of tidal marshes- remains limited.

Tidal marsh development usually takes place by transition from a bare mudflat to a vegetated marsh (van Belzen et al., 2017, 2022; Wang & Temmerman, 2013). This transition is initiated by the colonization of pioneer species. Essential requirements for successful pioneer plant establishment include an adequate supply of seeds and favorable environmental conditions (Erfanzadeh et al., 2010a; van Regteren et al., 2019). Abiotic disturbances (e.g. hydrodynamic forces from tidal currents and waves, and associated erosion and sedimentation) and biotic disturbances (e.g. herbivory) can impede vegetation establishment (Balke et al., 2016; Cao et al., 2018; Hu et al., 2015; Paramor & Hughes, 2004, 2005; Zhu et al., 2020). Therefore, seedling establishment relies on seed dispersal followed by sufficiently long disturbance-free periods, a concept known as "Windows of Opportunity", allowing germination and growth of seedlings until they are strong enough to survive the next disturbances (Balke et al., 2011, 2014). These Windows of Opportunity can become wider (i.e. extend over a longer period) if abiotic disturbances are weaker or less frequent (Balke et al., 2014; Hu et al., 2015, 2021; van Belzen et al. 2022) and biotic disturbances are reduced (e.g. Hughes, 1999; Hughes et al., 2000).

While the role of abiotic processes, such as hydrodynamic and sediment bed disturbances, in the initial establishment of tidal marshes, have been extensively studied (e.g. Callaghan et al., 2010; Cao et al., 2018; Hu et al., 2015; Schoutens et al., 2021), biotic processes, like herbivory, have received comparatively less attention despite their crucial role in vegetation establishment. This study addresses biotic processes, specifically focusing on the interactions among three key groups of organisms commonly found in early successional stages of tidal marshes in NW European estuaries: (1) polychaetes (e.g. *Hediste diversicolor*), (2) benthic filamentous algae (e.g. *Vaucheria* sp.) and (3) pioneer marsh plant species (e.g. *Aster tripolium*).

(1) Benthic invertebrates play an important role in the ecosystem functioning of tidal marshes. One of the most prevalent and influential species is the polychaete *Hediste diversicolor*, formerly known as *Nereis diversicolor*. *Hediste* is an intertidal macrobenthos species commonly found in the brackish water zones of estuaries in temperate climates of the northern hemisphere. This omnivorous polychaete builds burrows in the sediment bed and employs various feeding strategies such as deposit feeding, filter feeding, scavenging, herbivory on sprouting seeds and predation (Nielsen et al., 1995; Scaps, 2002; Zhu et al., 2016). In pioneer zones, *Hediste* predominantly acts as a surface deposit feeder (Paramor & Hughes, 2004), consuming sediment, microphytobenthos (Smith et al., 1996), filamentous algae (Engelsen & Pihl, 2008; Hughes, 1999), plant debris (Olivier et al., 1997; Scaps, 2002) and seeds (Hughes et al., 2000; Zhu et al., 2016). Several studies have documented the negative effects of *Hediste* on marsh development by herbivory and bioturbation. These effects include damage to plant roots (Hughes et al., 2000), increased sediment erosion (Hughes & Paramor, 2004; Widdows et al., 2009), and restricted vegetation establishment in pioneer zones (Paramor & Hughes, 2005, 2007; van Regteren et al., 2017). According to Hughes et al. (2000), *Hediste*'s activity can drive an alternation between two ecological states: one dominated by vegetation, which excludes burrowing macrobenthos, and another dominated by macrobenthos, which inhibits plant establishment through bioturbation and herbivory. During the early successional stages of tidal marshes, an intermediate transitional state may occur, where pioneer plant seedlings are able to establish despite the presence of polychaetes. However, the mechanisms regulating this balance remain unclear.

(2) Benthic algae are an ecologically important component of tidal marshes as they contribute to primary production, nutrient cycling, and sediment stabilization. Among them, benthic filamentous algae such as *Vaucheria* often play a key role in shaping sediment dynamics. The yellow-green algae, *Vaucheria* sp., form a dense mesh of filaments on intertidal mudflat and marsh sediment surfaces (Wilcox, 2012). The filaments can penetrate the sediment bed to a depth of 4-6 cm forming thick and patchy mats that can trap and bind sediment particles (Gallagher & Humm, 1981) and create elevated sediment hummocks (Gallagher & Humm, 1981; van de Vijsel et al., 2020, 2021). These hummocks could boost vegetation growth rates by increasing sediment drainage (Fivash et al., 2019) and reducing abiotic disturbance from sediment dynamics (Hu et al., 2015). Over the past decades, the biostabilizing effect of filamentous *Vaucheria* algae have attracted attention for their potential role as facilitator in vegetation establishment (van de Vijsel et al., 2020, 2021; Wilcox, 2012).

(3) Pioneer plant species are the first to colonize new or disturbed habitats, helping to stabilize sediments and pave the way for other plant species. *Aster tripolium* (also known as *Tripolium pannonicum*) is a marsh pioneer plant species of the *Asteraceae* family, typical for the brackish zone of NW European estuaries. It is a biennial plant

that flowers from July to October and reproduces through seed dispersal by wind and water flow from October to December (Hill et al., 2004; Huiskes et al., 1995; van Regteren et al., 2019). *Aster* seedlings and other marsh plant species tend to establish on elevated *Vaucheria* patches (personal observations and figures in Fivash et al., 2019; van de Vijsel et al., 2021; Van den Neucker et al., 2007) and along well-drained surfaces such as creek edges (Sanderson et al., 2000, 2001).

Field observations (Van den Bergh et al., 2005; Vandevoorde et al., 2011) indicate that these biota colonize intertidal mudflats following a typical pattern of subsequent successional stages in brackish tidal restoration sites. The process begins with *Hediste* dominating the colonization, followed by the formation of dense *Vaucheria* algal mats, which creates favorable conditions for the establishment of *Aster* (Fig. S3.1). This biotic succession suggests that the interactions between these species affect pioneer vegetation establishment during the early stages of tidal marsh development.

Although patterns of association between zoobenthos, algae, and pioneer marsh plant species have been observed, the underlying interactions and processes shaping these associations remain poorly understood. Specifically, while correlations suggest potential relationships, there is limited experimental evidence that explicitly examines the interactions among all three groups. For instance, it has been hypothesized that filamentous algae such as *Vaucheria* could mitigate the antagonistic effects of polychaetes (e.g. herbivory and reduced sediment stability due to bioturbation) on pioneer plants, potentially promoting plant establishment (van de Vijsel et al., 2021). However, experimental evidence supporting this hypothesis is still lacking. Clarifying the nature of these interactions -whether through mutual exclusion, facilitation, or other processes- is crucial for understanding tidal marsh development and informing more effective restoration strategies.

The current study aims to unravel the influence of the three-way interactions between polychaetes (i.e. *Hediste*), filamentous algae (i.e. *Vaucheria*), and pioneer marsh plant seedlings (i.e. *Aster*) during early successional stages of tidal marsh development. Specifically, we investigated whether *Vaucheria* could mitigate top-down control by polychaetes, potentially creating a biological "Window of Opportunity" for seedling establishment. We used a combination of field experiments, mesocosm experiments, and monitoring surveys to explore these dynamics.

We hypothesize that *Hediste* predation reduces *Aster* seedling survival, which we tested via an *Aster* transplantation experiment comparing a control and a defaunation treatment while monitoring *Aster* survival. Additionally, we hypothesize that *Vaucheria* algal mats counteract the top-down control of the polychaete *Hediste*

on seedling establishment by excluding the polychaetes (e.g. restricting their burrowing behavior). To test this, we conducted:

(1) A field monitoring survey quantifying *Aster* seedling densities in bare mud and *Vaucheria* patches;

(2) A field experiment transplanting *Aster* seedlings into *Vaucheria* and bare mud patches to assess the impact of *Vaucheria* on seedling survival;

(3) A polychaete survey in bare mud and *Vaucheria* patches to assess the effect of *Vaucheria* on *Hediste* densities;

(4) A mesocosm experiment monitoring *Aster* seedling survival in the presence/absence of *Hediste* and *Vaucheria* to determine whether *Vaucheria* algae exclude the polychaetes.

3.3 Materials and methods

Vegetation and macrobenthos monitoring surveys and field experiments (see overview in Table 1) were performed across two tidal marsh restoration sites along the Scheldt estuary (NE Belgium) (Fig. 3.1). Both sites are so-called 'managed realignment sites, that is: they were historically embanked areas (i.e. former wetlands embanked by dikes and drained by ditches), which were recently restored in tidal marshes by landward relocation of dikes and reintroduction of tidal flooding and drainage. The salinity in this part of the Scheldt estuary is between 5.5 and 8 PSU (Erfanzadeh et al., 2010b). At each site, the pre-existing terrestrial vegetation and infauna were initially killed by the reintroduction of tidal flooding with brackish water and deposition of sediment. This process created a bare sediment surface, allowing subsequent colonization by estuarine species.

Paardenschor (51°19'38.3" N, 4°15'45.5" E) is a managed realignment site located along the Scheldt estuary that was initiated in 2004 (Fig. 3.1, S3.2 & S3.3). The dike was relocated landward, and the area was excavated to achieve a soil surface level below mean high water level that is suitable for pioneer marsh plant establishment (Van den Neucker et al., 2007). The mean tidal range in this marsh is about 5.1 m (www.waterinfo.be).

Ketenisse (51°17'2.8" N, 4°18'37.4" E) is a formerly embanked agricultural area that was converted into a managed realignment site in 2003 using a similar restoration approach as in Paardenschor (Fig. 3.1 & S3.4). A new dike was constructed inland and the soil surface level was excavated below mean high water level to make it suitable for marsh development (Van den Neucker et al., 2007). The mean tidal range is about 5.25 m in this part of the Scheldt estuary (www.waterinfo.be).

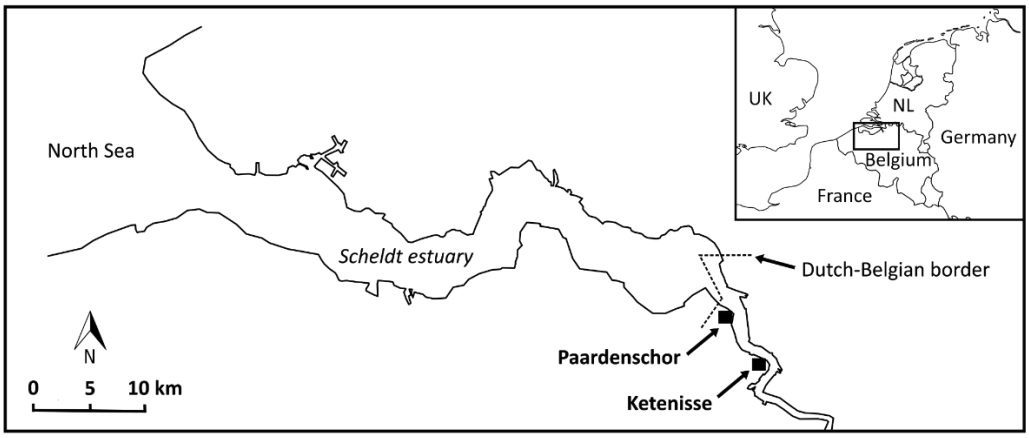


Figure 3.1: Overview of the study sites Paardenschor and Ketenisse along the Scheldt estuary (NE Belgium).

Table 3.1: Summary of which effects/relations were tested, the experiments and monitoring surveys that were conducted, and where the experiments/surveys took place.

Tested effects/relations	Experiments/surveys	Study site
T1 - Effect of *Hediste* predation on *Aster* seedling survival	*Field experiment 1*	Paardenschor
T2.1 - Effect of *Vaucheria* patches on *Aster* seedling establishment	*Field monitoring survey 1*	Paardenschor
T2.2 - Effect of *Vaucheria* patches on *Aster* seedling survival	*Field experiment 2*	Paardenschor
T3 - Observing *Hediste* densities within and outside *Vaucheria* patches	*Field monitoring survey 2*	Ketenisse
T4 - Role of *Vaucheria* - *Hediste* interactions in *Aster* seedling survival	*Mesocosm experiment*	Lab

3.3.1 Effect of *Hediste* predation on *Aster* seedling survival

Field experiment 1 (T1) - The effect of *Hediste* absence/presence on *Aster* seedlings was examined by transplanting *Aster* seedlings on 1 square meter plots across three plots along the intertidal elevation gradient: low, middle and high elevation zones (Fig. S3.2) in combination with two benthos treatments, being control plots (with presence of macrofauna) and defaunated plots (absence of macrofauna, explained below). The average elevation of the low zone was 2.27 ± 0.11 m NAP (i.e. Dutch Ordinance Level, approximately mean sea level), the mid zone 2.52 ± 0.02 m NAP, and the high zone 2.7 ± 0.06 m NAP. Each combination of elevation and benthos treatment was replicated five times (n = 5). Eight *Aster* seedlings (four weeks after

germination) were transplanted per plot in June 2015. Seedling survival was monitored at regular intervals (weekly during the first two weeks and then bi-weekly) by counting the number of seedlings per plot to track loss rates over time. The experiment was terminated after 86 days.

Defaunation treatment

To explore the impact of macrobenthic activity, a defaunation treatment was applied by creating anoxic conditions using a method proven effective in previous studies (Montserrat et al., 2008; Van Colen et al., 2008). The sediment of the plots was closed off from fresh air by covering the plots with two 2 m^2 waterproof polyethylene sheets (0.1 mm thick). The ends of the sheets were dug into the sediment (~ 0.3 m deep) at the edges of the plot until the start of the experiment. After 28 days of covering the sediment, the plastic sheets were removed.

3.3.2 Effect of *Vaucheria* algae on *Aster* seedling establishment and survival

Field survey 1 (T2.1): *Vaucheria*'s effect on *Aster* seedling establishment - The presence of *Aster* seedling establishment within and outside *Vaucheria* patches was examined by conducting a field monitoring survey in Paardenschor (Fig. 3.1 & S3.3) in 2015. As *Vaucheria* patches are observed typically along the edge of small tidal creeks draining from the intertidal flats, monitoring plots were chosen to assess the effects of distance from creek edge and presence/absence of *Vaucheria* patches on *Aster* seedling density. The seedling density was monitored by randomly placing 1 m^2 vegetation quadrats at different locations, including bare mud along creek edges (n = 20), bare mud away from creek edges (n = 20) and *Vaucheria* patches along creek edges (n = 20). No *Vaucheria* patches away from creek edges were selected as these were nearly absent.

Field experiment 2 (T2.2): *Vaucheria*'s effect on *Aster* seedling survival - Following this observation, *Aster* seedling survival probability was investigated in *Vaucheria* patches versus in bare mud by conducting another *Aster* field transplantation experiment in Paardenschor in 2015 (Fig. 3.1). In this study site, five replicate plots (0.25 x 0.25 m), each containing five transplanted *Aster* seedlings (the seedlings were grown for 6 weeks before transplantation), were set up in a *Vaucheria* patch and in bare mud. The plots were situated around the same location as the low and middle elevation levels discussed in the first field experiment (2.27 ± 0.11 m NAP, 2.52 ± 0.02 m NAP, and 2.7 ± 0.06 m NAP; see Fig. S3.2). The survival of the seedlings was monitored at least once a week by counting the number of seedlings. The experiment was terminated after five weeks (i.e. 42 days).

3.3.3 Effect of *Vaucheria* algae on *Hediste* densities

Field survey 2 (T3) - We examined whether the presence of *Vaucheria* algae affected *Hediste* densities by carrying out a macrobenthos sampling survey in Ketenisse in 2016 (Fig. S3.4). *Hediste* densities were quantified by sampling in random locations that included either bare mud or *Vaucheria* patches. At every sample location, three cores (Ø: 0.09 m, depth: 10 cm) were taken to cover a depth of 30 cm. This method was replicated three times (n = 3) for bare mud and *Vaucheria* patches. Afterwards, the sediment was rinsed over a sieve with a 1 mm mesh size to separate the smaller benthic species from the large polychaetes (i.e. *Hediste*), which were counted.

3.3.4 Role of *Vaucheria* - *Hediste* interactions in seedling survival

Mesocosm experiment (T4) - A laboratory mesocosm experiment was conducted in the summer of 2015 to test the effect of the absence/presence of the algae and polychaetes on *Aster* seedling survival. Four treatments were applied to PVC pots (height: 0.15 m, Ø: 12.5 cm) filled with sediment from Paardenschor: (1) one in which both *Hediste* and *Vaucheria* were absent (hereafter abbreviated to *H- V-*), (2) a second in which *Hediste* was present, but *Vaucheria* remained absent (*H+ V-*), (3) a third in which *Hediste* was absent but *Vaucheria* was present (*H- V+*) and, finally, (4) one in which both *Hediste* and *Vaucheria* were present (*H+ V+*). Seedlings were grown for 28 days before transplanting them into the pots and starting the mesocosm experiment. Ten PVC pots (n = 10) were used per treatment, with five seedlings transplanted into each pot. The sediment in the PVC pots containing treatments *H- V+* and *H- V-* was defaunated by freezing the pots at -20 °C for 48 h (Blackburn & Orth, 2013; Zhu et al., 2016). The PVC pots containing treatments *H- V+* and *H+ V+* contained *Vaucheria* algae that were collected at Ketenisse. All PVC pots were randomly distributed and equally spread over one mesocosm in a climate room kept at 18 °C. Wire netting (0.5 mm square mesh) was wrapped around the PVC pots to prevent the exchange of macrobenthos between the pots. The pots were inundated 2 times for 2 h with brackish water (5 PSU created from 32 PSU filtered Oosterschelde water and fresh tap water) per day with one simulated tidal cycle using artificial light and one in dark. A 14-hour day, and 10-hour night cycle was implemented with on average 250 µmol photons m^{-2} s^{-1} illuminated with fluorescent tubes above the upper tank (van Belzen, 2018; van de Vijsel et al., 2021). Seedling survival was monitored every two days after the first week until the end of the experiment (after 16 days) by counting the number of seedlings. The feeding behavior of *Hediste* on *Vaucheria* was monitored by taking pictures of the PVC pots containing both species (*H+ V+*) during the completion of the experiment. An estimation of the *Vaucheria* cover was made by calculating the Green Excess Index (GEI), a widely used index to distinguish vegetation from soil (Woebbecke et al., 1995), using the following formula:

$$GEI = 2 * G - R - B$$

where B, G, and R represent the images' blue, green, and red bands.

3.3.5 Statistical analysis

Before every analysis, we conducted Shapiro–Wilk tests to check for normality of the residuals and Levene's tests to check the homogeneity of variances. All analyses were performed in R version 4.2.2 (R Core Team, 2022), applying a significance level of $\alpha = 0.05$.

T1 - Field experiment 1

A survival analysis was performed to compare the daily seedling loss rates between the two treatments (control vs defaunated plots) across different sediment elevation zones (i.e. equivalent to different tidal inundation duration). This analysis was based on the principles of maximum likelihood estimation (Miller Jr., 2011; Schotanus et al., 2020). The seedling loss was assumed to follow an exponential decay model, where the loss rate ε is calculated using the following formula:

$$\varepsilon = \frac{n - c}{n * \bar{a}}$$

where n represents the total number of seedlings transplanted per plot at the start of the experiment, c is the number of seedlings that survived by the end of the experiment, and $\bar{a}$ is the average time each seedling was observed in the plot. This formulation accounts for censored observations, i.e. seedlings that survived until the end of the experiment. A two-way ANOVA was conducted on log-transformed loss rates to analyze the effect of macrobenthos (control vs defaunation) and inundation time (~low, middle and high elevation), followed by a Tukey HSD post-hoc test.

T2.1 - Field monitoring survey 1

A generalized linear model (GLM) of the quasi-poisson family was constructed to assess the effect of locations across a tidal marsh (bare mud away from creeks vs bare mud on creek edge vs *Vaucheria* on creek edge) on *Aster* seedling density using a Chi-squared test.

T2.2 - Field experiment 2

A one-way ANOVA was used to evaluate the role of *Vaucheria* - *Hediste* interactions on the survival probability of *Aster* seedlings.

T3 - Field monitoring survey 2

A GLM of the quasi-poisson family was fitted to assess the effect of different locations (*Vaucheria* patches and bare mud) on *Hediste* density using a Chi-squared test. Afterwards, pairwise comparisons were made.

T4 - Mesocosm experiment

Another binomial regression was fitted to determine the effect of four treatments (in which the presence of *Hediste* and *Vaucheria* was manipulated) on the survival probability of *Aster* seedlings using a Chi-squared test. This was followed by pairwise comparisons with Bonferroni correction.

Further, a paired t-test was carried out to compare *Vaucheria* algae cover at the start and the end of the mesocosm experiment in the replicates containing both *Hediste* and *Vaucheria* algae.

3.4 Results

3.4.1 Top-down control by *Hediste* hampers *Aster* establishment

Transplantation experiment 1 (Table 3.1 - T1) revealed that *Hediste diversicolor* exerts strong top-down control on *Aster tripolium* seedlings establishment. Seedling loss rates were consistently higher in control plots containing macrobenthos compared to defaunated plots across all elevations (Fig. 3.2). Loss rates also declined with decreasing inundation duration, with lowest losses observed at high elevation in defaunated plots. Both macrobenthos treatment ($F_{1, 24} = 29.19$, $p < 0.001$) and inundation duration ($F_{2, 24} = 31.59$, $p < 0.001$) significantly affected seedling loss rate, while no significant interaction was found ($F_{2, 24} = 0.65$, $p = 0.53$), indicating that the effect of defaunation was consistent across elevation levels. A Tukey HSD post-hoc test further confirmed that loss rates were significantly lower in defaunated plots compared to control plots ($p < 0.001$).

3.4.2 *Vaucheria* improves the establishment chances of *Aster* seedlings

The first field survey (Table 3.1 - T2.1) revealed that presence of *Aster* seedlings was significantly higher within *Vaucheria* patches as compared to outside *Vaucheria* patches. Seedling densities were highest in *Vaucheria* mats along creek edges, while considerably fewer seedlings were found in bare mud both near and away from creeks (Fig. 3.3a). Significant differences were found between the locations (likelihood-ratio χ^2 (2) = 31.77, $p < 0.001$). Pairwise comparisons showed that seedling densities were higher in *Vaucheria* patches on creek edges compared to seedling densities in bare mud away from creeks ($W = 85$, $p < 0.001$) and bare mud

along creek edges (W = 119, p = 0.015). Bare mud along creeks, however, did not significantly support more seedlings than bare mud further away (W = 242, p = 0.07).

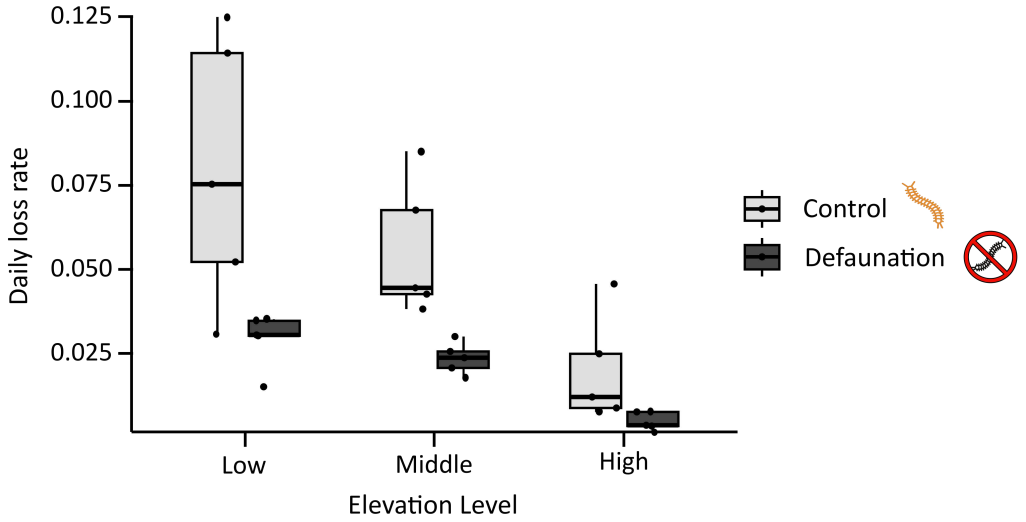


Figure 3.2: Overview of daily loss rates found in the *Aster* transplantation experiment in Paardenschor. The graph depicts the findings for three elevation levels and two treatments (n = 5 per combination): control (without defaunation, in light gray) and defaunation (in dark gray). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range.

3.4.3 *Vaucheria* improves the survival chances of *Aster* seedlings

Transplantation experiment 2 (Table 3.1 - T2.2) further indicated improved seedling survival in *Vaucheria* patches compared to bare mud (Fig. 3.3b). The seedlings within *Vaucheria* patches showed a significant survival advantage in contrast to the seedlings in bare mud ($F_{1,10} = 6.35$, $p = 0.03$).

3.4.4 *Vaucheria* and *Hediste* occur in mutually-exclusive environments

The results from the **second monitoring survey** (Table 3.1 - T3) showed a clear difference between *Hediste* densities in *Vaucheria* patches versus bare mud as *Vaucheria* algae seem to repress *Hediste* densities (Fig. 3.4). Statistical analysis confirmed this as significant differences were found between the *Hediste* densities in bare mud vs in *Vaucheria* patches (likelihood-ratio χ^2 (1) = 74.1, $p < 0.001$).

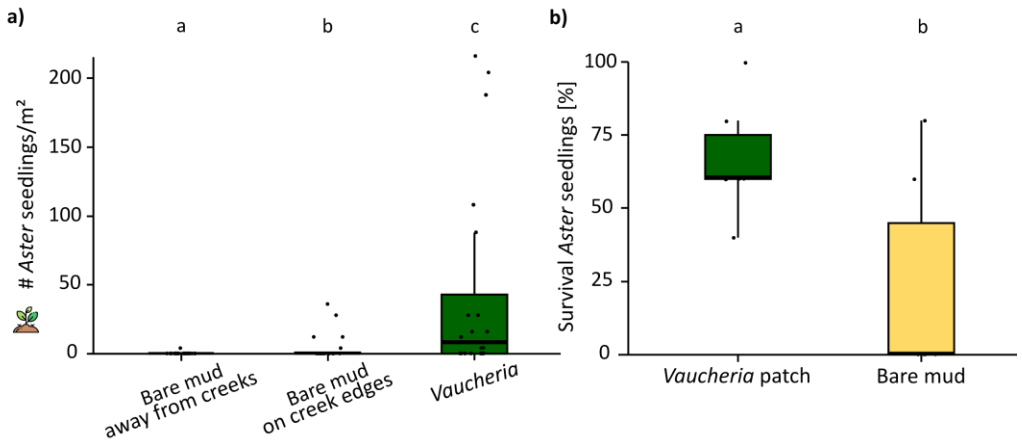


Figure 3.3: **a)** Comparison of distributions of the observed number of *Aster* seedlings per square meter in different locations in the Paardenschor: bare mud away from creeks (n = 20), bare mud on creek edges (n = 20) and *Vaucheria* patches on creek edges (n = 20). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference. **b)** The distribution of *Aster* seedling survival percentages after transplantation in *Vaucheria* patches (dark green) and on bare mud (light yellow) in Paardenschor. Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

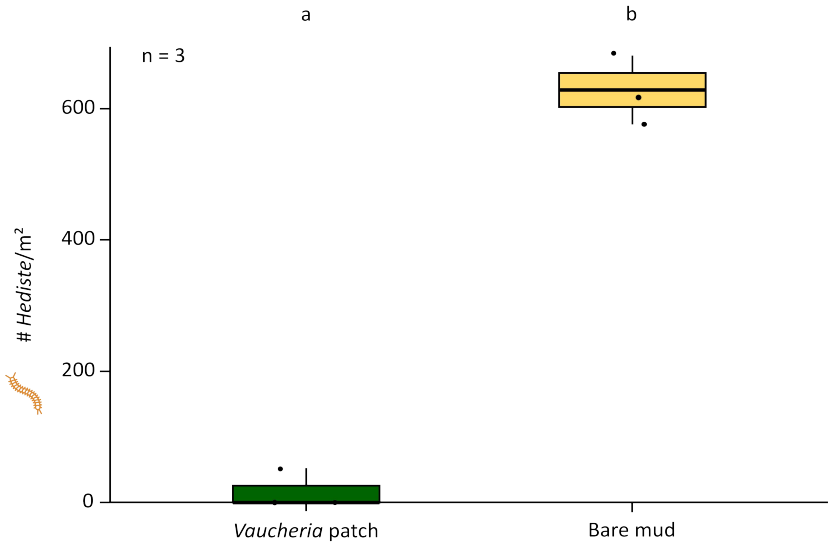


Figure 3.4: Overview of *Hediste* densities per square meter found in bare mud (light yellow) versus *Vaucheria* patches (dark green) during a sampling survey conducted in Ketenisse in September 2016 (n = 3). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

3.4.5 *Vaucheria* offers a refuge from top-down control by *Hediste*

A full-factorial **mesocosm experiment** (Table 3.1 - T4) was conducted to disentangle the biotic interactions between *Hediste diversicolor*, *Vaucheria* sp. algae, and *Aster tripolium* seedlings. Compared to the control treatment (*H- V-*), the presence of *Vaucheria* algae (*H- V+*) negatively affected seedling survival, causing a 25% decrease in survival percentage (Fig. 3.5a). The sole presence of *Hediste* (*H+ V-*), on the other hand, led to almost complete mortality of the *Aster* seedlings. However, seedling survival increased substantially once both *Hediste* and *Vaucheria* were present (*H+ V+*). Overall, the mesocosm results showed that *Vaucheria* algae counteracted the negative effect of *Hediste* on seedling survival. Direct observations indicated that *Hediste* grazed on both *Vaucheria* algae and *Aster* seedlings, frequently dragging the algae or seedlings into their burrows and biting off leaf fragments (documented via photos and timelapse – see public data repository). This grazing activity was supported by the reduction in *Vaucheria* algal cover in the *H+ V+* treatment as shown by Green Excess Index measurements (Fig. 3.5b).

A binomial model confirmed that treatment combinations had a significant effect on seedling survival (likelihood-ratio $\chi^2(3) = 130.99$, $p < 0.001$). Pairwise comparisons showed that the presence of either *Hediste* (*H+ V-*: W = 100, $p < 0.001$) or *Vaucheria* (*H- V+*: W = 95, $p < 0.001$) led to a significant decrease in seedling survival compared to the control treatment (*H- V-*). Seedling survival significantly improved in the combination of both *Hediste* and *Vaucheria* (*H+ V+*) compared to the *H+ V-* treatment (W = 0.5, $p < 0.001$). However, no significant difference was found between the *H+ V+* and *H- V+* treatments (W = 44.5, p = 0.676), suggesting that *Vaucheria* can offset the negative impact of *Hediste* on seedling establishment. Furthermore, *Hediste*'s grazing activity caused a significant reduction in *Vaucheria* algal cover at the end of the experiment compared to the start (paired t-test: t(9) = 3.29, p = 0.009).

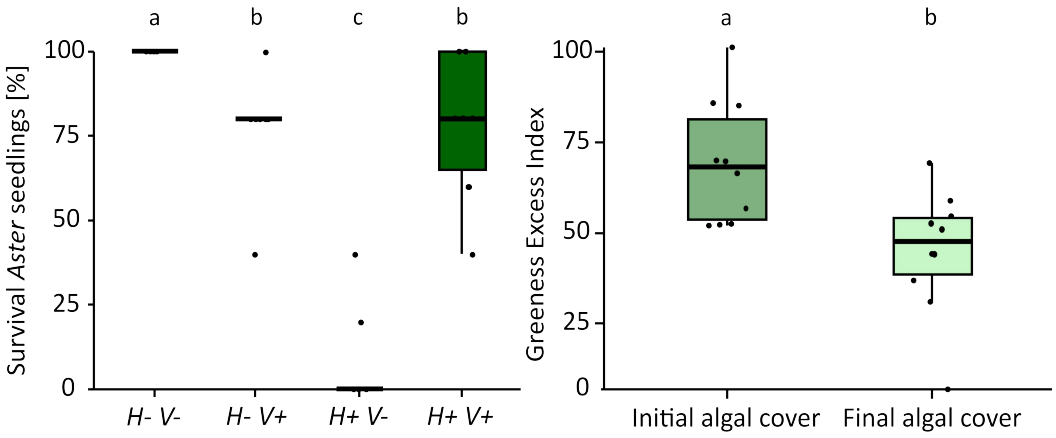


Figure 3.5: **a)** The distribution of *Aste*r seedling survival percentages at the end of the mesocosm experiment. Four treatments (n = 10) were used: (1) in absence of *Hediste* and *Vaucheria* algae (*H- V-*), (2) in absence of *Hediste* and presence of *Vaucheria* algae (*H- V+*) , (3) in presence of *Hediste* and absence of *Vaucheria* algae (*H+ V-*), and finally (4) in presence of both *Hediste* and *Vaucheria* algae (*H+ V+*). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference. **b)** Comparison between the *Vaucheria* algal cover, indicated by the Green Excess Index, found at the start of the mesocosm experiment versus the end of the mesocosm experiment for the *H+ V+* treatment. Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

3.5 Discussion

Understanding the mechanisms that drive tidal marsh development is crucial for the effective restoration of these ecosystems. While previous studies have examined bilateral interactions between zoobenthos, algae, and pioneer plants, the collective interactions among all three species, and their combined influence on early marsh development, remained poorly understood. Using a combination of controlled experiments and field monitoring, we demonstrate (Fig. 3.6) that the effects of zoobenthos and algae on pioneer plant establishment are context-dependent.

In isolation, both *Hediste* and *Vaucheria* negatively affect *Aster* seedling survival: *Hediste* strongly suppresses seedling establishment through grazing, while dense *Vaucheria* mats exert a weaker negative effect, likely through competition for nutrients and physical interference. However, when *Hediste* and *Vaucheria* co-occur, seedling survival increases markedly, as the presence of *Vaucheria* alleviates the strong grazing pressure exerted by *Hediste*. These algae enhance plant survival and establishment by (1) suppressing macrobenthos densities and (2) weakening top-down control exerted by *Hediste* (Fig. 3.6). The mitigating effects of *Vaucheria* most likely arise through both (i) providing *Vaucheria* as a preferred alternative food source for *Hediste* and (ii) physically restricting burrowing activity of *Hediste* via the formation of dense algal mats, as discussed below.

3.5.1 Polychaete predation negatively affects vegetation establishment

Our field and mesocosm experiments illustrate how *Hediste*'s seedling predation negatively affects *Aster tripolium* establishment by grasping (fragments of) the plant's leaves and dragging them in their burrow (Fig. 3.2 & 3.5a; photos in public data repository). Similar results were reported for the seagrass *Zostera noltii* and the salt marsh pioneer *Salicornia europaea* (Hughes & Paramor, 2004, Paramor & Hughes, 2004, 2005). In addition to seedling predation, polychaetes were found to hinder the establishment of *Spartina anglica* by collecting and burying seeds, then feeding on them once they sprout (Zhu et al., 2016). These findings highlight that

when *Hediste* densities become too high, which is typical in early successional stages of tidal marsh development (Fig. S3.1), they can significantly impede the colonization of bare tidal flats by tidal marsh plants.

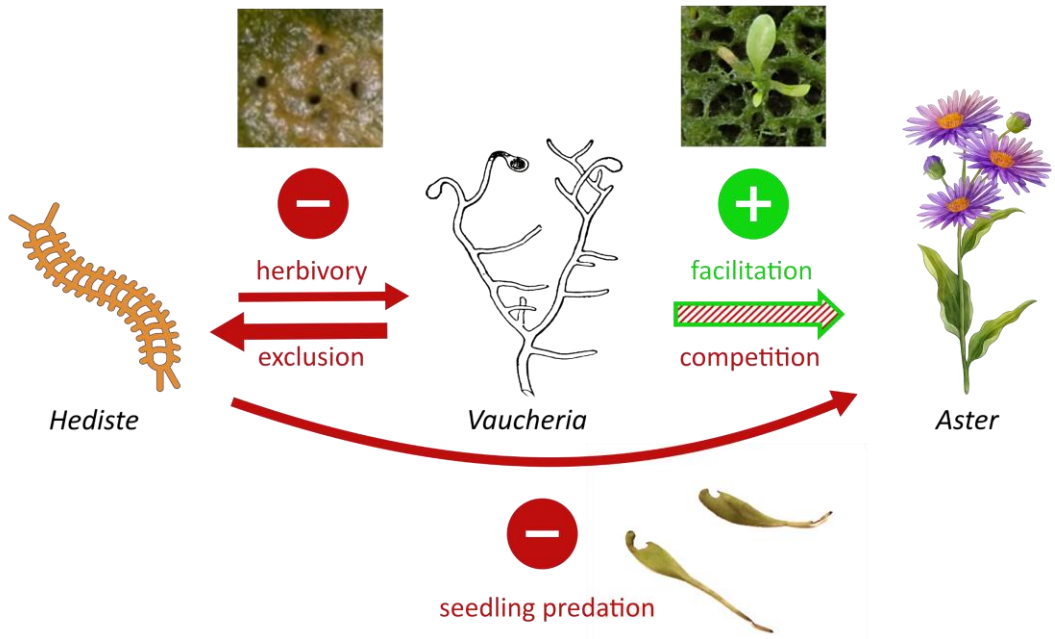


Figure 3.6: Conceptual diagram illustrating the biotic interactions among macrobenthos (*Hediste*), benthic algae (*Vaucheria*) and pioneer plants (*Aster*) driving the early establishment of brackish tidal marshes. *Hediste* negatively affects both *Vaucheria* algae and *Aster* seedling establishment by feeding on the algae and by disturbing or consuming seedlings (e.g. biting and dragging parts of the algal mats and seedlings into burrows). In the absence of *Hediste*, dense *Vaucheria* mats slightly reduce *Aster* seedling survival, potentially due to competition for nutrients or by physically hindering the seedlings. However, *Vaucheria* mitigates the negative effects of *Hediste* on *Aster* by 1) physically obstructing *Hediste*'s feeding and burrowing through the formation of dense algal mats, and 2) serving as a preferred alternative food source for *Hediste* due to its higher digestibility compared to *Aster*. Consequently, despite a direct competitive effect, *Vaucheria* has a net positive impact on *Aster*, facilitating its establishment.

3.5.2 Filamentous algae facilitate vegetation establishment in tidal marshes

Our results provide the first experimental evidence that *Vaucheria* algae can counteract the top-down effect of *Hediste* on vegetation establishment in brackish tidal marshes (Fig. 3.3, 3.4 & 3.5). This could be attributed to two potential mechanisms.

1) *Vaucheria* may offer an alternative, more easily digestible food source for the polychaetes as compared to *Aster.* This hypothesis may be supported by the fact that *Vaucheria* algae lack lignin and have lower cellulose concentrations making them more easily digestible for benthic organisms such as *Hediste* (Olivier et al., 1997). This hypothesis is supported by studies from Engelsen & Pihl (2008) and Nordström et al. (2006) who demonstrate that *Hediste* can contribute to a loss in macro-algal biomass, prevent initial algal growth by grazing on the propagules and partly reduce full-grown green macro-algal mats (e.g. *Ulva* spp.).

2) A second potential explanation may be that there is a mutual exclusion between *Vaucheria* and *Hediste*, as the dense algal filamentous mats could hinder the benthos mobility in and on top of the sediment bed. Evidence from macrobenthos survey 2 in this study suggests that *Vaucheria* algae can exclude *Hediste* (Fig. 3.4). Such exclusion likely results from restricted deposit feeding by *Hediste*, as the dense algal filaments form a barrier between the *Hediste*'s burrows and the sediment surface. This is in line with how rooted vegetation also hinders endobenthic communities (Bouma et al., 2009; Eklöf et al., 2015; Van Wesenbeeck et al., 2007). This barrier not only hinders *Hediste*'s access to seedlings but may also create prolonged anoxic conditions, visible as black sediments in our observations, that are detrimental to the polychaetes. Previous studies have shown that macroalgal mats, such as those formed by *Enteromorpha* and *Ulva*, can negatively impact mudflat invertebrate populations (Raffaelli, 2000; Raffaelli et al., 1999). Likewise, Paramor & Hughes (2007) demonstrated in a field experiment that porous biodegradable mats placed on the sediment surface excluded *Hediste,* comparable to our defaunation treatment, which consequently stimulated the establishment of algae and seedlings. However, we need to keep in mind that the defaunation treatment may have indirectly affected seedling survival results by creating initial anoxic conditions (visible as black sediment) and by changing sediment properties such as mud content. Previous studies have shown that defaunation can lead to an increase in sediment shear strength (i.e. erosion resistance) compared to control plots. This could be attributed to the lack of biodestabilizing organisms such as *Hediste* (Montserrat et al., 2008; Van Colen et al., 2008).

Based on our results we hypothesize that *Hediste* may graze on *Vaucheria* propagules and thin algal mats (i.e. low algal densities) creating a bare tidal flat, dominated by macrobenthos. However, due to the fast growth rate of *Vaucheria*, this grazing does not result in top-down control, allowing a *Vaucheria* mat to develop. Once a thick *Vaucheria* mat forms, the polychaetes avoid grazing as the dense algae impede their feeding strategy, which facilitates the transition to a vegetated state. Similar alternative stable state behavior has been described between seagrass meadows (*Zostera noltii*) and *Hediste* (Hughes et al., 2000) or the bioturbating lugworm *Arenicola marina* (Suykerbuyk et al., 2012). The potential role of antagonistic interactions between benthic algae and benthic organisms in guiding alternative

stable states shifting between bare tidal flats and vegetated marshes emphasizes the importance of biotic interactions in the establishment of intertidal vegetation as part of the tidal marsh restoration process.

In addition to direct biotic interactions, benthic algae such as *Vaucheria* are known for their bio-geomorphological interactions such as stabilizing sediments hence creating microtopographic features (Gallagher & Humm, 1981; van de Vijsel et al., 2020, 2021; Wilcox, 2012). *Vaucheria* algae, typically forming a dense network of filaments, reduce sediment erosion risk and enhance sediment stability, which are both essential for vegetation establishment (Balke et al., 2011; Cao et al., 2018). Additionally, the formation of microtopographic structures, such as elevated hummocks, provides favorable conditions for seedling establishment by improving drainage and oxygen availability (Cao et al., 2021; Fivash et al., 2019, 2021).

This dual function of *Vaucheria* as a physical sediment stabilizer and a biological buffer (i.e. mitigating herbivory) underlines its critical role in creating and widening "Windows of Opportunity" for pioneer vegetation establishment (Balke et al., 2014; van de Vijsel et al., 2021) during the early stages of tidal marsh restoration. Once mutualistic or facilitative interactions begin to align in the same direction, they can reinforce each other and give rise to positive feedbacks that amplify early differences in species composition or environmental conditions. Similarly, once the biotic interactions in a tidal marsh (for instance, between *Vaucheria*, *Hediste*, and *Aster*) begin to reinforce each other in favor of vegetation establishment (e.g. algae suppressing *Hediste*, thereby facilitating *Aster*), the system is more likely to continue evolving in that direction. This reinforcing feedback (Fig. 3.6) may underlie the emergence of stable vegetated patches within an otherwise bare tidal flat.

3.5.3 Broader ecological implications of biotic interactions

Overall, our findings underscore the complexity and significance of biotic interactions in ecosystem development, particularly during the early stages of (brackish) tidal marsh establishment. While abiotic factors such as hydrodynamic forces and sediment dynamics are often emphasized in marsh development, our study suggests that biotic interactions, including antagonistic (e.g. *Hediste* grazing on seedlings) and facilitative interactions (e.g. *Vaucheria* reducing *Hediste* densities), also significantly contribute to the resilience of emerging vegetated states by reinforcing positive feedbacks that support vegetation establishment (Fig. 3.6). Recognizing the effect of these complementary and reinforcing interactions on the resilience of bare or vegetated states, similar to patterns observed in other systems, is essential for improving tidal marsh restoration efforts.

3.5.4 Implications for tidal marsh management and restoration

The findings of this study provide insights for enhancing the success of tidal marsh restoration projects. Managing polychaete populations, particularly *Hediste diversicolor*, by placing porous biodegradable mats emerges as a strategy to reduce biotic disturbance (e.g. grazing) during the initial phases of vegetation establishment (Paramor & Hughes, 2007). Our findings show new evidence that promoting *Vaucheria* growth could serve as a practical intervention to enhance the success of marsh vegetation establishment in tidal marsh restoration projects. As *Vaucheria* patches are observed to concentrate along the edges of small creeks draining from intertidal flats (Cao et al., 2021; Fivash et al., 2019; van de Vijsel et al., 2023), restoration practitioners might consider engineering approaches, such as digging small channels, creating microtopography and/or making use of the pre-existing topographic heterogeneity like hummocks to promote drainage, hence facilitating establishment of algae and pioneer marsh plants (Fivash et al., 2019, 2021; Lawrence et al., 2018). These insights highlight several ways to make use of "Windows of Opportunity": (1) by mitigating environmental extremes, (2) by extending periods of favorable conditions, and/or (3) by strengthening biotic feedbacks to accelerate the development of the desired state (van Belzen et al., 2022). We recommend that future research explores (1) applying these findings in the context of tidal restoration projects, (2) investigating the effects of these measures, and (3) investigating the effect of climate change or pollution on "Windows of Opportunity". For instance, the observed increase in benthic biomass in the Scheldt and other estuaries following the ban on TBT (Herman, 2022; Rees et al., 2001; Smith et al., 2007) suggests that benthos may play an increasingly dominant role in species interactions, underscoring the need to better understand how environmental policy, pollution, climate change, or trophic rewilding might shift the balance of bottom-up and top-down controls during early marsh development.

3.6 Author contributions

All authors conceptualized the study. JvB conducted the experiments and monitoring surveys. OG, WM and BV collected the data from Lillo Potpolder. SH analyzed the data and wrote the original draft of the manuscript. The manuscript was reviewed and edited by JvB, GSF, KS, JvdK, TJB and ST. TJB and ST supervised the process.

3.7 Acknowledgments

We cordially thank Aniek van den Berg for assisting with experimental execution and data collection. This work was funded by the Fonds Wetenschappelijk Onderzoek (grant no. G031620N) and the European Commission through FP7 ENV2009-1, Contract 244104-THESEUS. JvB was further supported by the VNSC project "Vegetation modelling HPP" (contract 3109 1805) and TJB was supported by the NWO funded BE-SAFE project grant 850.13.011.

3.8 References

Balke, T., Bouma, T., Horstman, E., Webb, E., Erftemeijer, P., & Herman, P. (2011). Windows of opportunity: Thresholds to mangrove seedling establishment on tidal flats. *Marine Ecology Progress Series*, *440*, 1–9. https://doi.org/10.3354/meps09364

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: Identifying Windows of Opportunity for recovery. *Journal of Ecology*, *102*(3), 700–708. https://doi.org/10.1111/1365-2745.12241

Balke, T., Stock, M., Jensen, K., Bouma, T. J., & Kleyer, M. (2016). A global analysis of the seaward salt marsh extent: The importance of tidal range. *Water Resources Research*, *52*(5), 3775–3786. https://doi.org/10.1002/2015WR018318

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Blackburn, N., & Orth, R. (2013). Seed burial in eelgrass Zostera marina: The role of infauna. *Marine Ecology Progress Series*, *474*, 135–145. https://doi.org/10.3354/meps10103

Bouma, T. J., Olenin, S., Reise, K., & Ysebaert, T. (2009). Ecosystem engineering and biodiversity in coastal sediments: Posing hypotheses. *Helgoland Marine Research*, *63*(1), 95–106. https://doi.org/10.1007/s10152-009-0146-y

Callaghan, D. P., Bouma, T. J., Klaassen, P., Van Der Wal, D., Stive, M. J. F., & Herman, P. M. J. (2010). Hydrodynamic forcing on salt-marsh development: Distinguishing the relative importance of waves and tidal flows. *Estuarine, Coastal and Shelf Science*, *89*(1), 73–88. https://doi.org/10.1016/j.ecss.2010.05.013

Cao, H., Zhu, Z., Balke, T., Zhang, L., & Bouma, T. J. (2018). Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration: Sediment dynamics affect seedling establishment. *Limnology and Oceanography*, *63*(2), 647–659. https://doi.org/10.1002/lno.10657

Cao, H., Zhu, Z., Belzen, J., Gourgue, O., Koppel, J., Temmerman, O. S., Herman, P. M. J., Zhang, L., Yuan, L., & Bouma, T. J. (2021). Salt marsh establishment in poorly consolidated muddy systems: Effects of surface drainage, elevation, and plant age. *Ecosphere*, *12*(9). https://doi.org/10.1002/ecs2.3755

Eklöf, J. S., Donadi, S., Van Der Heide, T., Van Der Zee, E. M., & Eriksson, B. K. (2015). Effects of antagonistic ecosystem engineers on macrofauna communities in a patchy, intertidal mudflat landscape. *Journal of Sea Research*, *97*, 56–65. https://doi.org/10.1016/j.seares.2014.12.003

Engelsen, A., & Pihl, L. (2008). Grazing effects by Nereis diversicolor on development and growth of green algal mats. *Journal of Sea Research*, *59*(4), 228–236. https://doi.org/10.1016/j.seares.2008.02.001

Erfanzadeh, R., Garbutt, A., Pétillon, J., Maelfait, J.-P., & Hoffmann, M. (2010a). Factors affecting the success of early salt-marsh colonizers: Seed availability rather than site suitability and dispersal traits. *Plant Ecology*, *206*(2), 335–347. https://doi.org/10.1007/s11258-009-9646-8

Erfanzadeh, R., Hendrickx, F., Maelfait, J.-P., &

Hoffmann, M. (2010b). The effect of successional stage and salinity on the vertical distribution of seeds in salt marsh soils. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *205*(7), 442–448. https://doi.org/10.1016/j.flora.2009.12.010

Fivash, G. S., Temmink, R. J. M., D'Angelo, M., Dalen, J., Lengkeek, W., Didderen, K., Ballio, F., Heide, T., & Bouma, T. J. (2021). Restoration of biogeomorphic systems by creating windows of opportunity to support natural establishment processes. *Ecological Applications*, *31*(5). https://doi.org/10.1002/eap.2333

Fivash, G. S., van Belzen, J., Temmink, R. J. M., Didderen, K., Lengkeek, W., Heide, T. V. D., & Bouma, T. J. (2019). Elevated micro-topography boosts growth rates in Salicornia procumbens by amplifying a tidally driven oxygen pump: Implications for natural recruitment and restoration. *Annals of Botany*, *125*, 353–364. https://doi.org/10.1093/aob/mcz137

Gallagher, S. B., & Humm, H. J. (1981). Vaucheria (Xanthophyceae, Vaucheriaceae) of the central Florida gulf coast. *Bulletin of Marine Science*, *31*(1), 184-19.

Gedan, K. B., Silliman, B. R., & Bertness, M. D. (2009). Centuries of Human-Driven Change in Salt Marsh Ecosystems. *Annual Review of Marine Science*, *1*(1), 117–141. https://doi.org/10.1146/annurev.marine.010908.163930

Herman, P. (2022, November 10). *De Schelde, op weg naar een mooie toekomst?* Deltares.

Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Centre for Ecology and Hydrology. http://www.ceh.ac.uk/products/publications/plantatt-attributesofbritishandirishplantsstatussizelifehistorygeographyandhabitats.html

Hu, Z., Borsje, B. W., van Belzen, J., Willemsen, P. W. J. M., Wang, H., Peng, Y., Yuan, L., De Dominicis, M., Wolf, J., Temmerman, S., & Bouma, T. J. (2021). Mechanistic Modeling of Marsh Seedling Establishment Provides a Positive Outlook for Coastal Wetland Restoration Under Global Climate Change. *Geophysical Research Letters*, *48*(22). https://doi.org/10.1029/2021GL095596

Hu, Z., van Belzen, J., van der Wal, D., Balke, T., Wang, Z. B., Stive, M., & Bouma, T. J. (2015). Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: The importance of temporal and spatial variability in hydrodynamic forcing. *Journal of Geophysical Research: Biogeosciences*, *120*(7), 1450–1469. https://doi.org/10.1002/2014JG002870

Hughes, R. (1999). Saltmarsh erosion and management of saltmarsh restoration; the effects of infaunal invertebrates. *Aquatic Conservation-Marine and Freshwater Ecosystems*, *9*, 83–95. https://doi.org/10.1002/(SICI)1099-0755(199901/02)9:1<83::AID-AQC323>3.0.CO;2-9

Hughes, R. G., Lloyd, D., Ball, L., & Emson, D. (2000). The effects of the polychaete Nereis diversicolor on the distribution and transplanting success of Zostera noltii. *Helgoland Marine Research*, *54*(2–3), 129–136. https://doi.org/10.1007/s10152005011

Hughes, R. G., & Paramor, O. A. L. (2004). On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, *41*(3), 440–448. https://doi.org/10.1111/j.0021-8901.2004.00915.x

Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beeftink, W. G., Markusse, M. M., & Munck, W. D. (1995). Seed Dispersal of Halophytes in Tidal Salt Marshes. *The Journal of Ecology*, *83*(4), 559. https://doi.org/10.2307/2261624

Huyzentruyt, M., Belliard, J.-P., Saintilan, N., & Temmerman, S. (2024). Identifying drivers of global spatial variability in organic carbon sequestration in tidal marsh sediments. *Science of The Total Environment*, *957*, 177746. https://doi.org/10.1016/j.scitotenv.2024.177746

Lawrence, P. J., Smith, G. R., Sullivan, M. J. P., & Mossman, H. L. (2018). Restored saltmarshes lack the topographic diversity found in natural habitat. *Ecological Engineering*, *115*, 58–66. https://doi.org/10.1016/j.ecoleng.2018.02.007

Miller Jr., R. G. (2011). *Survival analysis* (Vol. 66). John Wiley and Sons.

Montserrat, F., Van Colen, C., Degraer, S., Ysebaert, T., & Herman, P. (2008). Benthic community-mediated sediment dynamics. *Marine Ecology Progress Series*, *372*, 43–59. https://doi.org/10.3354/meps07769

Nielsen, A., Eriksen, N., Iversen, J., & Riisgård, H. (1995). Feeding, growth and respiration in the polychaetes Nereis diversicolor (facultative filter-feeder) and N. virens (omnivorous)-a comparative study. *Marine Ecology Progress Series*, *125*, 149–158. https://doi.org/10.3354/meps125149

Nordström, M., Bonsdorff, E., & Salovius, S. (2006). The impact of infauna (Nereis diversicolor and Saduria entomon) on the redistribution and biomass of macroalgae on marine soft bottoms. *Journal of Experimental Marine Biology and Ecology*, *333*(1), 58–70. https://doi.org/10.1016/j.jembe.2005.11.024

Olivier, M., Desrosiers, G., Caron, A., Retière, C., & Caillou, A. (1997). Juvenile growth of Nereis diversicolor (O.F. Müller) feeding on a range of marine vascular and macroalgal plant sources under experimental conditions. *Journal of Experimental Marine Biology and Ecology*, *208*(1–2), 1–12. https://doi.org/10.1016/S0022-0981(96)02654-8

Paramor, O. A. L., & Hughes, R. G. (2004). The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on loss of saltmarsh in south-east England. *Journal of Applied Ecology*, *41*(3), 449–463. https://doi.org/10.1111/j.0021-8901.2004.00916.x

Paramor, O. A. L., & Hughes, R. G. (2005). Effects of the invertebrate infauna on early saltmarsh plant colonisation of managed realignment areas in south-east England. *Marine Ecology Progress Series*, *303*, 61–71. https://doi.org/10.3354/meps303061

Paramor, O. A. L., & Hughes, R. G. (2007). Restriction of Spartina anglica (C.E. Hubbard) marsh development by the infaunal polychaete Nereis diversicolor (O.F. Müller). *Estuarine, Coastal and Shelf Science*, *71*(1–2), 202–209. https://doi.org/10.1016/j.ecss.2006.07.012

Raffaelli, D. (2000). Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. *Helgoland Marine Research*, *54*(2–3), 71–79. https://doi.org/10.1007/s10152005004

Raffaelli, D., Balls, P., Way, S., Patterson, I. J., Hohmann, S., & Corp, N. (1999). Major long-term changes in the ecology of the Ythan estuary, Aberdeenshire, Scotland; how important are physical factors? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *9*(2), 219–

236. https://doi.org/10.1002/(SICI)1099-0755(199903/04)9:2<219::AID-AQC334>3.0.CO;2-P

Rees, H. L., Waldock, R., Matthiessen, P., & Pendle, M. A. (2001). Improvements in the Epifauna of the Crouch Estuary (United Kingdom) Following a Decline in TBT Concentrations. *Marine Pollution Bulletin*, *42*(2), 137–144. https://doi.org/10.1016/S0025-326X(00)00119-3

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91–95. https://doi.org/10.1038/s41586-019-0951-7

Sanderson, E. W., Foin, T. C., & Ustin, S. L. (2001). A simple empirical model of salt marsh plant spatial distributions with respect to a tidal channel network. *Ecological Modelling*, *139*(2–3), 293–307. https://doi.org/10.1016/S0304-3800(01)00253-8

Sanderson, E. W., Ustin, S. L., & Foin, T. C. (2000). The influence of tidal channels on the distribution of salt marsh plant species in Petaluma Marsh, CA, USA. *Plant Ecology*, *146*(1), 29–41. https://doi.org/10.1023/A:1009882110988

Scaps, P. (2002). A review of the biology, ecology and potential use of the common ragworm Hediste diversicolor (O.F. Müller) (Annelida: Polychaeta). *Hydrobiologia*, *470*(1/3), 203–218. https://doi.org/10.1023/A:1015681605656

Schotanus, J., Walles, B., Capelle, J. J., van Belzen, J., van de Koppel, J., & Bouma, T. J. (2020). Promoting self-facilitating feedback processes in coastal ecosystem engineers to increase restoration success: Testing engineering measures. *Journal of Applied Ecology*, *57*(10), 1958–1968. https://doi.org/10.1111/1365-2664.13709

Schoutens, K., Heuner, M., Minden, V., Schulte Ostermann, T., Silinski, A., Belliard, J., & Temmerman, S. (2019). How effective are tidal marshes as nature-based shoreline protection throughout seasons? *Limnology and Oceanography*, *64*(4), 1750–1762. https://doi.org/10.1002/lno.11149

Schoutens, K., Reents, S., Nolte, S., Evans, B., Paul, M., Kudella, M., Bouma, T., Möller, I., & Temmerman, S. (2021). Survival of the thickest? Impacts of extreme wave-forcing on marsh seedlings are mediated by species morphology. *Limnology and Oceanography*, *66*(7), 2936–2951. https://doi.org/10.1002/lno.11850

Smith, D., Hughes, R., & Cox, E. (1996). Predation of epipelic diatoms by the amphipod Corophium volutator and the polychaete Nereis diversicolor. *Marine Ecology Progress Series*, *145*, 53–61. https://doi.org/10.3354/meps145053

Smith, R., Bolam, S. G., Rees, H. L., & Mason, C. (2007). Macrofaunal recovery following TBT ban: Long-term recovery of subtidal macrofaunal communities in relation to declining levels of TBT contamination. *Environmental Monitoring and Assessment*, *136*(1–3), 245–256. https://doi.org/10.1007/s10661-007-9680-8

Suykerbuyk, W., Bouma, T. J., Van Der Heide, T., Faust, C., Govers, L. L., Giesen, W. B. J. T., De Jong, D. J., & Van Katwijk, M. M. (2012). Suppressing antagonistic bioengineering feedbacks doubles restoration success. *Ecological Applications*, *22*(4), 1224–1231.

https://doi.org/10.1890/11-1625.1

Temmerman, S., Horstman, E. M., Krauss, K. W., Mullarney, J. C., Pelckmans, I., & Schoutens, K. (2023). Marshes and Mangroves as Nature-Based Coastal Storm Buffers. *Annual Review of Marine Science*, *15*(1), 95–118. https://doi.org/10.1146/annurev-marine-040422-092951

van Belzen, J. (2018). Qualitative growth potential test for brackish Vaucheria species. *Protocol Exchange*. https://doi.org/10.1038/protex.2018.041

van Belzen, J., Fivash, G. S., Hu, Z., Bouma, T. J., & Herman, P. M. J. (2022). A probabilistic framework for windows of opportunity: The role of temporal variability in critical transitions. *Journal of The Royal Society Interface*, *19*(190), 20220041. https://doi.org/10.1098/rsif.2022.0041

van Belzen, J., van de Koppel, J., Kirwan, M. L., Van Der Wal, D., Herman, P. M. J., Dakos, V., Kéfi, S., Scheffer, M., Guntenspergen, G. R., & Bouma, T. J. (2017). Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. *Nature Communications*, *8*(1), 15811. https://doi.org/10.1038/ncomms15811

Van Colen, C., Montserrat, F., Vincx, M., Herman, P., Ysebaert, T., & Degraer, S. (2008). Macrobenthic recovery from hypoxia in an estuarine tidal mudflat. *Marine Ecology Progress Series*, *372*, 31–42. https://doi.org/10.3354/meps07640

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Borsje, B. W., Temmerman, S., Cornacchia, L., Gourgue, O., & van de Koppel, J. (2023). Vegetation controls on channel network complexity in coastal wetlands. *Nature Communications*, *14*(1), 7158. https://doi.org/10.1038/s41467-023-42731-3

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Cusseddu, V., Purkis, S. J., Rietkerk, M., & Koppel, J. (2020). Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. *Earth Surface Processes and Landforms*, *45*(5), 1141–1154. https://doi.org/10.1002/esp.4783

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., & van de Koppel, J. (2021). Algal-Induced Biogeomorphic Feedbacks Lay the Groundwork for Coastal Wetland Development. *Journal of Geophysical Research: Biogeosciences*, *126*(10). https://doi.org/10.1029/2021JG006515

Van den Bergh, E., Vandevoorde, B., Verbessem, I., Spanoghe, G., Lionard, M., Muylaert, K., Regge, N., Soors, J., Belder, W., Piesschaert, F., & Meire, P. (2005). *Tidal wetland restoration at Ketenisse polder (Schelde Estuary, Belgium): Developments in the first year*. 521–533.

Van den Neucker, T., Verbessem, I., Vandevoorde, B., Van Braeckel, A., Stevens, M., Spanoghe, G., Gyselings, R., Soors, J., De Regge, N., De Belder, W., & Van den Bergh, E. (2007). *Evaluatie van natuurontwikkelingsprojecten in het Schelde-estuarium.* Rapport van het Instituut voor Natuur-en Bosonderzoek. https://purews.inbo.be/ws/portalfiles/portal/5370095/VandenNeucker_etal_2007_EvaluatieNatuurontwikkelingsprojectenScheldeEstuarium.pdf

van Regteren, M., Colosimo, I., de Vries, P., van Puijenbroek, M. E. B., Freij, V. S., Baptist, M. J., & Elschot, K. (2019). Limited seed retention during winter inhibits vegetation establishment in spring, affecting lateral marsh expansion capacity. *Ecology and Evolution*, *9*(23), 13294–13308. https://doi.org/10.1002/ece3.5781

van Regteren, M., ten Boer, R., Meesters, E. H., &

de Groot, A. V. (2017). Biogeomorphic impact of oligochaetes (Annelida) on sediment properties and *Salicornia* spp. Seedling establishment. *Ecosphere*, *8*(7), e01872. https://doi.org/10.1002/ecs2.1872

Van Wesenbeeck, B. K., van de Koppel, J., Herman, P. M. J., Bakker, J. P., & Bouma, T. J. (2007). Biomechanical warfare in ecology; negative interactions between species by habitat modification. *Oikos*, *116*(5), 742–750. https://doi.org/10.1111/j.0030-1299.2007.15485.x

Vandevoorde, B., Gyselings, R., & Van den Bergh, E. (2011). *Short term vegetation development on restored brackish tidal marshes*. https://pureportal.inbo.be/en/publications/short-term-vegetation-development-on-restored-brackish-tidal-mars

Wang, C., & Temmerman, S. (2013). Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. *Journal of Geophysical Research: Earth Surface*, *118*(1), 229–240. https://doi.org/10.1029/2012JF002474

Widdows, J., Brinsley, M., & Pope, N. (2009). Effect of Nereis diversicolor density on the erodability of estuarine sediment. *Marine Ecology Progress Series*, *378*, 135–143. https://doi.org/10.3354/meps07864

Wilcox, M. (2012). Occurrence of the marine yellow-green algae *Vaucheria velutina* C. Agardh and *Vaucheria longicaulis* Hoppaugh (Xanthophyceae: Vaucheriaceae) in Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *46*(2), 285–290. https://doi.org/10.1080/00288330.2011.622444

Woebbecke, D. M., Meyer, G. E., Von Bargen, K., & Mortensen, D. A. (1995). Color Indices for Weed Identification Under Various Soil, Residue, and Lighting Conditions. *Transactions of the ASAE*, *38*(1), 259–269. https://doi.org/10.13031/2013.27838

Zhao, Q., Bai, J., Huang, L., Gu, B., Lu, Q., & Gao, Z. (2016). A review of methodologies and success indicators for coastal wetland restoration. *Ecological Indicators*, *60*, 442–452. https://doi.org/10.1016/j.ecolind.2015.07.003

Zhu, Z., van Belzen, J., Hong, T., Kunihiro, T., Ysebaert, T., Herman, P. M. J., & Bouma, T. J. (2016). Sprouting as a gardening strategy to obtain superior supplementary food: Evidence from a seed-caching marine worm. *Ecology*, *97*(12), 3278–3284. https://doi.org/10.1002/ecy.1613

Zhu, Z., van Belzen, J., Zhu, Q., van de Koppel, J., & Bouma, T. J. (2020). Vegetation recovery on neighboring tidal flats forms an Achilles' heel of saltmarsh resilience to sea level rise. *Limnology and Oceanography*, *65*(1), 51–62. https://doi.org/10.1002/lno.11249


© Ken Schoutens

4

Edges of opportunity: Tidal creek edge processes drive pioneer marsh vegetation establishment

Sarah Hautekiet, Gregory S. Fivash, Lauren Van Nimmen, Ken Schoutens, Jim van Belzen, Oberon Geunens, Wim Mertens, Bart Vandevoorde, Maarten G. Kleinhans & Stijn Temmerman

Submitted in Ecological Applications

4.1 Abstract

Tidal marshes provide many critical ecosystem services, yet extensive losses have occurred due to human land use change. This has created a demand for tidal marsh restoration. A key challenge in tidal marsh restoration projects is providing the conditions for early establishment of pioneer algae and plants, which are often limited by unfavorable environmental conditions. Observations reveal that pioneer species preferentially establish along tidal creek edges, yet the mechanisms causing this colonization pattern remain poorly understood. Here, we investigated the drivers of pioneer vegetation colonization along tidal creeks edges in a brackish marsh in the Scheldt estuary (Belgium). First, we characterized the spatio-temporal colonization pattern using geospatial analyses and seedling survival (via a field transplantation experiment). Then, we tested potential mechanisms underlying this pattern through field assessments of seed deposition and retention (via seed traps and seed bank sampling), and sediment characteristics. Higher seed retention and improved seedling survival were found near tidal creeks in association with increased sediment shear strength that was measured in the superficial sediment layer near tidal creeks. In contrast, other sediment properties measured at greater depth (up to 5 cm), such as dry bulk density, did not consistently explain these spatial patterns. Instead, we hypothesize that enhanced surface drainage and evaporation-driven consolidation near tidal creeks increase sediment erosion resistance of the thin sediment surface layer, which enhances seed retention and seedling survival. Overall, our results show that the superficial sediment bed of creek edges forms a hotspot for pioneer algal and plant establishment, demonstrating the importance of tidal creek networks to promote tidal marsh development in restoration projects.

4.2 Introduction

Tidal wetlands are valuable ecosystems that provide a range of essential ecosystem services, including carbon sequestration and shoreline protection (e.g. Barbier et al., 2011; Rogers et al., 2019; Temmerman et al., 2023). However, large tidal wetland areas have been lost historically due to conversion of human land use, and successful restoration of these valuable habitats requires informed and effective management strategies. A crucial aspect of tidal marsh restoration is understanding the process of pioneer vegetation colonization, which initiates the transition from a bare intertidal mudflat to a stable and resilient marsh (Brückner et al., 2019; van Belzen et al., 2017; Wang & Temmerman, 2013; Zhu et al., 2014).

Successful recruitment and establishment of vegetation on intertidal mudflats is a complex process influenced by multiple factors, including habitat suitability and the availability of propagules (Erfanzadeh et al., 2010; van Regteren et al., 2019). Plant colonization typically occurs through two mechanisms: (1) seed or propagule dispersal, driven by vectors such as wind and tides, or via deposition of rhizome fragments, and (2) in case of perennial species, lateral clonal expansion, whereby new shoots emerge from laterally outgrowing root systems (Huiskes et al., 1995; Silinski et al., 2016; Steinigeweg et al., 2023; Zhu et al., 2022). The proximity of mature marshes is essential for colonization through seed dispersal, as they serve as sources for propagules (Mossman et al., 2012; Wolters et al., 2005; Zhu et al., 2014). However, the mere arrival of propagules is insufficient for successful establishment. The environmental conditions must also be favorable for a specific period to enable seed germination, seedling survival and growth into mature plants.

Such favorable periods, often referred to as "Windows of Opportunity", are characterized by minimal physical disturbance from tidal currents, waves and sediment bed erosion, which allow seed retention, germination, and seedling survival (Balke et al., 2011, 2014; Hu et al., 2015, 2021). During the early stages of tidal marsh development, however, intense sediment dynamics -such as rapid sediment accretion- can produce soft, fluid sediment beds that hinder root anchorage and reduce seed retention (Cao et al., 2021; Oosterlee et al., 2020). For seedlings to establish successfully, the sediment must eventually transition to a more consolidated and erosion-resistant state (Cao et al., 2018). This state can develop through abiotic processes such as consolidation, sediment drainage, and evaporation (Brooks et al., 2021; Colosimo et al., 2023; Grabowski et al., 2011) or through biotic processes like vegetation growth (Brooks et al., 2021; Chen et al., 2012). Consolidation strengthens the sediment as porewater is expelled either under the weight of accumulating sediment (Torfs et al., 1996; Zhou et al., 2016) or through drying (Dong et al., 2020), which is often enhanced by drainage and evaporation (Cao et al., 2022; Colosimo et al., 2023). Vegetation can further enhance erosion resistance by modifying sediment properties and through its belowground biomass. In

particular, increased root biomass improves aggregate stability and cohesion, which leads to an increase in erosion resistance (Brooks et al., 2021; Feagin et al., 2015).

Observations from several tidal marshes - including the Tollesbury marsh restoration site in southeastern England (Garbutt et al., 2006), Petaluma Marsh in California, USA (Sanderson et al., 2000), and tidal marsh restoration sites in Belgium such as Fassaatpolder, Zennegat, and Lillo Potpolder (Fig. S4.1 & S4.6; Mertens et al., 2024) - reveal a distinct spatio-temporal vegetation colonization pattern. In these systems, pioneer species (e.g. *Vaucheria* algae and *Aster tripolium* plants in the Belgian sites) initially establish along creek edges before gradually spreading across the mudflat. This vegetation then facilitates colonization of other marsh species. Our understanding of the mechanisms driving this creek-edge focused colonization pattern is rather limited but will be instrumental to inform successful tidal marsh restoration projects.

Several hypotheses may explain why vegetation colonization often begins near tidal creek edges. One possibility is that seed availability is higher alongside creeks, due to enhanced seed supply by tidal flows, giving more opportunities for pioneers to attempt to successfully establish. Alternatively, tidal creeks may enhance seedling survival by locally enhancing sediment erosion resistance. For instance, we expect higher dry bulk density and lower sediment water content near tidal creeks due to increased subsurface drainage and sediment consolidation (Stoorvogel et al., 2024; Ursino et al., 2004; Xin et al., 2010), which are expected to reduce the sediment's vulnerability to erosion.

In this study, we first demonstrate the effects that tidal creek proximity has on the establishment of pioneer vegetation and algae using (1) geospatial analysis and (2) a field transplantation experiment in the managed realignment site of Lillo Potpolder in the brackish zone of the Scheldt estuary, Belgium. We then pursue a mechanistic explanation of this effect by evaluating the effects of a number of environmental parameters that depend on creek proximity. These include: (1) seed deposition and seed retention, measured using seed traps and by sampling the seed bank in the superficial sediment layer, (2) sediment shear strength measured by shear vane, and (3) changes in sediment characteristics, including grain size distribution, dry bulk density, and organic matter content.

4.3 Material and methods

4.3.1 Study area

This study was conducted at Lillo Potpolder (51°18'14.3" N, 4°17'50.5" E), a tidal marsh restoration site along the brackish portion of the Scheldt estuary in northeastern (NE) Belgium (see Fig. 4.1a). The mean tidal range in this part of the estuary is approximately 5.2 meters (van den Hoven et al., 2022) and the salinity of

the water varies between 5.5 and 8 PSU (Erfanzadeh et al., 2010). Lillo Potpolder was a formerly embanked polder, i.e. low-lying land adjacent to the estuary that was protected from tidal flooding by historical dike construction. This 13-hectare restoration site was de-embanked in late 2012 as part of the ongoing Belgian Sigmaplan, which aims to enhance flood protection combined with restoring tidal ecosystems by managed realignment of dikes. The polder was de-embanked by constructing a new landward dike in 2011, along with the construction of a dike that separated the area in two compartments, after which the pre-existing dike was breached in late 2012 (Peeters et al., 2014). Furthermore, the area was leveled to an elevation of 4 to 4.5 m TAW (i.e. Belgian reference level), while the local mean low and high water levels are at about 0.5 and 5.2 m TAW (Vandenbruwaene et al., 2022). All field research in this study was conducted in the largest compartment of 5.2 ha (Mertens et al., 2024). Following de-embankment and the reintroduction of tidal flooding by brackish water, the study site's original terrestrial vegetation and biota were killed and tidal deposition of mud started, creating a bare intertidal mudflat that was subsequently colonized by estuarine biota.

4.3.2 Geospatial analysis of vegetation establishment during the early developmental stages of brackish tidal marshes

In this study, we performed a geospatial analysis to identify the spatio-temporal patterns of vegetation establishment by two marsh pioneer species: (1) the filamentous algae, *Vaucheria* sp., and (2) the halophyte, *Aster tripolium* L. (also known as *Tripolium pannonicum*), during the early developmental stages of brackish tidal marshes. *Vaucheria* are yellow-green algae that can form thick filamentous mats on intertidal mudflats which can trap and bind sediment particles, creating elevated sediment hummocks (Gallagher & Humm, 1981; van de Vijsel et al., 2020, 2021). By acting as a biostabilizer, these algae can facilitate pioneer plant establishment. *Aster tripolium* (is a biennial marsh plant species of the *Asteraceae* family that flowers from July to October. The plants primarily reproduce through seeds, which are dispersed by wind and water flow from October to December (Hill et al., 2004; Huiskes et al., 1995; van Regteren et al., 2019).

We analyzed digital terrain models (DTMs) derived from aerial lidar surveys (1 x 1 m resolution) and vegetation maps (polygons created based on aerial images complemented with ground truthing of vegetation types in the field) constructed for every year from 2016 to 2020 by the Research Institute for Nature and Forest (Mertens et al., 2024). Annual vegetation mapping was done by visually delineating homogeneous vegetation units on the aerial images, which were classified into formations based on physiognomy and structural complexity. Per unit, the abundance of species with at least 10% vertical cover was recorded in the field using standardized cover classes (Van Ryckegem et al., 2020). The polygons were rasterized and the resulting raster maps (1 x 1 m resolution) for *Vaucheria* and *Aster*

were resampled to the same spatial resolution as the DTMs to allow analysis (see below).

The inundation frequency was calculated from water level time series of the Liefkenshoek tidal gauge station (www.waterinfo.be; measured every low and high tide) and the Lidar-derived DTMs (every year from 2016 to 2020) of the intertidal study area. These were used to map the spatial variations in the frequency of tidal inundations in the study area over the 1 x 1 m resolution grid. Following Fivash et al. (2023), the inundation frequency (i.e. the proportion of high tides that flood a specific intertidal elevation) was calculated and mapped by dividing the number of high tides that reached elevations above the local sediment surface elevation by the total number of tidal cycles within the measured period.

To determine how the proximity of tidal creeks correlates with the probability of vegetation presence, we computed the distance of each grid cell to the nearest tidal creek. This was done by first visually delineating the extent of the tidal creek with a polyline shapefile. The Euclidean distance (m) from each grid cell to the nearest point on this polyline was then computed as the distance from that cell to the nearest tidal creek.

4.3.3 Effect of inundation frequency & proximity to creek edges on vegetation presence

Next, we conducted a geospatial analysis to assess the combined effect of tidal inundation frequency and proximity to creeks on the presence of marsh pioneers, differentiating between *Vaucheria* algae and *Aster* seedlings using the vegetation map. Both explanatory variables (inundation frequency and distance to creek edge) were binned into categories as follows. Vegetation presence was binned across tidal inundation and creek distance categories, creating a 2D array where each bin represented a specific combination of these explanatory variables. The likelihood of vegetation presence within each bin was then determined as the proportion of vegetated cells relative to the total cells within each bin.

We found that tidal creek influence on pioneer establishment diminishes significantly beyond 7 m (see Supplementary information - Section S4.1 for detailed explanation). Therefore, further analysis focused on distances within that range.

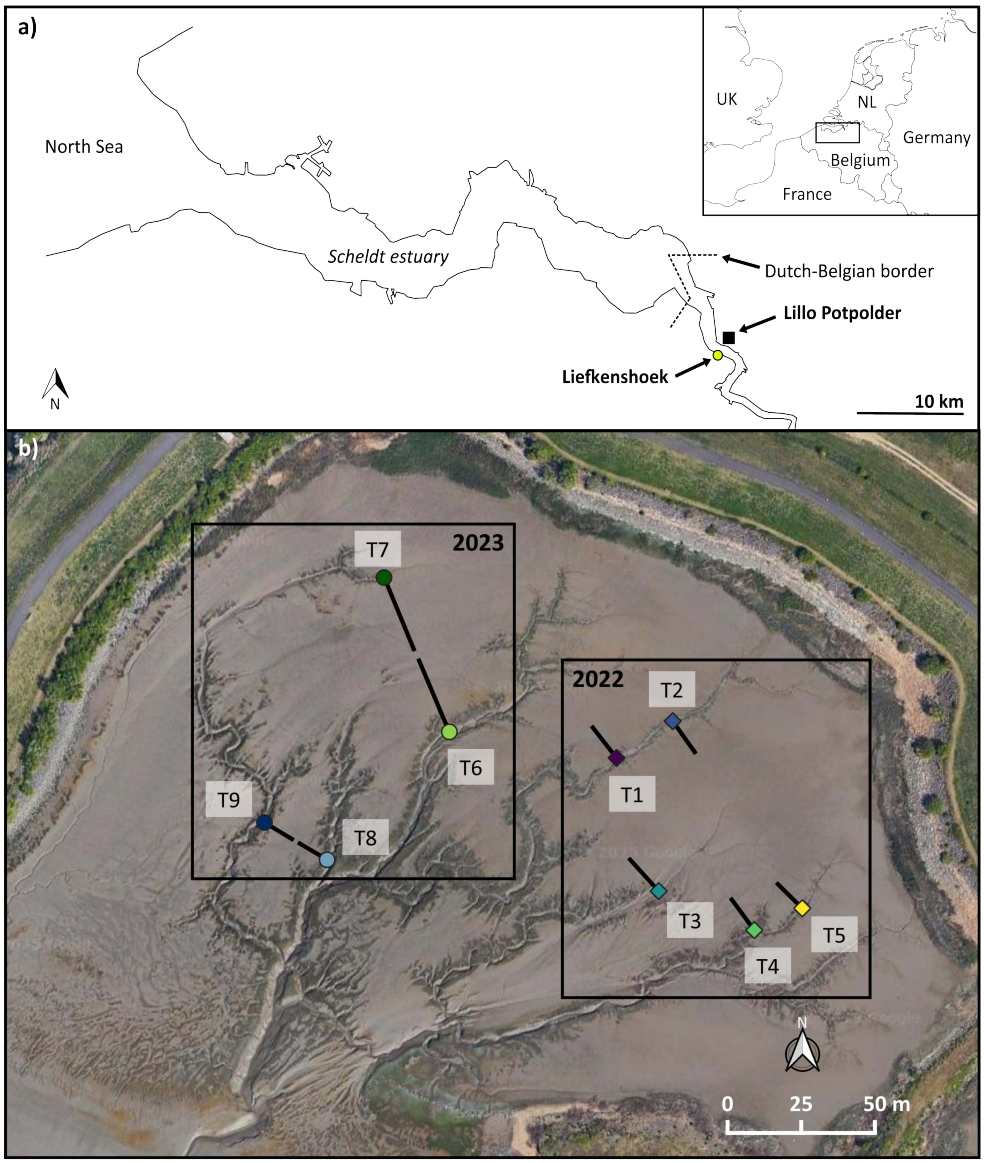


Figure 4.1: **a)** Overview of the study site (Lillo Potpolder) and tidal gauge station (Liefkenshoek) located along the Scheldt estuary (NE Belgium, see inset map); **b)** Overview of all transects that were used for the tests and field experiments. The rectangular box "2022" (referring to the year of fieldwork) includes five transects (T1 - T5) where we tested for spatial variation in seed deposition and retention along a gradient of increasing distance to the creek edge. Additionally, a field experiment testing the spatial variation in seedling survival along a creek edge distance gradient was carried out in three of the five transects (T1, T2 and T3). The four transects (T6 - T9) in the rectangular box "2023" were used to test the spatial variation in sediment drainage and erosion resistance in relation to creek edge distance. Map data obtained from © Google Earth, 28 April 2022.

4.3.4 Effect of creek edge proximity on seedling survival probability

A field experiment was conducted in June 2022 to investigate the survival probability of the pioneer plant species *Aster tripolium* at varying distances from a creek edge. *Aster* seedlings were transplanted into 1 x 1 m plots arranged along three transects at three distances from the creek edge (see Fig. 4.1b, T1 - T3 in box 2022): 0 m, i.e. directly adjacent to the creek edge (n = 6 plots), 5 m (n = 3 plots), and 10 m (n = 3 plots). A greater number of plots were selected at the creek edge because this was the only location where both areas with and without *Vaucheria* algae were present. Therefore, we set up three plots with and three plots without *Vaucheria* directly adjacent to the creek edge. The seedlings were germinated in the lab from seeds collected from plants in late 2021 in the Lillo Potpolder. Once the *Aster* seedlings reached an average height of 7.5 cm (approximately two months old), 15 individuals were transplanted into each field plot on June 8 and 10, 2022. Seedling survival was monitored throughout the growing season, with observations conducted weekly until the end of July, biweekly until the end of October, and approximately monthly until the end of November 2022.

A binomial regression was fitted to determine the effect of distance from the creek edge on the survival probability of *Aster* seedlings using a Chi-squared test. This was followed by pairwise comparisons with Bonferroni correction.

4.3.5 Effect of creek edge proximity on seed deposition and retention

Spatial variation in seed deposition relative to creek edge distance was assessed using AstroTurf® seed traps (45 x 45 cm), a synthetic mat consisting of a dense network of 18 mm high grass tufts (Wolters et al., 2004). The mats were positioned along five transects at three distances from the creek edge (see Fig. 4.1b, T1 - T5 in box 2022): 0 m, 5 m, and 10 m. The traps were securely anchored at each corner with steel pegs and deployed during the seed rain period (October 2022 - January 2023). To prevent sediment accumulation and seed loss due to tidal currents, the traps were replaced with fresh ones every three weeks, and the collected traps were stored in plastic bags at 4 °C. After collection, the mats were rinsed upright on a 1 mm mesh sieve to retrieve the seeds. The seeds were then dried at 40 °C for temporary storage before species identification and counting.

The spatial variation in seed retention (i.e. the actual seed bank in the sediment surface layer) was quantified at the same locations by scraping the upper 1 cm of the sediment surface over a 40 x 40 cm area at the end of the seed rain period (i.e. in January 2023). The sediment samples were stored in plastic bags and kept in a cooling cell until further processing.

One month after all seeds were collected (i.e. February 2023), a germination experiment was conducted in a greenhouse under controlled conditions, including

adequate light and a temperature of approximately 16 °C. After three weeks, the number of germinated *Aster tripolium* seedlings was recorded.

A negative binomial model was fitted to assess the effect of proximity to creek edge on the number of germinated seeds resulting from the seed deposition and seed retention samples using a Chi-squared test. Afterwards, pairwise comparisons were made.

4.3.6 Effect of creek edge proximity on sediment erosion resistance

Further we quantified environmental conditions that may vary with distance from creek edges and that may affect the seed deposition, retention and seedling survival and growth. In November 2023, sediment surface erosion resistance was tested using a pocket shear vane device (Eijkelkamp, the Netherlands) along four transects with increasing distance from creeks (see Fig. 4.1b, T6 - T9 in box 2023). Shear strength values were recorded by pressing the device into the superficial sediment layer up to a depth of maximum 1 cm and rotating it clockwise until sediment movement was observed. New transects with bare mud were selected for this test, as the previous transects were nearly entirely covered by vegetation by November 2023, making them unsuitable for measurements. For each transect, multiple measurements ($n \geq 3$) were taken at regular distance intervals and recorded using an RTK GPS (Leica Zeno GG04 plus).

To account for the variability in sample size, a generalized linear model with a gamma distribution was used to assess the effect of distance from the creek edge on sediment shear strength. The significance of the model was assessed using a Chi-squared test. Furthermore, the relationship between sediment shear strength and distance from the creek edge was characterized by using an exponential decay model with nonlinear least-squares regression.

4.3.7 Effect of creek edge proximity on sediment properties and nutrient content

Sediment samples up to a depth of 5 cm were collected using a Kopecky ring (Ø = 53 mm, height = 50 mm) in May 2024 to investigate the spatial variation in sediment properties in the field locations where the seed deposition and retention was assessed (Fig. 4.1b, T1 - T5 in box 2022) and in May 2024 along the transects where the sediment erosion resistance was measured (Fig. 4.1b, T6 - T9 in box 2023). Three replicates were taken per location (0 m, 5 m, and 10 m from the creek edge for **T1 - T5**; 0 m, 1 m, 2 m, 4 m, 6 m, and 10 m from the creek edge for **T6 - T9**). Before grain size analysis, the sediment samples were pre-treated with H_2O_2 and HCl to remove organic matter and disperse aggregates. The treated sediment was analyzed for its grain size distribution using a Mastersizer 2000 (Malvern) and classified according to the standard grain-size distribution categories: clay: < 2 μm, silt: 2-63 μm, sand:

63-2000 µm. Dry bulk density and sediment water content were calculated by weighing the fresh wet sediment mass and dry sediment mass after oven-drying the samples at 70 °C for 72 hours (until complete dryness was achieved). Finally, organic matter content was estimated by performing the loss on ignition (LOI) method (Heiri et al., 2001), which involves the combustion of sediment at 550 °C for four hours in a muffle furnace. The total nitrogen and phosphorus content of sediment was analyzed along the same five transects used for sediment property measurements (Fig. 4.1b, T1 - T5 in box 2022). The analysis was conducted in November 2023 using the previously collected sediment samples. These samples were first dried in an oven at 70 °C, then subjected to sulfuric acid (H_2SO_4) digestion for nutrient determination.

A linear mixed-effects model using restricted maximum likelihood estimation, with transect as a random effect was used to assess the effect of creek edge proximity (0 m, 5 m, and 10m) on the measured sediment properties in transects 1 to 5. These include dry bulk density, median grain size, the fraction below 63 µm (i.e. mud content) and organic matter content. A similar approach was used for the measured sediment water content and dry bulk density in transects 6 to 9.

A generalized linear model with gamma distribution was used to assess the effect of distance from the creek edge (0 m, 5 m, and 10 m) on total phosphorus and nitrogen content in transects 1 to 5. The significance of the model was assessed using a Chi-squared test.

4.3.8 Statistical analysis

Before every analysis, we conducted Shapiro-Wilk tests to check for normality of the residuals and Levene's tests to check the homogeneity of variances. All analyses were performed in R version 4.2.2 (R Core Team, 2022), applying a significance level of $\alpha = 0.05$.

4.4 Results

4.4.1 Algae and pioneer plants prefer to establish along creek edges

Our geospatial analysis showed that vegetation establishment is strongly influenced by tidal inundation frequency, and that this relationship is affected by proximity to tidal creeks. Specifically, pioneer species are more likely to establish under higher inundation frequencies when they are closer to the creek edge. This effect declines with distance from creeks and becomes negligible beyond 7 meters (as seen in Fig. S4.2 and explained in S4.1).

We observed this pattern for both *Vaucheria* and *Aster* (Fig. 4.2 & Fig. S4.3), but with a key distinction: *Vaucheria* proved to be a more robust pioneer, establishing at higher inundation frequencies (i.e. lower elevations in the tidal frame) than *Aster*

near the creek edge (see detailed analysis and statistics in S4.1). This suggests *Vaucheria* is less sensitive to inundation stress and more suited to early colonization under challenging conditions.

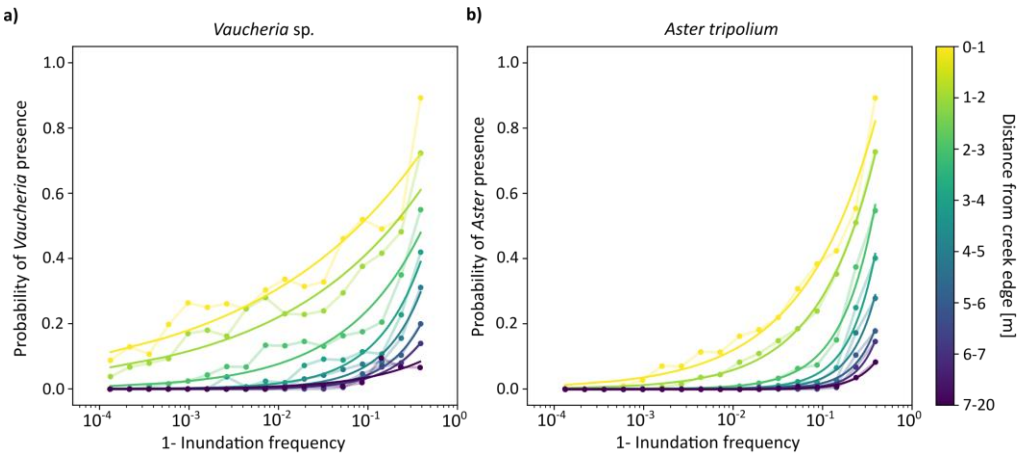


Figure 4.2: Relationship between the probability of **a)** *Vaucheria* sp. algae and **b)** *Aster tripolium* presence, inundation frequency, and distance from the creek edge. The probability of pioneer presence (y-axis) is shown in relation to "1 - Inundation frequency", the proportion of tidal cycles that the area is not submerged at high tide (x-axis) for a series of binned groups at various distances from the nearest creek edge (different colors). The points represent the observed proportion of vegetated cells at each inundation frequency and distance bin, while the lines represent the model fits.

4.4.2 *Aster* seedlings have higher survival probabilities closest to the creek edge

The transplantation experiment showed that *Aster* seedlings have higher survival probabilities when located closer to the creek edge (Fig. 4.3). A significant effect of distance on survival was found (likelihood-ratio $\chi^2(2) = 18.14$, $p < 0.001$). Pairwise comparisons indicated significant differences in survival between seedlings located closest to the creek edge (0 m) and those located at 5 m from the creek edge ($z = 3.68$, $p < 0.001$), as well as between 0 m and 10 m ($z = 3.23$, $p = 0.004$). No significant difference was found between seedlings located 5 m and 10 m from the creek edge ($z = -0.42$, $p = 0.91$).

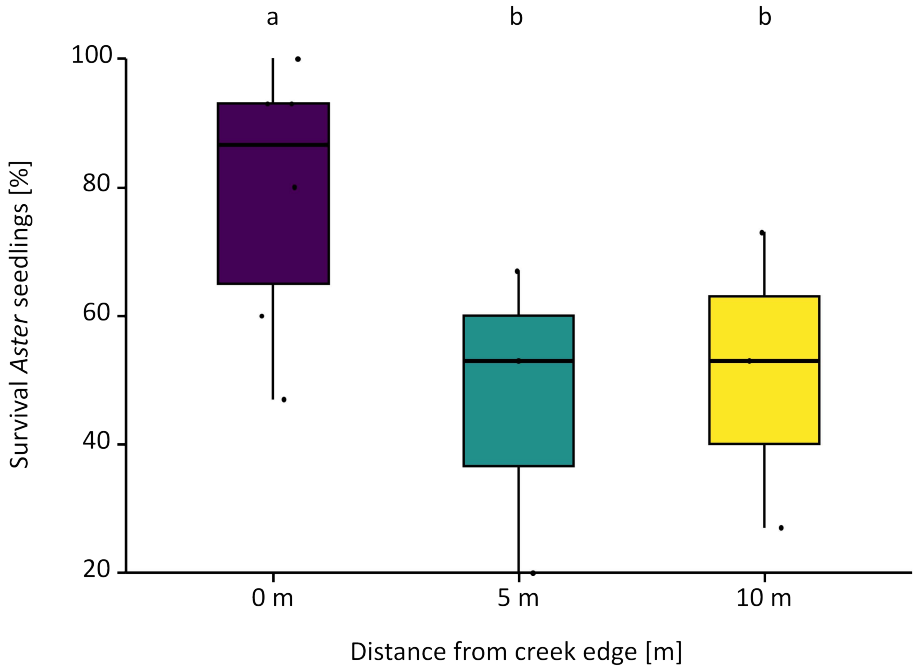


Figure 4.3: *Aster* seedling survival probability along varying distances from the creek edge (0 m, 5 m and 10 m), based on three transects (T1 - T3 in box 2022). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

4.4.3 Creek edge proximity influences seed retention but not deposition

Seed deposition (i.e. measured by germinating seeds collected on AstroTurf® mats) did not show significant differences along the creek edge distance gradient (Fig. 4.4). However, the results from the seed retention samples (i.e. seeds present in upper 1 cm of sediment surface) showed significant differences. Seed retention appears to be highest closest to the creek edge (0 m) and decreases with increasing distance (Fig. 4.4).

Significant differences in seed retention were found across distances from the creek edge (likelihood-ratio χ^2 (2) = 12.598, p = 0.002). Specifically, a significant difference was found between 0 m and 5 m (z = -3.62, p < 0.001), while the difference between 0 m and 10 m was not statistically significant (z = -1.9, p = 0.057). In contrast, no significant differences in seed deposition were detected along the creek edge distance gradient (likelihood-ratio χ^2 (2) = 3.841, p = 0.147).

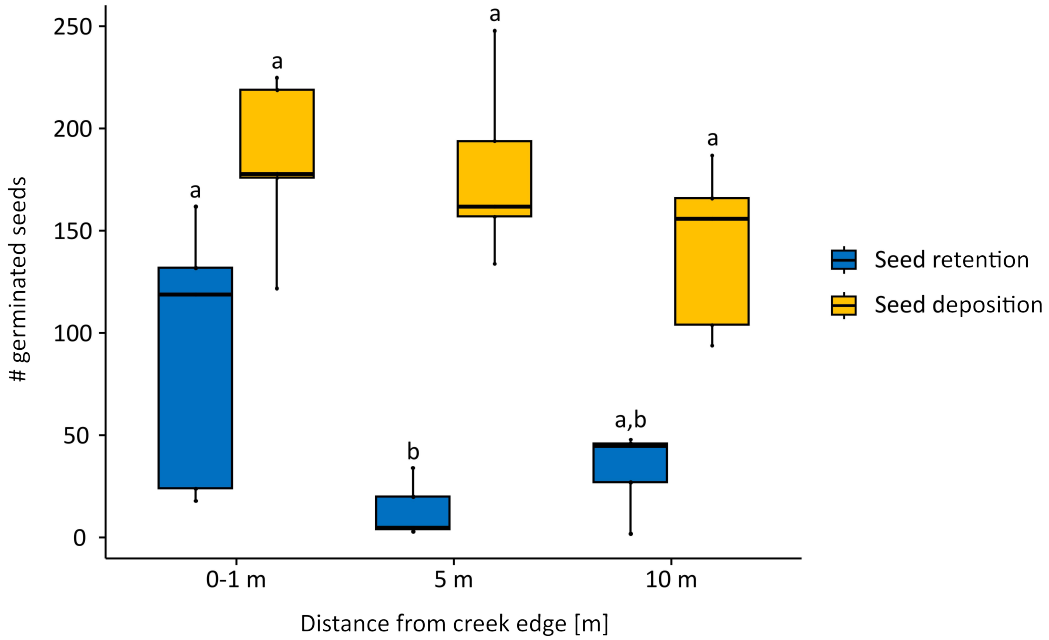


Figure 4.4: The number of germinated seeds found at varying distances from the creek edge based on five transects (T1 - T5 in box 2022). Seed deposition relates to the seeds collected during the seed rain period using seed traps, while seed retention refers to seeds collected at the end of the seed rain period by scraping the top 1 cm of the sediment surface. Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

4.4.4 Creek edge proximity enhances sediment erosion resistance

The sediment shear strength measurements revealed differences in sediment erosion resistance in relation to distance from the creek edge across all four transects. The highest shear strength values were found near the creek edge, gradually decreasing with distance (Fig. 4.5). A significant negative relationship was observed between shear strength and distance from the creek edge (β = -0.096, t = −12.24, $p < 0.001$), confirming that shear strength decreases with increasing distance. Model comparison (likelihood $\chi^2(2) = 69.58$, $p < 0.001$) showed that a quadratic model provided a significantly better fit than a linear model. The quadratic model suggests that shear strength initially decreases sharply with distance, but the rate of decline slows at greater distances ($\beta_1 = -8.94$, $\beta_2 = 8.24$, both $p < 0.001$).

Complementing this, an exponential decay model, fitted via nonlinear least-squares regression, captured the decreasing trend in shear strength with distance ($R^2 = 0.81$, $F_{3,205} = 289.4$, $p < 0.001$). This model supports the interpretation that sediment erosion resistance declines asymptotically with increasing distance from the creek edge.

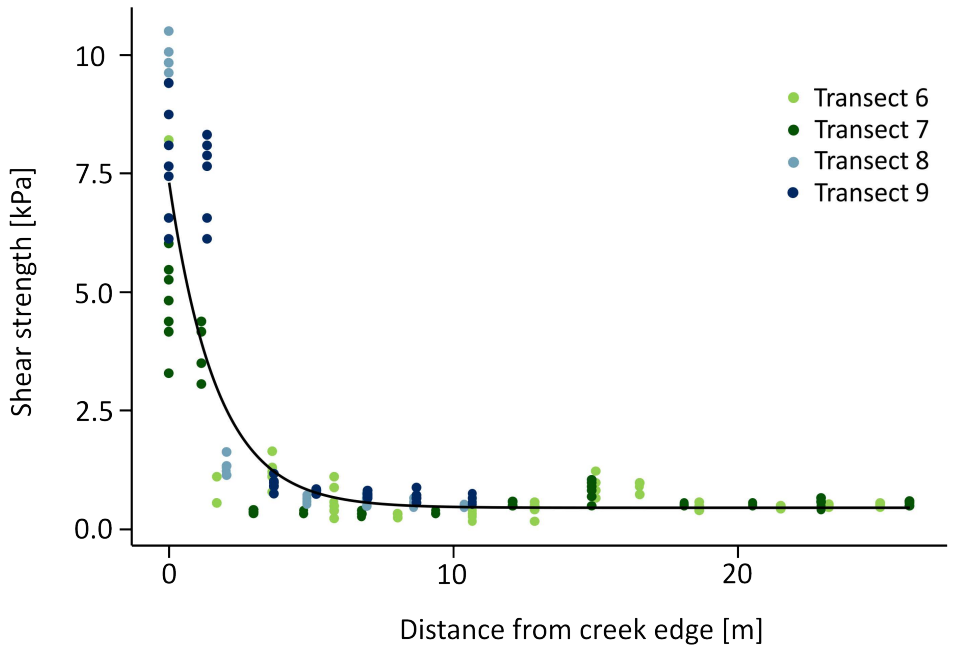


Figure 4.5: Relationship between sediment shear strength (kPa) and distance from the creek edge based on four transects (T6 - T9 in box 2023). The solid black line shows the fitted exponential decay function: $y(x) = a(e^{-bx}) + c$. The model captures a significant decline in shear strength with increasing distance from the creek edge.

4.4.5 Creek edge proximity does not (consistently) affect sediment properties and nutrient content

The measured sediment properties did not show clear patterns or trends in relation to distance from the creek edge in transects 1 to 5 (Fig. 4.1b, box 2022 & Fig. 4.6). Linear mixed-effects models with transect as a random effect confirmed that none of the sediment properties varied significantly with distance: organic matter content (β = –0.037 ± 0.059 %, p = 0.53), median grain size (β = 0.076 ± 0.095 µm, p = 0.43), fraction below 63 µm (β = –0.002 ± 0.096 %, p = 0.98), and dry bulk density (β = 0.000002 ± 0.000002 g/cm^3, p = 0.20). The distance effect differed among the transects.

The sediment water content (Fig. S4.4a) and dry bulk density (Fig. S4.4b) measured in transects 6 to 9 (Fig. 4.1b, box 2023) showed only slight spatial variation. We found lower sediment water content and higher dry bulk density values near the creek edge. These trends were particularly pronounced for transects 8 and 9, while transect 6 showed a less distinct pattern. Transect 7, however, appeared to follow a completely different trend.

Bulk density did not vary significantly with distance from the creek edge (β = −0.0048 ± 0.0040 g/cm^3, p = 0.236), nor did sediment water content (β = 0.29 ± 0.24 %, p = 0.228). Although no consistent distance-related patterns were detected, substantial variability was observed among transects.

Furthermore, our results did not show spatial variation in total nitrogen and phosphorus content along varying distances from the creek edge (Fig. S4.5), which is also confirmed by the generalized linear model. We did not find significant differences between the varying distances for total phosphorus (likelihood-ratio χ^2 (2) = 0.380, p = 0.827) and nitrogen (likelihood-ratio χ^2 (2) = 1.736, p = 0.420).

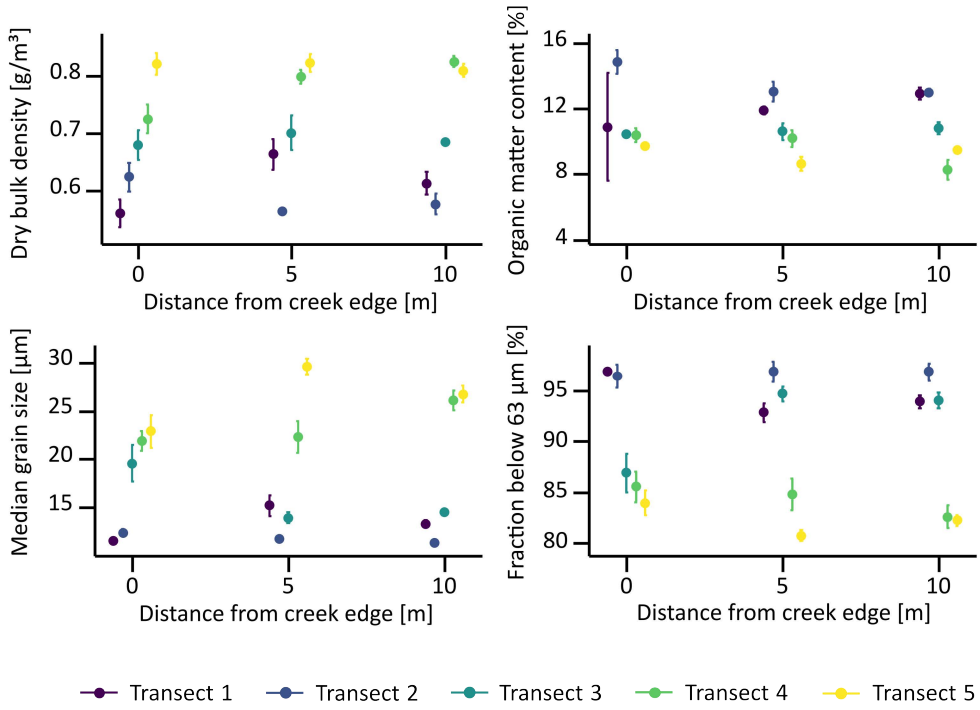


Figure 4.6: Sediment properties (i.e. dry bulk density, organic matter content, median grain size and fraction below 63 µm) at varying distances from the creek edge (0 m, 5 m and 10 m) across five transects within box 2022 (n = 3). Error bars represent standard errors of the mean. Points indicate mean values.

4.5 Discussion

Pioneer vegetation often establishes preferentially along tidal creek edges, but the underlying mechanisms causing this spatial pattern to remain poorly understood. Our study aimed to identify the mechanisms that promote early vegetation establishment near creeks during the transition from mudflat to marsh. Our findings confirmed that proximity to tidal creeks significantly enhances the establishment

success of both pioneer algae (*Vaucheria* sp.) and plants (*Aster tripolium*). Creek edges showed higher *Aster* seed retention and greater seedling survival compared to the interior tidal flat, which indicates that creek edges provide favorable conditions for early colonization. This was associated with higher sediment shear strength at the creek edges, implying that higher sediment erosion resistance along creek edges may promote enhanced seed retention and seedling survival. In contrast, these patterns were not consistently associated with spatial variations in other sediment properties, including grain size distribution, water content, dry bulk density and nutrient contents, indicating that these sediment properties had a negligible influence. Below we discuss the potential mechanisms underlying the higher seed retention and seedling survival near tidal creek edges.

4.5.1 Enhanced drainage near creek edges facilitates pioneer colonization

While inundation frequency typically poses a strong constraint on seedling survival (Balke et al., 2014; Friess et al., 2012; Hu et al., 2021), our findings indicate that proximity to tidal creeks enable pioneer establishment outside commonly tolerable inundation thresholds (Fig. 4.2, Fig. S4.2 & Fig. S4.3). This suggests that creek proximity effects mitigate the physiological stress typically associated with frequent inundation. This effect is likely caused by the enhanced drainage of the sediment surface layer that reduces waterlogging and improves sediment aeration (Ursino et al., 2004; Van Putte et al., 2022; Xin et al., 2022).

Support for this drainage hypothesis comes from the 2023 transects (Fig. 4.1b, box 2023), where we observed reduced sediment water content near creeks (Fig. S4.4), which is a pattern often associated with better-drained sediments (Cao et al., 2022; Stoorvogel et al., 2024). Furthermore, improved drainage conditions may enhance plant growth by reducing anoxic stress during early seedling development (Cao et al., 2012), which potentially explains the higher survival observed in the transplantation experiment (Fig. 4.3). However, dry bulk density (Fig. 4.6 & Fig. S4.4), also often used as a proxy for drainage, did not show similar spatial patterns, which does not support the hypothesis.

4.5.2 Drivers of sediment erosion resistance near tidal creeks

Creek proximity was also strongly associated with increased sediment shear strength (Fig. 4.5), a key factor in sediment erosion resistance. This increase in sediment erosion resistance was most pronounced within the first few meters from the creek edge coinciding with zones of algae and pioneer plant establishment (Fig. 4.2, Fig. S4.2 & Fig. S4.3). These patterns agree with previous studies showing that higher sediment shear strength facilitates early-stage marsh plant establishment by enhancing seedling anchorage and resistance to uprooting under the influence of tidal currents, waves and erosion (Cao et al., 2018, 2022).

Notably, the measured shear strength values reflect the superficial sediment layer (0-1 cm depth), where we observed a clear spatial variation. In contrast, sediment properties measured over a greater depth (0-5 cm), such as grain size distribution, organic matter content, nutrient contents and dry bulk density, did not show consistent spatial patterns (Fig. 4.6). We did not find trends typically associated with increased erosion resistance (i.e. higher dry bulk density and lower sediment water content values), apart from lower sediment water content near creeks in the 2023 transects. This contrasts with previous studies showing that sediment consolidation, which could be higher near creeks due to higher sediment deposition rates (Hill et al., 2013; Temmerman et al., 2003, 2004), is often accompanied by increased dry bulk density and organic matter content (Grabowski et al., 2011; Stoorvogel et al., 2025). The absence of consistent trends in our study suggests that other processes, such as surface drainage and evaporation of the thin upper sediment layer, may be more important drivers of sediment shear strength in dynamic, early-successional intertidal environments. This interpretation aligns with other recent findings that demonstrated that lateral porewater drainage and surface evaporation during low tide, and amplified by wind, can rapidly increase sediment shear strength of cohesive sediment beds, on the timescale of just a few hours (Colosimo et al., 2023; Fivash et al., 2024; van Rees et al., 2024).

Evaporation-induced sediment strengthening is especially pronounced in the upper few millimeters to centimeters of the sediment bed, where drying quickly increases shear strength (van Rees et al., 2024). This thin erosion-resistant surface layer appears to be a primary contributor to sediment shear strength on cohesive intertidal flats (Fivash et al., 2024). This process depends on the capacity for residual surface water to drain away, and for the sediment surface to dry between tidal cycles -conditions that appear more favorable near tidal creeks (Fagherazzi et al., 2017). Drone imagery of our study site, taken in 2020 during ebb (see Fig. S4.6), revealed visibly drier sediment along creek edges compared to the waterlogged tidal flat interior, which indicates that surface drainage is improved near tidal creeks. By enhancing sediment surface drying, added to the effect of evaporation, tidal creek proximity may create erosion resistant sediment zones, thereby improving (1) seed retention and (2) reducing seedling loss due to uprooting, ultimately supporting pioneer vegetation establishment.

In addition to these abiotic mechanisms, pioneer species themselves contribute to sediment erosion resistance. Vegetation growth enhances shear strength both indirectly, by trapping cohesive sediment particles (Feagin et al., 2015), and directly, through the binding effects of root biomass, which increases aggregation and sediment cohesion (Brooks et al., 2021; Gyssels et al., 2005; Lo et al., 2017). Filamentous benthic algae, particularly *Vaucheria*, also play a critical role in creating erosion resistant sediment beds. *Vaucheria* mats trap sediment, build elevated hummocks, and increase surface roughness, all of which effectively enhance the

probability of seed trapping and local sediment erosion resistance (van de Vijsel et al., 2021; Zhao et al., 2023). This could improve conditions for seed retention and seedling survival. As such, *Vaucheria* not only benefits from erosion resistant, well-drained conditions near creeks but may actively contribute to their formation, acting as an ecosystem engineering species during the critical early phases of tidal marsh development (in agreement with van de Vijsel et al., 2020, 2021). Together, these biostabilization processes likely increase sediment strength in zones near creek edges where algae and pioneer plants are most abundant, potentially creating a positive feedback that increases erosion resistance and promotes further colonization by other species.

4.5.3 Implications for restoration practices

This study confirms and explains the importance of creek edges as key zones for pioneer vegetation establishment. The improved seed retention and seedling survival is likely attributed to increased sediment erosion resistance by faster drainage and drying of the sediment surface near creek edges. These insights may help to improve restoration of tidal marshes. Specifically, the insights suggest that an appropriate platform elevation (potentially through raising the landscape) and creation of a creek network may accelerate vegetation establishment, which confirms and explains earlier work (Liu et al., 2020; Van Putte et al., 2022). This is particularly relevant in low-elevation or frequently inundated restoration sites where poorly drained fluid sediment would otherwise delay or prevent colonization (Oosterlee et al., 2020).

4.6 Acknowledgments

We cordially thank Allen Jun Anies and Harvey Rey Suello for assisting with experimental data collection. This work was funded by the Fonds Wetenschappelijk Onderzoek (grant no. G031620N).

4.7 References

Balke, T., Bouma, T. J., Horstman, E., Webb, E., Erftemeijer, P., & Herman, P. (2011). Windows of opportunity: Thresholds to mangrove seedling establishment on tidal flats. *Marine Ecology Progress Series*, *440*, 1–9. https://doi.org/10.3354/meps09364

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: Identifying Windows of Opportunity for recovery. *Journal of Ecology*, *102*(3), 700–708. https://doi.org/10.1111/1365-2745.12241

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Bouma, T. J., Temmerman, S., van Duren, L. A., Martini, E., Vandenbruwaene, W., Callaghan, D. P., Balke, T., Biermans, G., Klaassen, P. C., van Steeg, P., Dekker, F., van de Koppel, J., de Vries, M. B., & Herman, P. M. J. (2013). Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. *Geomorphology*, *180–181*, 57–65. https://doi.org/10.1016/j.geomorph.2012.09.005

Brooks, H., Möller, I., Carr, S., Chirol, C., Christie, E., Evans, B., Spencer, K. L., Spencer, T., & Royse, K. (2021). Resistance of salt marsh substrates to near-instantaneous hydrodynamic forcing. *Earth Surface Processes and Landforms*, *46*(1), 67–88. https://doi.org/10.1002/esp.4912

Brückner, M. Z. M., Schwarz, C., Dijk, W. M., Oorschot, M., Douma, H., & Kleinhans, M. G. (2019). Salt Marsh Establishment and Eco-Engineering Effects in Dynamic Estuaries Determined by Species Growth and Mortality. *Journal of Geophysical Research: Earth Surface*, *124*(12), 2962–2986. https://doi.org/10.1029/2019JF005092

Cao, H., Zhu, Z., Balke, T., Zhang, L., & Bouma, T. J. (2018). Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration: Sediment dynamics affect seedling establishment. *Limnology and Oceanography*, *63*(2), 647–659. https://doi.org/10.1002/lno.10657

Cao, H., Zhu, Z., Hu, Z., Wang, H., & Bouma, T. J. (2022). Drainage-Improved Sediment Strength Enhances Saltmarsh Seedling Establishment Chance. *Frontiers in Marine Science*, *9*, 874680. https://doi.org/10.3389/fmars.2022.874680

Cao, M., Xin, P., Jin, G., & Li, L. (2012). A field study on groundwater dynamics in a salt marsh – Chongming Dongtan wetland. *Ecological Engineering*, *40*, 61–69. https://doi.org/10.1016/j.ecoleng.2011.12.018

Chen, Y., Thompson, C. E. L., & Collins, M. B. (2012). Saltmarsh creek bank stability: Biostabilisation and consolidation with depth. *Continental Shelf Research*, *35*, 64–74. https://doi.org/10.1016/j.csr.2011.12.009

Colosimo, I., Van Maren, D. S., De Vet, P. L. M., Winterwerp, J. C., & Van Prooijen, B. C. (2023). Winds of opportunity: The effects of wind on intertidal flat accretion. *Geomorphology*, *439*, 108840. https://doi.org/10.1016/j.geomorph.2023.108840

Dong, Y., Lu, N., & Fox, P. J. (2020). Drying-Induced Consolidation in Soil. *Journal of Geotechnical and Geoenvironmental Engineering*,

146(9), 04020092. https://doi.org/10.1061/(ASCE)GT.1943-5606.0002327

Erfanzadeh, R., Garbutt, A., Pétillon, J., Maelfait, J.-P., & Hoffmann, M. (2010). Factors affecting the success of early salt-marsh colonizers: Seed availability rather than site suitability and dispersal traits. *Plant Ecology*, *206*(2), 335–347. https://doi.org/10.1007/s11258-009-9646-8

Erfanzadeh, R., Hendrickx, F., Maelfait, J.-P., & Hoffmann, M. (2010). The effect of successional stage and salinity on the vertical distribution of seeds in salt marsh soils. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *205*(7), 442–448. https://doi.org/10.1016/j.flora.2009.12.010

Fagherazzi, S., Bortoluzzi, A., Dietrich, W. E., Adami, A., Lanzoni, S., Marani, M., & Rinaldo, A. (1999). Tidal networks: 1. Automatic network extraction and preliminary scaling features from digital terrain maps. *Water Resources Research*, *35*(12), 3891–3904. https://doi.org/10.1029/1999WR900236

Fagherazzi, S., Viggato, T., Vieillard, A. M., Mariotti, G., & Fulweiler, R. W. (2017). The effect of evaporation on the erodibility of mudflats in a mesotidal estuary. *Estuarine, Coastal and Shelf Science*, *194*, 118–127. https://doi.org/10.1016/j.ecss.2017.06.011

Feagin, R. A., Figlus, J., Zinnert, J. C., Sigren, J., Martínez, M. L., Silva, R., Smith, W. K., Cox, D., Young, D. R., & Carter, G. (2015). Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Frontiers in Ecology and the Environment*, *13*(4), 203–210. https://doi.org/10.1890/140218

Fivash, G. S., Stoorvogel, M. M., De Smit, J. C., van Rees, F., Van Dalen, J., Grandjean, T. J., van de Vijsel, R. C., Bouma, T. J., Temmerman, S., & van Belzen, J. (2024). Abiotic origins of self-organized ridge-runnel patterns on tidal flats. *Limnology and Oceanography*, *69*(6), 1378–1389. https://doi.org/10.1002/lno.12581

Fivash, G. S., Temmerman, S., Kleinhans, M. G., Heuner, M., Van Der Heide, T., & Bouma, T. J. (2023). Early indicators of tidal ecosystem shifts in estuaries. *Nature Communications*, *14*(1), 1911. https://doi.org/10.1038/s41467-023-37444-6

Friess, D. A., Krauss, K. W., Horstman, E. M., Balke, T., Bouma, T. J., Galli, D., & Webb, E. L. (2012). Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biological Reviews*, *87*(2), 346–366. https://doi.org/10.1111/j.1469-185X.2011.00198.x

Gallagher, S. B., & Humm, H. J. (1981). *Vaucheria* (Xanthophyceae, Vaucheriaceae) of the central Florida gulf coast. *Bulletin of Marine Science*, *31*(1), 184-19.

Garbutt, R. A., Reading, C. J., Wolters, M., Gray, A. J., & Rothery, P. (2006). Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. *Marine Pollution Bulletin*, *53*(1–4), 155–164. https://doi.org/10.1016/j.marpolbul.2005.09.015

Gedan, K. B., Silliman, B. R., & Bertness, M. D. (2009). Centuries of Human-Driven Change in Salt Marsh Ecosystems. *Annual Review of Marine Science*, *1*(1), 117–141. https://doi.org/10.1146/annurev.marine.010908.163930

Grabowski, R. C., Droppo, I. G., & Wharton, G. (2011). Erodibility of cohesive sediment: The importance of sediment properties. *Earth-Science*

Reviews, *105*(3–4), 101–120. https://doi.org/10.1016/j.earscirev.2011.01.008

Gyssels, G., Poesen, J., Bochet, E., & Li, Y. (2005). Impact of plant roots on the resistance of soils to erosion by water: A review. *Progress in Physical Geography: Earth and Environment*, *29*(2), 189–217. https://doi.org/10.1191/0309133305pp443ra

Heiri, O., Lotter, A. F., & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. *Journal of Paleolimnology*, *25*(1), 101–110. https://doi.org/10.1023/A:1008119611481

Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Centre for Ecology and Hydrology. http://www.ceh.ac.uk/products/publications/plantatt-attributesofbritishandirishplantsstatussizelifehistorygeographyandhabitats.html

Hill, P. S., Newgard, J. P., Law, B. A., & Milligan, T. G. (2013). Flocculation on a muddy intertidal flat in Willapa Bay, Washington, Part II: Observations of suspended particle size in a secondary channel and adjacent flat. *Continental Shelf Research*, *60*, S145–S156. https://doi.org/10.1016/j.csr.2012.06.006

Hu, Z., Borsje, B. W., van Belzen, J., Willemsen, P. W. J. M., Wang, H., Peng, Y., Yuan, L., De Dominicis, M., Wolf, J., Temmerman, S., & Bouma, T. J. (2021). Mechanistic Modeling of Marsh Seedling Establishment Provides a Positive Outlook for Coastal Wetland Restoration Under Global Climate Change. *Geophysical Research Letters*, *48*(22). https://doi.org/10.1029/2021GL095596

Hu, Z., van Belzen, J., Van Der Wal, D., Balke, T., Wang, Z. B., Stive, M., & Bouma, T. J. (2015). Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: The importance of temporal and spatial variability in hydrodynamic forcing. *Journal of Geophysical Research: Biogeosciences*, *120*(7), 1450–1469. https://doi.org/10.1002/2014JG002870

Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beeftink, W. G., Markusse, M. M., & Munck, W. D. (1995). Seed Dispersal of Halophytes in Tidal Salt Marshes. *The Journal of Ecology*, *83*(4), 559. https://doi.org/10.2307/2261624

Huyzentruyt, M., Belliard, J.-P., Saintilan, N., & Temmerman, S. (2024). Identifying drivers of global spatial variability in organic carbon sequestration in tidal marsh sediments. *Science of The Total Environment*, *957*, 177746. https://doi.org/10.1016/j.scitotenv.2024.177746

Liu, Z., Fagherazzi, S., She, X., Ma, X., Xie, C., & Cui, B. (2020). Efficient tidal channel networks alleviate the drought-induced die-off of salt marshes: Implications for coastal restoration and management. *Science of The Total Environment*, *749*, 141493. https://doi.org/10.1016/j.scitotenv.2020.141493

Lo, V. B., Bouma, T. J., Van Belzen, J., Van Colen, C., & Airoldi, L. (2017). Interactive effects of vegetation and sediment properties on erosion of salt marshes in the Northern Adriatic Sea. *Marine Environmental Research*, *131*, 32–42. https://doi.org/10.1016/j.marenvres.2017.09.006

Mertens, W., Geunens, O., Van Beek, H., Van Braeckel, A., Van Ryckegem, G., Vandevoorde, B., Van Lierop, F., Terrie, T., Spanoghe, G., & Van den Bergh, E. (2024). *Ontpoldering van Lillo's potpolder. Vergelijking van*

twee inrichtingsvarianten. Instituut voor Natuur- en Bosonderzoek. https://doi.org/10.21436/inbor.116393830

Mossman, H. L., Brown, M. J. H., Davy, A. J., & Grant, A. (2012). Constraints on Salt Marsh Development Following Managed Coastal Realignment: Dispersal Limitation or Environmental Tolerance? *Restoration Ecology*, *20*(1), 65–75. https://doi.org/10.1111/j.1526-100X.2010.00745.x

Nijland, W., de Jong, R., de Jong, S. M., Wulder, M. A., Bater, C. W., & Coops, N. C. (2014). Monitoring plant condition and phenology using infrared sensitive consumer grade digital cameras. *Agricultural and Forest Meteorology*, *184*, 98–106. https://doi.org/10.1016/j.agrformet.2013.09.007

Oosterlee, L., Cox, T. J. S., Temmerman, S., & Meire, P. (2020). Effects of tidal re-introduction design on sedimentation rates in previously embanked tidal marshes. *Estuarine, Coastal and Shelf Science*, *244*, 106428. https://doi.org/10.1016/j.ecss.2019.106428

Peeters, P., Zhao, G., De Vos, L., & Visser, P. (2014). Large-scale dike breaching experiments at Lillo in Belgium. In L. Cheng, S. Draper, & H. An (Eds.), *Scour and Erosion* (pp. 289–297). CRC Press. https://doi.org/10.1201/b17703-36

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91–95. https://doi.org/10.1038/s41586-019-0951-7

Schoutens, K., Heuner, M., Minden, V., Schulte Ostermann, T., Silinski, A., Belliard, J., & Temmerman, S. (2019). How effective are tidal marshes as nature-based shoreline protection throughout seasons? *Limnology and Oceanography*, *64*(4), 1750–1762. https://doi.org/10.1002/lno.11149

Silinski, A., Fransen, E., Bouma, T. J., Meire, P., & Temmerman, S. (2016). Unravelling the controls of lateral expansion and elevation change of pioneer tidal marshes. *Geomorphology*, *274*, 106–115. https://doi.org/10.1016/j.geomorph.2016.09.006

Steinigeweg, C. S., Paul, M., Kleyer, M., & Schröder, B. (2023). Conquering New Frontiers: The Effect of Vegetation Establishment and Environmental Interactions on the Expansion of Tidal Marsh Systems. *Estuaries and Coasts*, *46*(6), 1515–1535. https://doi.org/10.1007/s12237-023-01220-y

Stoorvogel, M. M., Temmerman, S., Oosterlee, L., Schoutens, K., Maris, T., van de Koppel, J., Meire, P., & Bouma, T. J. (2024). Nature-based shoreline protection in newly formed tidal marshes is controlled by tidal inundation and sedimentation rate. *Limnology and Oceanography*, *69*(10), 2377–2390. https://doi.org/10.1002/lno.12676

Stoorvogel, M. M., Willemsen, P. W. J. M., van Belzen, J., Temmerman, S., De Jonge, J. M., van de Koppel, J., & Bouma, T. J. (2025). Nature-based mitigation of shoreline erosion risks in tidal marshes created by managed realignment vs. Sediment nourishment. *Ecological Engineering*, *210*, 107439. https://doi.org/10.1016/j.ecoleng.2024.107439

Temmerman, S., Govers, G., Meire, P., & Wartel, S. (2004). Simulating the long-term development of levee–basin topography on tidal marshes. *Geomorphology*, *63*(1–2), 39–55.

https://doi.org/10.1016/j.geomorph.2004.03.004

Temmerman, S., Govers, G., Wartel, S., & Meire, P. (2003). Spatial and temporal factors controlling short-term sedimentation in a salt and freshwater tidal marsh, Scheldt estuary, Belgium, SW Netherlands. *Earth Surface Processes and Landforms*, *28*(7), 739–755. https://doi.org/10.1002/esp.495

Temmerman, S., Horstman, E. M., Krauss, K. W., Mullarney, J. C., Pelckmans, I., & Schoutens, K. (2023). Marshes and Mangroves as Nature-Based Coastal Storm Buffers. *Annual Review of Marine Science*, *15*(1), 95–118. https://doi.org/10.1146/annurev-marine-040422-092951

Torfs, H., Mitchener, H., Huysentruyt, H., & Toorman, E. (1996). Settling and consolidation of mud/sand mixtures. *Coastal Engineering*, *29*(1–2), 27–45. https://doi.org/10.1016/S0378-3839(96)00013-0

Ursino, N., Silvestri, S., & Marani, M. (2004). Subsurface flow and vegetation patterns in tidal environments. *Water Resources Research*, *40*(5). https://doi.org/10.1029/2003WR002702

van Belzen, J., Fivash, G. S., Hu, Z., Bouma, T. J., & Herman, P. M. J. (2022). A probabilistic framework for windows of opportunity: The role of temporal variability in critical transitions. *Journal of The Royal Society Interface*, *19*(190), 20220041. https://doi.org/10.1098/rsif.2022.0041

van Belzen, J., Van De Koppel, J., Kirwan, M. L., Van Der Wal, D., Herman, P. M. J., Dakos, V., Kéfi, S., Scheffer, M., Guntenspergen, G. R., & Bouma, T. J. (2017). Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. *Nature Communications*, *8*(1), 15811. https://doi.org/10.1038/ncomms15811

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Cusseddu, V., Purkis, S. J., Rietkerk, M., & Koppel, J. (2020). Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. *Earth Surface Processes and Landforms*, *45*(5), 1141–1154. https://doi.org/10.1002/esp.4783

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., & van de Koppel, J. (2021). Algal-Induced Biogeomorphic Feedbacks Lay the Groundwork for Coastal Wetland Development. *Journal of Geophysical Research: Biogeosciences*, *126*(10). https://doi.org/10.1029/2021JG006515

van den Hoven, K., Kroeze, C., & Van Loon-Steensma, J. M. (2022). Characteristics of realigned dikes in coastal Europe: Overview and opportunities for nature-based flood protection. *Ocean & Coastal Management*, *222*, 106116. https://doi.org/10.1016/j.ocecoaman.2022.106116

Van Putte, N., Meire, P., Seuntjens, P., Joris, I., Verreydt, G., Hambsch, L., & Temmerman, S. (2022). Solving hindered groundwater dynamics in restored tidal marshes by creek excavation and soil amendments: A model study. *Ecological Engineering*, *178*, 106583. https://doi.org/10.1016/j.ecoleng.2022.106583

van Rees, F. F., Hanssen, J., Gamberoni, S., Talmon, A. M., & Van Kessel, T. (2024). Effect of air exposure time on erodibility of intertidal mud flats. *Frontiers in Marine Science*, *11*, 1393262. https://doi.org/10.3389/fmars.2024.1393262

van Regteren, M., Colosimo, I., de Vries, P., van Puijenbroek, M. E. B., Freij, V. S., Baptist, M. J., & Elschot, K. (2019). Limited seed retention during winter inhibits vegetation establishment in spring, affecting lateral marsh

expansion capacity. *Ecology and Evolution*, *9*(23), 13294–13308. https://doi.org/10.1002/ece3.5781

Van Ryckegem, G., Van Braeckel, A., Elsen, R., Vanoverbeke, J., Van de Meutter, F., Vandevoorde, B., Mertens, W., Breine, J., Speybroeck, J., Bezdenjesnji, O., Buerms, D., De Beukelaer, J., De Regge, N., Hessel, K., Soors, J., & Van Lierop, F. (2020). *MONEOS – Datarapport INBO: Toestand Zeeschelde 2018-2019: Monitoringsoverzicht en 1ste lijnsrapport Geomorfologie, diversiteit Habitats en diversiteit Soorten.* (p. 156). Instituut voor Natuur- en Bosonderzoek. https://doi.org/10.21436/inbor.18656743

Vandenbruwaene, W., Bertels, J., Michielsen, S., Thant, S., Van Den Berg, M., Brackx, M., Hertoghs, R., Claeys, S., Plancke, Y., Meire, D., Vereecken, H., & Deschamps, M. (2022). Monitoring Effecten Ontwikkelingsschets (MONEOS) – Jaarboek monitoring 2021: Data rapportage monitoring waterbeweging en fysische parameters in Zeeschelde en bijrivieren. *Title : WL Rapporten. Waterbouwkundig Laboratorium: Antwerpen. Volume : PA047_11*, 91 + 19 p. bijl. https://doi.org/10.48607/139

Wang, C., & Temmerman, S. (2013). Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. *Journal of Geophysical Research: Earth Surface*, *118*(1), 229–240. https://doi.org/10.1029/2012JF002474

Wolters, M., Garbutt, A., & Bakker, J. P. (2005). Plant colonization after managed realignment: The relative importance of diaspore dispersal: Plant colonization after managed realignment. *Journal of Applied Ecology*, *42*(4), 770–777. https://doi.org/10.1111/j.1365-2664.2005.01051.x

Wolters, M., Geertsema, J., Chang, E. R., Veeneklaas, R. M., Carey, P. D., & Bakker, J. P. (2004). Astroturf seed traps for studying hydrochory. *Functional Ecology*, *18*(1), 141–147. https://doi.org/10.1111/j.1365-2435.2004.00813.x

Xin, P., Gibbes, B., Li, L., Song, Z., & Lockington, D. (2010). Soil saturation index of salt marshes subjected to spring-neap tides: A new variable for describing marsh soil aeration condition. *Hydrological Processes*, *24*(18), 2564–2577. https://doi.org/10.1002/hyp.7670

Xin, P., Wilson, A., Shen, C., Ge, Z., Moffett, K. B., Santos, I. R., Chen, X., Xu, X., Yau, Y. Y. Y., Moore, W., Li, L., & Barry, D. A. (2022). Surface Water and Groundwater Interactions in Salt Marshes and Their Impact on Plant Ecology and Coastal Biogeochemistry. *Reviews of Geophysics*, *60*(1). https://doi.org/10.1029/2021RG000740

Zhao, Z., Zhang, L., Yuan, L., & Bouma, T. J. (2023). Seed settling and trapping during submerged secondary dispersal: Implications for saltmarsh recruitment and restoration. *Journal of Environmental Management*, *348*, 119301. https://doi.org/10.1016/j.jenvman.2023.119301

Zhou, Z., Van Der Wegen, M., Jagers, B., & Coco, G. (2016). Modelling the role of self-weight consolidation on the morphodynamics of accretional mudflats. *Environmental Modelling & Software*, *76*, 167–181. https://doi.org/10.1016/j.envsoft.2015.11.002

Zhu, Z., Bouma, T., Ysebaert, T., Zhang, L., & Herman, P. (2014). Seed arrival and persistence at the tidal *97*(12), 3278–3284. https://doi.org/10.1002/ecy.1613



5

Bottlenecks for pioneer plant establishment in restored tidal marshes: effect of subsoil, sediment drainage, and elevation

Sarah Hautekiet, Ken Schoutens, Denise Rosenbrand, Ignace Pelckmans, Mona Huyzentruyt, Gregory S. Fivash & Stijn Temmerman

5.1 Abstract

Tidal marsh areas have globally declined due to construction of seawalls and conversion to human land use, but are increasingly restored by re-introduction of tides on the formerly embanked land. Yet early marsh vegetation establishment in restored sites is often slow and mechanisms underlying the delayed establishment remain poorly understood. Here, we investigated how sediment surface elevation, sediment drainage, subsoil and bed level dynamics influence pioneer vegetation establishment in a recently de-embanked marsh restoration site in the Scheldt estuary (Belgium & the Netherlands). Using geospatial analysis, we characterized the spatial pattern of vegetation establishment in relation to initial sediment surface elevation, bed level change and degree of subsoil compaction. We then tested the effects of varying elevation levels, (sub)surface drainage, and sediment properties on seedling survival through a field mesocosm experiment and verified the findings by a field transplantation experiment in sites that varied in degrees of subsoil compaction. We found that the rate of bed level deposition was quite high across the restored area (on average ± 0.035 - 0.09 m/year), and that vegetation was largely restricted to higher elevations where the rate of bed level change was reduced (≤ 0.06 m/year). Adding reworked soil on top of a compacted subsoil layer did not notably affect vegetation establishment in the initial years after de-embankment. The experiments showed that the deposited, unconsolidated surface sediments had low erosion resistance (i.e. low shear strength), which might inhibit pioneer marsh establishment. However, effective (sub)surface drainage enhanced sediment shear strength and algal mat development, which improved seedling survival and extended the zone suitable for pioneer colonization towards lower elevations. This suggests the existence of a "sediment-vegetation" feedback mechanism, in which (sub)surface drainage and evaporation increase sediment shear strength. As a result, seedlings are less likely to be removed by tidal currents, waves and erosion. Hence, pioneer vegetation can establish, which further enhances sediment erosion resistance. Such a feedback mechanism may be key to successful transitions from bare mudflats to vegetated marshes. Overall, our results indicate that restoration measures that optimize sediment drainage (e.g. tidal creek network excavation and reworking the compacted subsoil) could be used to accelerate the transition from a bare tidal mudflat to a vegetated marsh.

5.2 Introduction

Tidal marshes have been widely lost due to centuries of human activities such as embankment, conversion to agricultural land and pollution (Gedan et al., 2009). Given the wide array of ecosystem services these tidal marshes provide, including carbon sequestration and shoreline protection (e.g. Rogers et al., 2019; Schoutens et al., 2019; Temmerman et al., 2023), their restoration is receiving growing attention. In places where tidal marshes were historically converted to embanked land (mostly agricultural land), by building of dikes and drainage of the wetland soils, so-called managed realignment of dikes has become a popular coastal management practice to reverse this trend. In such cases, a new dike is constructed more inland after which the old existing dike along the shoreline is breached to allow tidal inundation at high tides and drainage at low tides, to create an intertidal ecosystem (Airoldi et al., 2021; French, 2006). However, restored tidal marshes often show limitations compared to their natural counterparts, including reduced species richness (Mossman et al., 2012), lack of topographic diversity (Lawrence et al., 2018), and impaired groundwater dynamics (Spencer et al., 2017; Van Putte et al., 2020). In addition, many restoration sites experience a prolonged period during which marsh vegetation fails to establish (Cao et al., 2021). Understanding the mechanisms behind this delayed vegetation establishment is critical for designing interventions that accelerate the transition from bare intertidal mudflats to vegetated marshes.

Vegetation establishment in the early phases of tidal marsh restoration depends on environmental conditions that support seed retention, germination, and seedling survival. Specifically, tidal marsh plants require areas with sufficiently high soil surface elevation that fall within their inundation tolerance limits (van Belzen et al., 2017; Wang & Temmerman, 2013), as well as disturbance-free periods with limited hydrodynamic forcing (i.e. tides and waves), and limited bed level change (Balke et al., 2014; Hu et al., 2021). Such disturbance-free periods are key, as tidal currents and waves combined with sediment bed erosion may lead to loss of young seedlings. However, such favorable disturbance-free conditions are often lacking in recently de-embanked areas.

A few interacting mechanisms may be at the root of why marsh formation is so often delayed in managed realignment sites (also referred to as de-embanked areas). Restored sites typically start at lower relative elevations than adjacent natural marshes (Crooks et al., 2002). This can be attributed to the absence of tidal sediment supply for an extended period due to historical dike construction and the subsidence/compaction of the soil surface level due to soil drainage and the use of heavy agricultural machinery. Once tidal flow is reintroduced, high sediment deposition rates may occur as the intertidal system adjusts towards a new equilibrium elevation (Gerwing et al., 2020; Oosterlee et al., 2020; Vandenbruwaene et al., 2012). These deposited sediments are typically fine-grained and

unconsolidated, often remaining water-saturated due to the presence of compacted soil layers impeding porewater flow and tidal creek network development in the strongly consolidated subsoil (Fagherazzi et al., 2012; Grabowski et al., 2011; Van Putte et al., 2020; Vandenbruwaene et al., 2012). This reduces overall sediment drainage, which includes both surface drainage (runoff of overlying water at the sediment surface) and subsurface drainage (vertical and lateral porewater flow through the sediment). Due to poor drainage, the mud that is tidally deposited on the compacted subsoil may remain fluid and unconsolidated, preventing the development of sediment shear strength (Cao et al., 2021; Oosterlee et al., 2020). This leaves the sediment bed vulnerable to intense bed level change (i.e. erosion and accretion), which may in turn limit seed retention and seedling survival due to uprooting and burial (Cao et al., 2021, 2022).

Although the roles of sediment bed elevation and drainage in tidal marsh vegetation development are recognized, the mechanistic basis for delayed vegetation colonization in managed realignment sites remains poorly understood. We hypothesize that the combination of initially low site elevation, poor sediment drainage and their interaction affect reduced vegetation establishment probabilities on elevations that theoretically can be colonized by pioneer vegetation.

In this study, we investigate the factors affecting vegetation establishment in the early phases of tidal marsh restoration in a recently de-embanked site in the Scheldt estuary (Belgium). Specifically, we (1) use geospatial analyses to assess the spatial patterns of vegetation establishment in relation to initial elevation, bed-level change and degree of subsoil compaction; (2) experimentally test the effects of elevation, (sub)surface drainage, and sediment properties on seedling survival in a field mesocosm (marsh organ) experiment; and (3) verify these results under field conditions using a transplantation experiment. By combining geospatial analyses with targeted experiments, we aim to clarify the physical constraints on pioneer establishment and identify interventions that could accelerate the transition from a bare intertidal mudflat to a vegetated marsh.

5.3 Material and methods

5.3.1 Study area

This study was conducted at the Hedwige-Prosperpolder (51°20′ N, 4°13′ E), a formerly embanked agricultural area (i.e. protected from flooding by dikes) that was converted into an intertidal wetland restoration site by managed realignment of the dikes in November 2022 (Fig. 5.1). The Hedwige-Prosperpolder (hereafter referred to as HPP) is located within the brackish zone of the Scheldt estuary, where salinity levels range from 5 - 18 PSU (Van Damme et al., 2005). At this location, the Scheldt estuary experiences a semi-diurnal tidal regime with an average tidal range of about 5 m. High water levels vary from approximately 4.62 m TAW (i.e. Belgian reference

level, which is about 2.3 m below local mean sea level) during neap tides to 5.52 m TAW during spring tides, while low water levels vary from 0.45 m TAW during neap tides to -0.18 m TAW during spring tides (Vandenbruwaene et al., 2022). The soil surface elevation of the restoration site largely varies from 3.5 to 6.5 m TAW, i.e. it is intertidal between the local low and high water levels.

This 465-hectare site consists of two formerly embanked (diked) areas, called "polder" areas: the Belgian Prosperpolder and the Dutch Hedwigepolder (Fig. 5.1b). A new ring dike was constructed on the landward side of the polder areas, after which daily tidal inundation at high tides and drainage at low tides was introduced through the removal of sections of the old dike on the estuary side. Additionally, an initial channel network was excavated to facilitate drainage of the new intertidal area during low tides, and parts of the existing marshes and mudflats on the estuary side of the old dike were excavated. The excavated material (i.e. from the channel and marsh/mudflat excavation) was reused to create bird breeding islands and to raise the soil surface elevation in the Belgian Prosperpolder (Gourgue et al., 2022; Oranjewoud & Antea Group, 2013). This intervention was necessary to compensate for the relatively lower mean elevation in the Belgian site, which stemmed from differences in sediment accretion and embankment history –specifically, the Belgian polder was embanked 60 years earlier than its Dutch counterpart and hence experienced less sediment accretion.

Once daily brackish tidal flooding and drainage was reintroduced, following dike breaches, the original terrestrial vegetation and biota perished, resulting in a predominantly bare intertidal mudflat with small remnant patches of *Phragmites australis* and *Aster tripolium*.

5.3.2 Studied species

To test the influence of sediment surface elevation and sediment drainage on pioneer species establishment and survival, we selected two typical early-successional species from brackish tidal marshes in NW European estuaries: the benthic filamentous algae *Vaucheria* sp. and the pioneer plant *Aster tripolium* (also known as *Tripolium pannonicum*). *Vaucheria* algae typically form dense filamentous mats on intertidal mudflats that can stabilize the sediment bed and that can create topographic relief by building elevated sediment hummocks (Gallagher & Humm, 1981; van de Vijsel et al., 2020, 2021). The algae can facilitate the establishment of pioneer plant species, such as *Aster tripolium* (Chapter 3; van de Vijsel et al., 2021). *Aster* is a biennial marsh plant species belonging to the *Asteraceae* family that flowers from July to October and colonizes mudflats by seed dispersal via wind and water flow from October to December (Hill et al., 2004; Huiskes et al., 1995; van Regteren et al., 2019). Both pioneer species tend to establish in well-drained areas, such as tidal creek edges (Chapter 4; figures in Fivash et al., 2019; van de Vijsel et al., 2021).

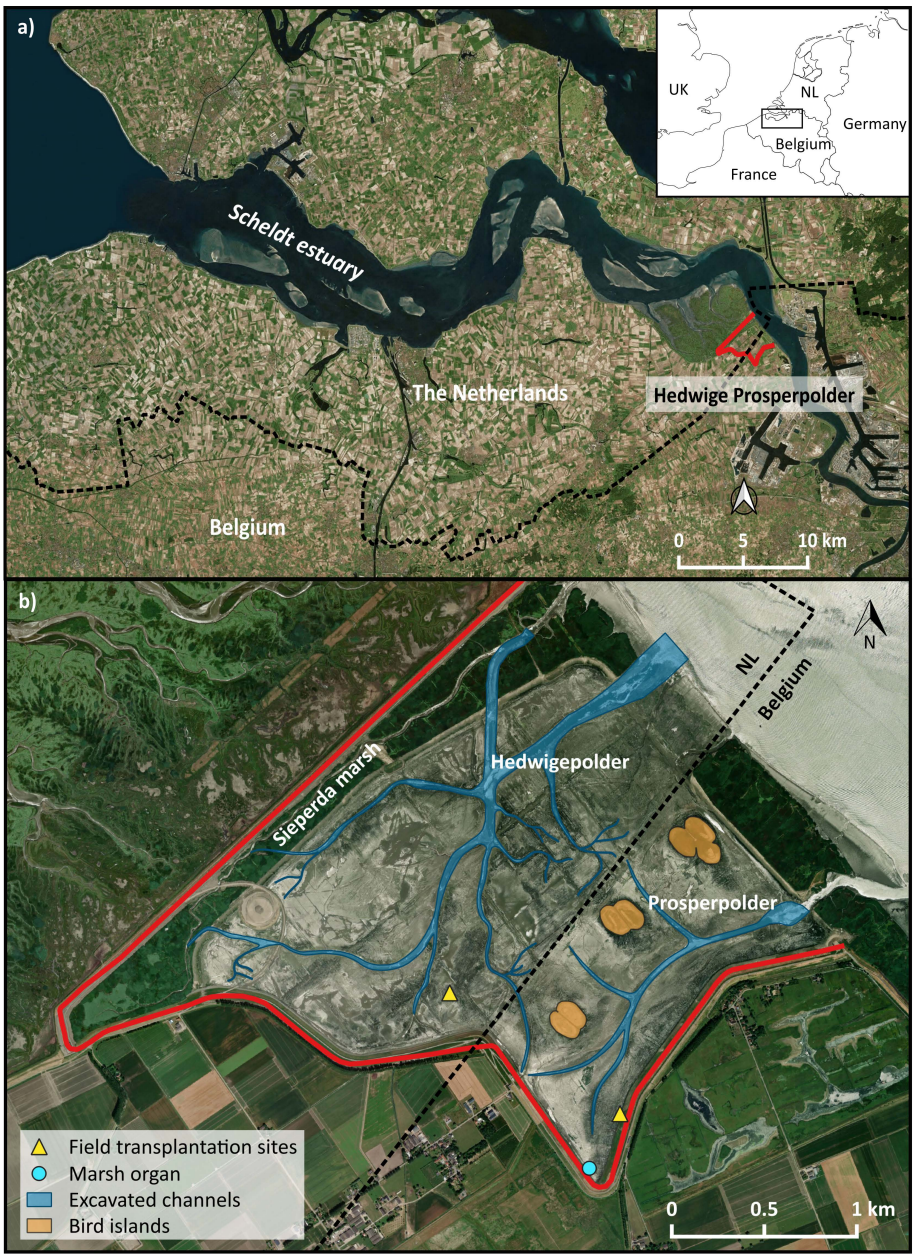


Figure 5.1: **a)** Overview of the study site (Hedwige-Prosperpolder) located along the Scheldt estuary (N Belgium & SW Netherlands) and **b)** the locations used for experimental tests (i.e. field transplantation and marsh organ experiment). Within the field transplantation sites, the effect of intertidal elevation was tested on *Aster* seedling survival. Additionally, the combined effect of intertidal elevation and (sub)surface sediment drainage on *Aster* seedling survival and *Vaucheria* establishment was investigated using a marsh organ experiment. The satellite imagery was extracted from Bing maps.

5.3.3 Geospatial analysis of pioneer vegetation establishment in HPP

We performed a geospatial analysis to explore relationships between abiotic conditions and the distribution of vegetation across the managed realignment site and separately for the Belgian and Dutch subareas. The Dutch Hedwigepolder (HP) is an area characterized by historical soil compaction due to former agricultural use and soil drainage. This is expected to hinder the porewater drainage from tidally deposited sediments on top of the compacted soil. The surface elevation of the Belgian Prosperpolder (PP) was raised with reworked soil material prior to de-embankment and was therefore considered "reworked". As a result, the Prosperpolder has a lower degree of subsoil compaction (since it was reworked and thereby decompacted) compared to the untouched subsoil of the Hedwigepolder. Hence, this offered an opportunity to investigate the effect of subsoil compaction on pioneer vegetation establishment.

Tidal inundation was re-introduced in HPP in October 2022. In April 2023 and March 2024, the Flemish Waterways Administration (De Vlaamse Waterweg) commissioned LIDAR flights over the area, producing two digital terrain models (DTMs) and resampled to 10 m horizontal resolution which are available in a data repository.

Vegetation classification

Sentinel satellite orthophotos (of 10 m horizontal resolution taken in September of 2024, acquired via Google Earth Engine) were used to determine the vegetation extent in 2024, by classifying vegetation according to an NDVI threshold of 0.266 (determined with reference to the NDVI probability distribution; see Fig. S5.1).

Identification of characteristic elevation zones

By dividing the 2024 DTM into vegetated and unvegetated zones, we were able to select three equidistant elevation levels that characterize the key states of the environment: **(1)** the low, unvegetated tidal flat (4.1 m TAW), **(2)** the transitional zone where unvegetated and vegetated states are equally likely (4.6 m TAW), and **(3)** the fully vegetated marsh zone (5.1 m TAW; see Fig. 5.3a). These characteristic elevations were then used to inform our later field experiments (see below).

Analysis of bed level change

The annual rate of bed level change across the study area ($\frac{\Delta z}{\Delta t}\ m/year$) was measured by comparing the DTMs of 2023 and 2024 as follows:

$$\frac{\Delta z}{\Delta t} = \left(\frac{z_1 - z_0}{t_1 - t_0}\right)$$

where z_0 and z_1 represent the bed elevation (m TAW) in years t_0 = 2023 and t_1 = 2024.

To evaluate how the rate of bed-level change varies as a function of the bed elevation, we grouped bed elevations from 2023 into 0.02 m bins and calculated the average annual rate of bed level change within each group. We then tested the relationship between elevation (z) and the average rate of bed level change, $r(z)$, by fitting an exponential function, such that:

$$r(z) = ae^{-zb}$$

Model performance was assessed using R^2, F-statistics, and p-values.

Lastly, to check if bed level dynamics inhibit the establishment of marsh vegetation, we tested whether the absolute rate of bed level change was larger in unvegetated areas than in vegetated areas, using a non-parametric Mann–Whitney U test (see Fig. 5.3c).

5.3.4 Effect of intertidal elevation and sediment drainage on *Aster* seedling survival

Controlled situation: marsh organ experiment

To investigate the effect of **(1)** different sediment surface elevations (i.e. corresponding to different inundation frequencies, depths and durations during high tides) and **(2)** sediment drainage (both surface and subsurface drainage during low tides) on pioneer vegetation establishment, an outdoor mesocosm experiment was set up in the summer of 2023 (Fig. 5.1b & Fig. 5.2). Specifically, a so-called 'marsh organ' was constructed (after Morris, 2007). A marsh organ is an experimental setup commonly used in tidal marsh ecology to study plant responses to varying inundation regimes. This can be achieved by growing plants in a set of sediment-filled vertical PVC pipes at different heights, thereby mimicking a gradient of tidal elevations. In our experiment, the marsh organ was adapted not only to test elevation effects but also to explicitly manipulate sediment drainage.

The structure consisted of 48 PVC pipes (height of pipe = 25 cm; Ø = 16 cm) vertically attached to a wooden framework at three elevation levels: 4.1 m TAW, 4.6 m TAW, and 5.1 m TAW (i.e. approximately 1 m, 0.5 m, and 0 m below mean high water levels). These levels correspond to inundation regimes typical of **bare, vegetation transition, and vegetated zones**. These elevations were selected based on our geospatial analysis (see Fig. 5.3a). The highest elevation level represents sediment surface elevations where pioneer vegetation is commonly observed in nearby tidal marshes (e.g. Lillo Potpolder). The intermediate level corresponds to a threshold associated with the transition from bare to vegetated states (following Wang &

Temmerman, 2013 & Fig. 5.3a), while the lowest level reflects non-vegetated low site elevations measured in the field (see Fig. 5.3a).

At each elevation, two sediment drainage treatments were applied (drained and non-drained). We had eight replicate cores per treatment, totaling 16 PVC pipes per elevation level and 48 in total. Each pipe was filled with sediment by pushing the pipe vertically into the sediment bed near the marsh organ up to a depth of 20 cm, after which the sediment-filled PVC pipe was extracted from the sediment bed and closed at the bottom with a lid. As such, the pipes functioned as individual planting pots. Pipes assigned to the "drained" treatment were perforated with 5 mm drainage holes scattered along the four sides of the PVC pipe and in the bottom lid to allow surface and subsurface drainage. To prevent sediment loss through these drainage holes, a filter sock was fitted over each pipe, including the bottom lid. Pipes in the "non-drained" treatment were not perforated to mimic poorly drained conditions typical of early stages of tidal marsh restoration.

At the end of August 2023, one *Aster* seedling was transplanted per pipe (48 *Aster* seedlings in total). The seedlings were grown from seeds collected in January 2023 in a nearby marsh site (Lillo Potpolder) and cultivated for about 4 weeks before being transplanted into the marsh organ. The transplanted seedlings had an average stem length of 7 ± 3 cm. Seedling survival was monitored every few days during the first two weeks, then weekly for five weeks, and finally monthly until the experiment was terminated after two and a half months (i.e. 78 days).

Situation in field: transplantation sites

A field transplantation experiment (i.e. transplanting young *Aster* seedlings in field plots) was set up in August 2023 to verify the marsh organ results under field conditions. Two field sites were selected in the aforementioned "vegetation transition zone" (i.e. 4.6 m TAW) using a RTK GPS (see Fig. 5.1b). The sediment composition of the sites is described in Table S5.1. One plot was located in the Dutch Hedwigepolder, and the other plot was situated in the Belgian Prosperpolder. Both plots had an elevation close to 4.6 m TAW upon transplantation of *Aster* seedlings.

Fifty *Aster tripolium* seedlings were transplanted into each plot (1.5 × 1.5 m). These seedlings were also cultivated from seeds collected in Lillo Potpolder and grown for about 4 weeks before transplantation. The seedlings transplanted in the field had an average stem length of 6 ± 2 cm. To protect the seedlings from bird disturbance, ropes were stretched between sticks placed around the perimeter of each plot, forming a bird exclosure. Seedling survival was monitored every few days during the first two weeks, then weekly for five weeks, and finally monthly until the experiment was terminated after two and a half months (i.e. 78 days).

5.3.5 Effect of sediment drainage on sediment properties

Sediment properties were measured at the end of the marsh organ experiment using the upper 10 cm of three randomly selected PVC pipes per treatment. Grain size analysis was conducted using a Mastersizer 2000 (Malvern) after pre-treating the sediment samples with H_2O_2 and HCl to remove organic matter and disperse aggregates. Afterwards, the sediment was classified according to the standard grain-size distribution categories: clay: < 2 µm, silt: 2-63 µm, sand: 63-2000 µm. Dry bulk density was determined by weighing the fresh wet sediment mass and dry sediment mass after oven-drying the samples at 70 °C for 72 hours to ensure complete dryness. Finally, organic matter content was quantified by performing the loss on ignition (LOI) method (Heiri et al., 2001). This entails heating the sediment samples for four hours at 550 °C in a muffle furnace.

5.3.6 Effect of sediment drainage on sediment shear strength

At the end of the experiment, we also assessed sediment shear strength to quantify the vulnerability of the sediment bed to erosion. Sediment shear strength of the surface (top 1 cm) was measured using a pocket shear vane (Eijkelkamp, the Netherlands). The device was gently inserted into the sediment, and surface shear strength was determined by rotating it clockwise until sediment movement was observed, at which point the reading (in kPa) was recorded.

5.3.7 Effect of sediment drainage on *Vaucheria* algae establishment

Fibrous *Vaucheria* algae began to cover the sediment surface of certain cores during the marsh organ experiment. After the experiment was concluded and all seedlings were removed algal biomass was measured by scraping algae from the sediment surface. The collected samples were rinsed to remove sediment, then dried at 72 °C to obtain their dry biomass.

5.3.8 Statistical analysis

Before every analysis, we conducted Shapiro-Wilk tests to check for normality of the residuals and Levene's tests to check the homogeneity of variances. When necessary, transformations were applied to satisfy model assumptions. All analyses were performed in R version 4.2.2 (R Core Team, 2022), applying a significance level of $\alpha = 0.05$.

A GLM of the binomial family was constructed to analyze the effect of varying elevation levels and drainage treatments on the survival probability of *Aster* seedlings at the end of the experiment, followed by pairwise comparisons. Afterwards, a Cox proportional hazards regression model was fitted to investigate the effects of drainage treatment and elevation level on seedling survival time. In this

analysis, we will report on the hazard ratio (HR) which indicates the risk of death relative to a reference group. A HR > 1 refers to a decreased probability of survival, while a HR < 1 refers to an increased probability of survival.

Afterwards, we tested the survival probability of *Aster* seedlings at one elevation level (i.e. the vegetation transition zone) in the field plots and marsh organ experiment by fitting a binomial GLM and a Cox proportional hazards regression model.

The effect of sediment drainage and intertidal elevation on sediment properties (i.e. grain size distribution, dry bulk density, organic matter content, and sediment shear strength) and on *Vaucheria* biomass was evaluated using a two-way ANOVA, followed by Tukey HSD post hoc tests.

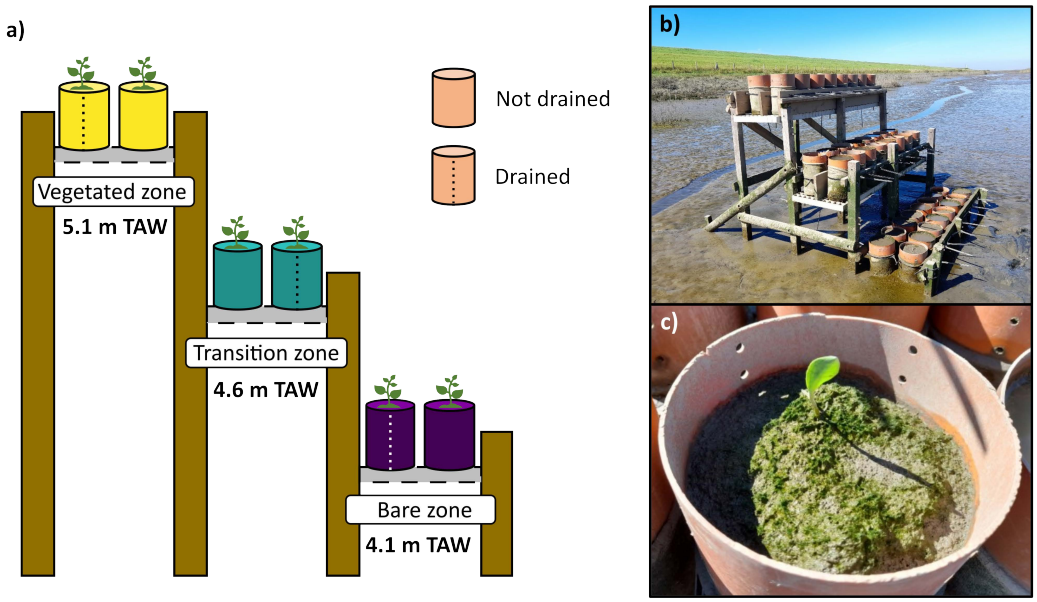


Figure 5.2: **a)** Schematic overview of the marsh organ setup. The highest level (yellow) represents the vegetated zone in intertidal wetlands (5.1 m TAW; i.e. Belgian reference level), the middle level (teal) represents the transition zone (4.6 m TAW), and the lowest level (dark purple) represents the bare unvegetated zone (4.1 m TAW). This color scheme is consistently used to represent elevation levels in other figures. **b)** Picture of the marsh organ setup. **c)** Close-up of a PVC pot subjected to the drained treatment showing an *Aster* seedling growing on *Vaucheria* algae and drilled holes that allow surface drainage.

5.4 Results

5.4.1 Intertidal elevation affects pioneer vegetation establishment

Our geospatial analysis indicated that the study site (from 2023 - 2024) was experiencing high rates of poorly consolidated, fine-grained sediment deposition (Fig. S5.3), which can be associated with the local intertidal elevation (Fig. 5.3b). Specifically, bed level change rates were greater at lower elevations and declined with increasing elevation ($F_{3,205}$ = 289.4, R^2 = 0.81, p < 0.001). This relationship between elevation, z, and the rate of bed level change, $r(z)$, can be described by the following regression model fit: $r(z) = ae^{-zb}$ in which a = 0.300 ± 0.032, b = 0.356 ± 0.023 ($F_{1,148}$ = 134, R^2 = 0.645, p < 0.001).

Vegetation establishment was closely associated with the intertidal elevation. Established marsh vegetation occurred at higher positions in the tidal frame (Fig. 5.3a) where bed level change was comparatively small, whereas unvegetated tidal flats were situated lower and experienced more intense elevation dynamics (Fig. 5.3c). A Mann-Whitney U test confirmed that the absolute rate of bed level change was significantly lower in vegetated than in bare areas (median of absolute rate of bed level change **vegetated areas** $\left(\frac{dz}{dt}\right)$ = 0.06 m/year vs. median of absolute rate of bed level change **bare areas** $\left(\frac{dz}{dt}\right)$ = 0.09 m/year; p < 0.001). The probability that a vegetated pixel had a smaller bed level change $\left(\frac{dz}{dt}\right)$ than a bare pixel was 0.636, demonstrating that vegetation preferentially established in zones experiencing weaker bed level dynamics.

The importance of intertidal elevation was also reflected by the findings of our field experiments (Fig. 5.4). The seedlings in the transplantation sites (located in the vegetation transition zone) showed a rapid decline in survival probability during the first 10 days, which then leveled off and led to complete mortality by day 30 (Fig. 5.4a). A similar pattern was observed in the marsh organ at the corresponding elevation (Fig. 5.4b). In contrast, survival probability was higher at the upper elevation level (representative for the vegetated zone) and declined even more rapidly at the lowest elevation level (bare zone), where complete mortality occurred within an even shorter period.

Overall, we found a significant effect of intertidal elevation on *Aster* seedling survival at the end of the marsh organ experiment (likelihood-ratio $\chi^2(2)$ = 12.7, p = 0.002). Specifically, the varying elevation levels resulted in significant differences in hazard ratios (i.e. the probability of mortality). Compared to the bare zone, the transition zone showed a 33% reduction in hazard ratio (HR = 0.67, z = –2.08, p = 0.038), while the vegetated zone showed a 55% reduction (HR = 0.45, z = –3.81, p < 0.001).

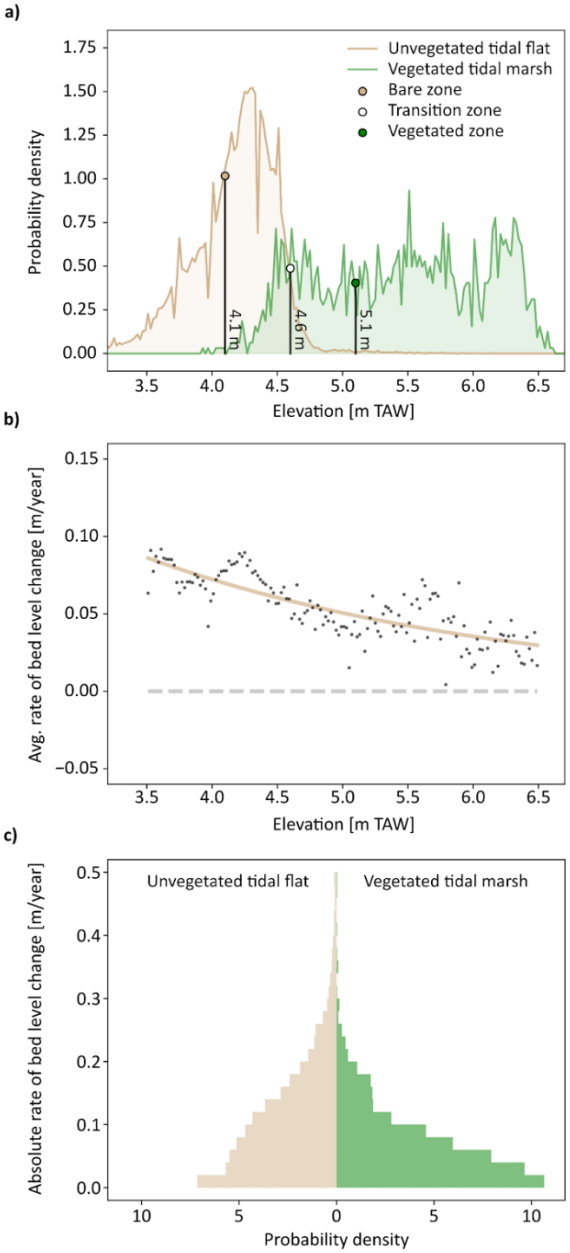


Figure 5.3: **a)** Histogram of bed elevation across the study site from 2024, divided into vegetated and unvegetated sectors. The elevations used in the field experiments are also indicated: the bare, transitional, and vegetated zones. **b)** The average annual change in bed level from 2023 to 2024 decays exponentially with increasing elevation. **c)** Paired histograms display the differences in the absolute annual change in bed level between vegetated and unvegetated areas in 2024. This may suggest that vegetation development is favored in areas where bed level dynamics are lower.

5.4.2 Subsoil compaction does not affect early vegetation establishment

We compared the effect of varying degrees of subsoil compaction across the Hedwigepolder (HP; historically compacted subsoil) and the Prosperpolder (PP; reworked subsoil). In both areas, vegetation preferentially started establishing above 4.6 m TAW (Fig. S5.4). We did not detect notable differences between HP and PP in the overall vegetation probability density and elevation relationship, although small vegetation patches tended to occur at slightly lower elevations in PP compared to HP. The difference in the tail of the S-curves can be attributed to the inclusion of a small part of Sieperda marsh (see Fig. 5.1b), a vegetated marsh adjacent to the Hedwige-Prosperpolder) in the analysis of Hedwigepolder.

5.4.3 (Sub)surface drainage enhances *Aster* seedling survival time

(Sub)surface drainage benefited seedling survival time in all elevation zones in the marsh organ experiment (Fig. 5.4b). It slightly reduced the mortality rate in the bare zone compared to the poorly drained treatment and enhanced survival in both the transition and vegetated zone.

Despite the visual trend in the graph described above, we did not find a significant effect of drainage treatment on seedling survival in the marsh organ experiment (likelihood-ratio $\chi^2(1) = 1.61$, $p = 0.204$). (Sub)surface drainage also did not significantly affect seedling survival time ($z = 1.08$, $p = 0.28$). However, seedling survival differed significantly among the treatments located in the transition zone, which included both the field plots and marsh organ experiment (likelihood-ratio $\chi^2(3) = 11.21$, $p = 0.01$). Seedlings transplanted in the field plots (i.e. compacted and reworked subsoil) exhibited significantly higher mortality rates compared to the seedlings transplanted in the drained treatment. Specifically, the seedlings in the compacted subsoil plot had the highest overall hazard ratio ($HR = 6.72$, $z = 11.057$, $p < 0.001$), while the seedlings in the reworked subsoil plot had a lower hazard ratio ($HR = 2.42$, $z = 5.139$, $p < 0.001$). The seedlings in the poorly drained treatment (i.e. marsh organ experiment) also experienced a slightly elevated risk of death compared to the drained treatment ($HR = 1.42$, $z = 1.731$, $p = 0.084$).

5.4.4 Sediment properties do not vary across drainage and elevation treatments

Sediment properties did not vary over the drainage and intertidal elevation treatments. The dry bulk density of the sediment cores was not significantly affected by elevation ($F_{2,14} = 2.19$, $p = 0.149$) and drainage treatment ($F_{1,14} = 0.031$, $p = 0.861$), nor was the median grain size ($F_{2,14} = 0.76$, $p = 0.490$ - elevation; $F_{1,14} = 1.18$, $p = 0.296$ - drainage treatment). Organic matter content was significantly affected by elevation

($F_{2,14}$ = 4.18, p = 0.038), but not by drainage treatment ($F_{1,14}$ = 0.080, p = 0.782). An overview of these results can be found in Table S5.2.

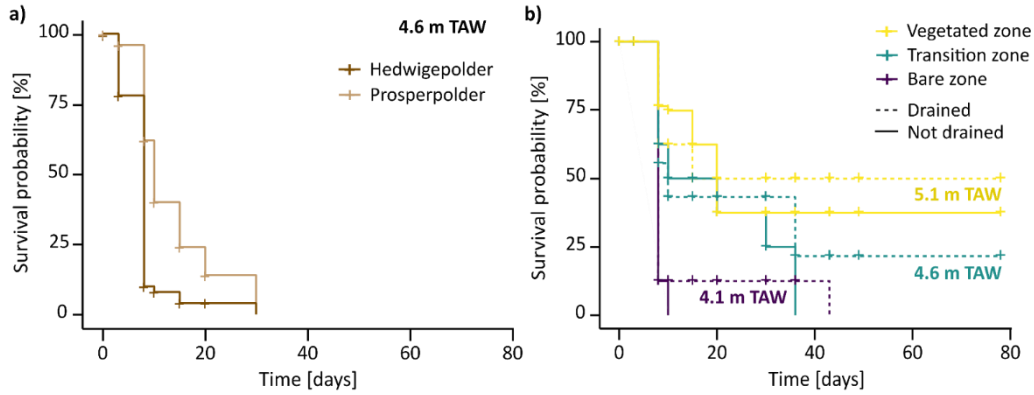


Figure 5.4: Kaplan Meier curves indicating the survival probability of transplanted *Aster* seedlings over the course of 78 days. In subplot **a)**, results are shown from the field transplantation plots (i.e. Dutch Hedwigepolder and the Belgian Prosperpolder), which were situated at an elevation of 4.6 m TAW, corresponding to the vegetation transition zone. In subplot **b)**, results from the marsh organ experiment are presented. The sediment cores were subjected to three elevation treatments (bare zone = 4.1 m TAW, transition zone = 4.6 m TAW, and vegetated zone = 5.1 m TAW) and two drainage treatments (not drained vs drained).

5.4.5 Increasing sediment drainage and elevation enhances shear strength

Sediment shear strength increased with both drainage and elevation level in the marsh organ experiment (Fig. 5.5a). The highest shear strength values were found in the vegetated zone, while the drained sediment cores showed consistently higher shear strength compared to their undrained counterparts. The most notable jump in shear strength can be found when comparing the drained and undrained sediment cores in the transition zone.

Both elevation level ($F_{2,42}$ = 37.73, p < 0.001) and drainage treatment ($F_{1,42}$ = 27.25, p < 0.001) had significant effects on sediment shear strength. A Tukey HSD post hoc test revealed significant differences between drained and undrained PVC pots in the vegetated zone (p = 0.019) and the transition zone (p < 0.001). No significant difference was found in the bare zone (p = 0.933), indicating that drainage treatment did not affect shear strength at this elevation.

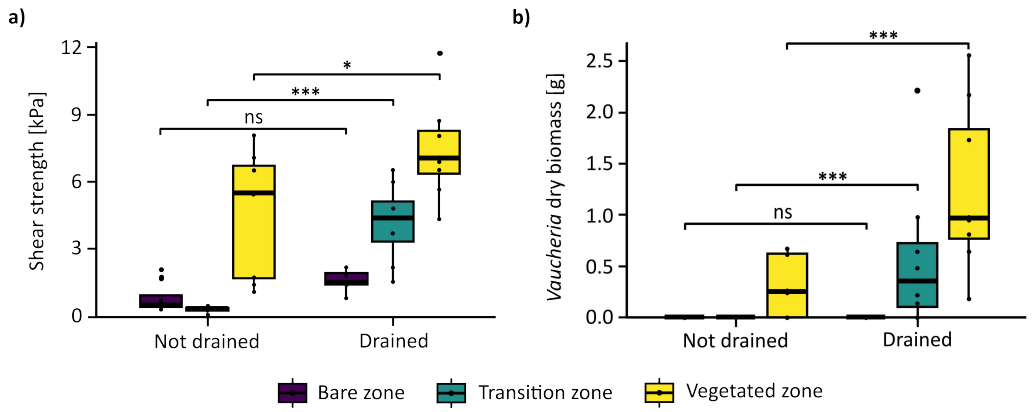


Figure 5.5: **a)** Superficial sediment shear strength across the different elevation zones (bare zone, transition zone and vegetated zone) and drainage treatments (not drained vs drained) in the marsh organ experiment. **b)** The recorded *Vaucheria* dry biomass across the different elevation zones and drainage treatments (n = 8). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Significant differences are indicated by * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

5.4.6 Sediment drainage promotes *Vaucheria* establishment

Vaucheria algae completely failed to establish in the bare zone (Fig. 5.5b) but started to cover the sediment surface in the slightly higher transition zone. However, this only occurred in the drained pots, where the algae were present in 75% of the pots (6 out of 8). At even higher elevations, in the vegetated zone, *Vaucheria* established in both drained (87.5%) and undrained pots (37.5%).

Statistical analysis confirmed that drainage treatment ($F_{1, 42} = 27.08$, $p < 0.001$), elevation levels ($F_{2, 42} = 27.88$, $p < 0.001$), and their interaction ($F_{2, 42} = 6.86$, $p = 0.003$) had significant effects on *Vaucheria* biomass. A Tukey HSD post hoc test revealed significant differences between drained and undrained pots in both the vegetated zone ($p = 0.002$) and transition zone ($p = 0.003$), while no such effect was found in the bare zone ($p = 1.000$).

5.5 Discussion

This study investigated the physical constraints limiting pioneer vegetation establishment (i.e. *Aster tripolium* and *Vaucheria* sp.) in a recently restored intertidal system, as well as potential interventions to promote successful colonization. Our geospatial analysis revealed that adding reworked soil on top of a compacted subsoil layer did not notably affect vegetation probability densities (Fig. S5.4). As expected, vegetation preferentially established at higher intertidal elevations, where bed level changes were less pronounced (Fig. 5.3). Our field experiment and marsh organ experiment with planted pioneer seedlings show that at elevations corresponding to

the vegetation transition zone, where initial vegetation establishment is theoretically possible, *Aster* seedling survival was strongly limited (Fig. 5.4). The marsh organ experiment showed that seedling survival improved under well-drained conditions at the same and higher elevation levels (Fig. 5.4b), which was associated with higher sediment shear strength, and the development of fibrous algae (Fig. 5.5).

Overall, these findings suggest the following. At low initial elevations, high rates of sediment deposition occur. In the absence of sufficient drainage, this may be expected to result in a waterlogged, unconsolidated mud bed. Such fluid mud bed is likely more susceptible to resuspension during high tides, making it therefore unsuitable for colonization by pioneer algae or vegetation. In addition, the anoxic conditions of waterlogged sediments may further impair seedling survival. Under well-drained conditions, however, surface shear strength can develop, even at comparatively lower elevations. This improves the sediment bed stability and reduces the risk of loss of algae and plant seedlings under the influence of tidal currents. This likely reflects a coupled feedback between (1) physical processes, i.e. drainage-induced development of cohesive sediment strength, and (2) biological processes, i.e. algal mat formation. Together, these processes may generate a "sediment-vegetation feedback", where improved sediment consolidation facilitates pioneer vegetation establishment, and vice versa. In the sections below, we will discuss this potential feedback mechanism in more detail.

5.5.1 Intertidal elevation and local sediment dynamics affect *Aster* seedling survival

The complete seedling loss observed in the field plots suggest that initial sediment surface elevation and local sediment dynamics form key constraints for vegetation establishment in early-stage tidal restoration. Since no dead standing biomass remained, this loss likely reflects physical removal of seedlings by tidal currents rather than local die-off caused by physiological stress such as prolonged inundation, anoxic conditions, or sulfide toxicity. Such loss could occur more easily in poorly drained and unconsolidated sediments with low shear strength, which are more vulnerable to erosion.

Geospatial analysis of the entire restoration site confirmed that vegetation establishment is largely confined to higher elevations within the tidal frame (Fig. 5.3a), where the bed level change is minimal (Fig. 5.3c). This can be attributed to the low initial platform elevation, as areas with low intertidal elevations experience a high rate of sediment deposition after de-embankment (Gerwing et al., 2020; Vandenbruwaene et al., 2012). The combination of low initial elevation and high deposition rates can contribute to the formation of an unconsolidated surface sediment layer that is prone to erosion and thus does not support vegetation establishment (Cao et al., 2018; Grabowski et al., 2011). At higher elevations,

however, it can be expected that tidally-deposited mud can dry out for a prolonged period during low tides as the mud bed is less frequently inundated. Hence, the sediment can gradually consolidate via porewater expulsion by the weight of the deposited sediments (Zhou et al., 2016) and lateral porewater drainage (Fivash et al., 2019; Van Putte et al., 2020). Additionally, porewater can get lost at the surface by prolonged drying of the sediment bed (Colosimo et al., 2023; Dong et al., 2020) and by evaporation (Colosimo et al., 2023; Fagherazzi et al., 2017; van Rees et al., 2024). During this process, the loss of porewater can create more erosion-resistant sediment beds (Colosimo et al., 2023; Fagherazzi et al., 2017; Fivash et al., 2024).

Overall, this indicates that although the transition zone may offer the right inundation regime, intense sediment dynamics (i.e. rapid accretion and erosion) might inhibit pioneer vegetation establishment, possibly by washing away seeds or due to the burial or uprooting of seedlings (e.g. Bouma et al., 2009; Cao et al., 2018; Zhu et al., 2014). As such, our results suggest that pioneer vegetation establishment is jointly controlled by initial site elevation and bed level change.

5.5.2 Sediment drainage and evaporation promote pioneer vegetation establishment and survival

Poor sediment drainage emerged as a factor that can limit seedling establishment. The marsh organ experiment demonstrated that even at the same elevation as the transplantation sites, *Aster* seedling survival markedly increased under drained conditions (Fig. 5.4b). A similar pattern was observed for *Vaucheria* establishment. Algal mats only developed in drained sediments in the transition zone (Fig. 5.5b). This suggests that both pioneer species can establish lower in the tidal frame, given the right drainage conditions. In the higher elevation zone, *Vaucheria* and *Aster* manage to establish and survive regardless of drainage, likely due to lower inundation frequencies and longer air exposure times that allowed surface drying (Fivash et al., 2024; van Rees et al., 2024).

Overall, the increase in seedling survival and algal establishment could be associated with the development of consolidated, erosion-resistant sediments (Fig. 5.5a). Interestingly, these trends were not reflected in higher dry bulk density, which is often linked to sediment beds with higher shear strength (Grabowski et al., 2011; Stoorvogel et al., 2025). Instead, our findings suggest that erosion resistance arises primarily from the combined effects of prolonged air exposure and effective (sub)surface drainage, consistent with previous studies (Cao et al., 2022; Fagherazzi et al., 2017; van Rees et al., 2024). Specifically, (sub)surface drainage contributes to shear strength development by dewatering the sediment: subsurface drainage reduces waterlogging, while surface drainage removes the overlying water layer allowing evaporation of the top layer during low tide (Cao et al., 2021, 2022; Dong et al., 2020; Xin et al., 2022). Evaporation further consolidates the upper sediment

layer, particularly under dry and windy conditions, thereby strengthening erosion resistance (Colosimo et al., 2023; Fivash et al., 2024; van Rees et al., 2024). These processes can take place because intertidal muddy sediment beds typically contain electrostatically charged clay minerals (Berlamont et al., 1993; Winterwerp & Van Kesteren, 2004b). In waterlogged conditions, clay particles are spaced farther apart, weakening electrostatic bonds and increasing erodibility. As porewater is expelled from the muddy sediment beds, flocs and aggregates settle into a denser arrangement, increasing the contact between the clay particles and strengthening electrostatic bonds (Chen et al., 2021; Torfs et al., 1996; Winterwerp & Van Kesteren, 2004a). Thus, the cohesive shear strength of muddy sediments increases as they increasingly dry out (Colosimo et al., 2023; Fagherazzi et al., 2017). Tidal creek proximity could amplify these processes as sediment drainage and surface evaporation are often more effective near tidal creeks, creating erosion-resistant zones that promote pioneer vegetation establishment (Chapter 4; Xin et al., 2022).

Over time, a positive loop may develop as the formation of the biostabilizing *Vaucheria* mats further promotes vegetation establishment (Chapter 3; van de Vijsel et al., 2020, 2021). Vegetation growth in turn enhances erosion resistance either directly through increasing belowground biomass (i.e. roots) or indirectly by trapping fine cohesive sediments (Brooks et al., 2021; Fagherazzi et al., 2012; Feagin et al., 2015; Gyssels et al., 2005).

5.5.3 Subsoil compaction history and implications for drainage

Our geospatial analysis did not reveal notable differences in the vegetation probability density between the Hedwigepolder (HP; historically compacted subsoil) and the Prosperpolder (PP; reworked subsoil) (Fig. S5.4). Both subareas showed vegetation establishment above ~4.6 m TAW, with only a slight tendency for vegetation to occur at lower elevations in PP compared to HP. This might indicate that, at least in the initial years following de-embankment, the degree of subsoil compaction has not yet resulted in strong differences in vegetation establishment patterns. In fact, the dry bulk density recorded in these areas did not substantially differ (Table S5.1), indicating that the addition of reworked soil had no measurable effect on subsoil compaction, and therefore had no significant impact on the vegetation.

Nonetheless, subsoil structure could influence restoration trajectories over longer timescales. Compacted subsoils are expected to hinder porewater drainage of newly deposited sediments, promoting prolonged waterlogging (Spencer et al., 2017; Van Putte et al., 2020). In contrast, reworked subsoils may facilitate drainage and thereby accelerate the development of surface shear strength, as suggested by the findings of our mesocosm experiment (Fig. 5.4 & 5.5). Thus, while our present results show little difference between HP and PP, future monitoring may reveal that vegetation

colonization proceeds more rapidly in areas with reworked subsoils that provide more favorable drainage conditions.

5.5.4 General implications for tidal marsh restoration practices

Our findings underline the importance of creating well-drained, erosion-resistant sediment surfaces at suitable elevations to promote pioneer vegetation establishment in restored tidal marshes. From a restoration perspective, this suggests that seedling survival might increase by combining interventions that (i) mitigate intense sediment dynamics, (ii) enhance sediment drainage, and (iii) promote air exposure time. Our results suggest that as surface elevation in restoration sites increases, the problems associated with waterlogged mud (e.g. low sediment shear strength and anoxic subsoil) should diminish, thereby allowing vegetation to establish. However, in well-drained areas (e.g. near tidal creeks or on locally raised sediment beds), vegetation might establish lower in the tidal frame, as improved drainage enhances sediment stability and oxygen availability, creating conditions favorable for colonization. Restoration measures such as raising the initial surface elevation, soil amendments to decompact the subsoils, creating topographic heterogeneity, or excavating tidal creeks may thus help accelerate the transition from a bare mudflat to vegetated marsh (Cao et al., 2022; Fivash et al., 2021; Mossman et al., 2020).

5.6 Acknowledgements

We cordially thank all people involved with the monitoring of the experiments. Special thanks go to Laura Bossaer, Liming Xue, Lauren Van Nimmen and Dawei Wang for assisting with the setup of the marsh organ experiment and collection of soil samples. This work was funded by the Fonds Wetenschappelijk Onderzoek (grant no. G031620N).

5.7 References

Airoldi, L., Beck, M. W., Firth, L. B., Bugnot, A. B., Steinberg, P. D., & Dafforn, K. A. (2021). Emerging Solutions to Return Nature to the Urban Ocean. *Annual Review of Marine Science*, *13*(1), 445–477. https://doi.org/10.1146/annurev-marine-032020-020015

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: Identifying Windows of Opportunity for recovery. *Journal of Ecology*, *102*(3), 700–708. https://doi.org/10.1111/1365-2745.12241

Berlamont, J., Ockenden, M., Toorman, E., & Winterwerp, J. (1993). The characterisation of cohesive sediment properties. *Coastal Engineering*, *21*(1–3), 105–128. https://doi.org/10.1016/0378-3839(93)90047-C

Bouma, T., Friedrichs, M., Klaassen, P., van Wesenbeeck, B., Brun, F., Temmerman, S., van Katwijk, M., Graf, G., & Herman, P. (2009). Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. *Marine Ecology Progress Series*, *388*, 293–297. https://doi.org/10.3354/meps08130

Brooks, H., Möller, I., Carr, S., Chirol, C., Christie, E., Evans, B., Spencer, K. L., Spencer, T., & Royse, K. (2021). Resistance of salt marsh substrates to near-instantaneous hydrodynamic forcing. *Earth Surface Processes and Landforms*, *46*(1), 67–88. https://doi.org/10.1002/esp.4912

Cao, H., Zhu, Z., Balke, T., Zhang, L., & Bouma, T. J. (2018). Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration: Sediment dynamics affect seedling establishment. *Limnology and Oceanography*, *63*(2), 647–659. https://doi.org/10.1002/lno.10657

Cao, H., Zhu, Z., Hu, Z., Wang, H., & Bouma, T. J. (2022). Drainage-Improved Sediment Strength Enhances Saltmarsh Seedling Establishment Chance. *Frontiers in Marine Science*, *9*, 874680. https://doi.org/10.3389/fmars.2022.874680

Cao, H., Zhu, Z., van Belzen, J., Gourgue, O., van de Koppel, J., Temmerman, O. S., Herman, P. M. J., Zhang, L., Yuan, L., & Bouma, T. J. (2021). Salt marsh establishment in poorly consolidated muddy systems: Effects of surface drainage, elevation, and plant age. *Ecosphere*, *12*(9). https://doi.org/10.1002/ecs2.3755

Chen, D., Zheng, J., Zhang, C., Guan, D., Li, Y., & Wang, Y. (2021). Critical Shear Stress for Erosion of Sand-Mud Mixtures and Pure Mud. *Frontiers in Marine Science*, *8*, 713039. https://doi.org/10.3389/fmars.2021.713039

Colosimo, I., Van Maren, D. S., De Vet, P. L. M., Winterwerp, J. C., & Van Prooijen, B. C. (2023). Winds of opportunity: The effects of wind on intertidal flat accretion. *Geomorphology*, *439*, 108840. https://doi.org/10.1016/j.geomorph.2023.108840

Crooks, S., Schutten, J., Sheern, G. D., Pye, K., & Davy, A. J. (2002). Drainage and Elevation as Factors in the Restoration of Salt Marsh in Britain. Restoration Ecology, 10(3), 591–602. https://doi.org/10.1046/j.1526-100X.2002.t01-1-02036.x

Dong, Y., Lu, N., & Fox, P. J. (2020). Drying-Induced Consolidation in Soil. *Journal of Geotechnical and Geoenvironmental Engineering*, *146*(9), 04020092. https://doi.org/10.1061/(ASCE)GT.1943-5606.0002327

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpaos, A., van de Koppel, J., Rybczyk, J. M., Reyes, E., Craft, C., & Clough, J. (2012). Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Reviews of Geophysics*, *50*(1), RG1002. https://doi.org/10.1029/2011RG000359

Fagherazzi, S., Viggato, T., Vieillard, A. M., Mariotti, G., & Fulweiler, R. W. (2017). The effect of evaporation on the erodibility of mudflats in a mesotidal estuary. *Estuarine, Coastal and Shelf Science*, *194*, 118–127. https://doi.org/10.1016/j.ecss.2017.06.011

Feagin, R. A., Figlus, J., Zinnert, J. C., Sigren, J., Martínez, M. L., Silva, R., Smith, W. K., Cox, D., Young, D. R., & Carter, G. (2015). Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Frontiers in Ecology and the Environment*, *13*(4), 203–210. https://doi.org/10.1890/140218

Fivash, G. S., Stoorvogel, M. M., De Smit, J. C., van Rees, F., Van Dalen, J., Grandjean, T. J., van de Vijsel, R. C., Bouma, T. J., Temmerman, S., & van Belzen, J. (2024). Abiotic origins of self-organized ridge-runnel patterns on tidal flats. *Limnology and Oceanography*, *69*(6), 1378–1389. https://doi.org/10.1002/lno.12581

Fivash, G. S., Temmink, R. J. M., D'Angelo, M., Dalen, J., Lengkeek, W., Didderen, K., Ballio, F., Heide, T., & Bouma, T. J. (2021). Restoration of biogeomorphic systems by creating windows of opportunity to support natural establishment processes. *Ecological Applications*, *31*(5). https://doi.org/10.1002/eap.2333

Fivash, G. S., van Belzen, J., Temmink, R. J. M., Didderen, K., Lengkeek, W., Heide, T. V. D., & Bouma, T. J. (2019). Elevated micro-topography boosts growth rates in Salicornia procumbens by amplifying a tidally driven oxygen pump: Implications for natural recruitment and restoration. *Annals of Botany*, *125*, 353–364. https://doi.org/10.1093/aob/mcz137

French, P. W. (2006). Managed realignment – The developing story of a comparatively new approach to soft engineering. *Estuarine, Coastal and Shelf Science*, *67*(3), 409–423. https://doi.org/10.1016/j.ecss.2005.11.035

Gallagher, S. B., & Humm, H. J. (1981). Vaucheria (Xanthophyceae, Vaucheriaceae) of the central Florida gulf coast. *Bulletin of Marine Science*, *31*(1), 184-19.

Gedan, K. B., Silliman, B. R., & Bertness, M. D. (2009). Centuries of Human-Driven Change in Salt Marsh Ecosystems. *Annual Review of Marine Science*, *1*(1), 117–141. https://doi.org/10.1146/annurev.marine.010908.163930

Gerwing, T. G., Davies, M. M., Clements, J., Flores, A.-M., Thomson, H. M., Nelson, K. R., Kushneryk, K., Brouard-John, E. K., Harvey, B., & Plate, E. (2020). Do you want to breach an embankment? Synthesis of the literature and practical considerations for breaching of tidally influenced causeways and dikes. *Estuarine, Coastal and Shelf Science*, *245*, 107024. https://doi.org/10.1016/j.ecss.2020.107024

Gourgue, O., van Belzen, J., Schwarz, C., Vandenbruwaene, W., Vanlede, J., Belliard, J.-P., Fagherazzi, S., Bouma, T. J., van de Koppel, J., & Temmerman, S. (2022). Biogeomorphic modeling to assess the resilience of tidal-marsh restoration to sea level rise and sediment supply. *Earth Surface Dynamics*, *10*(3), 531–553. https://doi.org/10.5194/esurf-10-531-2022

Grabowski, R. C., Droppo, I. G., & Wharton, G. (2011). Erodibility of cohesive sediment: The importance of sediment properties. *Earth-Science Reviews*, *105*(3–4), 101–120. https://doi.org/10.1016/j.earscirev.2011.01.008

Gyssels, G., Poesen, J., Bochet, E., & Li, Y. (2005). Impact of plant roots on the resistance of soils to erosion by water: A review. *Progress in Physical Geography: Earth and Environment*, *29*(2), 189–217. https://doi.org/10.1191/0309133305pp443ra

Heiri, O., Lotter, A. F., & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. *Journal of Paleolimnology*, *25*(1), 101–110. https://doi.org/10.1023/A:1008119611481

Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Centre for Ecology and Hydrology. http://www.ceh.ac.uk/products/publications/plantatt-attributesofbritishandirishplantsstatussizelifehistorygeographyandhabitats.html

Hu, Z., Borsje, B. W., van Belzen, J., Willemsen, P. W. J. M., Wang, H., Peng, Y., Yuan, L., De Dominicis, M., Wolf, J., Temmerman, S., & Bouma, T. J. (2021). Mechanistic Modeling of Marsh Seedling Establishment Provides a Positive Outlook for Coastal Wetland Restoration Under Global Climate Change. *Geophysical Research Letters*, *48*(22), e2021GL095596. https://doi.org/10.1029/2021GL095596

Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beeftink, W. G., Markusse, M. M., & Munck, W. D. (1995). Seed Dispersal of Halophytes in Tidal Salt Marshes. *The Journal of Ecology*, *83*(4), 559. https://doi.org/10.2307/2261624

Lawrence, P. J., Smith, G. R., Sullivan, M. J. P., & Mossman, H. L. (2018). Restored saltmarshes lack the topographic diversity found in natural habitat. *Ecological Engineering*, *115*, 58–66. https://doi.org/10.1016/j.ecoleng.2018.02.007

Morris, J. T. (2007). Estimating Net Primary Production of Salt Marsh Macrophytes. In T. J. Fahey & A. K. Knapp (Eds.), *Principles and Standards for Measuring Primary Production* (pp. 106–119). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195168662.003.0007

Mossman, H. L., Davy, A. J., & Grant, A. (2012). Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites? *Journal of Applied Ecology*, *49*(6), 1446–1456. https://doi.org/10.1111/j.1365-2664.2012.02198.x

Mossman, H. L., Grant, A., & Davy, A. J. (2020). Manipulating saltmarsh microtopography modulates the effects of elevation on sediment redox potential and halophyte distribution. *Journal of Ecology*, *108*(1), 94–106. https://doi.org/10.1111/1365-2745.13229

Oosterlee, L., Cox, T. J. S., Temmerman, S., & Meire, P. (2020). Effects of tidal re-introduction design on sedimentation rates in previously embanked tidal marshes. *Estuarine, Coastal and Shelf Science*, *244*, 106428. https://doi.org/10.1016/j.ecss.2019.106428

Oranjewoud, & Antea Group. (2013). *Ontwikkeling van een intergetijdengebied in Hedwige- en Prosperpolder: Definitief MER – tekstbundel*.

https://www.commissiemer.nl/docs/mer/p17/p1773/1773-132mer.pdf

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91–95. https://doi.org/10.1038/s41586-019-0951-7

Schoutens, K., Heuner, M., Minden, V., Schulte Ostermann, T., Silinski, A., Belliard, J., & Temmerman, S. (2019). How effective are tidal marshes as nature-based shoreline protection throughout seasons? *Limnology and Oceanography*, *64*(4), 1750–1762. https://doi.org/10.1002/lno.11149

Spencer, K. L., Carr, S. J., Diggens, L. M., Tempest, J. A., Morris, M. A., & Harvey, G. L. (2017). The impact of pre-restoration land-use and disturbance on sediment structure, hydrology and the sediment geochemical environment in restored saltmarshes. *Science of The Total Environment*, *587–588*, 47–58. https://doi.org/10.1016/j.scitotenv.2016.11.032

Stoorvogel, M. M., Willemsen, P. W. J. M., van Belzen, J., Temmerman, S., De Jonge, J. M., van de Koppel, J., & Bouma, T. J. (2025). Nature-based mitigation of shoreline erosion risks in tidal marshes created by managed realignment vs. Sediment nourishment. *Ecological Engineering*, *210*, 107439. https://doi.org/10.1016/j.ecoleng.2024.107439

Temmerman, S., Horstman, E. M., Krauss, K. W., Mullarney, J. C., Pelckmans, I., & Schoutens, K. (2023). Marshes and Mangroves as Nature-Based Coastal Storm Buffers. *Annual Review of Marine Science*, *15*(1), 95–118. https://doi.org/10.1146/annurev-marine-040422-092951

Torfs, H., Mitchener, H., Huysentruyt, H., & Toorman, E. (1996). Settling and consolidation of mud/sand mixtures. *Coastal Engineering*, *29*(1–2), 27–45. https://doi.org/10.1016/S0378-3839(96)00013-0

van Belzen, J., Van De Koppel, J., Kirwan, M. L., Van Der Wal, D., Herman, P. M. J., Dakos, V., Kéfi, S., Scheffer, M., Guntenspergen, G. R., & Bouma, T. J. (2017). Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. *Nature Communications*, *8*(1), 15811. https://doi.org/10.1038/ncomms15811

Van Damme, S., Struyf, E., Maris, T., Ysebaert, T., Dehairs, F., Tackx, M., Heip, C., & Meire, P. (2005). Spatial and temporal patterns of water quality along the estuarine salinity gradient of the Scheldt estuary (Belgium and The Netherlands): Results of an integrated monitoring approach. *Hydrobiologia*, *540*(1–3), 29–45. https://doi.org/10.1007/s10750-004-7102-2

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Cusseddu, V., Purkis, S. J., Rietkerk, M., & Koppel, J. (2020). Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. *Earth Surface Processes and Landforms*, *45*(5), 1141–1154. https://doi.org/10.1002/esp.4783

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., & van de Koppel, J. (2021). Algal-Induced Biogeomorphic Feedbacks Lay the Groundwork for Coastal Wetland Development. *Journal of Geophysical Research: Biogeosciences*, *126*(10). https://doi.org/10.1029/2021JG006515

Van Putte, N., Meire, P., Seuntjens, P., Joris, I., Verreydt, G., Hambsch, L., & Temmerman, S. (2022). Solving hindered groundwater dynamics in

restored tidal marshes by creek excavation and soil amendments: A model study. *Ecological Engineering*, *178*, 106583. https://doi.org/10.1016/j.ecoleng.2022.106583

Van Putte, N., Temmerman, S., Verreydt, G., Seuntjens, P., Maris, T., Heyndrickx, M., Boone, M., Joris, I., & Meire, P. (2020). Groundwater dynamics in a restored tidal marsh are limited by historical soil compaction. *Estuarine, Coastal and Shelf Science*, *244*, 106101. https://doi.org/10.1016/j.ecss.2019.02.006

van Rees, F. F., Hanssen, J., Gamberoni, S., Talmon, A. M., & Van Kessel, T. (2024). Effect of air exposure time on erodibility of intertidal mud flats. *Frontiers in Marine Science*, *11*, 1393262. https://doi.org/10.3389/fmars.2024.1393262

van Regteren, M., Colosimo, I., de Vries, P., van Puijenbroek, M. E. B., Freij, V. S., Baptist, M. J., & Elschot, K. (2019). Limited seed retention during winter inhibits vegetation establishment in spring, affecting lateral marsh expansion capacity. *Ecology and Evolution*, *9*(23), 13294–13308. https://doi.org/10.1002/ece3.5781

Vandenbruwaene, W., Bertels, J., Michielsen, S., Thant, S., Van Den Berg, M., Brackx, M., Hertoghs, R., Claeys, S., Plancke, Y., Meire, D., Vereecken, H., & Deschamps, M. (2022). Monitoring Effecten Ontwikkelingsschets (MONEOS) – Jaarboek monitoring 2021: Data rapportage monitoring waterbeweging en fysische parameters in Zeeschelde en bijrivieren. *Title : WL Rapporten. Waterbouwkundig Laboratorium: Antwerpen. Volume : PA047_11*, 91 + 19 p. bijl. https://doi.org/10.48607/139

Vandenbruwaene, W., Meire, P., & Temmerman, S. (2012). Formation and evolution of a tidal channel network within a constructed tidal marsh. *Geomorphology*, *151–152*, 114–125. https://doi.org/10.1016/j.geomorph.2012.01.022

Wang, C., & Temmerman, S. (2013). Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. *Journal of Geophysical Research: Earth Surface*, *118*(1), 229–240. https://doi.org/10.1029/2012JF002474

Winterwerp, J. C., & Van Kesteren, W. G. M. (2004a). Self-Weight Consolidation. In *Developments in Sedimentology* (Vol. 56, pp. 211–251). Elsevier. https://doi.org/10.1016/S0070-4571(04)80008-6

Winterwerp, J. C., & Van Kesteren, W. G. M. (2004b). The Nature of Cohesive Sediment. In *Developments in Sedimentology* (Vol. 56, pp. 29–85). Elsevier. https://doi.org/10.1016/S0070-4571(04)80004-9

Xin, P., Wilson, A., Shen, C., Ge, Z., Moffett, K. B., Santos, I. R., Chen, X., Xu, X., Yau, Y. Y. Y., Moore, W., Li, L., & Barry, D. A. (2022). Surface Water and Groundwater Interactions in Salt Marshes and Their Impact on Plant Ecology and Coastal Biogeochemistry. *Reviews of Geophysics*, *60*(1). https://doi.org/10.1029/2021RG000740

Zhou, Z., Van Der Wegen, M., Jagers, B., & Coco, G. (2016). Modelling the role of self-weight consolidation on the morphodynamics of accretional mudflats. *Environmental Modelling & Software*, *76*, 167–181. https://doi.org/10.1016/j.envsoft.2015.11.002

Zhu, Z., Bouma, T., Ysebaert, T., Zhang, L., & Herman, P. (2014). Seed arrival and persistence at the tidal mudflat:

Identifying key processes for pioneer seedling establishment in salt marshes. *Marine Ecology Progress Series*, *513*, 97–109. https://doi.org/10.3354/meps10920

6

General discussion

6.1 Synthesis

Tidal marshes are widely recognized as ecosystems of high ecological and societal value as they provide essential ecosystem services such as coastal protection and carbon sequestration (Barbier et al., 2011; Temmerman et al., 2023; Temmink et al., 2022). Yet, they are under increasing pressure from climate change and human disturbance (Kirwan & Megonigal, 2013; Schuerch et al., 2018). As a result, tidal marsh restoration has received growing interest. However, in many cases the restored tidal marsh landscapes exhibit slow or limited development compared to natural reference sites (Lawrence et al., 2018; Mossman et al., 2012; Spencer et al., 2017). Understanding the mechanisms that affect tidal marsh development is therefore important for future restoration projects.

The overarching aim of this thesis was to improve our mechanistic understanding of abiotic and biotic controls on tidal marsh development. To accomplish this, we investigated (1) the relative role of abiotic and biotic factors on tidal creek network development, followed by (2) the mechanisms controlling pioneer vegetation establishment in restored tidal sites. By combining flume experiments, field experiments, mesocosm experiments, and monitoring surveys with geospatial analysis, this thesis provides a better understanding of the mechanisms at play.

We found that tidal creek network development is primarily affected by the rate of vegetation colonization, rather than by the spatial colonization pattern (patchy versus homogenous). This biotic control on tidal creek development was especially present during the transition phase from a bare mudflat to vegetated marsh. Furthermore, an interdependency was found between abiotic factors (hydrodynamic energy) and biotic factors (vegetation recruitment strategy): the force of abiotic factors determines whether biotic factors have an additional effect on tidal creek network development. This suggests that tidal creek development is predominantly affected by abiotic processes, and only where abiotic processes have a minor influence, biotic factors play an additional role (Chapter 2). Next, our findings showed that pioneer vegetation establishment in a tidal marsh restoration site can be facilitated by mat-forming filamentous algae (i.e. *Vaucheria*) as they exclude predating polychaetes such as *Hediste diversicolor* (Chapter 3). These algae and pioneer plants prefer to establish along tidal creeks. We found that these zones promote seed retention and seedling survival (also on lower elevations in the tidal frame), in association with increased erosion-resistance of the sediment surface layer. We suggest that the latter can be related to faster drainage of subsurface porewater along tidal creek edges. This leads to faster drying of the surface sediment layer, which is known to increase the cohesive strength of the muddy sediments (Chapter 4).

Finally, our findings indicate that low intertidal elevation, intense bed level dynamics and poor sediment drainage restrict pioneer vegetation establishment in restored tidal marshes. Soil compaction does not affect vegetation probability in the early stages but might play a role in later stages (Chapter 5). The main findings and conclusions from the chapters are represented in Figure 6.1 and Figure 6.2.

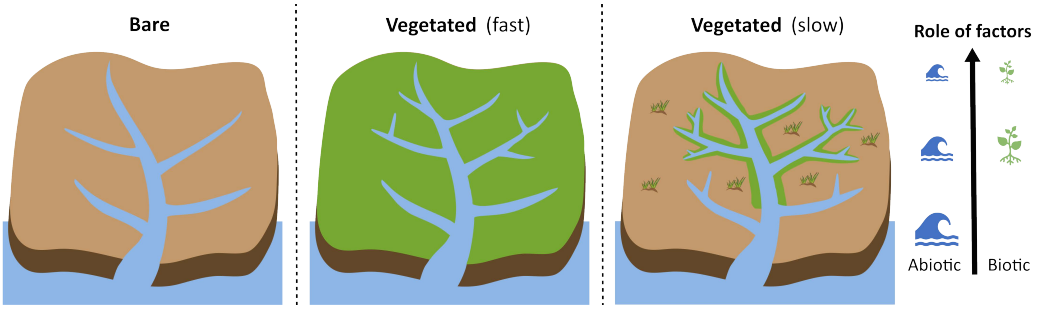


Figure 6.1: Tidal creek network development depends on abiotic and biotic factors. The geometric characteristics and drainage efficiency of these creek networks vary across different scenarios. In a bare tidal mudflat, creek networks remain relatively simple (e.g. lower drainage density and less branching) compared to the networks obtained in vegetated marshes. Vegetation establishment rate is an additional factor affecting creek network evolution. A fast colonization rate results in lower drainage efficiency compared to a slow colonization rate. The relative role of abiotic and biotic factors spatially differs across an intertidal basin. Near the seaward side, where tidal hydrodynamics are stronger, abiotic factors dominate creek development. More landward, where tidal hydrodynamics are weaker (smaller tidal prism), biotic factors start having an additional effect promoting further creek development. The effect of both abiotic and biotic factors starts diminishing at the most landward side of the intertidal basin as hydrodynamic energy (tidal prism) becomes too low to induce creek incision.

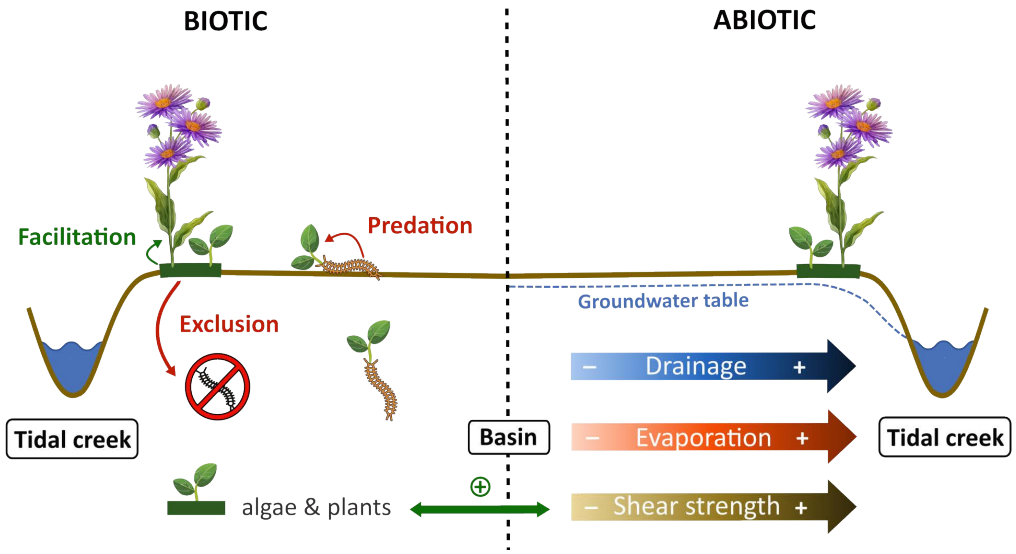


Figure 6.2: A cross-section of a tidal creek and mud basin depicting the investigated biotic and abiotic mechanisms affecting pioneer vegetation establishment. On the left side, the biotic interactions between polychaetes (e.g. *Hediste*), filamentous algae (e.g. *Vaucheria*) and plant seedlings (e.g. *Aster*) are depicted. Polychaetes predate plant seeds and seedlings thereby preventing plant establishment. This feeding behavior is however prevented when filamentous algae are present. We hypothesize that the dense filamentous mat created by these algae may exclude the polychaetes by either (1) limiting the benthos mobility, and/or by (2) creating anoxic conditions. This exclusion of benthos predation by the algae, along with the algal ability to stabilize the sediment bed, facilitate plant establishment. On the right side, the abiotic mechanisms influencing colonization are depicted. Plants prefer to establish along tidal creeks, which could be attributed to higher sediment drainage capacity and faster drying of surface sediment, which increases erosion resistance of cohesive muddy sediments. All these mechanisms positively affect algal and plant establishment, which in turn further promotes erosion resistance.

6.2 Interactions between creek network development and pioneer vegetation establishment

Our chapters demonstrate that tidal creek development and pioneer vegetation establishment are tightly coupled through interacting abiotic and biotic processes. The process is initiated by the emergence of tidal creeks during the early stages of marsh development, which introduce spatial heterogeneity in (sub)surface drainage conditions.

As shown in Chapters 4 and 5, sufficiently high areas with locally improved drainage conditions - such as tidal creeks - create zones with increased sediment surface drying time during low tide. The combination of efficient (sub)surface drainage and prolonged drying time can lead to the rapid development of erosion-resistant

sediment surfaces. These erosion-resistant zones provide favorable abiotic conditions for the establishment of filamentous mat-forming algae such as *Vaucheria*. Increased sediment stability and algal mat formation likely promote seed retention, thereby facilitating pioneer plant establishment.

However, favorable abiotic conditions alone are insufficient to guarantee successful vegetation establishment. As demonstrated in Chapter 3, biotic interactions, such as seedling predation, can strongly suppress pioneer plant survival. The presence of *Vaucheria* mitigates these antagonistic interactions by excluding the polychaetes. As such, the algae act as ecosystem engineers that create local refuges from physical and biotic disturbance.

Taken together, these results indicate that successful pioneer vegetation establishment emerges from a sequence of interacting processes. Hydrodynamic forcing initiates creek development during the earliest stages of tidal marsh development, creating the physical template required for pioneer vegetation establishment (Chapters 3, 4 & 5). Once pioneer plants start to establish, vegetation–landform interactions can further modify creek network development, potentially increasing creek network density (Chapter 2). This increased drainage density may in turn reinforce favorable abiotic conditions, creating a positive feedback that promotes further vegetation establishment.

In the sections below, we further disentangle the relative roles of abiotic and biotic processes governing early tidal marsh development and discuss how their interactions affect tidal creek development and pioneer vegetation establishment respectively.

6.3 Abiotic and biotic controls on tidal creek development

Tidal creek networks form the structural backbone of intertidal landscapes, regulating tidal marsh development and its ecosystem functions (Fagherazzi et al., 2012; Schwarz et al., 2018; Temmerman et al., 2007). As such, effective tidal marsh restoration requires understanding of the factors affecting tidal creek network development. The flume experiments conducted in this thesis revealed that the relative role of abiotic and biotic factors in creek network development shifts across spatial and temporal scales (Chapter 2). The following sections will focus on these factors shaping creek network development during the transition from bare mudflat to vegetated marsh, as our findings showed that creek network density and complexity are most susceptible to change during this stage.

In the initial stages of marsh development, tidal creek incision is driven entirely by physical processes (e.g. hydrodynamic energy) in a bare tidal mudflat. This initial formation of creek networks occurs fast, in the span of years (e.g. D'Alpaos et al., 2005, 2007; Fagherazzi & Furbish, 2001; Schwarz et al., 2014). In the next step,

vegetation colonizes the tidal flat, inducing vegetation-flow-sediment feedbacks which alter flow pathways. Within these vegetation patches, tidal flow velocity reduces and sediment gets trapped (Fagherazzi et al., 2012; Kirwan & Megonigal, 2013; Mudd et al., 2010). Conversely, around the vegetation patches, tidal flow velocity increases due to vegetation friction, initiating further creek incision (e.g. Temmerman et al., 2007; van Wesenbeeck et al., 2008; Vandenbruwaene et al., 2011). As a result, vegetated marshes exhibit higher creek network densities than bare tidal mudflats (e.g. Kearney & Fagherazzi, 2016; Schwarz et al., 2014; van de Vijsel et al., 2023; Vandenbruwaene et al., 2013). These tidal creek networks drain more efficiently than the networks found in bare intertidal flats because a larger portion of the marsh platform is located near a creek. The higher proximity to creeks can be attributed to differences in geometric characteristics due to increased branching and meandering of the creeks (Kearney & Fagherazzi, 2016; van de Vijsel et al., 2023). Specifically, spatio-temporal plant colonization patterns have been shown to affect creek network development and its geometry. Slow and patchy plant colonization (e.g. *Spartina* or *Scirpus* spp.) has been shown to promote creek network formation, while fast and homogenous plant colonization (e.g. mangrove species or *Salicornia* spp.) stabilizes pre-existing creeks (Schwarz et al., 2018, 2022). Our flume experiments suggest that vegetation colonization rate rather than vegetation patchiness controls creek network development (Chapter 2). In the hydrochorous seeding experiment (e.g. *Aster* spp.), vegetation expanded slowly. Consequently, flow concentration between the slowly developing vegetation zones could promote creek development, resulting in a more efficiently draining creek network compared to the patchy seeding experiment exhibiting faster and denser colonization. These findings highlight that the temporal dynamics of vegetation establishment (i.e. the rate of vegetation colonization), rather than the spatial recruitment pattern, may be the key driver of creek network development.

Furthermore, our flume experiments showed that spatial variability in hydrodynamic energy (tidal prism) within an intertidal basin affects tidal creek network development (Chapter 2). We hypothesize that at the seaward side, where the tidal prism (i.e. the flood and ebb water volumes) is largest, tidal flow velocities are strongest. Such conditions limit vegetation colonization and cause creek development to be dominated by abiotic hydrodynamic forcing. In more landward, lower hydrodynamic energy zones, vegetation-flow interactions can take place, enhancing creek network development. In the most landward side, the hydrodynamic energy is too low to induce creek incision. The resulting zonation suggests that the relevance of biotic factors depend upon abiotic thresholds: vegetation-flow feedbacks emerge only when hydrodynamic energy is moderate enough to allow colonization. This finding aligns with previous work indicating that abiotic processes predominantly control creek network development and complexity, while biotic processes play a secondary role (Liu et al., 2022).

6.4 Bottlenecks for pioneer vegetation establishment in restored tidal marshes

Restored tidal marshes often struggle to achieve vegetation establishment, which could be related to their low initial elevation, historically compacted subsoil (e.g. caused by agricultural activities prior to de-embankment), and poor drainage (Cao et al., 2021; Gerwing et al., 2020; Mossman et al., 2012; Spencer et al., 2017; Van Putte et al., 2020). These conditions likely result in rapid sediment deposition, long inundation periods, and slow sediment consolidation. In the absence of efficient drainage, the deposits often remain in an unconsolidated, waterlogged state that is easily erodible by tidal currents and wave action (Cao et al., 2021; Oosterlee et al., 2020; Vandenbruwaene et al., 2012). As a consequence of this poor sediment stability, seed retention and seedling anchorage are limited, delaying the transition from a bare mudflat to a vegetated marsh (Cao et al., 2021, 2022). Our findings indicate that successful vegetation establishment not only depends on overcoming these physical limitations but also on biotic interactions occurring within this environment. In particular, we showed that the development of erosion-resistant sediment beds (through increased subsurface sediment drainage and increased sediment surface elevation, both promoting sediment drying at low tides), and biotic interactions (e.g. seedling predation), collectively determine whether pioneer vegetation can establish successfully (Chapters 3, 4 & 5).

6.4.1 Erosion resistance as a prerequisite for pioneer vegetation establishment: the role of sediment drainage, intertidal elevation and sediment drying

We found that pioneer vegetation establishment critically depends on the erosion resistance of the sediment bed, which is affected by both abiotic and biotic processes (Chapters 4 & 5). Erosion resistance varied spatially across the tidal marsh, with significantly higher shear strength values in areas located higher in the tidal frame (Chapter 5) and in well-drained areas, such as tidal creek edges (Chapters 4 & 5).

Our findings in Chapters 4 and 5 suggest that sediment consolidation is enhanced in such areas, as they are less subjected to prolonged inundation and sediment disturbance. Sediment consolidation occurs via porewater expulsion from either prolonged drying of the sediment bed or the accumulating weight of sediment deposits (Dong et al., 2020; Winterwerp & Van Kesteren, 2004; Zhou et al., 2016). Drying-induced consolidation can be further aided during low tide by lateral porewater drainage, evaporation and wind when an overlying water layer is absent (Colosimo et al., 2023; Fagherazzi et al., 2017; Fivash et al., 2019, 2024; van Rees et al., 2024). During porewater expulsion, the void ratio decreases as sediment particles settle closer together, enhancing contact between the particles and their electrostatic bonds (Chen et al., 2021; Torfs et al., 1996; Winterwerp & Van Kesteren,

2004). As a result, cohesive shear strength and sediment erosion resistance increases in higher and/or well-drained areas. Such areas are thus less prone to sediment disturbance (i.e. accretion or erosion), which allows seedlings to establish more successfully (Chapters 4 & 5; Cao et al., 2018, 2021).

Interestingly, these spatial patterns in erosion resistance were not consistently reflected in higher dry bulk density (Chapters 4 & 5). This suggests that the observed increase in surface sediment shear strength was primarily driven by "short-term consolidation processes", such as sediment drying (by evaporation and lateral porewater drainage) rather than long-term self-weight consolidation. These findings align with recent studies reporting rapid increase in surface shear strength as mudflat sediment surfaces dry out during low tide (Colosimo et al., 2023; Fivash et al., 2024; van Rees et al., 2024).

In Chapter 4 we showed that tidal creek edges provide favorable establishment conditions even in lower parts of the tidal frame. This could be attributed to the efficient lateral porewater drainage in these zones, which may mitigate issues related to waterlogged conditions such as soil anoxia (Cao et al., 2012; Ursino et al., 2004; Xin et al., 2022). In addition, we found that the sediment surface along creek edges experience prolonged air exposure during low tide (see Fig. S4.6). Such prolonged air exposure potentially enables rapid sediment surface strengthening within hours through drying-induced consolidation and evaporation (Fivash et al., 2024; van Rees et al., 2024). Emergence periods and evaporation-induced consolidation (in absence of an overlying water layer) can thus play a crucial role in improving sediment stability and indirectly facilitate vegetation establishment.

Biological processes further contribute to the development of sediment erosion resistance. Filamentous algae such as *Vaucheria* sp. act as early biostabilizers by trapping and binding fine sediments, forming elevated hummocks and dense filamentous mats with increased surface roughness (van de Vijsel et al., 2020, 2021). These hummocks and algal mats provide improved drainage and oxygen conditions and typically exhibit higher shear strength compared to the surrounding bare mud (Fivash et al., 2019; van de Vijsel et al., 2020). As such, they create favorable conditions for seed retention and seedling survival (Chapters 3 & 4; van de Vijsel et al., 2021). Once seedlings establish, their root systems further enhance sediment consolidation, reinforcing erosion resistance and initiating a positive feedback loop between vegetation establishment and sediment stability (Brooks et al., 2021; Feagin et al., 2015; Gyssels et al., 2005).

Taken together, our findings demonstrated that erosion resistance depends on multiple interacting mechanisms. Drainage, intertidal elevation, and evaporation collectively determine whether the sediment surface can withstand prolonged tidal forcing and wave action. Where these processes align, such as along well-drained tidal creek edges offering longer emergence periods, seedlings are more likely to

survive. Where they do not, vegetation establishment remains limited. Low, poorly drained and unconsolidated sediment beds thus represent an important bottleneck in the early phases of tidal marsh development.

6.4.2 Competitive biotic interactions constrain or facilitate establishment

While developing erosion-resistant sediment beds is important, it does not guarantee successful colonization. Our experiments showed that three-way interactions between benthic algae, macrobenthos and plants actively shape pioneer plant establishment (Chapter 3). Predation by the polychaete *Hediste diversicolor* significantly reduced the survival of *Aster tripolium* seedlings, consistent with findings in other systems where benthic predators limit pioneer vegetation establishment (Hughes, 1999; Paramor & Hughes, 2004, 2005; van Regteren et al., 2017). Furthermore, the bioturbation of these polychaetes indirectly affects establishment success by reducing sediment stability (van Belzen, 2024). In Chapter 3, we show that these negative effects can be mitigated once filamentous algae (e.g. *Vaucheria*) start to establish. Filamentous algae are ecosystem engineers that positively modify environmental conditions for plant colonization by enhancing local sediment stability and creating elevated, well-drained hummocks (Fivash et al., 2019; van de Vijsel et al., 2020, 2021). Additionally, our findings indicated that the algae suppress polychaete densities and weaken their top-down control (Chapter 3). This can potentially be attributed to the algae acting as (1) a physical barrier to burrowing activity by the polychaetes, whilst creating prolonged anoxic conditions in the sediment bed beneath the dense algal mat, and as (2) an alternative, more digestible food source for the polychaetes (Chapter 3). As such, the filamentous algae form a refuge from environmental stress (e.g. polychaete predation and sediment disturbance) and facilitate plant establishment. This facilitative interaction seems especially important during the early stages of tidal marsh development and may decrease in strength over time due to decreasing stress (Bertness & Hacker, 1994; He et al., 2013; Silliman et al., 2015).

Our findings suggest that abiotic and biotic mechanisms are closely intertwined in shaping pioneer vegetation establishment. Abiotic processes, particularly sediment drainage and evaporation, create well-drained, erosion-resistant areas that provide the environmental foundation for facilitative biotic interactions (Chapters 4 & 5). In these areas, filamentous algae can establish, further enhancing sediment surface stability and suppressing predating polychaetes, which in turn facilitates the establishment of pioneer plants (Chapter 3). As such, abiotic factors act as the primary drivers that enable biotic facilitation to occur. Our results highlight that poor sediment drainage, low sediment stability and seedling predation form bottlenecks for tidal marsh development. Restoration efforts should thus aim to promote sediment drainage, sediment stability, and facilitative biotic interactions.

6.5 Implications for tidal marsh restoration practices

Based on our findings, some practical recommendations are proposed for future restoration projects that could help accelerate the transition from bare mudflat to vegetated marsh.

1. Consider the initial platform elevation of formerly embanked sites

Restored tidal marshes typically have a lower relative elevation compared to adjacent sites as the sites were cut off from tidal sediment supply during the embankment period (Crooks et al., 2002). Consequently, these restored marshes are subjected to high inundation frequencies and sediment deposition rates after the reintroduction of tidal cycles (Gerwing et al., 2020; Oosterlee et al., 2020; Vandenbruwaene et al., 2012). This can lead to waterlogged, unconsolidated and anoxic sediment beds in absence of sediment drainage which hinder vegetation establishment. Such issues can be mitigated by either slightly raising the landscape or by applying a controlled reduced tide (CRT) principle (described in detail in Cox et al., 2006; Maris et al., 2007). In the latter technique, high inlet and low outlet culverts can reduce inundation frequency and the volume of water entering the system (Beauchard et al., 2011; Jacobs et al., 2009; Maris et al., 2007; Oosterlee et al., 2020). As such, inundation frequency can be lowered, prolonging air exposure time and opportunities for porewater drainage. Properly balancing the hydroperiod is therefore crucial to ensure sufficient sediment supply for sediment accretion while maintaining conditions favorable for seedling survival.

2. Create improved sediment drainage conditions by excavating creeks and reworking the compacted subsoil layer

In addition to sediment surface elevation, improving (sub)surface sediment drainage should be a key design objective in restored tidal marshes. Many restored sites lack efficient drainage due to the lack of creek networks and the presence of historically compacted subsoil layers resulting from agricultural use. The compacted subsoil layers impede porewater flow and creek network development, maintaining waterlogged, unconsolidated sediment beds, deposited on top of the compacted subsoil, which hinder plant establishment (Cao et al., 2021, 2022; Fagherazzi et al., 2012; Van Putte et al., 2020; Vandenbruwaene et al., 2012).

Our findings indicate that well-drained areas, particularly along tidal creek edges, promote pioneer vegetation establishment by enhancing lateral porewater drainage and evaporation, resulting in erosion-resistant sediment beds (Chapters 4 & 5). Creek excavation prior to de-embankment can therefore be considered to accelerate creek network development (Wallace et al., 2005). However, such practices are often associated with high costs and the selected creek network design can substantially affect tidal marsh development (Gourgue et al., 2022). As such, their design should

be carefully optimized with the minimum amount of site preparations to achieve a naturally resembling creek network development. A recent study from Chirol et al. (2024) indicated that creeks in restored sites are often too widely spaced and unnaturally straight compared to natural systems, which leaves the system poorly drained. This can potentially be attributed to the lack of topographic diversity (Lawrence et al., 2018), presence of a compacted subsoil layer (Lawrence et al., 2018; Vandenbruwaene et al., 2012) and the presence of former agricultural drainage ditches (Chirol et al., 2024). Moreover, Chirol et al. (2024) showed that external (e.g. tidal range) and local conditions (e.g. site elevation and topographic diversity) can control how easily creeks develop. A thorough study of these external and local conditions should thus be conducted prior to making a restoration design. Furthermore, potential issues, such as the aforementioned compacted subsoil layer and drainage ditches, should be remediated prior to reintroduction of tides.

Based on our insights, focusing on an accelerated transition from bare mudflat to vegetated marsh, we propose to invest in the creation of a shallow, dense creek network with a dendritic pattern. Such designs might enhance drainage efficiency and soil aeration (Chapter 2; Kearney & Fagherazzi, 2016; Van Putte et al., 2022), which could promote pioneer vegetation establishment (Chapters 4 & 5). Over time, dense creek networks may also promote higher plant species diversity, as has been observed along tidal creek edges in natural marshes (Sanderson et al., 2000, 2001). However, the optimal creek design and spacing in relation to costs and site conditions remain poorly understood. Further research is needed to determine which configurations most effectively promote tidal marsh development toward natural reference conditions.

In addition to creek excavation, reworking the compacted subsoil layer could improve drainage conditions and creek network development in restored sites (Lawrence et al., 2018; Spencer et al., 2017; Van Putte et al., 2020; Vandenbruwaene et al., 2012). Although we did not observe significant effects of subsoil compaction on pioneer vegetation establishment during the early stages after restoration (Chapter 5), such effects may become more pronounced in later stages as vegetation cover increases and drainage pathways evolve.

3. Add topographic diversity to create higher vegetation diversity

Topographic diversity is a key feature of natural tidal marshes but is often absent in restored sites, leading to lower plant diversity (Lawrence et al., 2018, 2022; Mossman et al., 2020). Introducing microtopography can improve restoration outcomes by enhancing local oxygenation and sediment drainage (Fivash et al., 2019; Mossman et al., 2020). As such, microsites develop with higher shear strength, facilitating seed retention and seedling survival (Cao et al., 2018, 2022). Elevated hummocks can be created artificially by adding biodegradable lattice structures, bamboo poles, or other epibenthic structures that capture sediment (Bouma et al.,

2007; Fivash et al., 2019; Wang et al., 2020). The benefit of such features is that they can be applied post-restoration and are relatively cheap compared to measures such as creek excavation (Lawrence et al., 2018, 2022).

4. Account for biotic interactions

Finally, the role of biotic interactions should not be overlooked. Our findings indicated that biotic interactions strongly influence early vegetation establishment (Chapter 3). Filamentous algae, such as *Vaucheria* sp., can facilitate pioneer plant establishment by stabilizing sediments and mitigating the top-down control of benthic predators such as *Hediste diversicolor*. Encouraging early algal colonization, for instance by improving drainage via excavation of shallow creeks and adding microtopography, could therefore represent a cost-effective strategy to enhance plant establishment.

6.6 Limitations and future research

This thesis has provided new insights into the abiotic and biotic mechanisms affecting early tidal marsh development, yet several limitations and open questions remain. These arise partly from the spatial and temporal scope of the work and partly from the experimental simplifications required to isolate specific processes. Addressing these limitations offers valuable opportunities for future research and for translating these findings to a wider range of restoration contexts.

The scaled flume experiments in Chapter 2 offered a unique opportunity to investigate how spatio-temporal vegetation colonization patterns affect tidal creek network development under controlled conditions. However, the long runtime per experiment limited replication and thus the statistical power of the results. Furthermore, controlling vegetation cover in the vegetated experiments proved challenging. The intended homogeneous vegetation cover in the hydrochorous seeding experiment did not develop as fast and as dense as expected. In the patchy seeding experiment, a dense vegetation patch at the landward boundary likely restricted tidal flow and limited further tidal creek network development. Besides, our findings mainly apply to tidal systems characterized by a landward gradient of decreasing hydrodynamic energy (e.g. tidal flats-marsh complexes with an overall seaward sloping topography) lacking topographic complexity. Future research could address these limitations by performing additional flume runs, potentially incorporating variation in spatio-temporal colonization patterns and more topographic complexity. Furthermore, the effect of biostabilizing organisms (such as *Vaucheria*) on tidal creek network development should be investigated. A recent modelling study from van de Vijsel et al. (2023) showed that systems colonized by biofilms (without plants) induced enhanced creek network development, similar to plants. This indicates that enhanced shear strength might play an important role in

creating creek network complexity. Such effects could be further investigated by for instance using scaled flume experiments including diatoms.

The field studies presented in this thesis were conducted in brackish tidal marshes. Consequently, the observed three-way interactions in Chapter 3 between *Vaucheria* sp., *Hediste diversicolor*, and *Aster tripolium* are specific to this setting. Future research should explore whether comparable dynamics exist in saline or freshwater tidal marshes, where different macrofaunal and algal assemblages dominate. Moreover, the mechanisms by which *Vaucheria* suppresses *Hediste* remain uncertain. It is unclear whether this effect is primarily driven by the physical density of algal mats, restricting deposit feeding, the creation of anoxic conditions, or by the provision of an alternative, more digestible food source. Controlled experiments exposing *Hediste* to varying algal mat densities (e.g. no algal mat, thin algal mat, and dense algal mat) could clarify the relative importance of this mechanism and refine our understanding of how biostabilizers mediate trophic interactions during early marsh development.

Temporal constraints also limited the interpretation of field surveys and geospatial analyses in Chapters 4 and 5. Sediment sampling in Chapter 4 could not be conducted simultaneously and only occurred outside the growing season, which may have influenced dry bulk density and water content measurements. Furthermore, vegetation colonization in the recently restored Hedwige-Prosperpolder was assessed within the first two years after de-embankment, an early stage dominated by intense hydrodynamics and sediment dynamics and sparse vegetation establishment. The two subareas in this study site were considered to consist of varying degrees of subsoil compaction since loose, reworked subsoil was added in the Belgian subarea. However, the measured sediment properties do not reflect this difference in subsoil compaction. As such, this could explain the lack of clear effects on vegetation probability density during the short time since tidal restoration (two years). Overall, this thesis highlights the need to better understand how to improve abiotic processes and facilitative biotic interactions to create restored tidal marshes without developmental limitations. While abiotic processes such as drainage and sediment consolidation set the physical foundation, biotic interactions, ranging from antagonistic (e.g. herbivory) to facilitative (e.g. reducing herbivore densities), appear to determine whether the system tips toward a bare or vegetated state. Future research should further explore the effect of such biotic interactions to improve marsh restoration efforts and how these interactions will be affected by environmental changes. Climate-driven changes in temperature and salinity may alter the balance of these interactions as these factors can affect the physiology and behavior of macrobenthos (Bhuiyan et al., 2021; Scaps & Borot, 2000). Furthermore, effects might be more pronounced in restored tidal marshes as they have been shown to be less resilient to for instance salt intrusion (Saccon et al., 2025). Increased salinity can affect seed germination in certain marsh species (Greenwood

& MacFarlane, 2006) and could change the overall distribution of algae, macrobenthos and marsh vegetation. Such changes might potentially reshape the top-down and bottom-up controls in tidal marsh systems. Moreover, environmental policy changes may also influence biotic interactions. The observed recovery of macrobenthic communities in the Scheldt and other estuaries following the ban on tributyltin (TBT) (Herman, 2022; Rees et al., 2001; Smith et al., 2007) illustrates how reducing pollution could enhance benthic biomass. As such, benthos may play an increasingly dominant role in regulating sediment stability and vegetation establishment. Understanding how climate change, environmental policy, and pollution together shift the balance between facilitation and inhibition during early tidal marsh development remains an important challenge for future research.

6.6 References

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs, 81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Beauchard, O., Jacobs, S., Cox, T. J. S., Maris, T., Vrebos, D., Van Braeckel, A., & Meire, P. (2011). A new technique for tidal habitat restoration: Evaluation of its hydrological potentials. *Ecological Engineering, 37*(11), 1849–1858. https://doi.org/10.1016/j.ecoleng.2011.06.010

Bertness, M. D., & Hacker, S. D. (1994). Physical Stress and Positive Associations Among Marsh Plants. *The American Naturalist, 144*(3), 363–372. https://doi.org/10.1086/285681

Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T., & Herman, P. M. J. (2007). Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. *Continental Shelf Research, 27*(8), 1020–1045. https://doi.org/10.1016/j.csr.2005.12.019

Brooks, H., Möller, I., Carr, S., Chirol, C., Christie, E., Evans, B., Spencer, K. L., Spencer, T., & Royse, K. (2021). Resistance of salt marsh substrates to near-instantaneous hydrodynamic forcing. *Earth Surface Processes and Landforms, 46*(1), 67–88. https://doi.org/10.1002/esp.4912

Cao, H., Zhu, Z., Balke, T., Zhang, L., & Bouma, T. J. (2018). Effects of sediment disturbance regimes on Spartina seedling establishment: Implications for salt marsh creation and restoration: Sediment dynamics affect seedling establishment. *Limnology and Oceanography, 63*(2), 647–659. https://doi.org/10.1002/lno.10657

Cao, H., Zhu, Z., Hu, Z., Wang, H., & Bouma, T. J. (2022). Drainage-Improved Sediment Strength Enhances Saltmarsh Seedling Establishment Chance. *Frontiers in Marine Science, 9*, 874680. https://doi.org/10.3389/fmars.2022.874680

Cao, H., Zhu, Z., van Belzen, J., Gourgue, O., van de Koppel, J., Temmerman, O. S., Herman, P. M. J., Zhang, L., Yuan, L., & Bouma, T. J. (2021). Salt marsh establishment in poorly consolidated muddy systems: Effects of surface drainage, elevation, and plant age. *Ecosphere, 12*(9). https://doi.org/10.1002/ecs2.3755

Cao, M., Xin, P., Jin, G., & Li, L. (2012). A field study on groundwater dynamics in a salt marsh – Chongming Dongtan wetland. *Ecological Engineering, 40*, 61–69. https://doi.org/10.1016/j.ecoleng.2011.12.018

Chen, D., Zheng, J., Zhang, C., Guan, D., Li, Y., & Wang, Y. (2021). Critical Shear Stress for Erosion of Sand-Mud Mixtures and Pure Mud. *Frontiers in Marine Science, 8*, 713039. https://doi.org/10.3389/fmars.2021.713039

Chirol, C., Pontee, N., Gallop, S. L., Thompson, C. E. L., Kassem, H., & Haigh, I. D. (2024). Creek systems in restored coastal wetlands: Morphological evolution and design implications. *Science of The Total Environment, 921*, 171067. https://doi.org/10.1016/j.scitotenv.2024.171067

Colosimo, I., Van Maren, D. S., De Vet, P. L. M., Winterwerp, J. C., & Van Prooijen, B. C. (2023). Winds of opportunity: The effects of wind on intertidal flat accretion. *Geomorphology, 439*, 108840. https://doi.org/10.1016/j.geomorph.2023.108840

Cox, T., Maris, T., De Vleeschauwer, P., De Mulder, T., Soetaert, K., & Meire, P. (2006). Flood control areas as an

opportunity to restore estuarine habitat. *Ecological Engineering, 28*(1), 55–63. https://doi.org/10.1016/j.ecoleng.2006.04.001

Crooks, S., Schutten, J., Sheern, G. D., Pye, K., & Davy, A. J. (2002). Drainage and Elevation as Factors in the Restoration of Salt Marsh in Britain. *Restoration Ecology, 10*(3), 591–602. https://doi.org/10.1046/j.1526-100X.2002.t01-1-02036.x

D'Alpaos, A., Fagherazzi, S., & Rinaldo, A. (2005). Tidal network ontogeny: Channel initiation and early development. *Journal of Geophysical Research, 110*(F2), F02001. https://doi.org/10.1029/2004JF000182

D'Alpaos, A., Lanzoni, S., Marani, M., & Rinaldo, A. (2007). Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. *Journal of Geophysical Research: Earth Surface, 112*(F1), 2006JF000537. https://doi.org/10.1029/2006JF000537

Dong, Y., Lu, N., & Fox, P. J. (2020). Drying-Induced Consolidation in Soil. *Journal of Geotechnical and Geoenvironmental Engineering, 146*(9), 04020092. https://doi.org/10.1061/(ASCE)GT.1943-5606.0002327

Fagherazzi, S., & Furbish, D. J. (2001). On the shape and widening of salt marsh creeks. *Journal of Geophysical Research: Oceans, 106*(C1), 991–1003. https://doi.org/10.1029/1999JC000115

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpaos, A., van de Koppel, J., Rybczyk, J. M., Reyes, E., Craft, C., & Clough, J. (2012). Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Reviews of Geophysics, 50*(1), RG1002. https://doi.org/10.1029/2011RG000359

Fagherazzi, S., Viggato, T., Vieillard, A. M., Mariotti, G., & Fulweiler, R. W. (2017). The effect of evaporation on the erodibility of mudflats in a mesotidal estuary. *Estuarine, Coastal and Shelf Science, 194*, 118–127. https://doi.org/10.1016/j.ecss.2017.06.011

Feagin, R. A., Figlus, J., Zinnert, J. C., Sigren, J., Martínez, M. L., Silva, R., Smith, W. K., Cox, D., Young, D. R., & Carter, G. (2015). Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Frontiers in Ecology and the Environment, 13*(4), 203–210. https://doi.org/10.1890/140218

Fivash, G. S., Stoorvogel, M. M., De Smit, J. C., van Rees, F., Van Dalen, J., Grandjean, T. J., van de Vijsel, R. C., Bouma, T. J., Temmerman, S., & van Belzen, J. (2024). Abiotic origins of self-organized ridge-runnel patterns on tidal flats. *Limnology and Oceanography, 69*(6), 1378–1389. https://doi.org/10.1002/lno.12581

Fivash, G. S., van Belzen, J., Temmink, R. J. M., Didderen, K., Lengkeek, W., Heide, T. V. D., & Bouma, T. J. (2019). Elevated micro-topography boosts growth rates in Salicornia procumbens by amplifying a tidally driven oxygen pump: Implications for natural recruitment and restoration. *Annals of Botany, 125*, 353–364. https://doi.org/10.1093/aob/mcz137

Gerwing, T. G., Davies, M. M., Clements, J., Flores, A.-M., Thomson, H. M., Nelson, K. R., Kushneryk, K., Brouard-John, E. K., Harvey, B., & Plate, E. (2020). Do you want to breach an embankment? Synthesis of the literature and practical considerations for breaching of tidally influenced causeways and dikes. *Estuarine, Coastal and Shelf Science, 245*,

107024. https://doi.org/10.1016/j.ecss.2020.107024

Gourgue, O., van Belzen, J., Schwarz, C., Vandenbruwaene, W., Vanlede, J., Belliard, J.-P., Fagherazzi, S., Bouma, T. J., van de Koppel, J., & Temmerman, S. (2022). Biogeomorphic modeling to assess the resilience of tidal-marsh restoration to sea level rise and sediment supply. *Earth Surface Dynamics, 10*(3), 531–553. https://doi.org/10.5194/esurf-10-531-2022

Greenwood, M. E., & MacFarlane, G. R. (2006). Effects of salinity and temperature on the germination of Phragmites australis, Juncus kraussii, and Juncus acutus: Implications for estuarine restoration initiatives. *Wetlands, 26*(3), 854–861. https://doi.org/10.1672/0277-5212(2006)26%255B854:EOSATO%255D2.0.CO;2

Gyssels, G., Poesen, J., Bochet, E., & Li, Y. (2005). Impact of plant roots on the resistance of soils to erosion by water: A review. *Progress in Physical Geography: Earth and Environment, 29*(2), 189–217. https://doi.org/10.1191/0309133305pp443ra

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters, 16*(5), 695–706. https://doi.org/10.1111/ele.12080

Herman, P. (2022, November 10). De Schelde, op weg naar een mooie toekomst? Deltares.

Hughes, R. (1999). Saltmarsh erosion and management of saltmarsh restoration; the effects of infaunal invertebrates. *Aquatic Conservation-Marine and Freshwater Ecosystems, 9*, 83–95. https://doi.org/10.1002/(SICI)1099-0755(199901/02)9:1%3C83::AID-AQC323%3E3.0.CO;2-9

Jacobs, S., Beauchard, O., Struyf, E., Cox, T., Maris, T., & Meire, P. (2009). Restoration of tidal freshwater vegetation using controlled reduced tide (CRT) along the Schelde Estuary (Belgium). *Estuarine, Coastal and Shelf Science, 85*(3), 368–376. https://doi.org/10.1016/j.ecss.2009.09.004

Kearney, W. S., & Fagherazzi, S. (2016). Salt marsh vegetation promotes efficient tidal channel networks. *Nature Communications, 7*(1), 12287. https://doi.org/10.1038/ncomms12287

Kirwan, M. L., & Megonigal, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature, 504*(7478), 53–60. https://doi.org/10.1038/nature12856

Lawrence, P. J., Smith, G. R., Sullivan, M. J. P., & Mossman, H. L. (2018). Restored saltmarshes lack the topographic diversity found in natural habitat. *Ecological Engineering, 115*, 58–66. https://doi.org/10.1016/j.ecoleng.2018.02.007

Lawrence, P. J., Sullivan, M. J. P., & Mossman, H. L. (2022). Restored saltmarshes have low beta diversity due to limited topographic variation, but this can be countered by management. *Journal of Applied Ecology, 59*(7), 1709–1720. https://doi.org/10.1111/1365-2664.14179

Liu, Z., Gourgue, O., & Fagherazzi, S. (2022). Biotic and abiotic factors control the geomorphic characteristics of channel networks in salt marshes. *Limnology and Oceanography, 67*(1), 89–101. https://doi.org/10.1002/lno.11977

Maris, T., Cox, T., Temmerman, S., De Vleeschauwer, P., Van Damme, S., De Mulder, T., Van Den Bergh, E., & Meire, P. (2007). Tuning the tide: Creating ecological conditions for tidal marsh development in a flood control area. *Hydrobiologia, 588*(1), 31–43.

https://doi.org/10.1007/s10750-007-0650-5

Mossman, H. L., Davy, A. J., & Grant, A. (2012). Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites? *Journal of Applied Ecology, 49*(6), 1446–1456. https://doi.org/10.1111/j.1365-2664.2012.02198.x

Mossman, H. L., Grant, A., & Davy, A. J. (2020). Manipulating saltmarsh microtopography modulates the effects of elevation on sediment redox potential and halophyte distribution. *Journal of Ecology, 108*(1), 94–106. https://doi.org/10.1111/1365-2745.13229

Mudd, S. M., D'Alpaos, A., & Morris, J. T. (2010). How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on biologically mediated sedimentation. *Journal of Geophysical Research, 115*(F3), F03029. https://doi.org/10.1029/2009JF001566

Oosterlee, L., Cox, T. J. S., Temmerman, S., & Meire, P. (2020). Effects of tidal re-introduction design on sedimentation rates in previously embanked tidal marshes. *Estuarine, Coastal and Shelf Science, 244*, 106428. https://doi.org/10.1016/j.ecss.2019.106428

Paramor, O. A. L., & Hughes, R. G. (2004). The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on loss of saltmarsh in south-east England. *Journal of Applied Ecology, 41*(3), 449–463. https://doi.org/10.1111/j.0021-8901.2004.00916.x

Paramor, O. A. L., & Hughes, R. G. (2005). Effects of the invertebrate infauna on early saltmarsh plant colonisation of managed realignment areas in south-east England. *Marine Ecology Progress Series, 303*, 61–71. https://doi.org/10.3354/meps303061

Rees, H. L., Waldock, R., Matthiessen, P., & Pendle, M. A. (2001). Improvements in the Epifauna of the Crouch Estuary (United Kingdom) Following a Decline in TBT Concentrations. *Marine Pollution Bulletin, 42*(2), 137–144. https://doi.org/10.1016/S0025-326X(00)00119-3

Saccon, E., Hendrickx, G. G., Hulscher, S. J. M. H., Bouma, T. J., & Van De Koppel, J. (2025). Wetland topography drives salinity resilience in freshwater tidal ecosystems. *Ecological Engineering, 217*, 107650. https://doi.org/10.1016/j.ecoleng.2025.107650

Sanderson, E. W., Foin, T. C., & Ustin, S. L. (2001). A simple empirical model of salt marsh plant spatial distributions with respect to a tidal channel network. *Ecological Modelling, 139*(2–3), 293–307. https://doi.org/10.1016/S0304-3800(01)00253-8

Sanderson, E. W., Ustin, S. L., & Foin, T. C. (2000). The influence of tidal channels on the distribution of salt marsh plant species in Petaluma Marsh, CA, USA. *Plant Ecology, 146*(1), 29–41. https://doi.org/10.1023/A:1009882110988

Schuerch, M., Spencer, T., Temmerman, S., Kirwan, M. L., Wolff, C., Lincke, D., McOwen, C. J., Pickering, M. D., Reef, R., Vafeidis, A. T., Hinkel, J., Nicholls, R. J., & Brown, S. (2018). Future response of global coastal wetlands to sea-level rise. *Nature, 561*(7722), 231–234. https://doi.org/10.1038/s41586-018-0476-5

Schwarz, C., Gourgue, O., van Belzen, J., Zhu, Z., Bouma, T. J., van de Koppel, J., Ruessink, G., Claude, N., &

Temmerman, S. (2018). Self-organization of a biogeomorphic landscape controlled by plant life-history traits. *Nature Geoscience, 11*(9), 672–677. https://doi.org/10.1038/s41561-018-0180-y

Schwarz, C., van Rees, F., Xie, D., Kleinhans, M. G., & van Maanen, B. (2022). Salt marshes create more extensive channel networks than mangroves. *Nature Communications, 13*(1), 2017. https://doi.org/10.1038/s41467-022-29654-1

Schwarz, C., Ye, Q. H., van der Wal, D., Zhang, L. Q., Bouma, T., Ysebaert, T., & Herman, P. M. J. (2014). Impacts of salt marsh plants on tidal channel initiation and inheritance: Salt marsh plants channel development. *Journal of Geophysical Research: Earth Surface, 119*(2), 385–400. https://doi.org/10.1002/2013JF002900

Silliman, B. R., Schrack, E., He, Q., Cope, R., Santoni, A., Van Der Heide, T., Jacobi, R., Jacobi, M., & Van De Koppel, J. (2015). Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proceedings of the National Academy of Sciences, 112*(46), 14295–14300. https://doi.org/10.1073/pnas.1515297112

Smith, R., Bolam, S. G., Rees, H. L., & Mason, C. (2007). Macrofaunal recovery following TBT ban: Long-term recovery of subtidal macrofaunal communities in relation to declining levels of TBT contamination. Environmental *Monitoring and Assessment, 136*(1–3), 245–256. https://doi.org/10.1007/s10661-007-9680-8

Spencer, K. L., Carr, S. J., Diggens, L. M., Tempest, J. A., Morris, M. A., & Harvey, G. L. (2017). The impact of pre-restoration land-use and disturbance on sediment structure, hydrology and the sediment geochemical environment in restored saltmarshes. *Science of The Total Environment, 587–588*, 47–58. https://doi.org/10.1016/j.scitotenv.2016.11.032

Temmerman, S., Bouma, T. J., Van de Koppel, J., Van der Wal, D., De Vries, M. B., & Herman, P. M. J. (2007). Vegetation causes channel erosion in a tidal landscape. *Geology, 35*(7), 631. https://doi.org/10.1130/G23502A.1

Temmerman, S., Horstman, E. M., Krauss, K. W., Mullarney, J. C., Pelckmans, I., & Schoutens, K. (2023). Marshes and Mangroves as Nature-Based Coastal Storm Buffers. *Annual Review of Marine Science, 15*(1), 95–118. https://doi.org/10.1146/annurev-marine-040422-092951

Temmink, R. J. M., Lamers, L. P. M., Angelini, C., Bouma, T. J., Fritz, C., Van De Koppel, J., Lexmond, R., Rietkerk, M., Silliman, B. R., Joosten, H., & Van Der Heide, T. (2022). Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots. *Science, 376*(6593), eabn1479. https://doi.org/10.1126/science.abn1479

Torfs, H., Mitchener, H., Huysentruyt, H., & Toorman, E. (1996). Settling and consolidation of mud/sand mixtures. Coastal Engineering, 29(1–2), 27–45. https://doi.org/10.1016/S0378-3839(96)00013-0

Ursino, N., Silvestri, S., & Marani, M. (2004). Subsurface flow and vegetation patterns in tidal environments. *Water Resources Research, 40*(5). https://doi.org/10.1029/2003WR002702

van Belzen, J. (2024). Ragworms Anecdotes – Shared by Jim van Belzen. *Journal of Trial and Error.* https://doi.org/10.36850/d17f-489b

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Borsje, B. W., Temmerman, S., Cornacchia, L.,

Gourgue, O., & Van De Koppel, J. (2023). Vegetation controls on channel network complexity in coastal wetlands. *Nature Communications, 14*(1), 7158. https://doi.org/10.1038/s41467-023-42731-3

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., Cusseddu, V., Purkis, S. J., Rietkerk, M., & Koppel, J. (2020). Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. *Earth Surface Processes and Landforms, 45*(5), 1141–1154. https://doi.org/10.1002/esp.4783

van de Vijsel, R. C., van Belzen, J., Bouma, T. J., van der Wal, D., & van de Koppel, J. (2021). Algal-Induced Biogeomorphic Feedbacks Lay the Groundwork for Coastal Wetland Development. *Journal of Geophysical Research: Biogeosciences, 126*(10). https://doi.org/10.1029/2021JG006515

Van Putte, N., Temmerman, S., Verreydt, G., Seuntjens, P., Maris, T., Heyndrickx, M., Boone, M., Joris, I., & Meire, P. (2020). Groundwater dynamics in a restored tidal marsh are limited by historical soil compaction. *Estuarine, Coastal and Shelf Science, 244*, 106101. https://doi.org/10.1016/j.ecss.2019.02.006

van Rees, F. F., Hanssen, J., Gamberoni, S., Talmon, A. M., & Van Kessel, T. (2024). Effect of air exposure time on erodibility of intertidal mud flats. *Frontiers in Marine Science, 11*, 1393262. https://doi.org/10.3389/fmars.2024.1393262

van Regteren, M., ten Boer, R., Meesters, E. H., & de Groot, A. V. (2017). Biogeomorphic impact of oligochaetes (Annelida) on sediment properties and *Salicornia* spp. Seedling establishment. *Ecosphere, 8*(7), e01872. https://doi.org/10.1002/ecs2.1872

van Wesenbeeck, B. K., Van De Koppel, J., M. J. Herman, P., & J. Bouma, T. (2008). Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems? *Oikos, 117*(1), 152–159. https://doi.org/10.1111/j.2007.0030-1299.16245.x

Vandenbruwaene, W., Bouma, T. J., Meire, P., & Temmerman, S. (2013). Bio-geomorphic effects on tidal channel evolution: Impact of vegetation establishment and tidal prism change. Earth Surface Processes and Landforms, 38(2), 122–132. https://doi.org/10.1002/esp.3265

Vandenbruwaene, W., Meire, P., & Temmerman, S. (2012). Formation and evolution of a tidal channel network within a constructed tidal marsh. *Geomorphology, 151–152*, 114–125. https://doi.org/10.1016/j.geomorph.2012.01.022

Vandenbruwaene, W., Temmerman, S., Bouma, T. J., Klaassen, P. C., de Vries, M. B., Callaghan, D. P., van Steeg, P., Dekker, F., van Duren, L. A., Martini, E., Balke, T., Biermans, G., Schoelynck, J., & Meire, P. (2011). Flow interaction with dynamic vegetation patches: Implications for biogeomorphic evolution of a tidal landscape. *Journal of Geophysical Research: Earth Surface, 116*(F1), F01008. https://doi.org/10.1029/2010JF001788

Wallace, K. J., Callaway, J. C., & Zedler, J. B. (2005). Evolution of tidal creek networks in a high sedimentation environment: A 5-year experiment at Tijuana Estuary, California. *Estuaries, 28*(6), 795–811. https://doi.org/10.1007/BF02696010

Wang, D., Bai, J., Wang, W., Ma, X., Guan, Y., Gu, C., Zhang, S., & Lu, F. (2020). Micro-Topography Manipulations Facilitate Suaeda Salsa Marsh Restoration along the Lateral Gradient of a Tidal Creek. *Wetlands, 40*(5), 1657–1666. https://doi.org/10.1007/s13157-

020-01308-2

Winterwerp, J. C., & Van Kesteren, W. G. M. (2004). Self-Weight Consolidation. In Developments in Sedimentology (Vol. 56, pp. 211–251). Elsevier. https://doi.org/10.1016/S0070-4571(04)80008-6

Xin, P., Wilson, A., Shen, C., Ge, Z., Moffett, K. B., Santos, I. R., Chen, X., Xu, X., Yau, Y. Y. Y., Moore, W., Li, L., & Barry, D. A. (2022). Surface Water and Groundwater Interactions in Salt Marshes and Their Impact on Plant Ecology and Coastal Biogeochemistry. *Reviews of Geophysics, 60*(1). https://doi.org/10.1029/2021RG000740

Zhou, Z., Van Der Wegen, M., Jagers, B., & Coco, G. (2016). Modelling the role of self-weight consolidation on the morphodynamics of accretional mudflats. *Environmental Modelling & Software, 76*, 167–181. https://doi.org/10.1016/j.envsoft.2015.11.002

7

Supplementary information

S2 Supplementary information Chapter 2

Section S2.1

Sowing protocol

For our plant species selection, we relied on (1) the work from Lokhorst et al. (2019), in which the growth rate, hydraulic resistance, and bank strength of 19 different plant species were tested in Metronome-like tidal flume conditions, (2) previous experience/research done in the Metronome (e.g. Weisscher et al., 2022) and (3) observations from pilot tests.

(1) The fast growth rate of *Lotus pedunculatus* in the applied timescale (four days) is one of the main reasons it was selected. Furthermore, the results of Lokhorst et al. (2019) indicate that *Lotus* can represent grass-like species (like those found in natural marshes) in scaled landscape experiments as it can trap sediments and grow in dense patches with high flow resistance.

(2) The results from Weisscher et al. (2022) and Kleinhans et al. (2022) suggest that vegetation (including this species) could stabilize channel banks and influence the morphological development of (partially-filled) estuaries.

(3) Pilot tests were conducted to select a plant species that could rapidly germinate in both vegetated experiments where different sowing procedures were applied. Since previous experiments only relied on seed dispersal via the tidal flow, we had to examine whether seed viability would not suffer from the sowing procedure used in the patchy experiment. This was done by a simple test in which *Lotus* and *Veronica beccabunga* seeds, subjected to the procedures used in the experiments (i.e. soaking seeds for 24 hours and soaking seeds for 24 hours followed by drying them the next day), were deposited in buckets filled with poorly sorted sand. Afterwards, the seeds were watered daily and the fraction of germinated seeds along with germination time was monitored. We observed a very low fraction of germinated *Veronica* seeds in both procedures, while the *Lotus* seeds showed more promising results. Approximately 50% of the seeds germinated and we could not discern major differences in germination between the different procedures.

The number of seeds supplied to the tidal inlet was based on the vegetation protocol used in Weisscher et al. (2022). The authors of this study aimed to obtain vegetation covering half the Metronome flume by supplying 400 000 seeds per sowing event (160 000 seeds at the seaward tidal inlet and 240 000 seeds at the landward river inlet). Since, in our case, only one-half of the flume was used and no landward river inlet was present, but instead a closed landward boundary, we decided to use the same quantity supplied at the tidal inlet in Weisscher et al. (2022). The plant density obtained within vegetation patches in the hydrochorous experiment (ca. five plants/cm^2) was subsequently used to decide what plant density we wanted to

achieve in the patchy experiment, i.e. how many seeds were sown in the pre-defined patches.

The timing of the sowing events was also based on previous experiments conducted in the Metronome (Kleinhans et al., 2022; Weisscher et al., 2022). We initiated sowing events after 1000 tidal cycles, as channel network formation had started by then but had not reached equilibrium yet, hence trying to prevent fixation of the network by establishing vegetation. Every sowing event occurred with an interval of 440 (hydrochorous vegetation experiment) or 500 tidal cycles (patchy vegetation experiment). Each sowing event started by acquiring a DSM. Therefore, we had to drain the flume and refill it afterwards. Hence, every sowing event of the hydrochorous experiment required a short wetting phase (during 10 tidal cycles) to re-establish a normal flow pattern, followed by the release of seeds (during 25 tidal cycles) and dispersal of seeds (during another 25 tidal cycles). After a four-day germination period, a new 440 tidal cycle interval was run to obtain a total of 1500 tidal cycles since the start of the experiment. At this point, the procedure was repeated until 5000 tidal cycles were run, starting with a new DSM acquisition and a new sowing event (during 60 tidal cycles), followed by 440 tidal cycles. Etcetera.

In the patchy experiment, the number of patches and their sizes were determined as such that 60% of the tidal basin would be covered by vegetation patches after 5000 tidal cycles, with a first sowing event after 1000 tidal cycles followed by subsequent sowing events every 500 tidal cycles, i.e. totaling eight sowing events after 4500 tidal cycles. Apart from that, we wanted to ensure that the patch size and number would create sufficient interaction between vegetation patches and tidal flow. Moreover, the decision had to be practically feasible since all patches were manually sown (which required a lot of work).

Image calibration

The lens distortion was corrected in the standard Matlab toolbox. A pinhole camera model was applied for calibration, which uses calibration techniques involving the checkerboard method. Afterward, the “undistortImage” function was used to correct the images for lens distortion. The geometric rectification was carried out in Matlab by applying a projective transformation using the “fitgeotrans” function based on a correspondence between fixed (coordinates in real world) and moving points (corresponding points in images captured by the cameras).

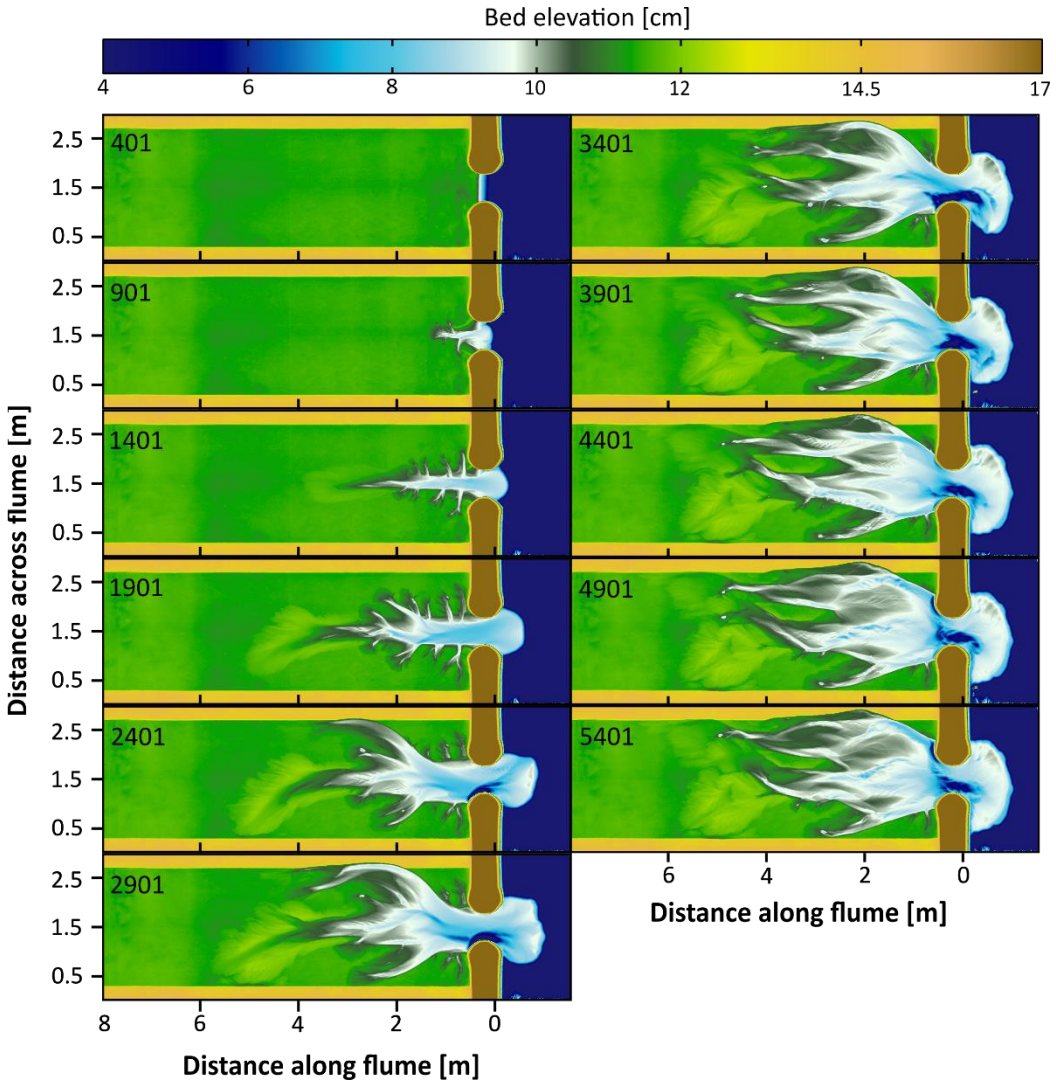


Figure S2.1: Plan view of DSMs showing the morphological development of the first control experiment. Numbers indicate the corrected number of tidal cycles after which the DSM is shown.

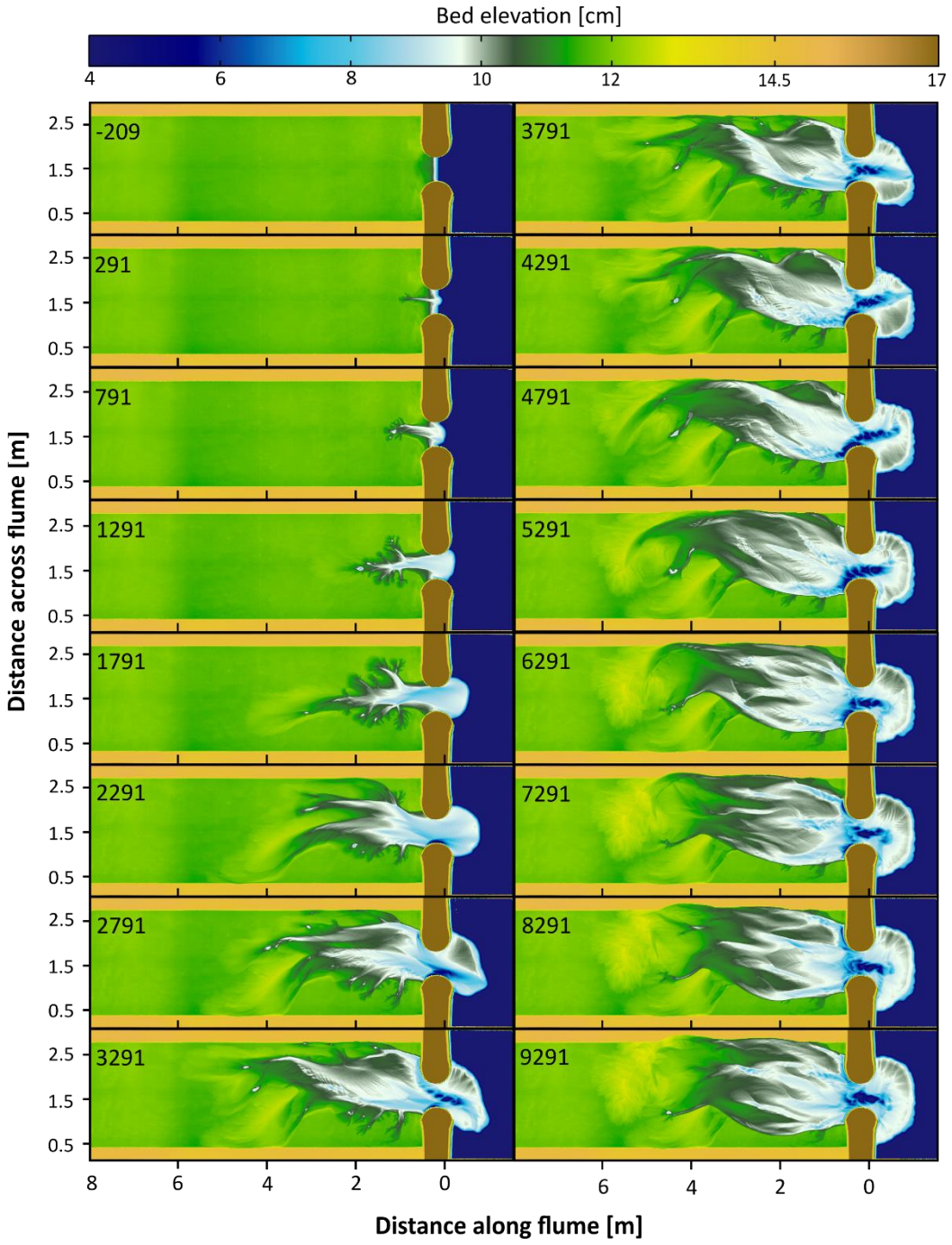


Figure S2.2: Plan view of DSMs showing the morphological development of the second control experiment. Numbers indicate the corrected number of tidal cycles after which the DSM is shown.

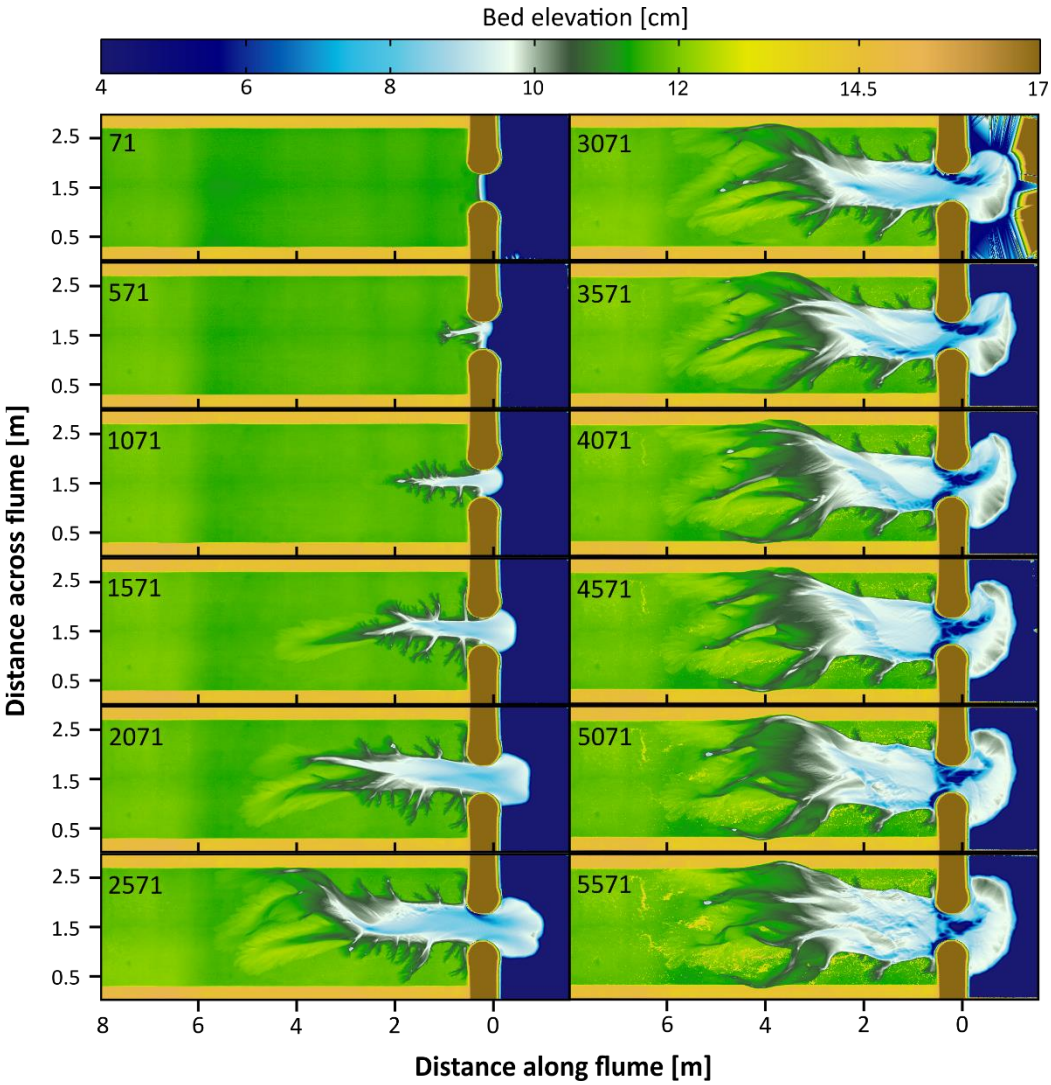


Figure S2.3: Plan view of DSMs showing the morphological development of the hydrochorous sowing experiment. Numbers indicate the corrected number of tidal cycles after which the DSM is shown.

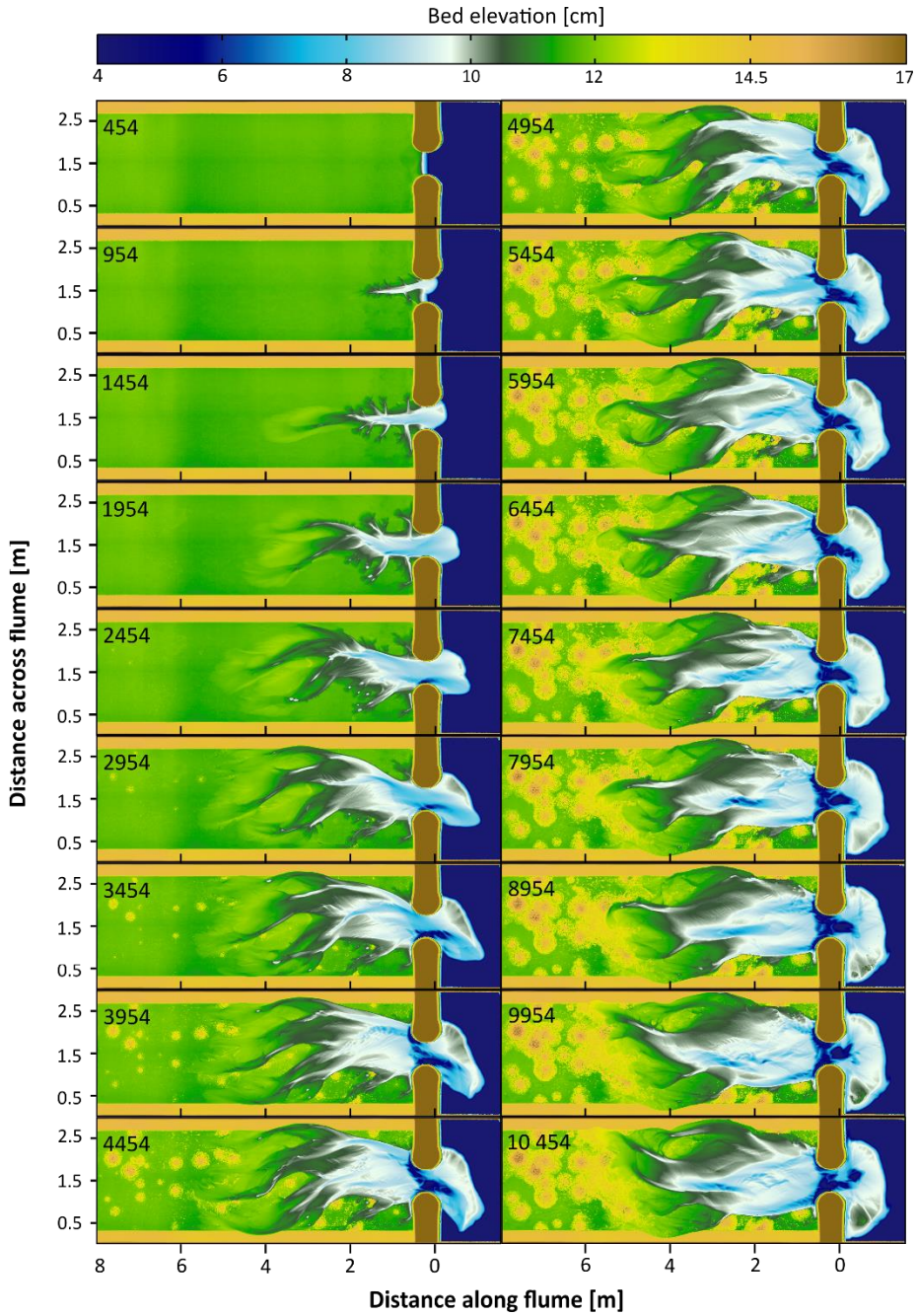


Figure S2.4: Plan view of DSMs showing the morphological development of the patchy sowing experiment. Numbers indicate the corrected number of tidal cycles after which the DSM is shown. Note that for densely vegetated surfaces, the DSM also includes the top of the vegetation canopy, which is most apparent after 5000 tidal cycles.

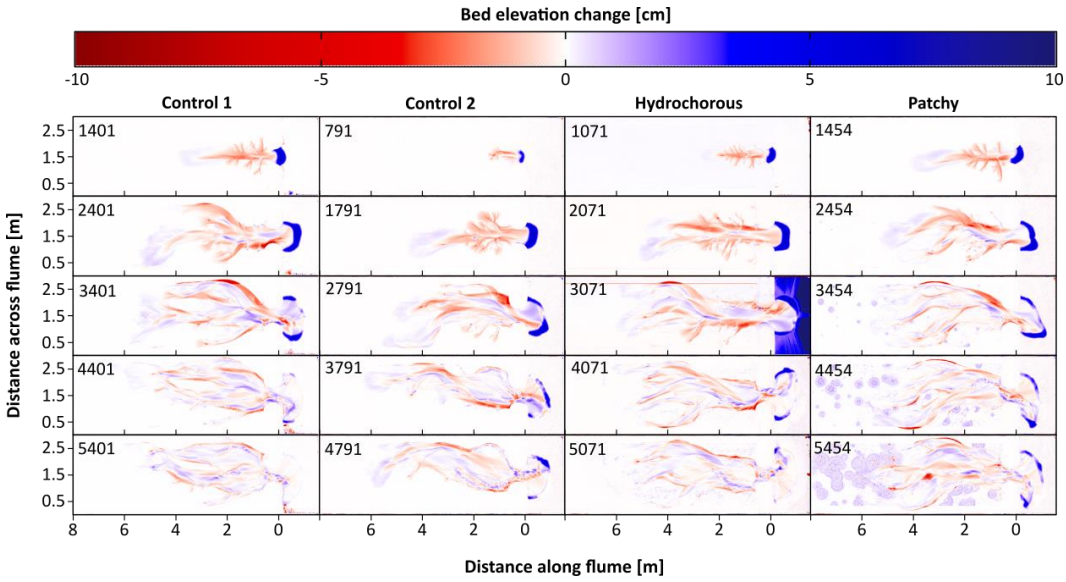


Figure S2.5: Erosion (red color scale) and sedimentation (blue color scale) during the salt marsh experiments with respect to the previous DSM. Numbers indicate the corrected tidal cycles. The visibility of the seafloor in the hydrochorous experiment at 3071 cycles is due to remaining water after draining the flume.

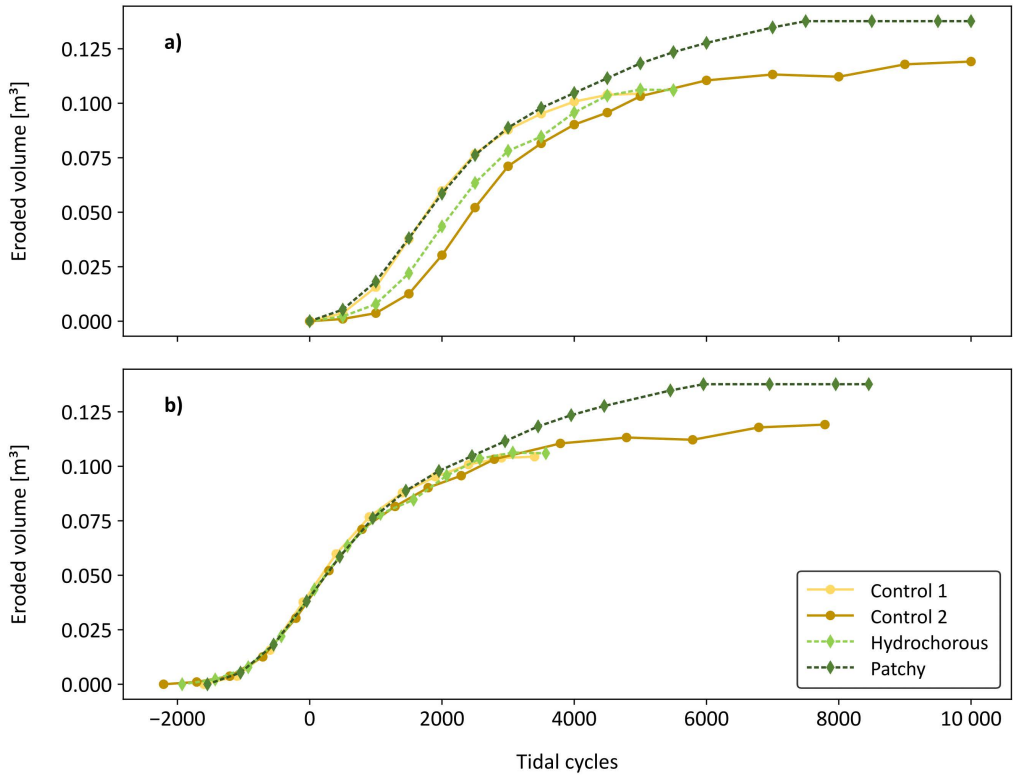


Figure S2.6: The evolution of eroded volume over time during the salt marsh experiments: **a)** represents the uncorrected data, which display variability attributed to differences in system development, while the data have been corrected in **b)** for this initial system development variability by shifting the time scale. The correction was based on a linear interpolation.

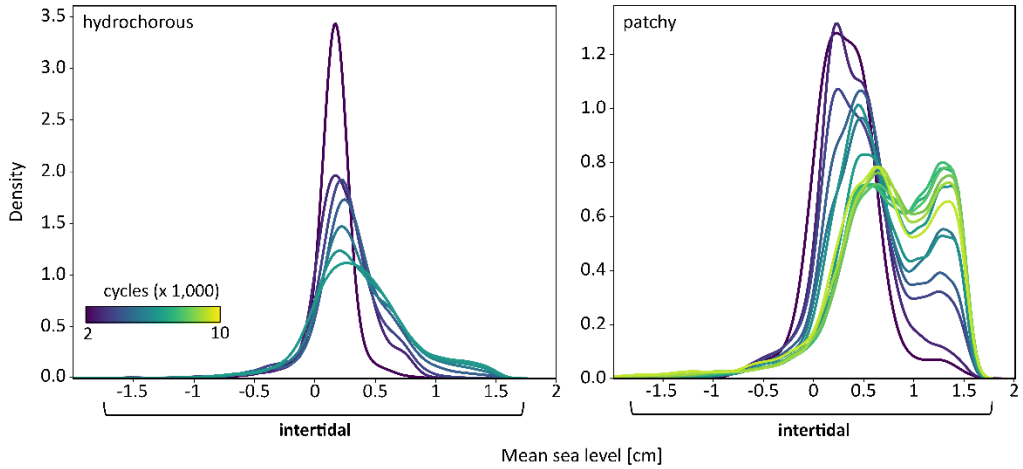


Figure S2.7: Vegetation density as function of mean sea level over time in the hydrochorous and patchy vegetation experiments.

S3 Supplementary information Chapter 3

Section S3.1

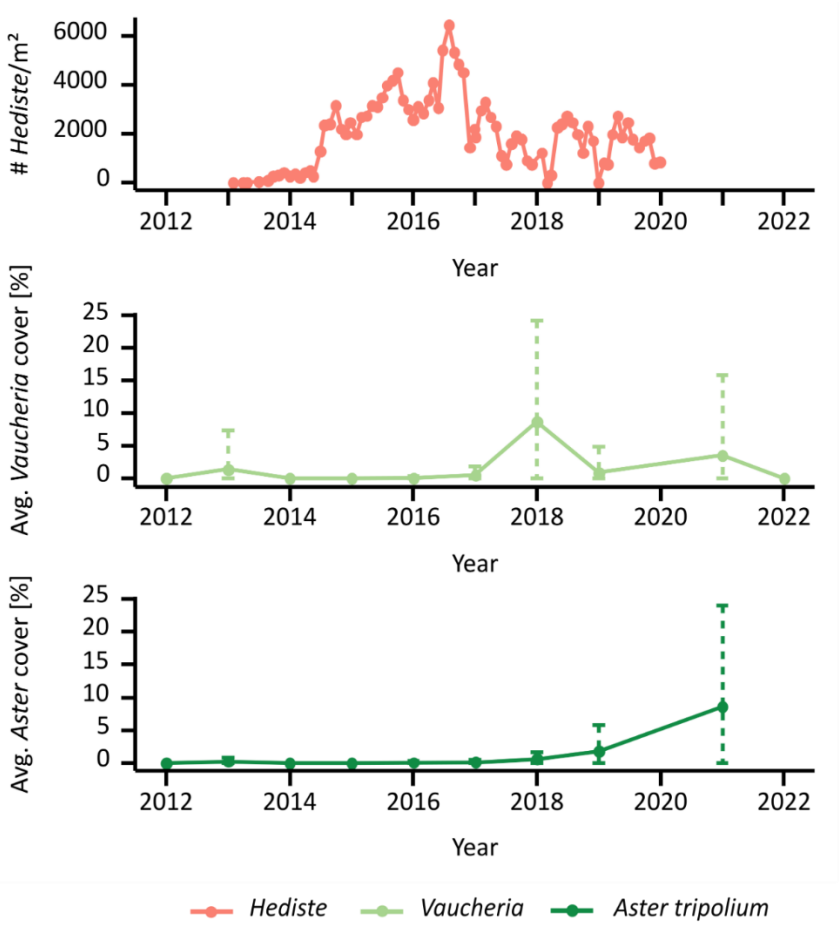


Figure S3.1: Data graphs (mean ± SD) showing the biotic colonization of a newly restored brackish tidal marsh (Lillo Potpolder) in the Scheldt estuary by the polychaete *Hediste diversicolor*, the fibrous algae *Vaucheria* and the plant pioneer species *Aster tripolium*.

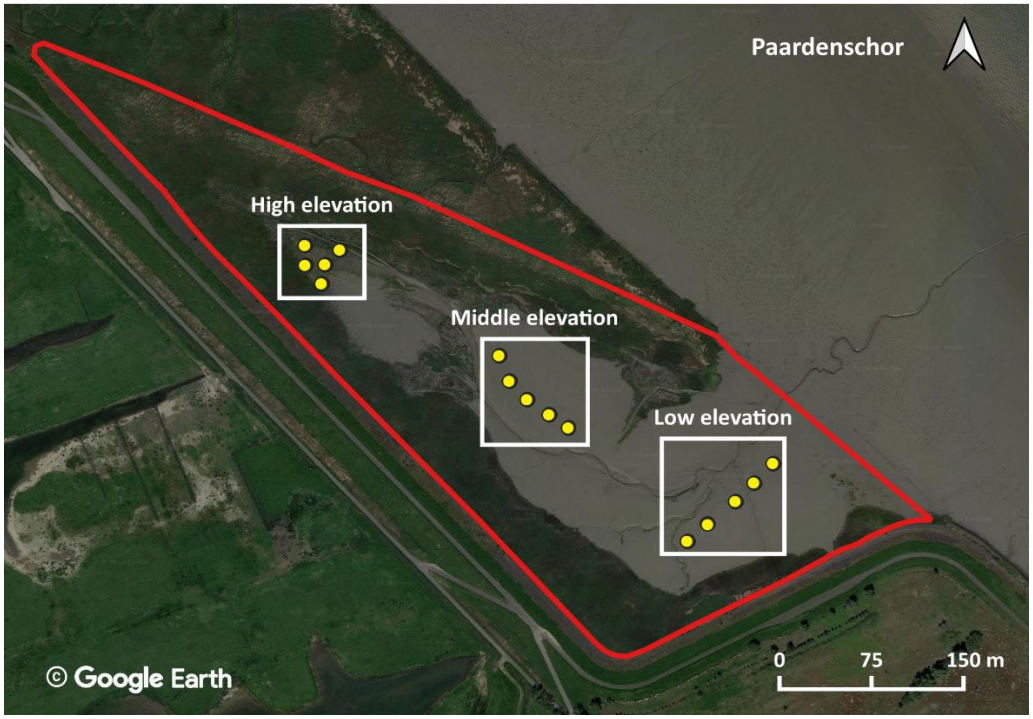


Figure S3.2: Locations used in the field transplantation experiment conducted in Paardenschor, where sea aster seedlings were transplanted along an elevation gradient: low elevation of 2.27 ± 0.11 m NAP (i.e. Dutch Ordinance Level, approximately mean sea level), mid elevation of 2.52 ± 0.02 m NAP, and high elevation of 2.7 ± 0.06 m NAP. Each location included a defaunated plot and a control plot at short distance (1 m) from each other. The transplantation in a control and defaunated plot was replicated five times per elevation level (as indicated by the yellow dots). The satellite imagery was extracted from Google Earth.

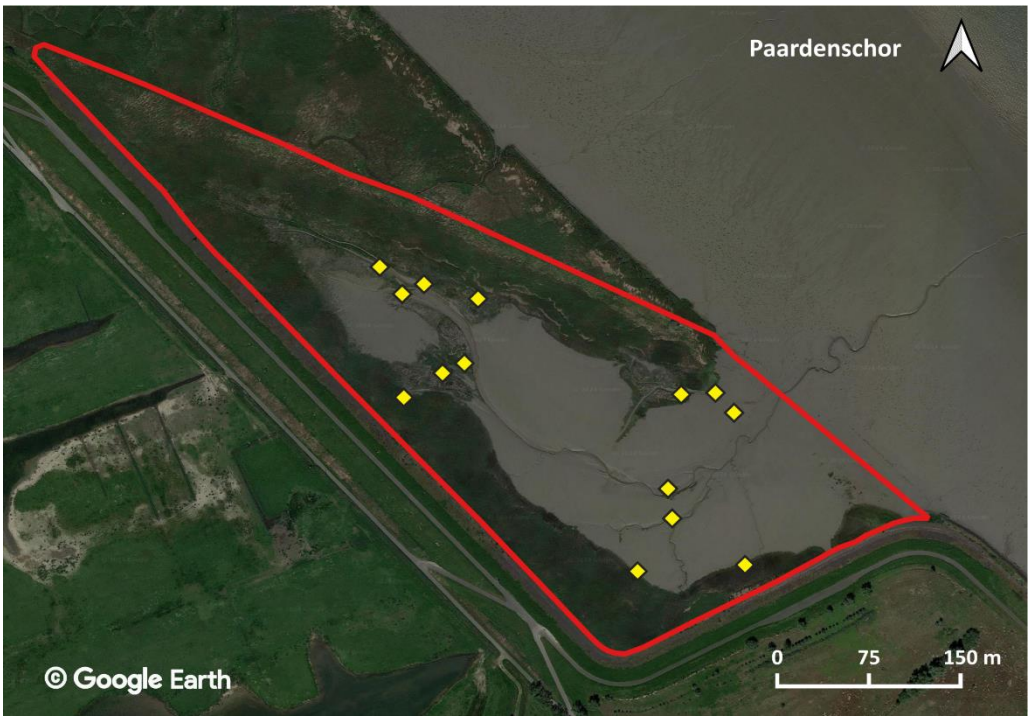


Figure S3.3: Locations used in the observation field survey conducted in Paardenschor. Permanent quadrats were thrown in transects along locations indicated by the yellow diamonds to quantify *Aster* seedling densities. These locations consisted of either bare mud, creek edges or creek edges covered with *Vaucheria* algae. The satellite imagery was extracted from Google Earth.

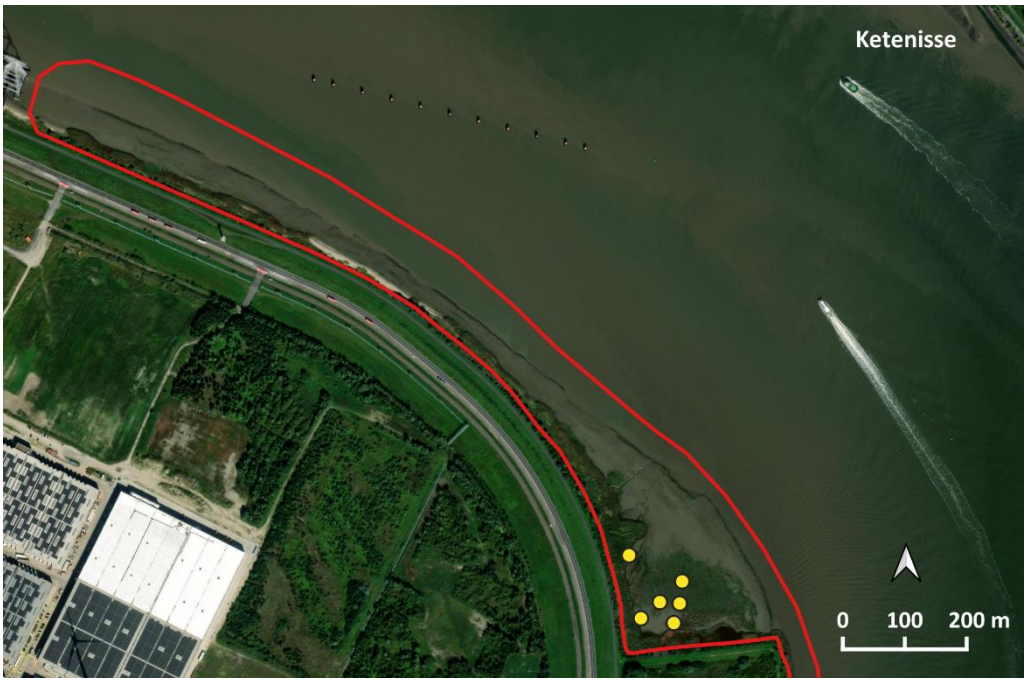


Figure S3.4: Locations used in the macrobenthos sampling survey conducted in Ketenisse. The sampling locations consisted of either bare mud or *Vaucheria* patches (n = 3) and are indicated by the yellow dots. The satellite imagery was extracted from Bing Maps.

S4 Supplementary information Chapter 4

Section S4.1

Geospatial analysis of vegetation establishment during the early developmental stages of brackish tidal marshes

The relationship between the presence of pioneer vegetation and the inundation frequency was described using a linear regression fitted to the log-log-transformed data (i.e. a power function). We tested how the proximity to a tidal creek affected this relationship by refitting the regression to a series of binned groups at 1 m increments from creeks between 0 - 7 m, and an additional group for distances > 7 m, at which the creek no longer had a distinguishable effect (see Fig. S4.2 and S4.3). For distances between 0 - 7 m, we tested how the fitted exponent, b, varied as a function of the distance from the creek, again using a linear regression. Lower b values indicate a higher likelihood for *Aster* or *Vaucheria* to be found at higher inundation frequencies. Together, this analysis assessed how the presence of pioneer plants and algae varied as both a function of tidal inundation frequency and creek proximity.

The probability of pioneer algae or plants presence (P) is best expressed as a power law function of the inundation frequency (I_f) (see Fig. 4.2):

$$P = a\,(1 - I_f)^b$$

Here, the exponent b determines how fast the likelihood of pioneer presence declines with increasing inundation frequency. Beyond 7 meters from a creek edge, the creek influence disappears (Fig. S4.2), and the parameters stabilize, in the case of *Aster* these are: scale a = 0.44 ± 0.04 (mean ± standard error) and exponent b = 1.75 ± 0.09 ($F_{1,15}$ = 755, R^2 = 0.99, p < 0.001). However, within the 7-meter zone of creek influence (Fig. S4.3), the exponent b can be expressed as a function of the distance to the nearest creek (D): $b(D) = sD + i$ with slope s = 0.43 and intercept i= 0.25 ($F_{1,5}$ = 74.9, R^2 = 0.968, p < 0.001). This indicates that proximity to tidal creeks facilitates pioneer algae/plant establishment in otherwise less favorable, more frequently inundated zones (Fig. S4.3).

As mentioned in the main text, we observed this pattern for both *Vaucheria* and *Aster* (see Fig. 4.2 & Fig. S4.3), but *Vaucheria* proved to be a more robust pioneer, establishing at higher inundation frequencies (i.e. lower elevations in the tidal frame) than *Aster* near the creek edge (beyond 7 m: scale a = 0.153 ± 0.04 and exponent b = 0.627 ± 0.16 ($F_{1,15}$ = 22.92, R^2 = 0.75, p = 0.001). The creek-proximity effect on *Vaucheria* was also captured by a similar relationship (Fig. S4.3): slope s = 0.139 and intercept i = 0.167 ($F_{1,5}$ = 24.37, R^2 = 0.907, p < 0.001).



Figure S4.1: Drone image (taken in the Lillo Potpolder by Ken Schoutens in 2020) showing a distinct spatio-temporal vegetation colonization pattern, where the pioneer marsh species *Aster tripolium* establishes along creek edges.

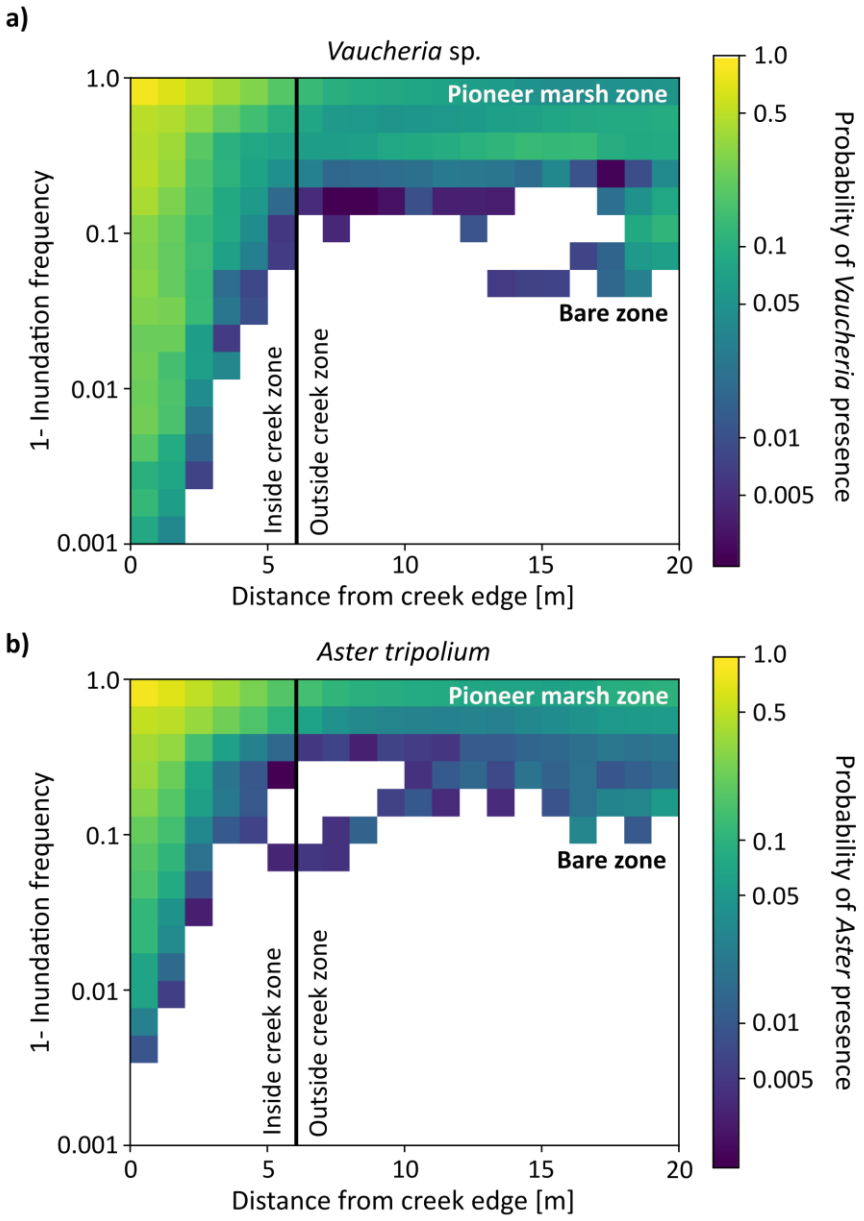


Figure S4.2: Relationship between the probability of **a)** *Vaucheria* sp. algae and **b)** *Aster tripolium* presence, inundation frequency, and distance from the creek edge. The x-axis shows the proportion of tidal cycles during which the area is not submerged at high tide (denoted as "1 – Inundation frequency") plotted against distance from the creek edge. Colored squares represent binned groups with varying probabilities of pioneer presence. A vertical line at 7 m marks the boundary of the creek influence zone, within which tidal creek proximity affects the probability of pioneer presence.

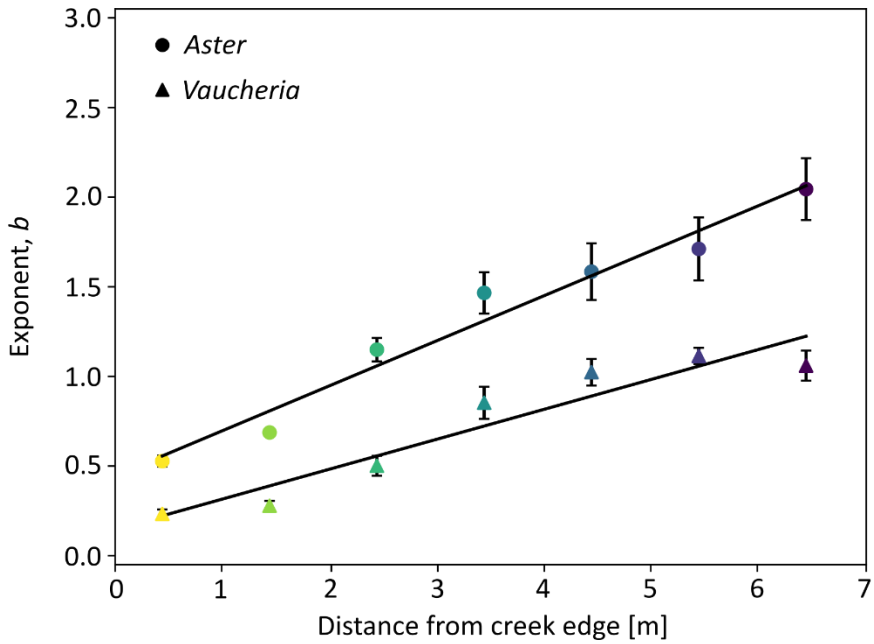


Figure S4.3: Linear regressions showing changes in the change in the fitted exponent, *b*, across a gradient of creek proximity between 0 - 7 m. Lower *b* values indicate a higher likelihood for *Aster* or *Vaucheria* to be found at higher inundation frequencies. These fits demonstrate that both *Aster* and *Vaucheria* benefit from proximity to tidal creeks, and that *Vaucheria* is more prevalent at lower intertidal elevations (due to its overall lower *b* values). Points represent the mean value and error bars represent standard error around each point. Point colors correspond to the fitted curves found in Figure 5.2.

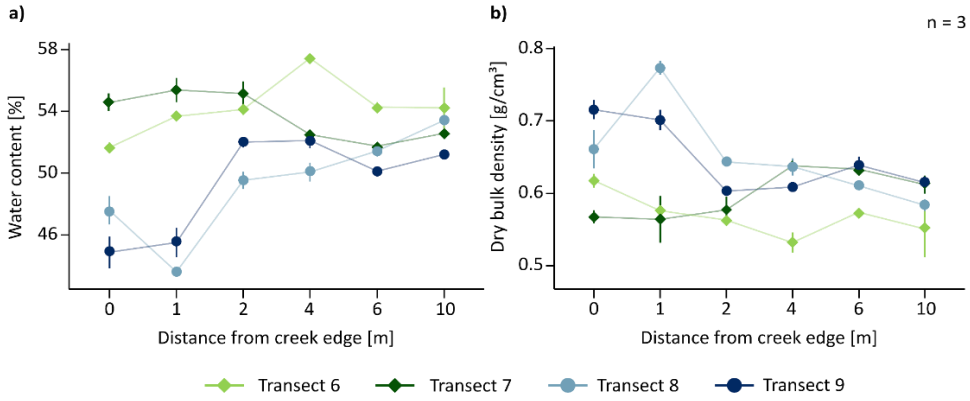


Figure S4.4: Sediment water content **a)** and dry bulk density **b)** at varying distances from the creek edge (0 m, 1 m, 2 m, 4 m, 6 m, and 10 m) across four transects (T6 = light green - diamond shape, T7 = dark green - diamond shape, T8 = light blue - circle and T9 = dark blue - circle). Error bars represent standard errors of the mean. Points indicate mean values, while lines connect mean measurements for each transect.

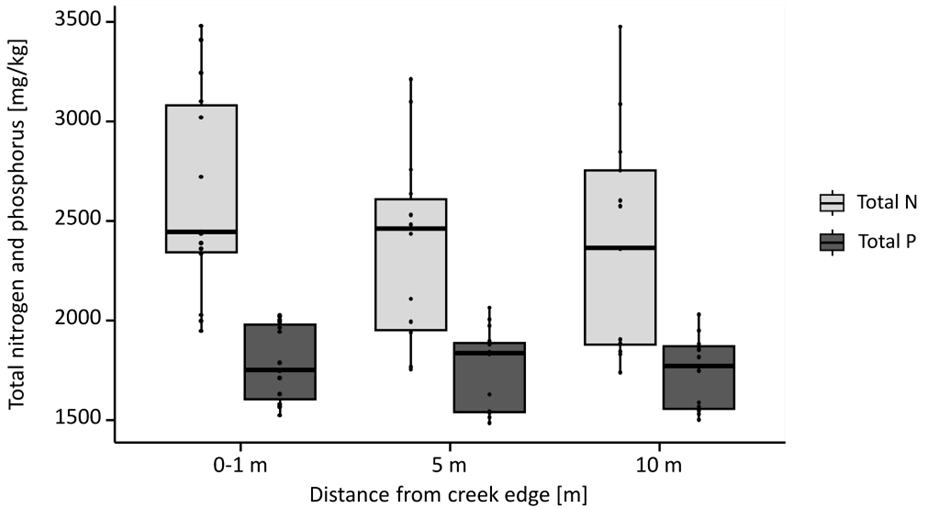


Figure S4.5: The sediment's total nitrogen and phosphorus content at varying distances from the creek edge (0 m, 5 m and 10 m) across five transects (see Fig. 5.1b, T1 - T5 in box 2022). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range.



Figure S4.6: Drone image (taken in the Lillo Potpolder by Ken Schoutens in 2020) illustrating the tendency of surface drying close to the channels during ebb.

S5 Supplementary information Chapter 5

Section S5.1

Analysis of grain size distribution across HPP

The grain size distribution of the deposited sediment in the study area was analyzed using median grain size data from sediment samples (0 - 3 cm depth) collected in 56 measuring stations (Fig. S5.3). The samples were freeze-dried, homogenized and sieved. Grain size analysis was then conducted using a Mastersizer 2000 (Malvern) after pre-treating the sediment samples with H_2O_2 and HCl to remove organic matter, prevent clogging and to remove salts. Afterwards, the sediment was classified according to the standard grain-size distribution categories: clay: < 2 µm, silt: 2-63 µm, sand: 63-2000 µm.

These data were binned into 30 intervals between 10 µm and 300 µm. Probability density functions were calculated by normalizing the counts in each bin by the total number of samples and bin width.

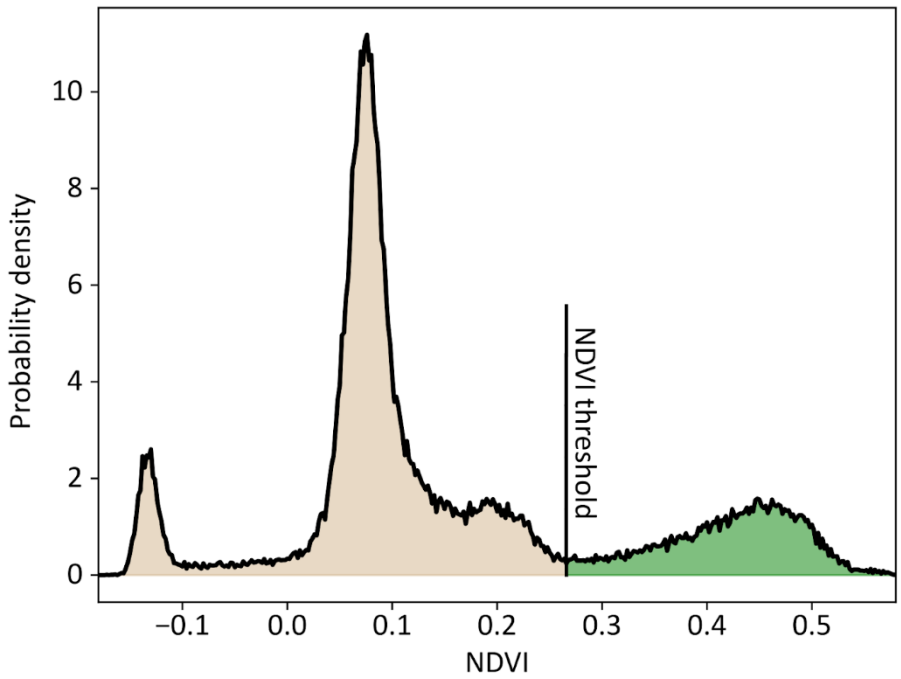


Figure S5.1: NDVI histogram of HPP in 2024 used for vegetation classification. The NDVI threshold delineating unvegetated and vegetated areas was determined automatically at the trough (lowest NDVI value) between two peaks, corresponding to bare tidal flat (−0.03) and tidal marsh (0.45).

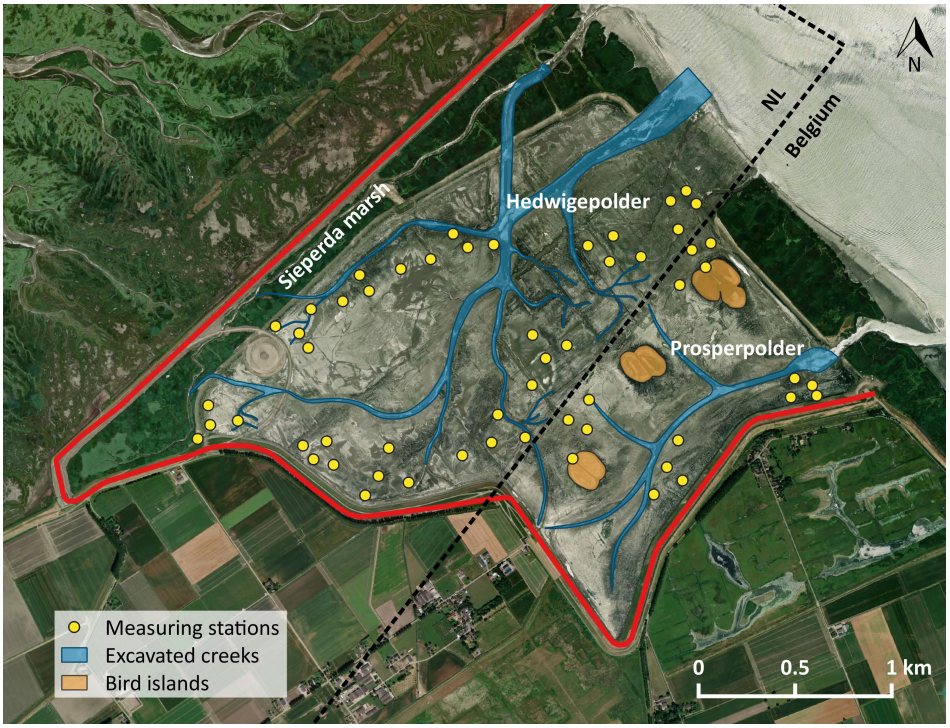


Figure S5.2: Overview of all measuring stations that were used to quantify the grain size distribution over the study site from 2023 to 2024. The satellite imagery was extracted from Bing maps.

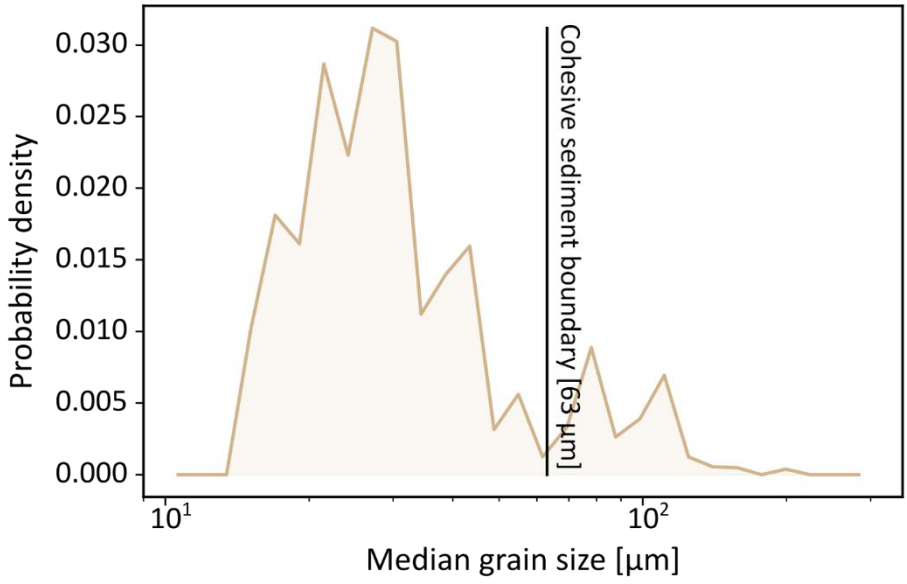


Figure S5.3: Measured sediment properties across the study site from 2023 to 2024: the probability density of mean median grain size with a vertical line indicating the cohesive sediment boundary (i.e. 63 µm).

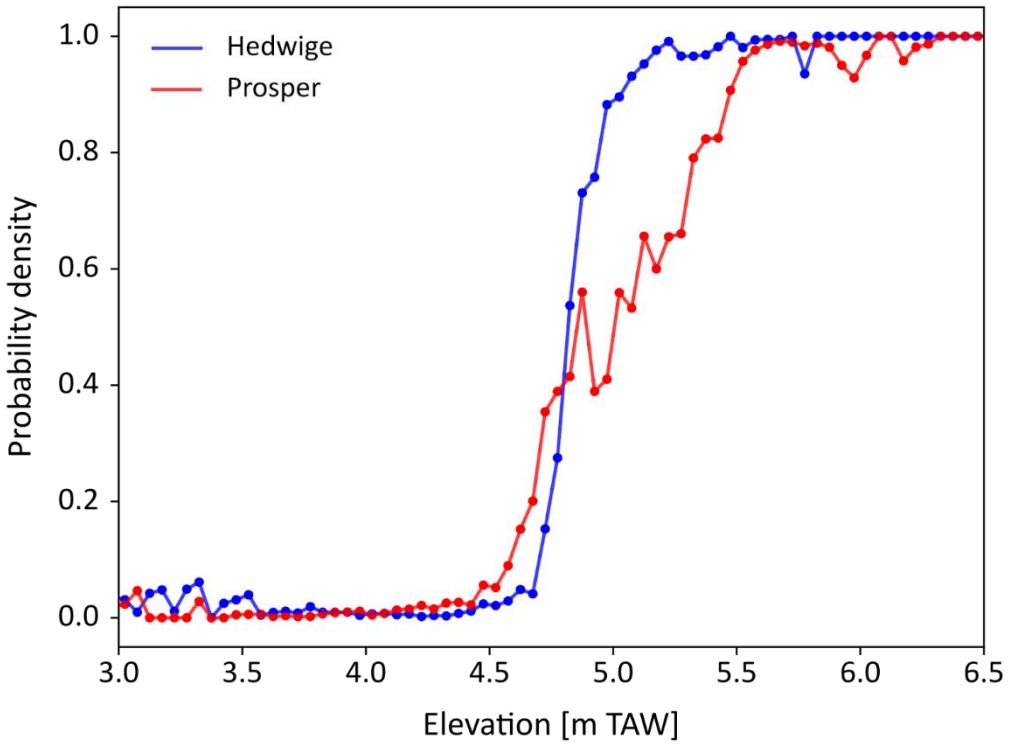


Figure S5.4: Vegetation probability density over intertidal elevation in the subareas Hedwigepolder and Prosperpolder, which differ in degree of subsoil compaction: i.e. Hedwigepolder has a compacted soil layer, while Prosperpolder has a reworked soil layer on top of the compacted soil.

Table S5.1: The sediment properties (i.e. median grain size, dry bulk density and organic matter content) measured along a 30 cm depth profile and shear strength measured at the surface of the two locations used for the field transplantation experiment.

Depth profile	Compacted	Reworked
Median grain size [µm]		
0 - 10 cm	15.45 ± 0.65	14.36 ± 2.16
10 - 20 cm	65.37 ± 0.73	26.99 ± 2.42
20 - 30 cm	55.32 ± 15.32	28.47 ± 7.9
Dry bulk density [g/cm^3]		
0 - 10 cm	0.93 ± 0.02	0.91 ± 0.07
10 - 20 cm	1.98 ± 0.30	2.00 ± 0.02
20 - 30 cm	2.38 ± 0.14	2.19 ± 0.07
Organic matter content [%]		
0 - 10 cm	8.31 ± 0.43	8.86 ± 0.93
20 - 30 cm	2.71 ± 0.5	3.46 ± 0.99
Surface shear strength [kPa]		
Surface layer (0-1 cm)	0.68 ± 0.13	0.92 ± 0.96

Table S5.2: Sediment properties (i.e. median grain size, dry bulk density and organic matter content) measured at the end of the marsh organ experiment along the varying elevation levels (i.e. bare zone, transition zone, and vegetated zone: 4.1 m TAW, 4.6 m TAW, and 5.1 m TAW).

Elevation zone	Not-drained	Drained
Median grain size [µm]		
Bare zone (4.1 m TAW)	12.53 ± 2.03	12.12 ± 1.21
Transition zone (4.6 m TAW)	11.45 ± 0.82	12.5 ± 1.45
Vegetated zone (5.1 m TAW)	14.54 ± 4.61	13.58 ± 1.97
Dry bulk density [g/cm^3]		
Bare zone	0.66 ± 0.14	0.53 ± 0.09
Transition zone	0.47 ± 0.09	0.62 ± 0.08
Vegetated zone	0.69 ± 0.12	0.69 ± 0.09
Organic matter content [%]		
Bare zone	8.37 ± 0.97	9.13 ± 0.39
Transition zone	9.67 ± 1.60	10.15 ± 0.58
Vegetated zone	8.29 ± 2.12	7.47 ± 1.09

7.1 References

Kleinhans, M. G., Roelofs, L., Weisscher, S. A. H., Lokhorst, I. R., & Braat, L. (2022). Estuarine morphodynamics and development modified by floodplain formation. *Earth Surface Dynamics*, *10*(2), 367–381. https://doi.org/10.5194/esurf-10-367-2022

Lokhorst, I. R., Lange, S. I., Buiten, G., Selaković, S., & Kleinhans, M. G. (2019). Species selection and assessment of eco-engineering effects of seedlings for biogeomorphological landscape experiments. *Earth Surface Processes and Landforms*, *44*(14), 2922–2935. https://doi.org/10.1002/esp.4702

Weisscher, S. A. H., Van den Hoven, K., Pierik, H. J., & Kleinhans, M. G. (2022). Building and Raising Land: Mud and Vegetation Effects in Infilling Estuaries. *Journal of Geophysical Research: Earth Surface*, *127*(1). https://doi.org/10.1029/2021JF006298