

Modelling Interspecific Competition between the *Salicornia* and *Spartina* species and its effect on the Bio-geomorphological Development of Salt Marshes

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Preface

This research is the final work of my MSc Civil Engineering and Management at the Water Engineering and Management department at the University of Twente. This research presents the influence of the interspecific competition between the *Salicornia* species and the *Spartina* species on the biogeomorphological development of salt marshes. I worked on this project from February 2020 till July 2020 under the supervision of Erik Horstman, Pim Willemsen and Pieter Roos.

During the last 2.5 years, I enjoyed (most of) the courses of the River and Coastal Engineering track. I especially enjoyed the subjects on the course Building with Nature. Therefore, I was very glad to get the opportunity to work on a project in this field.

This research would not have been possible without the help of some people. I would like to thank Erik Horstman for all his helpful input, intermediate feedback and the motivating weekly meetings, which were very welcome during the corona crisis. Secondly, I would like to thank Pim Willemsen for his explanations of the model and feedback on the report. I would also like to thank Pieter Roos for his feedback on the report and the new insights he gave on the population dynamics model.

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Abstract

Salt marshes are known for their contribution to coastal protection, their ecological importance and their sediment trapping ability. Under the right circumstances, salt marshes can keep up with sea-level rise, which makes them a good addition to conventional coastal protection. Several studies have concluded that physical forces and the interspecific competition between salt marsh vegetation species influence the development of salt marsh vegetation. Furthermore, it is known that vegetation development and colonisation behaviour influences the bio-geomorphological development of salt marshes. Still, it is unknown how interspecific competition works and how it influences the bio-geomorphological development of salt marshes. Therefore, this study aims to examine the influence of the interspecific competition between two salt marsh vegetation species (the *Salicornia europaea* and the *Spartina anglica*) on the bio-geomorphological development of salt marshes.

In this research, the interspecific competition between the *Salicornia* species and the *Spartina* species is schematised with the Lotka-Volterra competition framework, which is included in the vegetation module. This framework determines the growth of a salt marsh species depending on its vegetation density, the vegetation density of the competing species and the competition parameter. For the bio-geomorphological development of a multi-species salt marsh, three types of competition are tested: The development of a salt marsh without competition, with equal competition and with spatial competition. The actual simulations of 10 years of the bio-geomorphological development of salt marshes are preformed by including the Lotka-Volterra competition framework in the vegetation module in Python. This vegetation module is coupled to Delft3D Flexible Mesh (DFM), which is a numerical model that determines the hydrodynamics and the morphodynamics based on the vegetation development.

From the different model simulations, it is concluded that the differences in the morphological development between the mono-species simulation and the multi-species simulation are relatively small. On the contrary, the influence of interspecific competition on vegetation development is large, especially on the vegetation density. The extent to which the interspecific competition influences the vegetation development depends on the type of competition. When considering no competition, the vegetation density of both salt marsh vegetation species can grow towards their maximum carrying capacity. When considering equal competition, the *Spartina* species has an advantage caused by its higher maximum carrying capacity, which results in a decrease in the vegetation density for the *Salicornia* species compared to the mono-species simulation. When considering spatial competition, both salt marsh vegetation species grow till they meet their combined maximum carrying capacity, which results in a decrease in the mean vegetation density for both species compared to the mono-species simulation. When considering the vegetation cover, the *Salicornia* species proves to be more constant during the different simulations (i.e. the change in vegetation cover is limited). The vegetation cover of the *Spartina* species is more strongly affected by the competition. When considering interspecific competition the vegetation cover decreases compared to the mono-species run.

This research gives insight into the interspecific competition between different salt marsh vegetation species and shows the importance of the inclusion of interspecific competition on the vegetation development. Likewise, it has set the foundation for (long-term) simulations of a multi-species salt marsh, which can contribute to the construction of artificial salt marshes.

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Symbols

C	Bed roughness	$m^{1/2}s^{-1}$
C_b	Bed roughness of the bed without vegetation	$m^{1/2}s^{-1}$
C_D	Drag coefficient	-
C_{inund}	Plant mortality coefficient related to inundation stress	-
C_{τ}	Plant mortality coefficient related to bed shear stress	$yr^{-1}(N m^{-2})^{-1}$
D	Plant diffusion coefficient	m^2yr^{-1}
d_v	Diameter stems	m
$d_{v,Sal}$	Diameter <i>Salicornia</i> vegetation	m
$d_{v,Spar}$	Diameter <i>Spartina</i> vegetation	m
g	the gravitational acceleration	$m s^{-2}$
H	Inundation height	m
H_v	Height stems	m
$H_{cr,p}$	Critical inundation height for plant mortality	m
K	Maximum carrying capacity of stem density	stems m^{-2}
P_{est}	Chance of plant establishment	y^{-1}
n_b	Population density salt marsh vegetation	stems m^{-2}
$n_{b,est}$	Population density salt marsh vegetation new vegetated cells	stems m^{-2}
$n_{b,Sal}$	Vegetation density <i>Salicornia</i> species	stems m^{-2}
$n_{b,Spar}$	Vegetation density <i>Spartina</i> species	stems m^{-2}
$n_{b,total}$	Total vegetation density	stems m^{-2}
r	Growth rate	y^{-1}
z	Bed level elevation	m
α	Interaction coefficient	-
α_{Sal}	Interaction coefficient <i>Salicornia</i> species	-
α_{Spar}	Interaction coefficient <i>Spartina</i> species	-
$(\partial n_b / \partial t)$	Total change in stem density	stems $m^{-2}y^{-1}$
$(\partial n_b / \partial t)_{diff}$	Lateral expansion of plants to neighbouring cells	stems $m^{-2}y^{-1}$
$(\partial n_b / \partial t)_{est}$	Initial plant establishment in bare grid cells	stems $m^{-2}y^{-1}$

$(\partial n_b / \partial t)_{flow}$	Plant mortality caused by tidal flow	<i>stems</i> $m^{-2}y^{-1}$
$(\partial n_b / \partial t)_{growth}$	Logarithmic growth of stem density within a cell	<i>stems</i> $m^{-2}y^{-1}$
$(\partial n_b / \partial t)_{inund}$	Plant mortality caused by tidal inundation stress	<i>stems</i> $m^{-2}y^{-1}$
$\tau_{cr,p}$	Critical shear stress for plant mortality	Nm^{-2}
κ	the Nikuradse equivalent roughness	<i>m</i>

Chapter 1

Introduction

Because of the changing climate conditions (e.g. sea-level rise), subsidence, coastal erosion, frequent flooding and extreme storm surges, there are many concerns considering the protection of the coast. In the meantime, the number of people in the coastal areas is increasing (McGranahan et al., 2007). Temmerman et al. (2013) described how conventional coastal systems (e.g. sea walls, dykes and embankments) have high maintenance costs and in some cases can not keep up with sea-level rise scenarios. Furthermore, these conventional approaches can result in increased land subsidence and in most cases restrain the natural accumulation of sediments. Likewise, the conventional approaches often result in negative impacts on the local ecology and the ecosystem on a larger scale (Borsje et al., 2011).



Figure 1.1: Aerial view of the salt marshes at Schiermonnikoog, The Netherlands by J. van Houdt (RUG, 2014)

Another approach to ensure coastal safety is ecosystem-based engineering. This approach uses ecosystem engineers to ensure both coastal safety and the quality and quantity of habitat. Ecosystem engineers are organism that modify, maintain, create or destroy a habitat and can therefore alter the availability of a resources to other species (Jones et al., 1994). Several ecosystems engineers can be integrated in coastal protection/engineering: mangroves, salt marshes, seagrass beds, coral reefs and oyster domes, which all have different applications in coastal defences (Barbier et al., 2008; Gedan et al., 2011). Most ecosystem-based coastal approaches are used in front of the conventional coastal defences and can be used as an extra buffer, which often means that the requirements of the conventional coastal defences can be decreased. So, when using ecosystem engineering, it can enhance the protection of the area and can also provide better biological habitat and water quality (Hall, 2005).

This research will focus on bio-geomorphological development of salt marshes Figure 1.1. The application of salt marshes for coastal engineering is also considered as ecosystem-based engineering. Salt marshes are vegetated ecosystems between land and sea. They mainly occur between mean high water spring (MHWS) and the mean high water neap (MHWN) (Winterwerp & van Kesteren, 2004). This means that salt marshes are frequently flooded, therefore the vegetation growing in this area must be salt tolerant. Salt marshes can develop when the salt marsh vegetation is sheltered against waves and the inundation depth is small (Baptist et al., 2017). When the salt marsh vegetation starts to develop, the pioneer salt marsh starts to accumulate sediment and creeks start to develop. Salt marshes can be divided into several zones: The high marsh, the lower marsh, the pioneer zone and the intertidal mudflat (De Vlas et al., 2013), see Figure 1.2. A distinction between these different zones can be made according to the bed level elevation relative to the tide, but the vegetation development also depends on the salinity, inundation duration and oxygen levels (Winterwerp & van Kesteren, 2004). This research will focus on the most seaward part of the salt marsh: the pioneer zone, which is above the MHWN and below the mean high tide (MHT) and is flooded up to three hours every tidal cycle, see Figure 1.2. The *Salicornia europaea* known as glasswort (hereafter referred to as *Salicornia*) and the *Spartina anglica* also known as common cordgrass (hereafter referred to as *Spartina*) are the most common salt marsh species in the pioneer zone. In Figure 1.1, an aerial view of a salt marsh can be seen. Several characteristics can be noted in this figure: The creeks winding through the salt marsh, the bare mudflat in front of the salt marsh and the different shades of green, caused by the different salt marsh vegetation species.

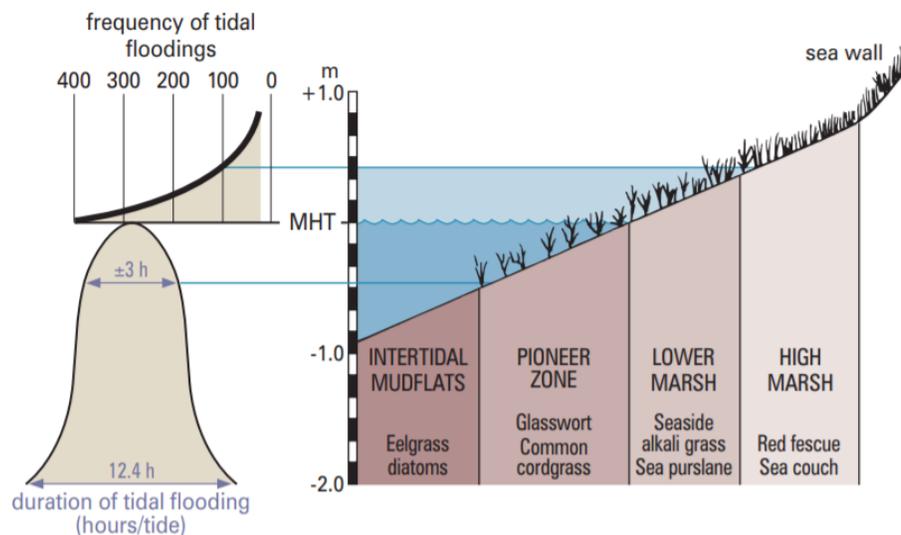


Figure 1.2: A schematisation of a salt marsh with different vegetation zones, depending on the inundation duration and inundation frequency (De Vlas et al., 2013).

The *Salicornia* species (Figure 1.3 (a)) is an annual plant species which is approximately 10-40 cm. The *Spartina* species (Figure 1.3 (b)) is slightly thinner and taller (≈ 50 cm) compared to the *Salicornia* species. The *Salicornia* species is a fast-colonising species and the *Spartina* species a slow-colonising species (Schwarz et al., 2018), which will be further explained in Chapter 2. These difference in colonisation behaviour, makes the *Salicornia* species and the *Spartina* species an interesting combination to examine.

Salt marshes in the Netherlands are considered as one of the most important habitats considering ecosystem services (Temmerman et al., 2013). Salt marshes can improve the water quality, the infiltration of water and the nutrient cycle (Baptist et al., 2017). Besides, salt marshes are important habitats for (migrating) birds, fishes and invertebrate species (van Loon-Steensma, 2015) and can be used for recreational purposes (Gedan et al., 2011; Temmerman et al., 2013). De Groot et al. (2012) estimated that the total monetary value of coastal wetlands is approximately 193,845 \$/ha/year, which is relatively large compared to e.g. tropical forest (5264 \$/ha/year) but still smaller than e.g. coral reefs (352,249 \$/ha/year). Salt marshes also contribute to coastal safety (Borsje et al., 2011). This protection is mostly caused by the wave attenuating effect of the marsh and their ability to trap sediment and therefore the ability to expand the salt marsh platform and increase the bed level elevation. Salt marshes can also reduce wave action, tidal currents and erosion (this will be further explained in Section 1.1) (Baptist et al., 2017).



Figure 1.3: A picture of the two salt marsh vegetation species, which are considered in this research. (a) A picture of the *Salicornia* species by W. Milliken (Zappi, 2009) and (b) the *Spartina* species by Alcántara (2006).

1.1 Bio-geomorphological development of a salt marsh

Several environmental factors influence the bio-geomorphological development of salt marshes. It is necessary to understand the dominant dynamics of a system when making predictions of the bio-geomorphological development of a coastal system (Larsen, 2019). Especially, when it must be decided which processes to include and exclude when making simulations. Baptist (2005a) describes bio-geomorphology as the study that considers the interaction between geomorphology and ecology. Geomorphology is the study of the physical factors influencing land forms and ecology studies the relationship between biota and the environment. In this study, the geomorphology is the bed of the salt marsh and

the biota is the salt marsh vegetation on the pioneer marsh.

The environmental factors, that influence the bio-geomorphological development of salt marshes consist of the abiotic factors, biotic factors and external factors (Baptist, 2005a). The abiotic factors that influence the bio-geomorphological development of salt marshes are physical processes. The biotic factors are the salt marsh vegetation development and interspecific interaction between salt marsh vegetation species. The external factors that influence the bio-geomorphological development of salt marshes mainly consist of the processes that humans impose e.g. sediment supply and salt marsh (re)construction. Next, the feedbacks between abiotic and biotic factors will be presented. Thereafter, the external factors will be discussed.

1.1.1 Feedbacks between abiotic and biotic factors

In Figure 1.4 the morphodynamic feedback loop is shown, including salt marsh vegetation development and interspecific interaction. The relevant abiotic factors at salt marshes are all the factors that influence the bio-geomorphological development of salt marshes and are not caused by living organisms. Abiotic factors can be chemical and physical, but the abiotic processes on salt marshes mainly consist of the physical processes (Baptist, 2005a). Salt marsh vegetation is considered to be an ecosystem engineer, which means that salt marsh vegetation is also able to alter the abiotic conditions (Jones et al., 1994). So, the vegetation development also influences the hydrodynamic processes, sediment transport and morphodynamics. These feedbacks between the hydrodynamics, sediment dynamics, morphodynamics and vegetation dynamics can be found in Figure 1.4. In Figure 1.4, the abiotic factors can be found in the blue box and the biotic factors in the green box. The numbered arrows between the different boxes are the feedback processes between the hydrodynamics, morphodynamics and vegetation dynamics. In this Chapter, the morphodynamic feedback loop and the influence of the vegetation development on the morphodynamic feedback loop will be discussed. In Chapter 2, the effect of the hydrodynamics and morphodynamics on the vegetation development will be discussed in more detail.

1. Hydrodynamic processes → sediment transport

The hydrodynamic processes are all the processes that result in a motion of water. When considering a salt marsh, waves and currents are important, also the turbulence that is caused by the waves and currents. The waves are caused by winds and tides. The currents are caused by tides, winds and differences in density. The combination of the waves, tides and currents determine the net direction and magnitude of the flow, which highly depends on time and place.

Sediment transport is the transport of sediments in suspension and as bedload, depending on the hydrodynamic conditions and the grain size. The transport of sediment in salt marshes can be divided into three stages: 1) the erosion, 2) transport and 3) the deposition of sediment (The Open University, 1999). All these stages are highly dependent on hydrodynamic conditions. Erosion of sediments will occur if the shear stress at the bed exceeds the critical shear stress. These shear stresses are caused by the flow stresses. The flow shear stresses are proportional to the square of the flow velocity (The Open University, 1999). So, if the flow velocity near the bottom increases, the shear stress is more likely to exceed the critical bed shear stress and the sediment will be more likely to be transported. The settling of the sediment depends on the grain size and the flow velocity. If the flow velocity is below a certain deposition threshold (depending on the grain size) the suspended sediment can deposit (The Open University, 1999). Besides, cohesive sediments form flocs when the flow velocity decreases, therefore the total size of the sediment increases and the deposition chance increases (Furukawa & Wolanski, 1996).

The supply of sediment to salt marshes mainly originates from the sea and enters the salt marsh because of waves and currents. During flood, the suspended sediment enters the salt marsh directly from the sea or can be transported by the creek. Sediments originating from the sea, are

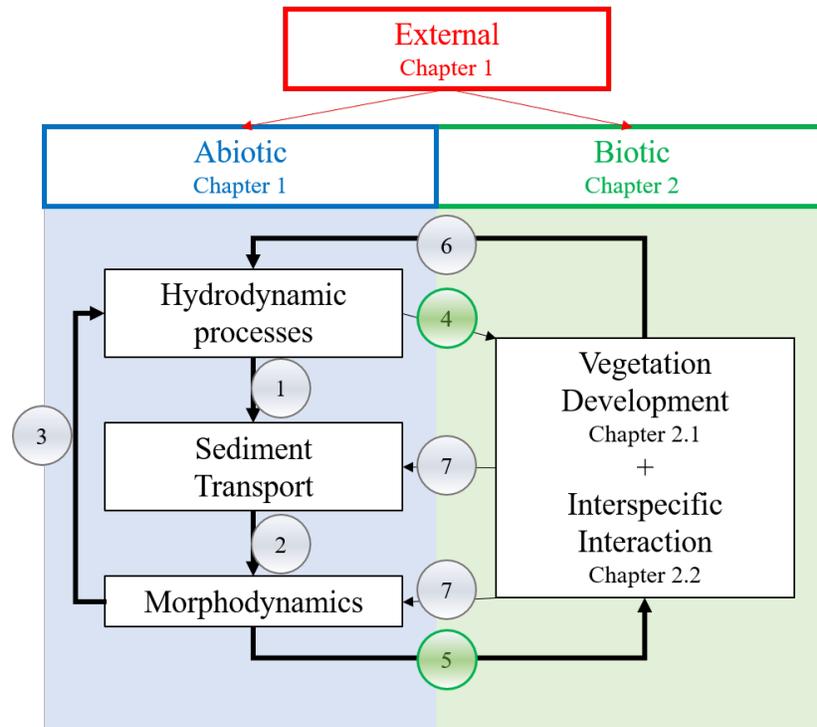


Figure 1.4: The morphodynamic feedback loop including the salt marsh vegetation development and interaction. The environmental factors (abiotic, biotic and external factors) that influence the biogeomorphological development of salt marshes are also shown. The thick arrows represent the main processes and thin arrows represent the secondary effects. The abiotic factors, external factors and arrows with a grey number are discussed in this Chapter. The biotic factors and arrows with a green number are further explained in Chapter 2. Altered from Baptist (2005a); Attema (2014)

transported by shallow water waves: When a wave enters the shallow water region, the orbital velocity and the shear stress at the bed increases as the water depth decreases. The waves move the sediment landwards through the crest and seaward through the trough. The relatively larger shore-wards orbital velocity results in a net sediment supply landwards and therefore the salt marsh (The Open University, 1999).

2. Sediment transport → morphodynamics

Bed level change is the increase (accretion) or decrease (erosion) of the bed level. So, the bed level elevation is the result of the deposition and erosion of sediments.

3. Morphodynamics → hydrodynamic processes

The change in bed level influences the hydrodynamic processes. The hydroperiod depends on the local bed level elevation. If the tidal range and the hydroperiod are large, a larger part of the salt marsh can be inundated for a longer period. Likewise, all the hydrodynamic and morphodynamic processes highly depend on the bathymetry and the bed composition. The bed of a salt marsh typically consists of cohesive sediments and has a slope between the $10\text{-}100\text{ cm km}^{-1}$, which is considered as low-gradient (Larsen, 2019).

4. hydrodynamic processes → vegetation development

For salt marsh vegetation to develop, the inundation depth and the bed shear stresses must be limited (Temmerman et al., 2007). The extent to which hydrodynamics effects the salt marsh vegetation development and the interspecific interaction, will be further explained in Chapter 2.

5. **Morphodynamics** → **vegetation development**

The bed level elevation highly influences the ability of vegetation to establish on a salt marsh. But, this is mostly because at a higher bed level elevation, salt marsh vegetation is less inundated and more sheltered against waves. The slope of the salt marsh also affects the salt marsh vegetation development. When the gradient decreases, the gradient in vegetation density increases and the vegetation plays a more important role in the transformation of the salt marsh (Jones et al., 1997; Larsen, 2019; Temmerman et al., 2005).

Besides, the erosion or deposition of sediments can withhold the establishment of salt marsh vegetation, which will also be explained further in Chapter 2.

6. **Vegetation** → **hydrodynamic processes**

The cylindrical-shaped salt marsh vegetation exerts a drag force on the water flowing by (Gedan et al., 2011). Therefore, salt marsh vegetation reduces the hydrodynamic energy from waves (Bouma et al., 2005; Möller et al., 2014). This also applies to unidirectional flow (e.g. currents): the current velocities decrease due to the drag of the salt marsh vegetation species (Bouma et al., 2005). Depending on the exact situation, salt marshes can reduce waves during storm surges and small tsunami waves (Mullarney, 2018). However, till a certain point. Severe tsunamis and storm surges can reduce the damping effect of vegetation (Gedan et al., 2011). This depends on the inundation depth and the wave energy. If the inundation depth increases, the salt marsh vegetation is further submerged and the flow velocity will increase above the salt marsh vegetation. So, the damping effect of the vegetation decreases as the inundation depth increases. Besides, storm surge waves are waves with a large wavelength. When the wavelength is large, the wave energy increase as the water depth decreases and the wave is moving towards land. The high wave energy of the long tsunami waves and storm surges can, therefore, overcome the wave attenuating ability of salt marsh vegetation (Gedan et al., 2011). Still, Möller et al. (2014) found that under the extreme storm surge conditions, the bed of the salt marsh remains stable and resistant to surface erosion (Möller et al., 2014).

7. **Vegetation development** → **sediment transport and morphodynamics**

The erosion of sediments can be reduced by the vegetation. Because of the salt marsh vegetation, an extra drag force arises, which decreases the near bed velocity and reduces erosion. Flexible vegetation can cover the ground when the flow velocity increases (Bouma et al., 2013). Also, the roots of salt marsh vegetation bind the sediments together, which results in a larger critical bed shear stress (Möller et al., 2014). Therefore, the roots of the salt marsh vegetation stabilise the bed of the salt marsh and increase the critical shear stress for erosion (Fagherazzi et al., 2012; Howes et al., 2010). So, they can be considered as sediment traps, which can also contribute to the expansion of the salt marsh (Best et al., 2018). Likewise, the salt marshes produce organic material, which also contributes to an increase in the accretion rate.

1.1.2 External factors

The most important external factor, influencing the bio-geomorphological development of salt marshes, is the impact of human activity on salt marshes. Human activity can influence the development of salt marshes in several ways: humans can damage salt marshes with their presence, they can remove salt marshes, can decide to let cattle graze on the salt marsh or can construct salt marshes. Besides, salt marshes are often located in front of a sea dike for coastal protection. This means that the requirements of the width of the salt marsh can increase or decrease, depending on the requirements of the sea dike (e.g. a decrease in the width of a salt marsh because the sea dike must be heightened or an increase in the width of the salt marsh to prevent the heightening of the sea dike). Human behaviour also indirectly influences the dynamics on salt marshes e.g. through human induced sea-level rise and the sediment supply.

Both the sediment supply and the sea-level rise are important factors that determine whether a salt marsh can survive. Kirwan and Murray (2007) found that with moderate sea-level rise, the deposition

rate increases and the bed level elevation of salt marshes can keep up with sea-level rise if the provided sediment supply is sufficient. When the sea-level rise increases or the sediment supply decreases, the bed level elevation of salt marshes will not be able to keep up with the rate of sea-level rise and the salt marsh vegetation will drown. Best et al. (2018) also found an increase in salt marsh elevation when simulating over a period of 120 years. The inclusion of sea-level rise resulted in a (partial) drowning of the salt marsh platform, which can be prevented if the accretion rates are higher than the sea-level rise.

1.1.3 Time and space scales of the abiotic and external factors

All the processes mentioned above have different time scales. In this research, we are especially interested in the smallest common time scale of the most important processes. When knowing the smallest timescale, one can decide what minimum time step can be considered when implementing the processes numerically. Furthermore, this research is interested in the time scales of the different biotic processes. Based on the time needed for a salt marsh vegetation to interaction with each other, the duration of the simulation can be determined.

Cowel and Thom (1994) and later Woodroffe (2002) developed a framework in which the time and space scales of the hydrodynamics and morphodynamics can be found. The finding of these two studies are summarised and shown in Figure 1.5. In this figure, the processes mentioned in this chapter are placed in the space-time domain. The hydrodynamics are displayed in blue, the morphodynamics in brown and the external factors in red. Four time scales can be distinguished: 1) instantaneous, 2) event, 3) planning/engineering and 4) geological. In the instantaneous time scale, the physical processes and the results of the physical processes are shown, which are mainly occurring stochastically. One can think of the waves caused by winds. The second scale is the event time scale. In this time scale several processes are reoccurring with a interval e.g. storm events during the winter. Also, the results of the longer morphodynamics start to develop, such as bars and dunes. The next time scale is the planning/engineering time scale, which is the result of the processes in the smaller scales. This is also the time scale that is related to the future, which means that coastal engineers are planning for this time scale when making designs for future coasts. The last time scale is the geological time scale, which is the result of mean trends of the environmental conditions for several millennia e.g. the variations in sea-level.

Figure 1.5 only shows the abiotic and external phenomena, discussed in this Chapter. So, the next step is to determine the important biotic factors and include these factors in the space-time diagram. In this way, the minimal time step and the appropriate duration of the simulation can be determined.

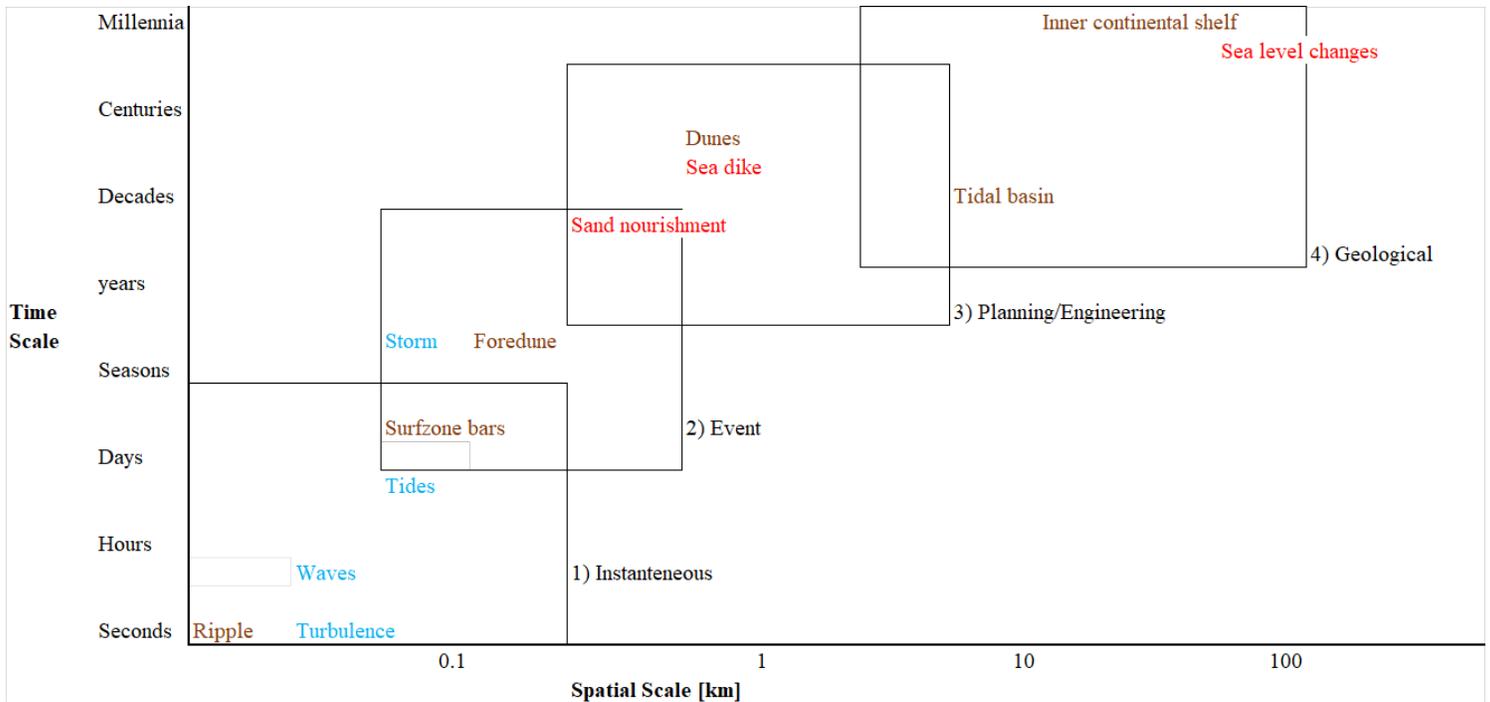


Figure 1.5: The space-time diagram of the abiotic and external factors, discussed in this chapter. The hydrodynamic phenomena are shown in blue, the morphodynamic phenomena in brown and the external phenomena in red. In Chapter 2 Altered from Cowell and Thom (1994) and Woodroffe (2002)

1.2 Knowledge gap

From the literature it can be concluded that salt marshes have great ecological importance and, under the right circumstances, can keep up with sea-level rise. The research of the bio-geomorphological development of salt marshes in the pioneer zone is important since these landscapes are among the first to inundate when the relative sea-level increases (Larsen, 2019). Roman (2011) concluded that salt marshes are continuously changing while being influenced by environmental factors and therefore pointed out the importance of predicting salt marsh development under different human and natural interactions. Several studies found that interaction between salt marsh vegetation species influence the development and the zonation of salt marsh vegetation (e.g. (Bertness, 1991; Bertness & Ellison, 1987; Gollasch & Nehring, 2006; Scholten et al., 1987)). Furthermore, several salt marsh vegetation species are considered as an ecosystem engineer, which means that they can alter their environment and therefore changing the biotic and abiotic conditions (Jones et al., 1994). Also, different salt marsh vegetation species can have different colonisation behaviour, which can influence the evolution of a salt marsh (Schwarz et al., 2018).

So, it is known that interspecific interaction between salt marsh vegetation species influence the development and the zonation of salt marsh vegetation, and it is known that the development and zonation of salt marsh vegetation influence the evolution of the bed of the salt marsh. Still, it is unknown how the interaction between salt marsh vegetation species influences the morphological development of salt marshes, and how the vegetation development and morphological development influence the interspecific interaction. Due to the competition e.g. the salt marsh width, morphology or the strength of the bed can change, which can result in favourable conditions for a certain salt marsh vegetation species, which results in a change in interspecific interaction. This means that this interaction has not yet been included in assessing the bio-geomorphological development of salt marshes. Therefore, it is unknown how the multi-species salt marsh develops compared to a single species salt marsh.

1.3 Research aim and research questions

This research aims to examine the influence of interspecific interaction between two salt marsh vegetation species on the bio-geomorphological development of salt marshes. To do this, the following research question is composed:

What is the influence of interspecific interaction between different salt marsh vegetation species on the bio-geomorphological development of salt marshes in the pioneer zone?

This research question can be answered, by answering the following research sub-questions:

1. What biotic factors are relevant when making models of the bio-geomorphological development of salt marshes and what are the timescales of these biotic factors?
2. How can the interaction between different salt marsh vegetation species in the pioneer zone be included in the models of the bio-geomorphological development of salt marshes?
3. What is the bio-geomorphological development of mono-species salt marsh versus the bio-geomorphological development of a multi-species salt marsh?

1.4 Reading guide

1.4.1 Outline of methodology

The first research question aims to determine how biotic factors influence the bio-geomorphological development of salt marshes. The biotic factors that influence the bio-geomorphological development of salt marshes are the vegetation development characteristics of the salt marsh vegetation species and the interspecific interaction between salt marsh vegetation species. To gain insight into the salt marsh vegetation development characteristics, the establishment and seasonal change are examined through literature. Likewise, through literature, it is studied what abiotic factors are dominant for the vegetation development. Finally, the timescales of the biotic factors will be included in the time-space diagram (Figure 1.5), to give an indication of the smallest time step in the simulation and the simulation duration.

The second research question will be answered by investigating how the interaction between different salt marsh vegetation species can be classified. After this, the interaction between two salt marsh vegetation species will be captured in an interaction framework. This will be done by examining the literature. Finally, the interaction framework will be included in the vegetation module.

In the last research question, the bio-geomorphological development of a mono-species salt marsh will be compared to the development of a multi-species salt marsh. This will be done by making numerical simulations of the bio-geomorphological development of salt marshes, with no vegetation, with only *Salicornia* vegetation, with only *Spartina* vegetation and three runs including both salt marsh vegetation species. In the three runs with both salt marsh vegetation species, the competition parameter will be varied for both species to represent a simulation without competition, with equal competition and with spatial competition. This results in a total of six simulations, which will be simulated by coupling the adjusted population vegetation module to Delft3D Flexible Mesh.

1.4.2 Outline of report

In Chapter 2 the biotic factors will be discussed, which consist of the salt marsh vegetation development and the interspecific interaction, see Figure 1.4. Also in Chapter 2, the interspecific interaction will be captured in an interaction framework, which will be included in vegetation module. In Chapter 3, the numerical implementation of a mono-species salt marsh versus a multi-species salt marsh is described

and in Chapter 4 the results of this numerical implementation are described. In Chapter 5 the results will be discussed and in Chapter 6 a conclusion will be drawn.

Chapter 2

Literature review

In Chapter 1 the abiotic and external factors are already discussed. This Chapter will focus on the biotic factors that influence the bio-geomorphological development of salt marshes and how these factors can be parameterized in a bio-geomorphological model. The biotic factors are all the factors caused by living organisms. This research will focus on the biotic factors caused by the salt marsh vegetation, so the development of the vegetation and the interaction between different salt marsh vegetation species. First, salt marsh vegetation development will be discussed. The different types of interaction will be discussed and it will be explained how these different types of interaction can be included in the Lotka-Volterra competition framework. The different processes, important for the development of salt marshes and the interaction between the different salt marsh vegetation species, are then included in the time-space diagram (Figure 1.5), to indicate the minimum time step and the simulation duration.

2.1 Salt marsh vegetation development

When considering the morphodynamic feedback-loop again (Figure 1.4) one can see that the vegetation development is influenced by the bed level change and the hydrodynamics. Besides, the development of salt marsh vegetation depends on the establishment and seasonal change.

The dominant hydrodynamics and morphodynamics that influence the vegetation development are the bed shear stresses, inundation depths, the bed level elevation and the net erosion rate. Temmerman et al. (2007) investigated the feedbacks between hydrodynamics, morphodynamics and vegetation development on the colonisation and channel formation. They concluded that the biomass of salt marsh vegetation can decrease due to high bed shear stresses ($\approx 0.25 \text{ N m}^{-2}$) and large inundation depths ($\approx 0.21 \text{ m}$). The extent to which salt marsh vegetation is exposed to these bed shear stresses and inundation is determined by the bed level elevation. If the bed level elevation is high, the inundation is likely to be smaller. Besides, high erosion rates ($\approx 5 \text{ mm/week}$) or deposition rates ($\approx 15 \text{ mm/week}$) can cause salt marsh vegetation seedlings not to establish (Poppema et al., 2019).

As explained in Chapter 1, the salt marsh vegetation on the pioneer marsh is considered in this research. Two common salt marsh pioneer vegetation species are the *Spartina* species and the *Salicornia* species. In Figure 2.1 a picture can be seen, showing both vegetation species. The large patch of vegetation is the *Spartina* species and the smaller vegetation surrounding the patch is the *Salicornia* species. It can already be seen from this Figure that both species differ both in their sizes, establishment pattern and expansion pattern. Therefore, these species will now be discussed in more detail.



Figure 2.1: A picture of the *Spartina* and *Salicornia* species. The large vegetated patch solely consists of the *Spartina* species and the plants surrounding the patch are the *Salicornia* species. Picture taken at Moddergat, the Netherlands by Braam (n.d.) obtained through Poppema (2017)

Establishment *Spartina* species

The establishment of the *Spartina* species can be divided into three stages: 1) the seedling establishment, 2) patch development and 3) salt marsh platform succession (Attema, 2014). The first two stages describe the transition from a bare mudflat to a pioneer marsh and the evolution of this pioneer marsh. The last stage describes the evolution of a mature marsh and how the structure of the community changes over time.

1. **Seedling establishment:** Whether pioneer salt marsh vegetation species can develop on a bare mudflat or sandflat depends on the seedling availability and the shelter against waves (Baptist, 2005a). Besides, the environmental factors (e.g. the bed shear stresses, sedimentation rate, erosion rate and water depth) should be minimal. In nature, salt marsh vegetation is only able to arise by seeds and plant parts originating from other salt marshes, which often are transported by the sea. For the seedling establishment of salt marsh vegetation species, the Windows of Opportunity (WoO) framework is developed initially by Balke et al. (2011) and later altered by Hu et al. (2015) and Poppema et al. (2019). The WoO framework states that an inundation free period of approximately 2.5 days is needed, followed by a period of limited bed shear stresses, sedimentation rate and net erosion rate. When these conditions are met for the next 80 days, the salt marsh vegetation reaches maturity.
2. **Patch development:** Patches are circle-shaped vegetated areas (see Figure 2.1), in which the *Spartina* species develops on pioneer marshes. Initially, these patches are scattered over the bare mudflat or sand flat and can expand but also erode (Wesenbeeck, 2007). The stem density and the bed level are relatively high in the patches, which can result in a positive feedback loop and expansion of the patch. But the patch can also cause a gully adjacent to the patch, which can

result in erosion of the patch (Wesenbeeck, 2007; Attema, 2014).

3. **Salt marsh platform succession:** This stage describes the growth from patch to a mature salt marsh platform. Schwarz et al. (2018) described the *Spartina* species as a slow colonising salt marsh species. This means that the establishment probability is relatively low caused by the relatively low viable seed produced, but the lateral expansion rate is large (Marks & Truscott, 1985). The lateral expansion rate describes the chance of vegetation to expand to directly adjacent bare substrate through tillering. Since the establishment probability is small and the lateral expansion rate large, the *Spartina* vegetation density is large at the areas where vegetation is occurring, but it takes a longer period to colonise an area.

Seasonal change *Spartina* species

During one year, the biomass of the *Spartina* species varies. During winter, there is more wave-induced stem breakage caused by e.g. the storm frequency and intensity (Vuik et al., 2018). Likewise, salt marsh vegetation loses the above-ground biomass during the winter: The paper of Drake (1976) researched variability of the green standing crop dry weight (i.e. the total dried biomass of an organism) for the period May-July for several salt marsh communities. The grass communities, which included the *Spartina* species, have maximum biomass during the month July after which the biomass decreases. Mid-May, new vegetation starts to develop again while the old growth from the previous season decays. Vuik et al. (2018) also observed these seasonal changes in the vegetation properties, which were then found to affect the wave attenuation: The highest wave attenuation for the *Spartina angilca* occur during the summer (when the above-ground biomass was at its maximum) and a decrease of wave attenuation from September till March (when the above-ground biomass reduces). The new vegetation starts to develop between March and May, which can also be seen in a change in stem height and diameter: The mean value of the height for the *Spartina angilca* decreased from 327 mm in December to 285 mm in April, thereafter the value increased again to 544 mm in September (Vuik et al., 2018). The diameter of the *Spartina angilca* almost follows the same pattern: from December, the mean diameter increases from 3.1 mm to 4.1 mm, after which it decreases to 3.7 mm in November (Vuik et al., 2018). Zhu et al. (2019) analysed the patch expansion rate of the *Spartina alterniflora* and also found a seasonal variation. During spring and summer the expansion rates were relatively large (0.52 mm/month and 0.66 mm/month respectively) and during autumn and winter small (0.08 m/month and 0.00 m/month respectively). An overview of the seasonal change of the *Spartina* species can be found in Figure 2.2. The studies mentioned above analysed different aspects of the *Spartina* species. But it can be seen that generally, the vegetation increases in biomass during the summer and decreases during the winter.

Establishment *Salicornia* species

The establishment of the *Salicornia* species consists of the seedling establishment and the salt marsh succession. In contrary to the *Spartina* species, the *Salicornia* does not form patches, but spreads due to a large establishment probability:

1. **Seedling establishment:** The higher establishment probability of the *Salicornia* species causes relatively more seeds to establish. After the seedling starts to grow roots, the chance of establishment of the vegetation can be also described with the WoO-framework. When considering the WoO-framework, the *Salicornia* establishment is quite similar to the *Spartina* establishment: The *Salicornia* species requires an inundation free period of 2.5 days. Thereafter, the *Salicornia* species requires a period of 90 days of small bed shear stresses and net erosion rate. But, there are some differences: The increasing shoot length of the *Salicornia* species can have a negative influence on the maximum net erosion rate. Therefore, the initial critical erosion rate for the *Salicornia* species is lower than the *Spartina* species (Poppema, 2017).
2. **Salt marsh platform succession:** The *Salicornia* species has no lateral expansion, but a large seed establishment occurs with a large survival rate (Adam, 1993; Wolters, Garbutt, Bekker,

Spartina												
Month	January	February	March	April	May	June	July	August	September	October	November	December
Season	Winter			Spring			Summer			Autumn		
Vuik (2018)	Gradually decline of biomass			New shoots			Development of dense vegetation			Gradually decline of biomass		
Drake (1976)	Decline of dead biomass			Start growth		Increase biomass		Maximum biomass		Decrease biomass		
Zhu (2019)	0.00 m/month patch expansion rate			0.52 m/month patch expansion rate			0.66 m/month patch expansion rate			0.08 m/month patch expansion rate		
Salicornia												
Month	January	February	March	April	May	June	July	August	September	October	November	December
Season	Winter			Spring			Summer			Autumn		
Ungar (1987)	Growing season											
Jefferson (1981)	Declining			Seed		Slow Growth		Moderate Growth			Reaching Maturity and Declining	
Ball & Brown (1970)	Declining			Seed germination			Grow vegetatively			Completion flowering		Reaching Maturity and Declining
van den Broek	Declining			Growing season						Dies off		

Figure 2.2: The seasonal change of the *Spartina* species according to Vuik et al. (2018); Drake (1976); Zhu et al. (2019) and of the *Salicornia* species according to Ungar (1987); Jefferies et al. (1981); Ball and Brown (1970); Van den Broek (2020) through one year. The green boxes indicate a increase of salt marsh vegetation and the yellow boxes indicate a decrease in salt marsh vegetation.

Bakker, & Carey, 2008). So, no patches will occur, but independent plants will be scattered over the salt marsh, which can also be seen in Figure 2.1. This makes the *Salicornia* species a fast colonising species (Schwarz et al., 2018).

Seasonal change *Salicornia* species

Like the *Spartina* species, the biomass of the *Salicornia* species varies during one year. The *Salicornia* species is an annual vegetation species, which means that the whole life cycle occurs in one year. So every year, a completely new population is build up (Beeftink, 1985). Most of the seeds germinate during the early spring (Egan & Ungar, 1999; Jefferies et al., 1981; Ball & Brown, 1970). Thereafter, the growing season starts in which a slow vegetation growth occurs until mid-July. Then the growth rate increases because of the flowering (Jefferies et al., 1981). Late-September the seed reaches maturity and the flowering season ends (Jefferies et al., 1981; Ball & Brown, 1970). Mid-autumn the growing season ends and the vegetation starts to decay (Ungar, 1987). The seeds for the new generation fall from the mature plants during November and December. The seeds are relatively heavy and posses mucilaginous hairs, which both contribute to the attachment of the seeds to the sediment (Jefferies et al., 1981). Again, these findings are summarised, see Figure 2.2. It can be seen from this Figure that, generally, the growing season occurs during the spring and summer. During autumn and winter, the *Salicornia* vegetation reaches maturity and dies off.

2.1.1 Salt marsh vegetation development: population dynamics model

The feedback between the hydrodynamic, morphodynamics and vegetation development is a complex system. Therefore, numerical models are an important tool when making predictions of the bio-geomorphological development of salt marshes. Temmerman et al. (2005) developed a three-dimensional hydrodynamic and sediment transport model and studied the impact of vegetation in the Westerschelde estuary. They found that the vegetation cover is a key factor is that controls the bio-geomorphological development of salt marshes. Later, Temmerman et al. (2007) further developed this model and coupled the hydrodynamics, morphodynamic and a population dynamics model to simulate the salt marsh vegetation colonisation and the formation of creek patterns. In the research of Temmerman et al. (2007), the hydrodynamics and morphodynamics are calculated with the Delft3D modelling system, which was coupled

with the population dynamics model. This coupling of the population dynamics model with the Delft3D is successfully used in several studies (e.g. Schwarz et al. (2014); Best et al. (2018); Poppema et al. (2019)).

In the populations dynamics model, the increase in vegetation density is the result of the growth of the salt marsh vegetation, the establishment of new salt marsh vegetation and the diffusion of the vegetation. The decrease of the salt marsh vegetation density is caused by mortality due to inundation of the vegetation or high bed shear stresses:

$$\frac{\partial n_b}{\partial t} = \left(\frac{\partial n_b}{\partial t}\right)_{growth} + \left(\frac{\partial n_b}{\partial t}\right)_{diff} + \left(\frac{\partial n_b}{\partial t}\right)_{flow} + \left(\frac{\partial n_b}{\partial t}\right)_{inund} + \left(\frac{\partial n_b}{\partial t}\right)_{est} \quad (2.1)$$

Here, $\partial n_b/\partial t$ is the change in vegetation density over time. The increase in vegetation density is caused by the growth $(\partial n_b/\partial t)_{growth}$, the diffusion $(\partial n_b/\partial t)_{diff}$ and the establishment $(\partial n_b/\partial t)_{est}$. The decrease in vegetation density is caused by high bed shear stresses $(\partial n_b/\partial t)_{flow}$ and high inundation depths $(\partial n_b/\partial t)_{inund}$.

Logistic growth

In Equation 2.2 the logistic growth function can be found according to Temmerman et al. (2007). The logistic growth function states that the growth rate decreases as the species is reaching the maximum carrying capacity of a species.

$$\left(\frac{\partial n_b}{\partial t}\right)_{growth} = r \cdot n_b \left(1 - \frac{n_b}{K}\right) \quad (2.2)$$

Here, $(\partial n_b/\partial t)_{growth}$ is the increase in vegetation density caused by growth in *stems* $m^{-2} yr^{-1}$. This depends on the growth rate r per *yr*, the current vegetation density n_b in *stems* m^{-2} and the maximum carrying capacity K in *stems* m^{-2} .

Diffusion

Equation 2.3 calculates the change in vegetation density due to the diffusion $((\partial n_b/\partial t)_{diff})$ in *stems* $m^{-2} yr^{-1}$. So, the diffusion of the salt marsh vegetation to the neighbouring cells in x-direction and y-direction depends on the vegetation density n_b in *stems* m^{-2} and the diffusion coefficient D in $m^2 y^{-1}$.

$$\left(\frac{\partial n_b}{\partial t}\right)_{diff} = D \left(\frac{\partial^2 n_b}{\partial x^2} + \frac{\partial^2 n_b}{\partial y^2}\right) \quad (2.3)$$

This means that when the vegetation density is large in a cell, the vegetation density will be redistributed to the neighbouring cells. This also means that when the vegetation density is large in a cell and small in the surrounding cells, the vegetation density in the surrounding cells will increase but vegetation density in the original cell will decrease.

Flow

Equation 2.4 shows the decrease in vegetation density caused by high bed shear stresses, caused by flow $(\partial n_b/\partial t)_{flow}$ in *stems* $m^{-2} yr^{-1}$. In this equation, τ is the bed shear stress and $\tau_{cr,p}$ the critical bed shear stress in $N m^{-2}$. This means that there will only be a decrease in the vegetation density caused by the flow if the bed shear stress is larger than the critical bed shear stress. The decrease in vegetation density then depends on how much larger the bed shear stress is compared to the critical bed shear stress, the vegetation density n_b in *stems* m^{-2} and the plant mortality coefficient caused by bed shear stress C_{tau} in $yr^{-1}(N m^{-2})^{-1}$.

$$\left(\frac{\partial n_b}{\partial t}\right)_{flow} = \begin{cases} 0, & \tau < \tau_{cr,p} \\ -n_b \cdot C_{tau}(\tau - \tau_{cr,p}), & \tau > \tau_{cr,p} \end{cases} \quad (2.4)$$

Inundation depth

The decrease in vegetation density caused by large inundation depths $(\partial n_b / \partial t)_{inund}$ in *stems* $m^{-2} yr^{-1}$ is described in Equation 2.5. One can note that it has the same structure as the decrease in vegetation density caused by bed shear stresses. There will only be a decrease if the inundation depth H in m is larger than the critical inundation depth $H_{cr,p}$ in m . If the inundation depth is larger than the critical inundation depth, the decrease in vegetation density depends on the plant mortality coefficient caused by inundation depth C_{inund} in $m^{-1} yr^{-1}$ and the difference between the actual inundation depth and the critical inundation depth $(H - H_{cr,p})$.

$$\left(\frac{\partial n_b}{\partial t}\right)_{inund} = \begin{cases} 0, & H < H_{cr,p} \\ -C_{inund}(H - H_{cr,p}), & H > H_{cr,p} \end{cases} \quad (2.5)$$

Establishment

The increase in vegetation density caused by vegetation establishment $(\partial n_b / \partial t)_{est}$ (in *stems* $m^{-2} yr^{-1}$) is described in Equation 2.6. Here, the increase in vegetation density depends on the chance of seed establishment P_{est} per year. Besides, the bed shear stress must be smaller than the critical bed shear stress, the inundation depth must be smaller than the critical inundation depth, the bed level elevation z must be above $-2.32m$ and the vegetation density in the cell must be smaller than 0.1 *stems* m^{-2} . If all these requirements are met, the vegetation density is equal to the vegetation density in a new cell $n_{b,est}$ in *stems* m^{-2} .

$$\left(\frac{\partial n_b}{\partial t}\right)_{est} = \begin{cases} 0, & H > H_{cr,p} \vee \tau > \tau_{cr,p} \vee n_b > 0.1 \vee z < -2.32 \\ P_{est} \cdot n_{b,est}, & H < H_{cr,p} \wedge \tau < \tau_{cr,p} \wedge n_b < 0.1 \wedge z > -2.32 \end{cases} \quad (2.6)$$

2.2 Interspecific interaction

There are several ways in which different species can interact with each other. This interaction between different species is called interspecific interaction. The interspecific interaction can be positive (+), negative (-) or neutral (0). A positive effect results in an increase in the population density of species 1 due to species 2 and a negative effect results in a decrease in the population density of species 1 due to species 2 (Hacker & Gaines, 1997). Neutral interaction is used to describe a negligible small interaction between different species. Also, the interaction between species can be direct and indirect. E.g. when considering salt marsh vegetation, the patch formation of the *Spartina* species can increase flow stresses around the patch, which can have a negative effect on the survival of the *Salicornia* species (Wesenbeeck, 2007). This is an example of negative indirect interaction since the negative interaction is a result of the hydrodynamic forces. An example of negative direct interspecific interaction for a salt marsh vegetation species, is the unavailability for a species to grow at a certain location, caused by the presence of another species at that location.

In this research, two salt marsh vegetation species on the pioneer marsh are considered. This means that the *Spartina* species can have a positive, negative or neutral effect on the *Salicornia* species, and vice versa. This results in six different scenarios which are visualised in Figure 2.3 (Zélé et al., 2018). Positive interaction is occurring in the blue area of Figure 2.3. Mutualism is the interaction that results in a benefit for both species and commensalism is the interaction that is beneficial for species 1, without influencing species 2. One example of mutualism are birds that are eating parasites from larger mammals or the flowering of plants by insect pollinators (Hacker & Gaines, 1997). An example of commensalism is the providing of living space by trees for birds (Hacker & Gaines, 1997). Parasitism is the interaction where species 1 benefits at the cost of species 2. An obvious example of this type of interaction is a parasite living on another organism. Neutralism is, as mentioned above, used to describe an interaction of which no negative or positive effect is observed by both species. Amensalism is the interaction where one species harms another species without receiving any costs or benefit. E.g. one organism produces

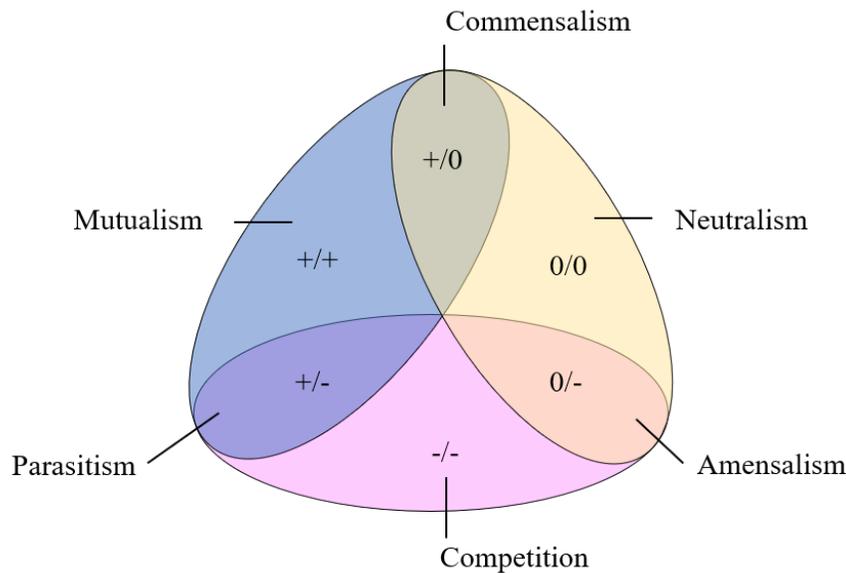


Figure 2.3: A visualisation of the six different types of interaction, when considering the interaction between two species. Here, '+' represents a positive effect, the '-' a negative effect and the '0' a neutral effect. This results in the following six types of interaction: mutualism, commensalism, neutralism, amensalism, competition and parasitism. Altered from Z  l   et al. (2018)

a toxin, which has an ill effect on another organism (Begon et al., 1996). The last type of interaction is competition. In this type of interaction, species 1 and species 2 both depend on the availability of a resource or a set of resources (Begon et al., 1996).

2.2.1 Interspecific competition salt marsh vegetation species

In Section 2.1 can be found that the during the establishment, both the *Spartina* species and the *Salicornia* species require shelter against waves, and require a limited amount of bed shear stresses, inundation depths and net erosion rates. Also, both salt marsh vegetation species are halophytes, which means they require saltwater and are located near the sea. This means that the area in which both salt marsh vegetation species can grow are overlapping. Therefore these species interact with each other on the pioneer zone of the salt marsh.

Several studies found that the interspecific competition between salt marsh vegetation species highly influence the spatial patterns of the salt marsh community (Bertness & Ellison, 1987; Pennings & Callaway, 1992; Egan & Ungar, 2001). E.g. Bertness (1991) looked at the role of the interspecific interaction on the salt marsh zonation and found that the distribution of the salt marsh vegetation species is influenced by interspecific competition. He also found a large difference in the interaction between the salt marsh species during the colonisation of a bare mudflat, compared to the dense vegetation: The colonisation of a bare mudflat by the *Spartina patens* and the *Distichlis spicata* facilitate the colonisation of the *Juncus gerardi* species. But after that, the *Juncus gerardi* species becomes the competitive dominant. Gollasch and Nehring (2006) researched the impact of introduced aquatic species in Germany. They found that the *Spartina anglica* species, which was introduced in the 1920s, is displacing the native *Salicornia stricta* population in the tidal zone in the Wadden Sea.

It can be concluded from the previously mentioned studies that the interspecific interaction between

salt marsh vegetation species can be described as interspecific competition for the available space. For this type of interaction, the Lotka-Volterra competition framework can be used as a tool to examine the interspecific competition.

2.2.2 Lotka-Volterra competition framework

The interspecific competition between two species can be described with the Lotka-Volterra competition framework. In this framework, an extra term is added to the logistic growth term to determine how different species, occurring in the same habitat, interact with each other (Hernandez, 1998). The standard logistic growth term is already defined in Section 2.1.1. When considering two species, the logistic growth term of each species individually can be defined as follows:

$$\begin{aligned}\frac{\partial n_{b,1}}{\partial t} &= r_1 \cdot n_{b,1} \cdot \left(1 - \frac{n_{b,1}}{K_1}\right) \\ \frac{\partial n_{b,2}}{\partial t} &= r_2 \cdot n_{b,2} \cdot \left(1 - \frac{n_{b,2}}{K_2}\right)\end{aligned}\tag{2.7}$$

Here, $\partial n_{b,1}/\partial t$ and $\partial n_{b,2}/\partial t$ is the increase in population density caused by growth. This depends on the growth rate r_1 and r_2 , the current biomass $n_{b,1}$ and $n_{b,2}$ and the maximum bearing capacity K_1 and K_2 , for species 1 and 2, respectively.

In the Lotka-Volterra competition framework, an extra term is added to the logistic growth term, which represents the decrease of species 1 caused by species 2, and vice versa, see Equation 2.8 (Hernandez, 1998; Wesenbeeck, 2007; Wang & Wu, 2011):

$$\begin{aligned}\frac{\partial n_{b,1}}{\partial t} &= r_1 \cdot n_{b,1} \left(1 - \frac{n_{b,1}}{K_1} - \alpha_{12} \frac{n_{b,2}}{K_1}\right) \\ \frac{\partial n_{b,2}}{\partial t} &= r_2 \cdot n_{b,2} \left(1 - \frac{n_{b,2}}{K_2} - \alpha_{21} \frac{n_{b,1}}{K_2}\right)\end{aligned}\tag{2.8}$$

In Equation 2.8 α_{12} and α_{21} represent the competition parameters for species 1 and species 2. The competition parameter α can also be described as the maximum limiting effect of species 2 on species 1, and vice versa. The influence of α will be further explained in Section 2.2.3.

In Equation 2.8, the sign in front of the α is negative, which will cause the last term to be negative. This indicates that the interaction between the two species can be described as direct negative interspecific interaction. When one wants to describe direct positive interaction, the sign in front of the α and therefore the last term must be positive (i.e. the increase in population density of species 2 would result in an increase in population density of species 1) (Hernandez, 1998). When one wants to describe no interspecific interaction (0), the last term of Equation 2.8 will be zero. In this way, the six different types of interaction (Figure 2.3) can be represented with this Lotka-Volterra framework.

2.2.3 Competition parameter α

As described above, α_{12} describes the maximum limiting effect of species 2 on species 1 and vice versa. In other words, α_{12} represents how much an individual of species 1 uses of a certain resource, compared to an individual of species 2 (Hernandez, 1998). If $0 < \alpha < 1$, the species is only partly effected by the competing species (Wesenbeeck, 2007). This also means that the effect of its own species is larger than the effect of the competing species. However, if $\alpha > 1$ the species is more effected by the competing species compared to its own species (Wesenbeeck, 2007). So, the effect of the competing species is larger.

To understand the Lotka-Volterra competition model and the influence of the competition parameter, a state-space diagram can be made. These state-space diagrams show the population density increase or

decrease based on its population density and the population density of the competing species (Begon et al., 1996). In these diagrams, the population density of species 1 is shown on the x-axis and the population density of species 2 on the y-axis. In these state-space diagrams, two lines are plotted, which are called zero isoclines. The zero isoclines can be determined by assuming the salt marsh is in equilibrium. So, every point on the zero isocline of species 1 represents a combination of the population density of species 1 at a certain population density of species 2 and vice versa. When the salt marsh is in equilibrium, the change in salt marsh vegetation density ($\partial n_b / \partial t$) is zero. This means that Equation 2.8 is equal to zero (Begon et al., 1996):

$$\begin{aligned} r_1 \cdot n_{b,1} \left(1 - \frac{n_{b,1}}{K_1} - \alpha_{12} \frac{n_{b,2}}{K_1} \right) &= 0 \\ r_2 \cdot n_{b,2} \left(1 - \frac{n_{b,2}}{K_2} - \alpha_{21} \frac{n_{b,1}}{K_2} \right) &= 0 \end{aligned} \quad (2.9)$$

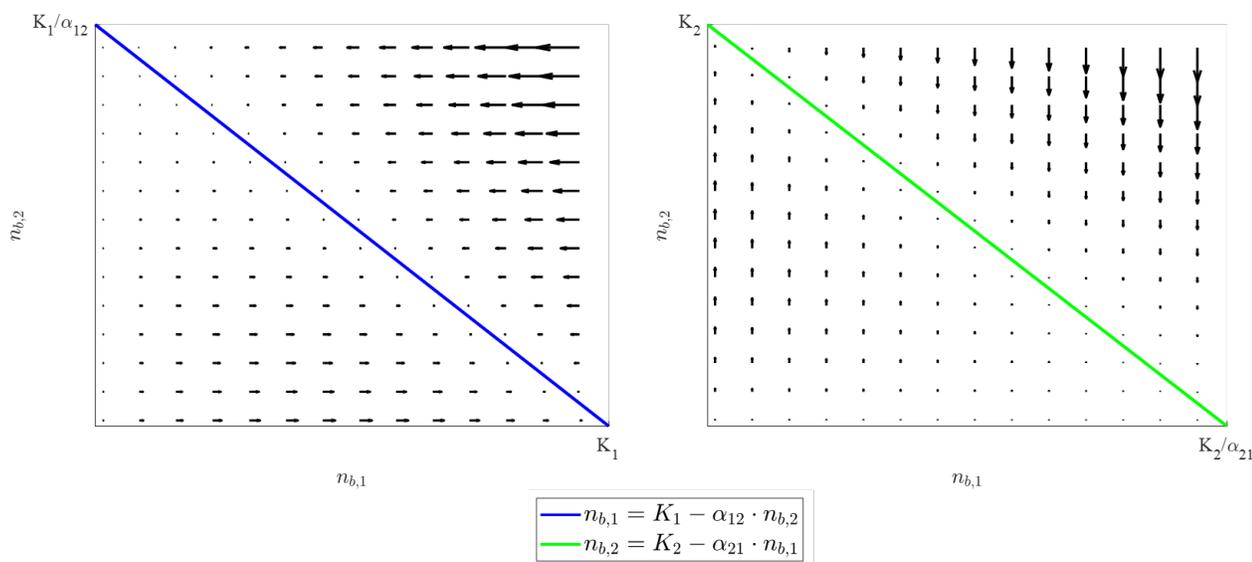


Figure 2.4: (a) The blue line represents the isocline for species 1 ($N_1 = K_1 - \alpha_{12} \cdot N_2$), so the line at which the population density is in equilibrium. The zero isocline depends on the maximum carrying capacity of species 1 K_1 and the competition parameter of species 1 α_{12} . (b) The green line represents the isocline of species 2 ($N_2 = K_2 - \alpha_{21} \cdot N_1$). This is the line in which the species 2 is in equilibrium. This line depends on the carrying capacity of species 2 K_2 and the competition parameter for species 2 α_{21} . The black arrows show the direction in which the population density is moving: If the population density is (a) on the right side of the zero isocline or (b) above the zero isocline, the population density decreases, and if the population density is (a) left or (b) below the zero isocline, the population density will increase. Based on Begon et al. (1996).

$$\begin{aligned} n_{b,1} &= K_1 - \alpha_{12} \cdot n_{b,2} \\ n_{b,2} &= K_2 - \alpha_{21} \cdot n_{b,1} \end{aligned} \quad (2.10)$$

Solving Equation 2.9 for $n_{b,1}$ and $n_{b,2}$ results in Equation 2.10. In Figure 2.4 the two equations are plotted for species 1 (Figure 2.4 (a)) and species 2 (Figure 2.4 (b)). When considering Figure 2.4 (a), the population density of species 1 is considered (so the x-axis). One can note that if the population density is on the left side of the zero isocline, the population can grow and when the population density is on the right side from the zero isocline, the population will decrease. When considering Figure 2.4 (b), the population density of species 2 is considered (so the y-axis). Therefore, if the population density is

below the zero isocline, the population will grow. If the population density is above the zero isocline, the population density will decrease. In Figure 2.4, one can also note that the intercepts with the x-axis and the y-axis depend on the maximum carrying capacity (K_1 and K_2) and the value of α_{12} and α_{21} .

When considering the dynamics of two species, the zero isoclines can be plotted for both species in one graph (so a combination of Figure 2.4 (a) and (b)). In this way, the position of the zero isoclines determines whether the population density of a species will increase or decrease. As explained before, the zero isoclines depend on the maximum carrying capacity K and the competition parameter α . By varying values for these parameters, four different situations can occur, which are shown in Figure 2.5 (Begon et al., 1996). In Figure 2.5 (a) and (b), one of the zero isoclines is situated above the other zero isocline. This means that the population density will move towards the upper isocline and the black dot (stable equilibrium), which will result in the extinction of the weak interspecific competitor and a population density equal to the carrying capacity for the strong interspecific competitor. Figure 2.5 (c) shows a situation where the interspecific competition is strong for both species (so α is large). This results in an unstable equilibrium (white dot) where the zero isoclines intersect and will eventually in the extinction of one of the two species. Which of the species will extinct, depends on the initial population densities of the two species. In the last scenario Figure 2.5 (d), the interspecific competition is small. Therefore a stable equilibrium occurs at the population densities, where the two zero isoclines intersect. These different outcomes are also summarised in Table 2.1.

Situation	Outcome
(a)	Extinction of species 2
(b)	Extinction of species 1
(c)	Unstable equilibrium at the intersection. Extinction of species 1 or species 2 depending on the initial conditions
(d)	Stable equilibrium at intersection

Table 2.1: A summary of outcomes of the scenarios, sketched in Figure 2.5.

From this it can be concluded that the interspecific competition between the *Salicornia* species and the *Spartina* species can be captured in the Lotka-Volterra competition framework. By including the Lotka-Volterra competition framework in the populations dynamics model, the vegetation dynamics of the two species can be examined. But, the Lotka-Volterra framework is highly dependent of the competition parameter α and the carrying capacity K (as can be seen in Figure 2.5 and Table 3.4). The maximum carrying capacity of the *Salicornia* species and the *Spartina* species are known, but values for the competition parameter, which represents the competition between the *Salicornia* species and the *Spartina* species, are not yet available in the literature.

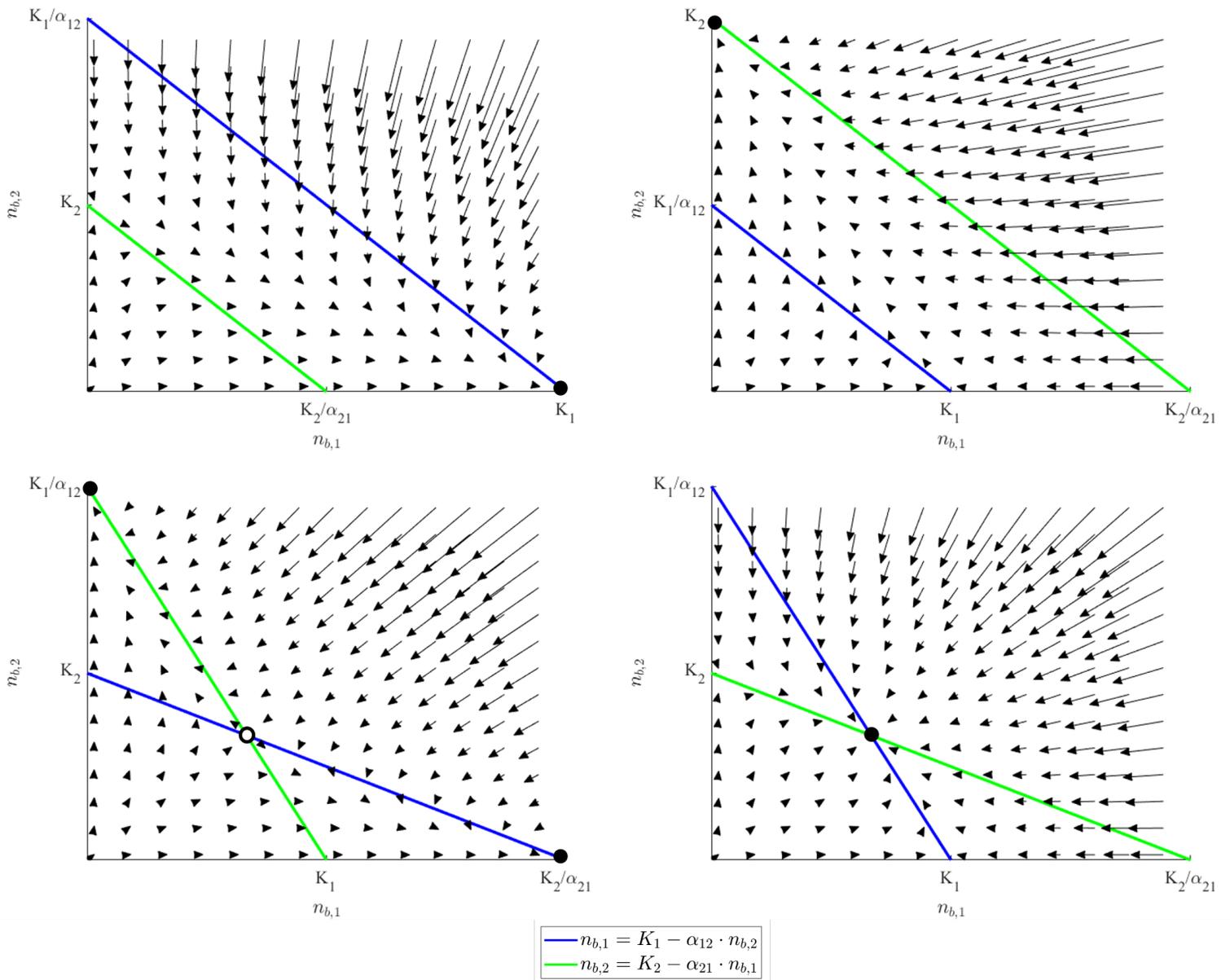


Figure 2.5: The four different scenarios for the zero isoclines for species 1 and species 2. The blue lines are the zero isoclines for species 1 and the green lines the zero isoclines for species 2. The x-axis shows the population density for species 1 $n_{b,1}$ and y-axis for species 2 $n_{b,2}$. The black dot represents a stable equilibrium, the white dot an unstable equilibrium and the black arrows show the direction in which the population density is moving. Whether a stable or unstable equilibrium occurs depends on the maximum carrying capacity of species 1 (K_1) and species 2 (K_2), and the value for the competition parameters (α_{12} and α_{21}), based on Begon et al. (1996)

2.3 Time and space scales of the biotic factors

Since it is clear which biotic factors influence the bio-geomorphological development of salt marshes, these processes can be included in the space-time diagram, which was introduced in Section 1.1.3. In Figure 2.6 the space-time diagram is shown, including the biotic factors. It can be seen in this Figure that the seedling establishment and the seedling reaching maturity have the smallest time scales. The biomass increase during the summer and decrease during the winter has the next smallest time scale. The succession of the salt marsh by the salt marsh vegetation takes longer: Schwarz et al. (2018) found that the *Spartina* species needs five years to cover an area and the *Salicornia* species needs two years to cover an area.

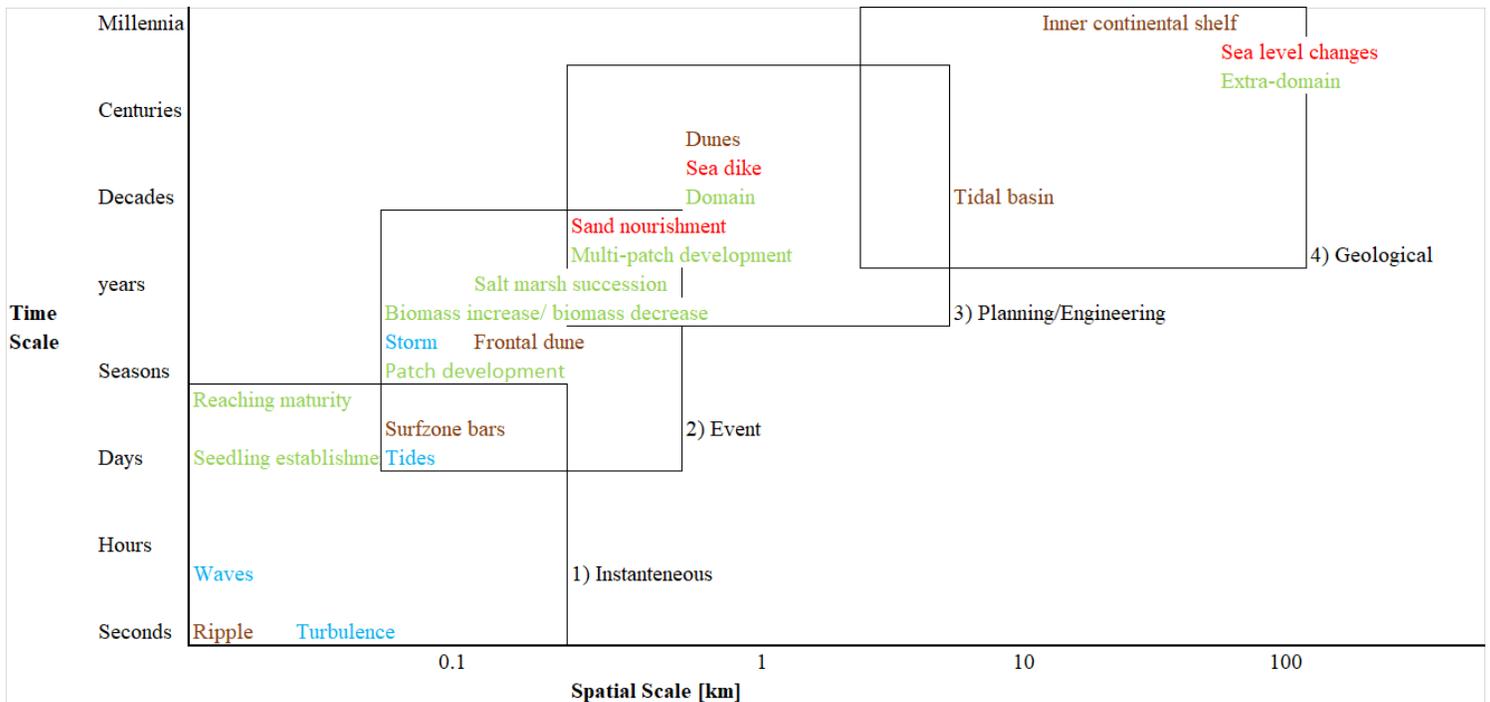


Figure 2.6: The time and space scale of the different environmental factors. In Chapter 1 the hydrodynamic phenomena (in blue), the morphodynamic phenomena (in brown) and the external phenomena (in red) are explained and displayed in Figure 1.5. In this Chapter the vegetation development is examined and included in the time-space diagram.

Larsen (2019) also investigated the scales of the flow-vegetation-sediment feedbacks. She found that it takes hours to days for stems to establish, days to weeks for patches to develop and weeks to decades for a multi-patch system to develop. From this, it can be concluded that the salt marsh succession and competition occur after several years. So, for the numerical implementation a simulation duration between five years (succession time of *Spartina* species) and several years must be considered.

Chapter 3

Methodology

This Chapter presents the methods used in this research. This research aims to investigate the influence of interspecific competition on the bio-geomorphological development of salt marshes. The influence of interspecific competition can be investigated by comparing the bio-geomorphological development of a mono-species salt marsh to a multi-species salt marsh. The bio-geomorphological development is determined by coupling Delft3D Flexible Mesh (DFM) with a vegetation module in Python. First, a description will be given of computation of the hydrodynamics, morphodynamic in DFM and the vegetation dynamics in the vegetation module. Next, the physical setting and the considered parameters will be presented. Finally, the mono-species and multi-species simulations will be explained.

3.1 Model description

The bio-geomorphological development of salt marshes is determined by coupling DFM to the vegetation module in Python. Figure 3.1 shows a flowchart of the coupling between DFM and the vegetation module. The right side of the Figure shows the vegetation dynamics and the left side of the Figure the hydrodynamics and morphodynamics. On the left side of the flowchart, one can notice three squares: the hydrodynamics calculated in D-Flow FM, the morphodynamics calculated in D-Morphology and the waves calculated in D-Waves (Deltares, 2019a, 2019b, 2019c). D-Flow FM, D-Morphology and D-Waves are the three modules that are included in this research. These three modules are part of DFM, which is the successor of Delft3D. Delft3D is used in several studies for rivers or coastal areas (e.g. Horstman et al. (2015); Kernkamp et al. (2011); Borsje et al. (2011)). Besides, the coupling of Delft3D to the vegetation module has also successfully been used in several studies (e.g. Schwarz et al. (2014); Best et al. (2018); Poppema et al. (2019)). Since this coupled model is widely used and includes the feedbacks between hydrodynamics, morphodynamics and vegetation dynamics, it is proven to be a suitable model for this research.

3.1.1 Hydrodynamics

As mentioned before, the hydrodynamics are determined in D-Flow FM. D-Flow FM, a numerical shallow water model, is computer software for multidisciplinary 2D and 3D computations for coastal areas. For every time step, D-Flow FM calculated the water depth, flow velocities and direction, turbulence characteristics and the bed shear stress, by solving the depth-averaged unsteady shallow water equations. In this research, the two-dimensional horizontal (2DH) model is used, which limits the computation time. Also, the differences in results between 2DH and 3D are small (Horstman et al., 2015). The other modules will use D-Flow FM as the basis of their calculations.

The D-Waves module is used to determine the development of waves in the coastal area. It is based on the third generation of SWAN, which stands for Simulating Waves Near Shore (Booij, Ris, & Holthuijsen, 1999). In D-Waves, the waves are computed with the two-dimensional spectral balance equation

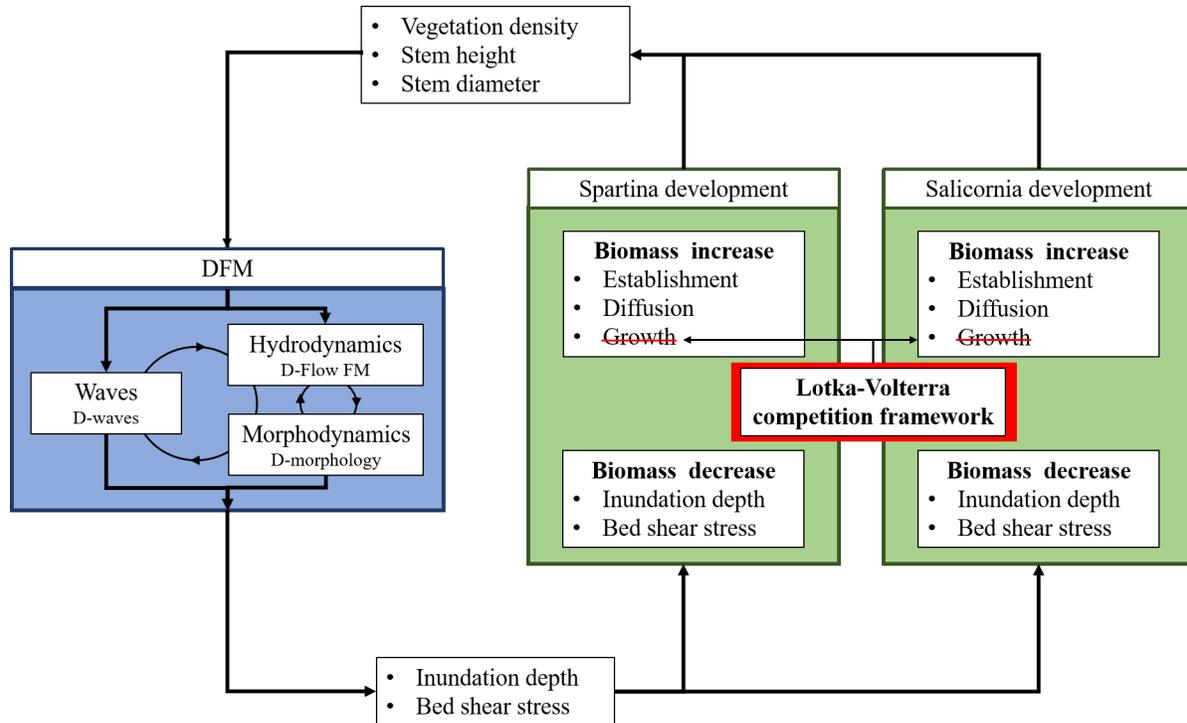


Figure 3.1: A flowchart of the coupling of DFM with the vegetation growth module. The vegetation growth models for the *Salicornia* species and the *Spartina* species are shown in the green boxes. In this module, the standard logistic growth term is replaced by the Lotka-Volterra competition framework. The vegetation growth module is coupled to DFM by the BMI-wrapper. In the blue box, the hydrodynamics are calculated in D-flow FM, the morphodynamics in D-morphology and the waves in D-waves based on the current vegetation density, stem height and stem diameter. From DFM, the inundation depth and bed shear stress are used as input for the vegetation growth module.

(Deltares, 2019c). This computes the wave propagation, wave interaction and the wave dissipation, based on the topography, wind direction and the water level.

3.1.2 Morphodynamics

The change in the bed of the salt marsh is caused by the transport of sediment, which can consist of suspended load and bedload, mainly depending on the grain size. In this research, a muddy environment with cohesive sediment is considered. The cohesiveness is a result of clay particles in the sediment. These clay particles are relatively small ($\approx 0.5\mu\text{m} - 2\mu\text{m}$) and are therefore transported through suspension. The transport of suspended sediment is calculated based on the advection-diffusion equations. The sediment erosion and deposition is calculated with the Krone-Partheniades equations for fine sediments.

3.1.3 Vegetation dynamics

On the right side of Figure 3.1, the vegetation development is displayed for the *Salicornia* species and the *Spartina* species. The vegetation development is calculated in the vegetation module in Python with the population dynamics model by Temmerman et al. (2007), see Section 2.1.1. As explained in Chapter 2.1.1, the vegetation density of both species can increase due to the establishment, diffusion and growth. The vegetation density can decrease due to high inundation depths and bed shear stress. As explained in Section 2.2.1 that the interaction between different salt marsh vegetation species can be described as

interspecific competition. The interspecific competition is included by replacing the growth term of the population dynamics model with the Lotka-Volterra competition framework.

Inclusion Lotka-Volterra competition framework

In Section 2.2.2 the Lotka-Volterra competition framework is explained. When considering the *Salicornia* species as species 1 and the *Spartina* species as species 2, Equation 2.8 can be rewritten as follows:

$$\begin{aligned} \left(\frac{\partial n_{b,Sal}}{\partial t}\right)_{growth} &= r_{Sal} \cdot n_{b,Sal} \left(1 - \frac{n_{b,Sal}}{K_{Sal}} - \alpha_{Sal} \frac{n_{b,Spar}}{K_{Sal}}\right) \\ \left(\frac{\partial n_{b,Spar}}{\partial t}\right)_{growth} &= r_{Spar} \cdot n_{b,Spar} \left(1 - \frac{n_{b,Spar}}{K_{Spar}} - \alpha_{Spar} \frac{n_{b,Sal}}{K_{Spar}}\right) \end{aligned} \quad (3.1)$$

Here, $(\partial n_{b,Sal}/\partial t)_{growth}$ and $(\partial n_{b,Spar}/\partial t)_{growth}$ are the change of the vegetation density over time caused by the growth and the competition. r_{Sal} and r_{Spar} are the growth rate per year, $n_{b,Sal}$ and $n_{b,Spar}$ the current vegetation density in *stems m⁻²*, and K_{Sal} and K_{Spar} the maximum carrying capacity in *stems m⁻²*. α_{Sal} and α_{Spar} are the competition parameters for the *Salicornia* species and the *Spartina* species. One must note that the value of $(\partial n_b/\partial t)_{growth}$ can also be negative as a result of the interspecific competition.

During the simulation of the vegetation development, first, the increase or decrease in vegetation density of the *Salicornia* species is determined based on the vegetation density of the *Spartina* species of the previous time step. Thereafter, the increase of the vegetation density of the *Spartina* species is determined with the vegetation density of the *Salicornia* species of the current time step. This sequence is chosen based on the colonisation behaviour of both salt marsh vegetation species. The *Spartina* species has a lower establishment probability compared to the *Salicornia* species. This means that the chance is smaller that vegetation of the *Spartina* species will occur in a cell, which was empty on the previous time step. So, for the *Spartina* species it is more likely that cells that are vegetated in the current time step were already vegetated in the previous time step.

3.1.4 Bio-geomorphological coupling

DFM and the vegetation module in Python are two separate models. The vegetation module in Python is the main model, which calls on DFM to compute the hydrodynamic and morphodynamics. These two programmes are coupled through a BMI-wrapper (Peckham, Hutton, & Norris, 2013). This makes it possible to obtain the hydrodynamic and morphodynamic characteristics (inundation depth and bed shear stress) from DFM to calculate the vegetation development. After the vegetation development is determined, the vegetation density, stem diameter and stem height are used as input in DFM.

Figure 3.1 also shows a smaller loop between the D-Flow FM, D-Morphology and D-waves modules. This is because the hydrodynamic, morphodynamics and waves are calculated several times, before returning to the vegetation module: For every minute, the hydrodynamics are calculated in D-Flow FM. Thereafter, the morphodynamic change is calculated in D-Morphology and after one hydrodynamic hour, the waves are calculated in D-Waves. These results are multiplied with a morphodynamic factor (MorFac), in this case 100. This loop is repeated for 1 hydrodynamic day and therefore 100 morphodynamic days. Then, the vegetation development is determined, based on the outcomes of D-Flow, D-morphology and D-Waves. This also means that the salt marsh vegetation development is updated every 100 morphological days.

The MorFac, mentioned above, accelerates the bed level variations. The MorFac can be applied if it can be assumed that the hydrodynamics and morphodynamics are similar for every neap-spring cycle. One can imagine that the accuracy of the prediction decreases as the morphological factor increases. But, the

simulation time also decreases as the morphological factor increases. Therefore, a trade-off must be made between the simulation time and the accuracy of the prediction. Therefore, in this research, a MorFac of 100 is used, which has already successfully been used in several studies (e.g. Lesser et al. (2004) Best et al. (2018)).

Output vegetation module

In DFM the bed roughness C is determined based on the vegetation density, stem height and stem density. The bed roughness is determined according to Baptist (2005b) (Deltares, 2019a). This means that the presence of the vegetation will result in an increase in roughness, which will be used as input for the hydrodynamic and morphodynamic calculation in DFM. Equation 3.2 shows the calculation of the bed roughness for submerged vegetation and Equation 3.3 for emerged vegetation.

$$C = \frac{1}{\sqrt{\frac{1}{C_b^2} + \frac{C_D n H_v}{2g}}} + \frac{\sqrt{g}}{\kappa} \ln\left(\frac{h}{H_v}\right) \quad (3.2)$$

$$C = \frac{1}{\sqrt{\frac{1}{C_b^2} + \frac{C_D n h}{2g}}} \quad (3.3)$$

Here, C is the bed roughness in $m^{1/2}s^{-1}$, C_b the roughness of the bed without vegetation in $m^{1/2}s^{-1}$, C_d the drag coefficient [-], H_v the vegetation height in m , g the gravitational acceleration in $m s^{-2}$, κ the Nikuradse equivalent roughness in m and h the inundation depth in m . Also, $n = n_b \cdot d_v$ where n_b the stem density is in $stems m^{-2}$ and d_v the diameter in m . In the current model, Equations 3.2 and 3.3 can only consider one value for the vegetation density, stem height and stem diameter for every cell. Since this research considers two salt marsh vegetation species, different values for the vegetation density, stem height and stem diameter can occur in one cell. Therefore, the values of the vegetation density of the *Salicornia* species and the *Spartina* species are added:

$$n_{b,total} = n_{b,Sal} + n_{b,Spar} \quad (3.4)$$

Here, $n_{b,total}$ is the total vegetation density in $stems m^{-2}$, $n_{b,Sal}$ the vegetation density of the *Salicornia* species in $stems m^{-2}$ and $n_{b,Spar}$ the vegetation density of the *Spartina* species in $stems m^{-2}$. Next, the weighted average of the vegetation diameter and height are calculated according to Equations 3.5 and 3.6. Here, $d_{v,Sal}$ and $d_{v,Spar}$ are the diameters of a single *Salicornia* and *Spartina* canopy and $H_{v,Sal}$ and $H_{v,Spar}$ the height of a single *Salicornia* and *Spartina* species.

$$d_v = \frac{d_{v,Sal} \cdot n_{b,Sal} + d_{v,Spar} \cdot n_{b,Spar}}{n_{b,total}} \quad (3.5)$$

$$H_v = \frac{H_{v,Sal} \cdot n_{b,Sal} + H_{v,Spar} \cdot n_{b,Spar}}{n_{b,total}} \quad (3.6)$$

With the summation of the vegetation density and the weighted average of the stem diameter and stem height, the bed roughness is determined in DFM. This will then be used for the next step of the hydrodynamic and morphodynamic simulation.

3.2 Model set-up

Next, the model set-up will be discussed. First the physical settings of this research will be explained. Thereafter, the bathymetry and the model parameters based on the physical settings will be discussed.

3.2.1 Physical settings

In this research, a framework is created which makes it possible to examine the competition between multiple salt marsh vegetation species in the bio-geomorphological development of salt marshes. It is desirable that this framework is applicable to different salt marsh cases. Therefore, this research is not based on an actual salt marsh. But, a schematic salt marsh is considered, based on North-European values. E.g. the South Western Delta, the Wadden Sea and the Ems Estuary in the Netherlands and the Thames Estuary in Great Britain (e.g. Van der Wal et al. (2008); van Maren et al. (2015); Willemsen et al. (2018); Best et al. (2018)).

3.2.2 Domain and time frame

A sketch of the domain can be seen in Figure 3.2 (a). In this Figure, three different grids can be distinguished: the flow grid, the nested grid and large wave grid. The flow grid represents the area of interest in this research and is also the grid on which the salt marsh vegetation dynamics is determined. The flow grid has a cell size of $5m \times 5m$, an along-shore distance of $1000m$ and a cross-shore distance of $2500m$ upon which the hydrodynamic and morphodynamic processes are calculated. The waves are determined in the two wave grids: the most outer wave grid, with a cell size of $15m \times 15m$ and the nested grid with a cell size of $5m \times 5m$. The wave grids are larger than the flow grid to prevent boundary effects caused by the waves. On the boundary of the flow grid and the wave grid, the bed roughness, caused by the vegetation, is extended onto the wave grids and is used for the wave calculations. In 3.2 (a), an open boundary can also be observed on the south side of the domain. At this open boundary, different forcings are imposed to the domain: Tides, waves and sediment supply, which will be further explained in Section 3.2.4. One can notice that only the Southern boundary is an open boundary: The other boundaries are closed. A summary of the domain and time scale is given in Table 3.1.

Flow grid		
Number of cells along-shore direction	200	cells
Number of cells cross-shore direction	500	cells
Length and width cells	5×5	m
Nested grid		
Number of cells along-shore direction	220	cells
Number of cells cross-shore direction	510	cells
Length and width cells	5×5	m
Wave grid large		
Number of cells along-shore direction	400	cells
Number of cells cross-shore direction	510	cells
Length and width cells	15×15	m
Bed level elevation		
Minimum bed level elevation	-2.8	m
Maximum bed level elevation	2.7	m
slope	0.001	m/m
Time scale		
Duration simulation	10	years
MorFac	100	-

Table 3.1: A summary of the domain and time scale.

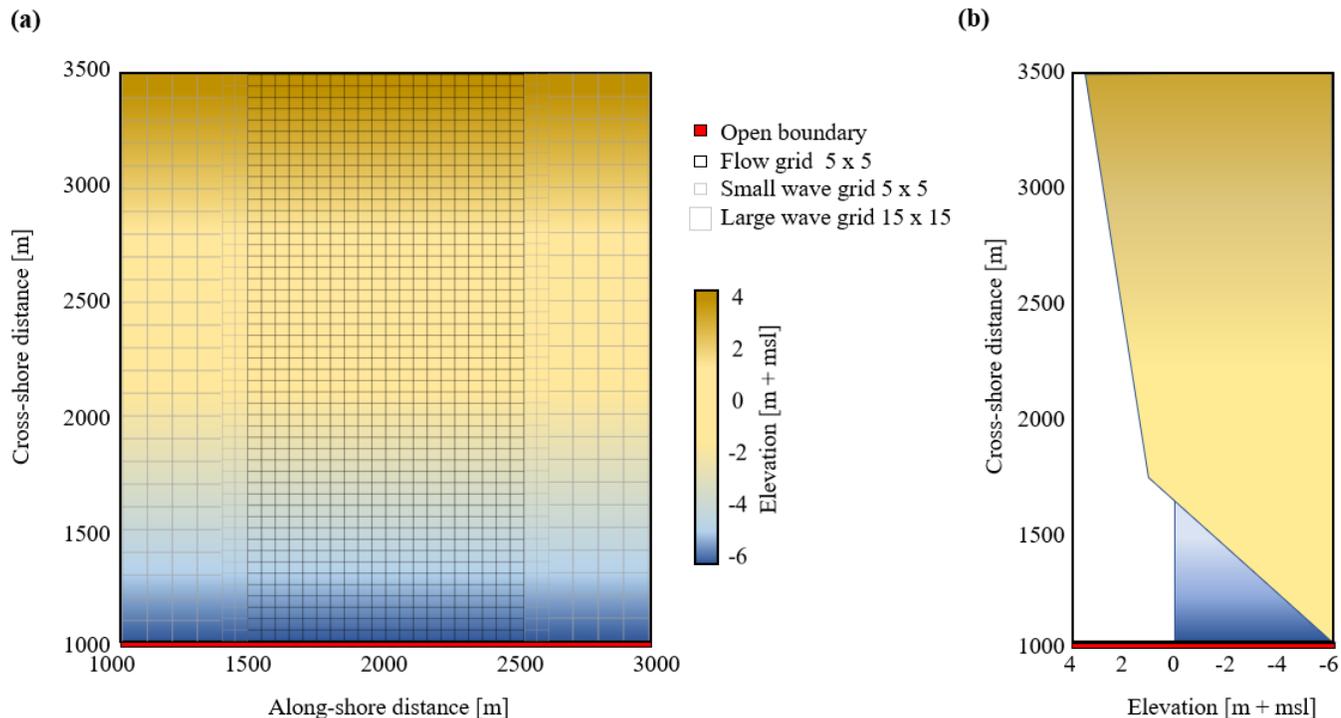


Figure 3.2: A sketch of the domain. (a) The top view of the domain, including the flow grid, the small wave grid and the large wave grid. The open boundary is also shown, which is located seawards, at a cross-shore distance of 1000 m. (b) A cross section of the bed with the bed level elevation.

Simulation duration

In Section 2.3 the different time scales of the biotic processes for the *Salicornia* species and the *Spartina* species are discussed. In Section 2.3 it is also explained that it takes about 5 years for the *Spartina* species to colonise a new area (Schwarz et al., 2018). Therefore, a simulation period of 5 years is considered as the lower limit. Next, a trade-off is made between the simulation time (the time needed for the model to finish) and the simulation period. Eventually, it has been decided to use a simulation period of ten years, which takes approximately 14 hours to simulation, which is acceptable.

3.2.3 Bathymetry

The bed profile of the salt marsh influences several factors, for instance, the inundation depth and duration, the bed shear stresses and the net sedimentation rate. This makes the bed profile an important initial condition. This research is not based on an actual study area, which means that the initial bed profile must be determined based on the literature and the aim of this research. This results in the following requirements for the bed profile:

1. In this research, the competition between different salt marsh vegetation species is examined. In the field, the competition between the different salt marsh vegetation species generally occurs in areas where the vegetation density has not reached its maximum carrying capacity and a gradient in the

vegetation density can be noted. So, a bed level slope, which causes a gradient in the vegetation density is preferred.

2. The slope of a salt marsh is considered as low-gradient (Larsen, 2019). Larsen (2019) found that the slope of salt marshes generally ranges between the 0.0001 m/m and 0.001 m/m . This agrees with the slopes used by Schwarz et al. (2018), which are 0.00075 m/m and 0.0009 m/m . But, larger slopes ($\approx 0.002 \text{ m/m}$ or 0.003 m/m) have also been used to represent the slope of a salt marsh (Mariotti & Fagherazzi, 2010).
3. At the open boundary the water level varies, in order to represent tides. This water level varies between the -2.3 m and the 2.6 m . This means that the bed profile must at least smaller than -2.3 m and larger than 2.6 m . The salt marsh vegetation occurs between MHWN and MHWS (Winterwerp & van Kesteren, 2004), which means that the vegetation will occur between approximately 1.8 m and 2.6 m . So, the slope in this vegetated area should be small.

Ideally, one wants to use a small slope, because as the slope decreases, the gradient in vegetation density increases and the vegetation plays a more important role in the transformation of the salt marsh (Jones et al., 1997; Larsen, 2019; Temmerman et al., 2005). But, a small slope requires a large width of the salt marsh, since a decrease in slope would result in an increase in width, as the minimum bed level elevation is -2.3 m and the maximum bed level elevation is 2.6 m . But, the width of the salt marsh is limited to 2500 m , since an increase in width would result in an increase in simulation time, which is not desirable. Therefore, a slope of 0.001 m/m is chosen at the bed level elevation where salt marsh vegetation can occur (approximately between MHWN and MHWS). In front of this area, a larger slope is chosen to reach the minimal bed level elevation of -2.3 m . This results in the bed profile as shown in Figure 3.2 (b).

3.2.4 Model parameters

Next, the parameters used in this research will be mentioned. As explained in Section 3.2.1, the parameters are based on North-European values. First, the boundary conditions and hydrodynamics will be discussed. Thereafter, the sediment characteristics and the parameters for the parameters used for the vegetation dynamics will be discussed.

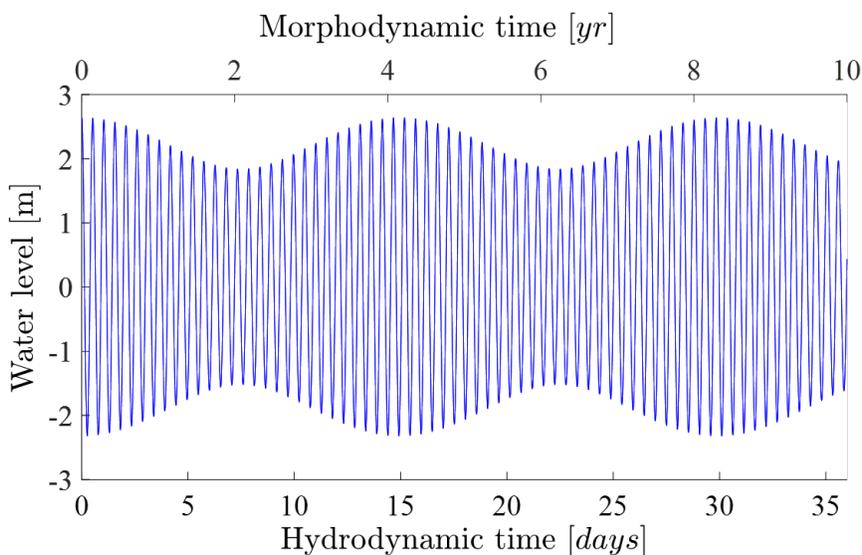


Figure 3.3: The water level variation at the open boundary in hydrodynamic days and morphodynamic years.

Boundary conditions and hydrodynamics

The open-water boundary of the salt marsh is an open boundary (Figure 3.2). At this open boundary, the water level varies to represent the semidiurnal M2 and S2 tide, which can be seen in Figure 3.3. In this Figure can also be seen that this spring-neap cycle is reoccurring approximately every two weeks. the range of the tide is 4.9 m with a mean tide level of 0.16 m (Van der Wal et al., 2008). During neap, the mean low water level (MLWN) is -1.5 m and the mean high water (MHWN) level 1.9 m (Van der Wal et al., 2008). During spring, the mean low water level (MLWS) is -2.3 m and mean high water level (MHWS) 2.6 m. At this open boundary, waves with a significant wave height of 0.1 m and a wave period of 2.5 s are imposed (based on Willemsen et al. (2018)). Finally, a uniform concentration of 0.01 kg/m^3 of suspended sediment is supplied at the open boundary (van Maren et al., 2015). Table 3.2 shows a summary of the boundary conditions used in this research. Besides that, when considering the hydrodynamics, a Manning coefficient of $0.023 s m^{-1/3}$ is used and the horizontal eddy viscosity and diffusivity is both set at $10 m^2 s^{-1}$.

Water level			
Mean tide level	0.16	m	Van der Wal et al. (2008)
Tidal range	4.9	m	Van der Wal et al. (2008)
MLWN	-1.5	m	Van der Wal et al. (2008)
MHWN	1.9	m	Van der Wal et al. (2008)
MLWS	-2.3	m	Van der Wal et al. (2008)
MHWS	2.6	m	Van der Wal et al. (2008)
Sediment supply			
Uniform sediment supply	0.01	kg/m^3	van Maren et al. (2015)
Waves			
Wave height	0.1	m	Willemsen et al. (2018)
Wave period	2.5	s	Willemsen et al. (2018)

Table 3.2: Summary of the boundary conditions.

Sediment dynamics

Salt marshes typically grow on cohesive sediments, so a soil consisting of cohesive sediments is applied. Cohesive sediments usually have a specific density of $2650 kg m^{-3}$ and a dry bed density of $500 kg m^{-3}$. A critical bed shear stress for the erosion of $0.5 N m^{-2}$ is used. A value of $1000 N m^{-2}$ for the critical deposition bed shear stress is used, which means that the deposition bed shears is not affected by the critical bed shear stress. Table 3.3 shows a summary of the sediment dynamics.

Vegetation dynamics

In the vegetation module in Python, the vegetation dynamics are computed with the populations dynamics model. In Section 2.1.1 the population dynamics model by Temmerman et al. (2007) is explained. The parameters for the *Salicornia* species and the *Spartina* species are shown in Table 3.4. In Table 3.4, one can also note the several values for α . These different values for α will translate into different three types of competition, which will be explained in the next section.

Hydrodynamics			
Manning coefficient	0.023	$s m^{-1/3}$	Deltares (2019a)
Horizontal eddy viscosity	10	$m^2 s^{-1}$	Deltares (2015)
Horizontal eddy diffusivity	10	$m^2 s^{-1}$	Deltares (2015)
Sediment dynamics			
Specific density	2650	$kg m^{-3}$	Best et al. (2018); Deltares (2019a)
Dry bed density	500	$kg m^{-3}$	Best et al. (2018); Deltares (2019a)
Erosion parameter	$5 \cdot 10^{-5}$	$kg m^{-2} s^{-1}$	Best et al. (2018); Deltares (2019a)
Critical bed shear stress erosion	$5 \cdot 10^{-1}$	$N m^{-2}$	Best et al. (2018); Deltares (2019a)
Critical bed shear stress deposition	1000	$N m^{-2}$	Best et al. (2018); Deltares (2019a)
Settling velocity	$5 \cdot 10^{-4}$	$m s^{-1}$	Willemsen et al. (2018)

Table 3.3: A summary of the parameters, used for the sediment dynamics.

Symbol	Parameter	Unit	value <i>Spartina</i>	Ref. <i>Spartina</i>	Value <i>Salicornia</i>	Ref. <i>Salicornia</i>
n_b	Vegetation density	$stems m^{-2}$				
P_{est}	Seed establishment	yr^{-1}	0.01	Temmerman et al. (2007)	0.08	Schwarz et al. (2018)
$n_{b,est}$	Veg. density new cell	m^{-2}	66	Schwarz et al. (2018)	19	Schwarz et al. (2018)
r	Growth rate	yr^{-1}	1	Temmerman et al. (2007)	1	Schwarz et al. (2018)
K	Carrying capacity	m^{-2}	658	Schwarz et al. (2018)	189	Schwarz et al. (2018)
D	Diffusion coefficient	$m^2 yr^{-1}$	0.2	Temmerman et al. (2007)	0	Schwarz et al. (2018)
τ_{cr}	Critical shear stress	$N m^{-2}$	0.25	Schwarz et al. (2018)	0.25	Schwarz et al. (2018)
H_{cr}	Critical inund. depth	m	0.21	Schwarz et al. (2018)	0.21	Schwarz et al. (2018)
C_{tau}	Plant mortality coeff. related to shear stress	$m^{-2} yr^{-1}$	30	Temmerman et al. (2007)	30	Temmerman et al. (2007); Van den Broek (2020)
C_{inund}	Plant mortality coeff. related to inund. depth	$m^{-3} yr^{-1}$	3000	Temmerman et al. (2007)	3000	Temmerman et al. (2007); Van den Broek (2020)
H_v	Height stems	m	0.59	Bouma et al. (2013)	0.28	Bouma et al. (2013)
d_v	Diameter stems	m	0.00304	Bouma et al. (2013)	0.005	Bouma et al. (2013)
α	Competition coefficient	-	0		0	
			1		1	
			3.5		0.3	

Table 3.4: The population dynamics parameters for the *Spartina* and *Salicornia* species.

3.3 Model simulations

This research aims to investigate the influence of the interspecific competition on the bio-geomorphological development of salt marshes. The influence of the interspecific competition can be tested by comparing the results of a mono-species salt marsh with the results of a multi-species. In Chapter 2 is concluded that it is still unclear what the appropriate values are for the competition parameters, which represents the competition between *Salicornia* species and *Spartina* species (α_{Sal} and α_{Spar}). Therefore, three different combinations for α will be tested, based on different assumptions, to represent the competition for available space. First, it is assumed that there is no competition between the *Salicornia* species and the *Spartina* species. Secondly, it is assumed that the competition between the two salt marsh vegetation species is equal. Finally, it is assumed that competition depends on the available space. These multi-species simulations will be further explained below. An overview of the six simulations can be found in Table 3.5. Next, the different simulations will be discussed in more detail.

Simulation	Description
1	No salt marsh vegetation
2	Mono-species salt marsh: only the <i>Salicornia</i> species
3	Mono-species salt marsh: only the <i>Spartina</i> species
4	Multi-species salt marsh excluding competition
5	Multi-species salt marsh with equal competition
6	Multi-species salt marsh with spatial competition

Table 3.5: The 6 different simulations, that will be tested on the bio-geomorphological development of salt marshes.

No salt marsh vegetation

In the first simulation, no salt marsh vegetation is considered. By comparing the morphological development of the bed of a salt marsh with and without salt marsh vegetation, the influence of the vegetation species on the morphology can be investigated.

Mono-species salt marsh

Two mono-species salt marshes will be simulated: one with solely *Salicornia* vegetation and one with solely *Spartina* vegetation. By comparing the mono-species simulations with the multi-species simulations, the influence of the interspecific competition can be investigated.

Multi-species salt marsh excluding competition

During the first multi-species simulation, it is assumed that there is no competition between the two salt marsh vegetation species, i.e. $\alpha_{Sal} = 0$ and $\alpha_{Spar} = 0$. In this way, the influence of the α parameter can be determined by comparing the simulation excluding competition to the simulation with equal competition and spatial competition. In Figure 3.4 the state space diagram (explained in Section 2.2.3) for the *Spartina* and the *Salicornia* species can be found. The black arrows show the direction, in which the vegetation density would move when the Lotka-Volterra competition framework is considered. One can see that these arrows are moving toward a stable equilibrium (black dot in Figure 3.4). Since both salt marsh vegetation species are not affected by the competing species, both species will grow towards their maximum carrying capacity (189 *stems m*⁻² for the *Salicornia* species and 658 *stems m*⁻² for the *Spartina* species). This also means, that it is assumed that both salt marsh vegetation species can reach their maximum carrying capacity in the same cell.

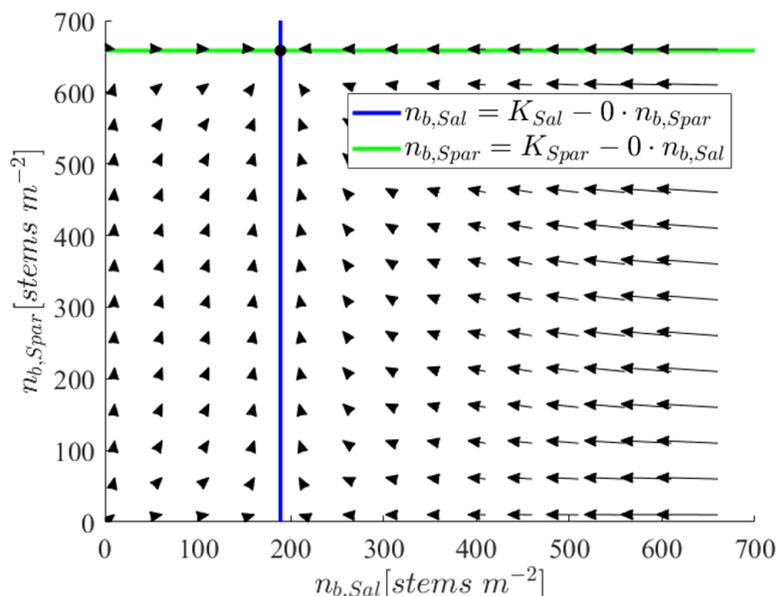


Figure 3.4: The space-state diagram with the isoclines for the *Spartina* species (in green) and the *Salicornia* species (in blue) for the simulation without competition. In this simulation it is assumed that vegetation development is not limited by interspecific competition, hence $\alpha_{Spar} = \alpha_{Sal} = 0$

Multi-species salt marsh with equal competition

In the second multi-species simulation, it is assumed that the interspecific competition is equal to the intraspecific competition. This means that the competition between two *Spartina* canopies is equal to the competition between a *Spartina* canopy and a *Salicornia* canopy. In Figure 3.5, the state space diagram with $\alpha_{Sal} = 1$ and $\alpha_{Spar} = 1$ can be seen. In this figure, one can note that the isocline of the *Spartina* species is located above the isocline of the *Salicornia* species. This means that a situation is occurring as sketched in Figure 2.5 (b), which results at a stable equilibrium at the maximum carrying capacity of the *Spartina* species. So, if only the space-state diagram would be considered, the *Spartina* species would eventually survive and the *Salicornia* species would go extinct. Still, one must keep in mind that this is not a necessary outcome of the bio-geomorphological simulation, because these outcomes also depend on the sensitivity of the salt marsh vegetation species to the abiotic and external factors.

Multi-species salt marsh with spatial competition

For the determination of α , the common resource can also be used as a starting point. One of the common resources is available space. The maximum carrying capacity is $189 \text{ stems } m^{-2}$ for the *Salicornia* species and $658 \text{ stems } m^{-2}$ for the *Spartina* species. This means that the *Salicornia* species takes up approximately $(K_{Spar}/K_{Sal} = 658/189 =) 3.5$ times as much space as the *Spartina* species. Therefore, in terms of the common resource, one *Spartina* plant is the equivalent of $(K_{Sal}/K_{Spar} = 189/658 =) 0.3$ of the *Spartina* plant, hence $\alpha_{Sal} = 0.3$ and $\alpha_{Spar} = 3.5$. In Figure 3.6 can be seen that in this situation, the lines are identical. In contrary to Figures 5.1 and 3.5, the black arrows are not moving toward one equilibrium situation, but are pointing towards the zero-isoclines. This means that an equilibrium situation can occur anywhere on the zero isoclines. So, it is not more likely for one salt marsh vegetation species to go extinct and the survival or extinction of the salt marsh vegetation species depends on the abiotic conditions.

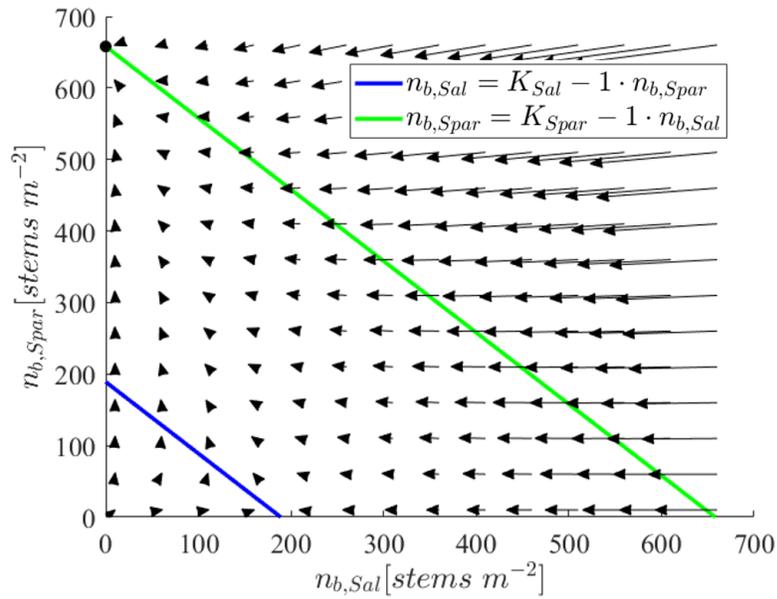


Figure 3.5: The space-state diagram with the isoclines for the *Spartina* species (in green) and the *Salicornia* species (in blue) for the simulation with equal competition. In the situation where the interspecific competition is equal to the intraspecific competition, hence $\alpha_{Spar} = \alpha_{Sal} = 1$.

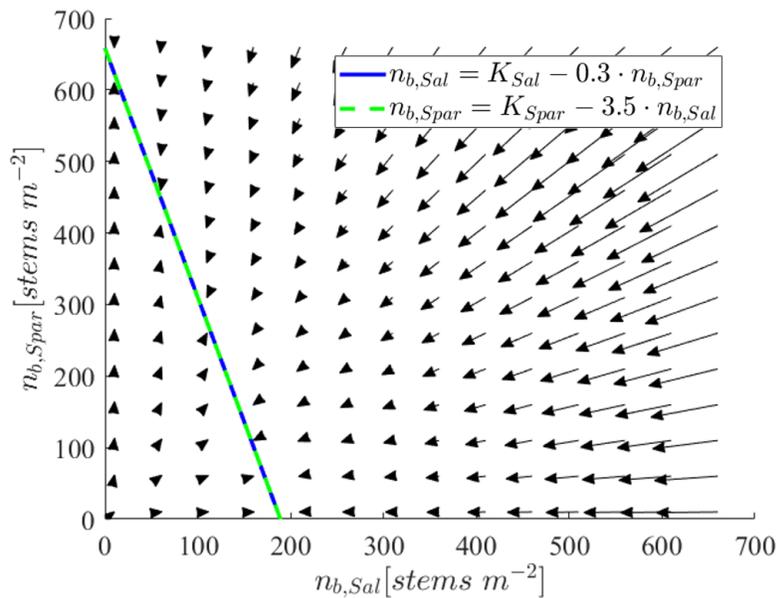


Figure 3.6: The space-state diagram with the isoclines for the *Spartina* species (in green) and the *Salicornia* species (in blue) for the simulation with spatial competition. In this simulation it is assumed that the interspecific competition depends on the available space, hence $\alpha_{Sal} = 0.3$ and $\alpha_{Spar} = 3.5$.

Chapter 4

Results

Next, the results of the six simulations will be discussed (Table 3.5). Chapter 3 explains which six simulations will be examined: one without vegetation, two mono-species simulations and three multi-species simulations. Of these simulations, the bio-geomorphological development of the salt marshes over ten years will be discussed. In Chapter 1 it is already explained that the bio-geomorphological development of salt marshes consists of the development of the bed of the salt marsh and the development of the salt marsh vegetation. First, the hydrodynamic and morphodynamic results are shown. Thereafter, the results of the vegetation development is shown.

4.1 Hydrodynamic results

The hydrodynamic results consist of the inundation depth and the bed shear stress. These two are discussed because they both directly influence the vegetation development. The along-shore averaged inundation depth is shown in Figure 4.1 and the along-shore averaged bed shear stress in Figure 4.2. The along-shore averages are shown, because there is not much variation in inundation depth and bed shear stress in the along-shore direction, see Figures C.4 and C.5 in Appendix C. The along-shore averaged is shown with an average of one year. So, Figures 4.1 (a) and 4.2 (a) show the values for year five and 4.1 (b) and 4.2 (b) for year ten.

Generally, in Figures 4.1 and 4.2, it can be noted that the results of the different simulations are almost similar. The lines of the different simulations are plotted on top of each other. This means that vegetation development does not (yet) influence the inundation depth and the bed shear stress. In Figure 4.2, several peaks in the bed shear stress can be noticed, which are caused by tidal currents. The mean bed shear stress of one year is considered. This means that 360 morphodynamic days are considered and 3.6 hydrodynamic days. When considering Figure 3.3 again, one can see that during these 3.6 hydrodynamic days, approximately seven high tides and seven low tides are occurring. Since the water level per tide differs, the tidal range differs per tide and, therefore, the location of the maximum bed shear stress. This explains the different peaks occurring in Figure 4.2. This also means that the results for the inundation depth and the bed shear stress can differ, depending on whether a neap or spring cycle is considered. When considering Figure 3.3 again, one can note that the hydrodynamics in year five and year ten is represented by a tide that is between neap and spring cycle. To test the effect of extreme hydrodynamic, the bed shear stress of a neap cycle (year 6.2) and a spring cycle (year 8.2) are also considered and can be found in Figures C.2 and C.3 in Appendix C. In these Figures can be seen that during spring tide (year 8.2), the inundation depth is larger, the water is moving more landwards and the bed shear stresses are also occurring more landwards. During neap tide, the inundation depth is smaller and the bed shear stresses and the bed shear stresses are occurring more seaward. Similar to Figures 4.1 and 4.2, one large peak can be noted around a cross-shore distance of 1300 *m*, several peaks can be noted in the bed shear stress and no clear difference be found between the different simulations.

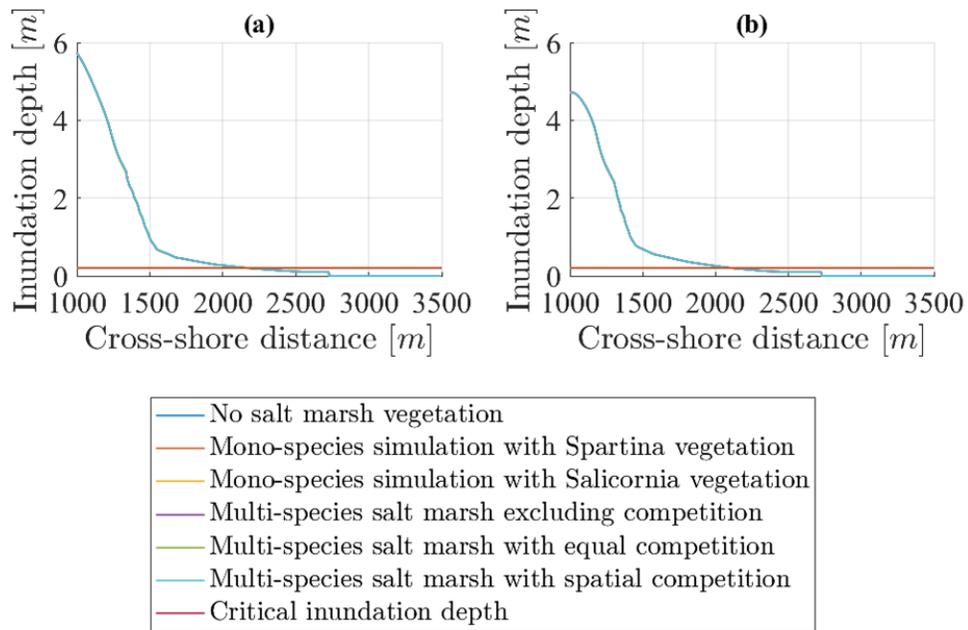


Figure 4.1: The along-shore averaged inundation depth at (a) year five and (b) year ten for the all the simulations. The red line represents the critical inundation depth (i.e. the inundation depth at which a decrease in biomass occurs).

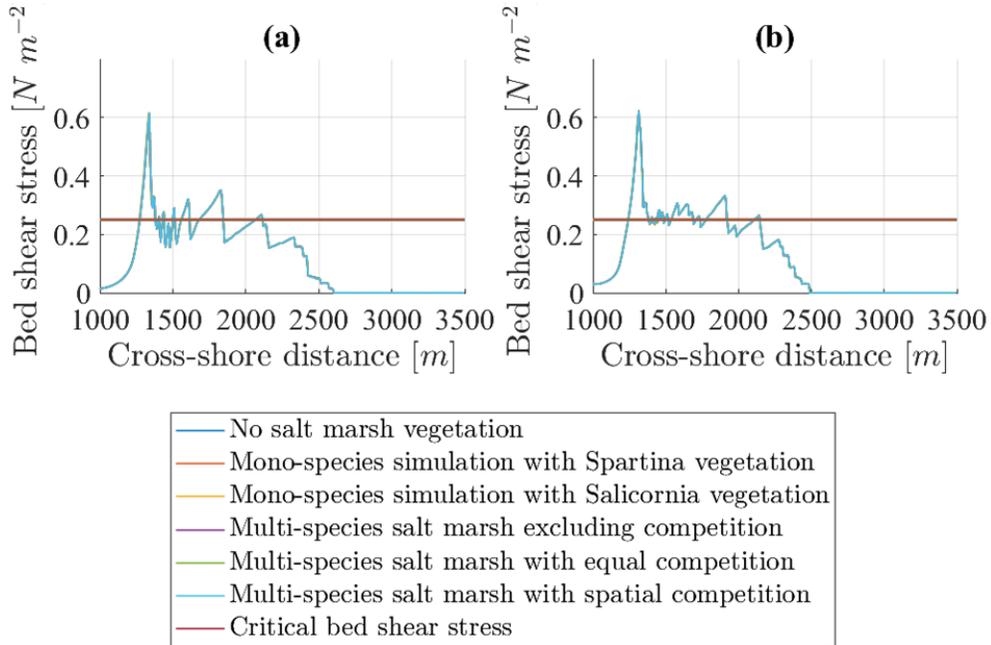


Figure 4.2: The along-shore averaged bed shear stress at (a) year five and (b) year ten for the all the simulations. The red line represents the critical bed shear stress (i.e. the bed shear stress at which a decrease in biomass occurs).

In Figures 4.2 (a) and (b), the large peak occurring at a cross-shore distance of 1300 m , is caused by the berm. At this location, the slope of the bed decreases, which results in higher flow velocities above this berm. The bed shear stresses remain larger than the critical bed shear stress till a cross-shore distance of approximately 2200 m . Because of these high bed shear stresses, erosion is occurring in this area. This sand is moved towards the front of the beach, where sedimentation occurred.

4.2 Morphological development

In Figure 4.3, the bed level elevation for the simulation without vegetation and the simulation of the multi-species salt marsh excluding competition are shown. These two simulations are shown, because one would expect a difference in bed level elevation caused by vegetation. But (again), In Figure 4.3, it can be seen that the differences are small in the along-shore direction, which is also the case for the other simulations (see Figure C.6). Even when zooming in to a smaller section one can hardly observe a variation in bed level elevation (see Figure C.9). Therefore, the along-shore averaged results are shown.

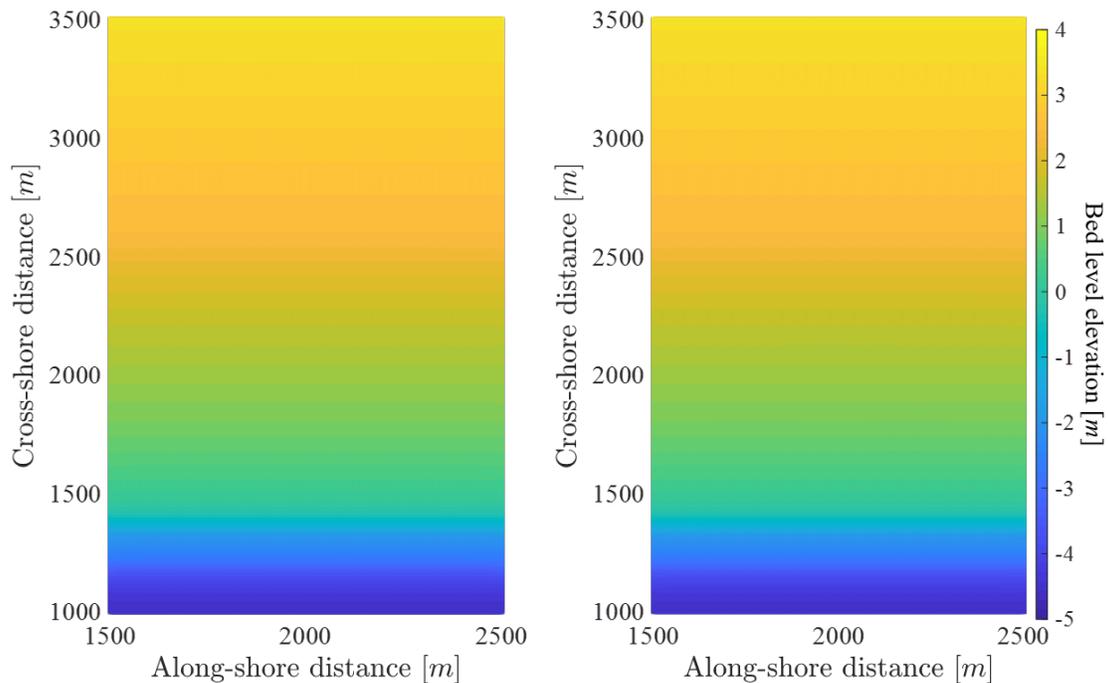


Figure 4.3: The bed level elevation after ten years for (a) the simulation without vegetation and (b) the multi-species simulation excluding competition (the results of the other simulations can be found in Figure C.6).

In Figure 4.4, the bed level elevation for the different simulations for (a) year five and (b) year ten are shown. In these two plots, it can be seen that the differences between the simulations are small. The lines are on top of each other. Therefore, the change in bed level elevation relative to the initial bed level elevation is also included, which can be seen in Figure 4.4 (c) and (d).

Figures 4.4 (c) and (d) can again be seen that the bed level change between the different simulations is small. This Figure is made by subtracting the initial bed level elevation from the bed level elevation of the simulations. This means that a positive value for the relative bed level elevation indicates sedimentation

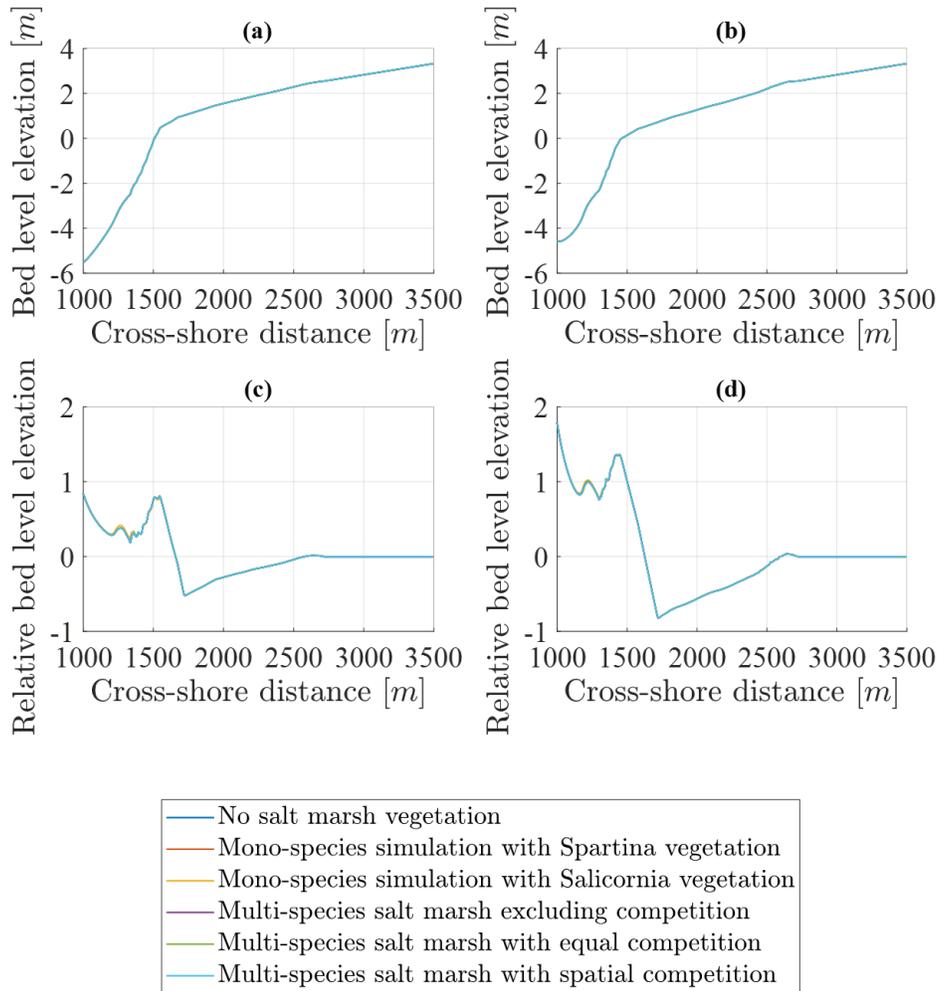


Figure 4.4: The along-shore averaged bed level elevation for all the simulations at (a) year five and (b) year ten and the along-shore averaged bed level elevation relative to the initial bed level elevation at (c) year five and (d) year ten.

and the negative values indicate erosion. When considering Figure 4.4 (c) and (d) again, it means that sedimentation occurs between a cross-shore distance of 1000 m and 1700 m and erosion between a cross-shore distance of 1700 m and 2600 m. At a cross-shore distance of approximately 2600 m the erosion stops after which the bed level elevation stabilises. When comparing the Figures 4.4 (c) with (d) one can see that the before the cross-shore distance of 1700 m the sedimentation patterns continue and behind the cross-shore distance of 1700 m the erosion patterns continue. This pattern also appears when considering other time steps (e.g. year 2 or year seven), therefore only year five and year ten are shown.

4.3 Vegetation development

Next, the salt marsh vegetation development will be shown. First, an overview of the total vegetation density is shown. Next, the along-shore averaged vegetation density will be examined for the different simulations and different time steps. To examine the zonation and the colonisation behaviour of the salt marsh vegetation species, the top view of the vegetation density will also be shown for the different simulations. Finally, the frequency of the vegetation density and the total vegetation cover will be discussed.

Total vegetation density

Figure 4.5 shows the total vegetation density, which is the summation of the vegetation density of the *Spartina* species and the *Salicornia* species. In this Figure can be seen that the vegetation for both species start to develop at a cross-shore distance of approximately 2300 m. One can also note that the variations in along-shore direction are relatively small. Even when zooming in at a cross-shore distance of 2300 m, a clear distinction between the vegetated and unvegetated area can be seen and no large differences in the along-shore direction can be noticed. Therefore, the along-shore averaged vegetation density will be discussed in the next paragraph.

Along-shore averaged vegetation density

In Figure 4.6 the along-shore averaged vegetation density relative to the maximum carrying capacity (n_b/K) for the *Spartina* species and the *Salicornia* species can be seen for the five simulations including vegetation. In this Figure, in general, it can be noted that the vegetation starts occurring at a cross-shore distance of approximately 2000 m, which is at a bed level elevation of approximately 1.2 m. Between a cross-shore distance of 2000 m and 2300 m an area is occurring with a low vegetation density. In this area, the vegetation density is able to establish and increase during neap tides, but is disappearing during spring tides. Therefore, the vegetation density in this area will remain small. At a cross-shore distance of approximately 2300 m the vegetation density increases rapidly. Since the resilience of both salt marsh vegetation species to the inundation depth and bed shear stresses are similar ($\tau_{cr,Sal} = \tau_{cr,Spar} = 0.25$ and $H_{cr,Sal} = H_{cr,Spar} = 0.21$), the vegetation starts to appear at the same cross-shore distance. So, the hydrodynamics and morphodynamics determine the starting point of the vegetation development in cross-shore direction, but hardly influence the vegetation development after this point.

In Figure 4.6 (a) the vegetation density of the mono-species simulation with the *Spartina* species can be found. In this Figure, it can be seen that the relative average vegetation density is approximately 60 %. Besides, one can see that the minimum vegetation density is around the value for the vegetation density in a new cell (= 10%) and the maximum vegetation density is around its maximum carrying capacity (100%). In Figure 4.6 (b), vegetation density of the mono-species simulation with the *Salicornia* species can be seen. The mean vegetation density of the *Salicornia* species is around 90 %, which is higher than the *Spartina* species. This can probably be explained by the colonisation behaviour of both species. Because of the higher establishment probability of the *Salicornia* species, more vegetation is establishing faster, which results in a higher average vegetation density. Besides, the *Spartina* species expands by diffusion. This means that when the *Spartina* species is expanding to a neighbouring cell, the vegetation density of the original cell decreases. The decrease in vegetation density in the original cell and the small vegetation density in the diffused cells results in a smaller average vegetation density for the *Spartina* species. The *Salicornia* also shows a minimum vegetation density equal to the vegetation density in a new cell and a maximum vegetation density at the maximum carrying capacity.

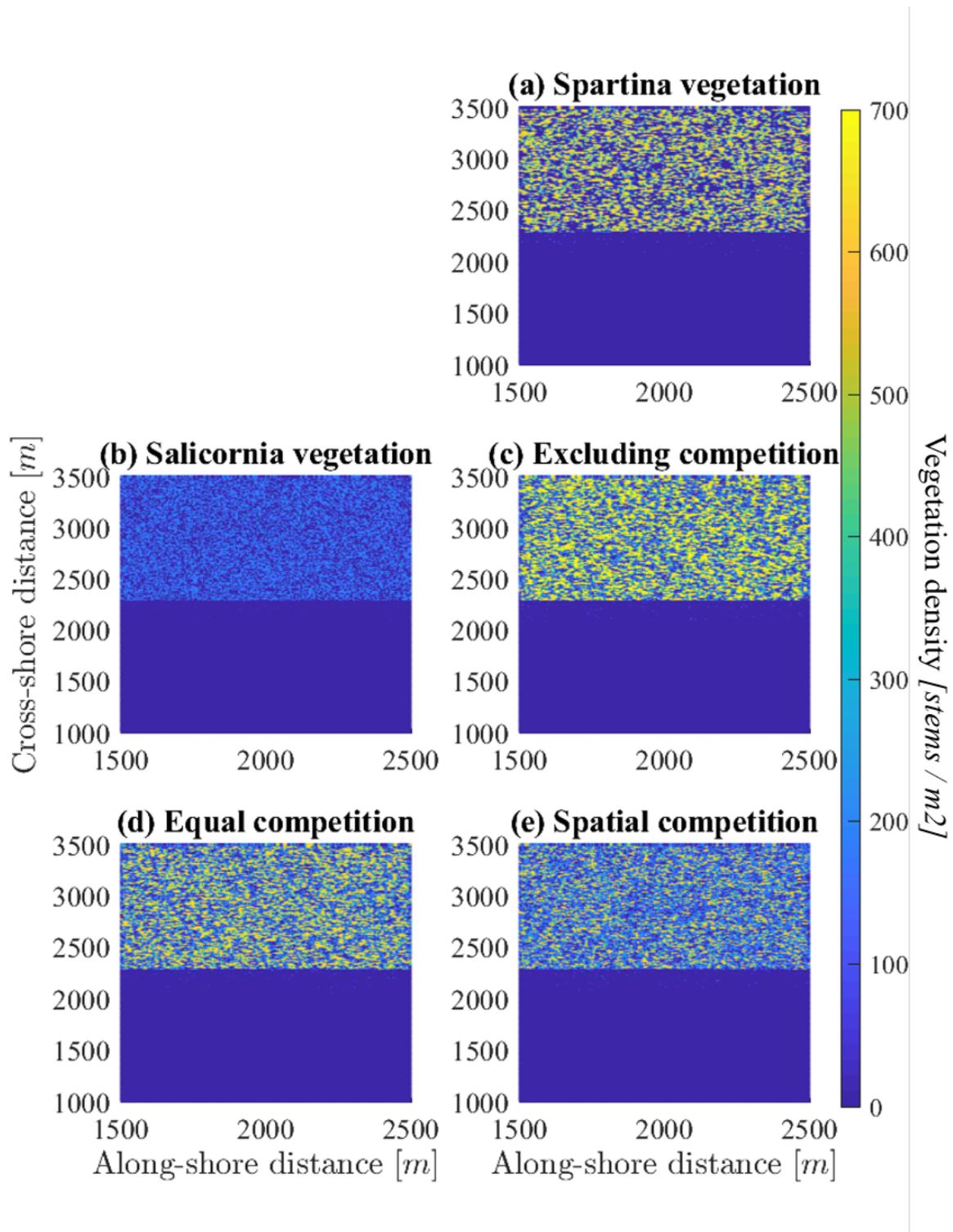


Figure 4.5: The total vegetation density during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

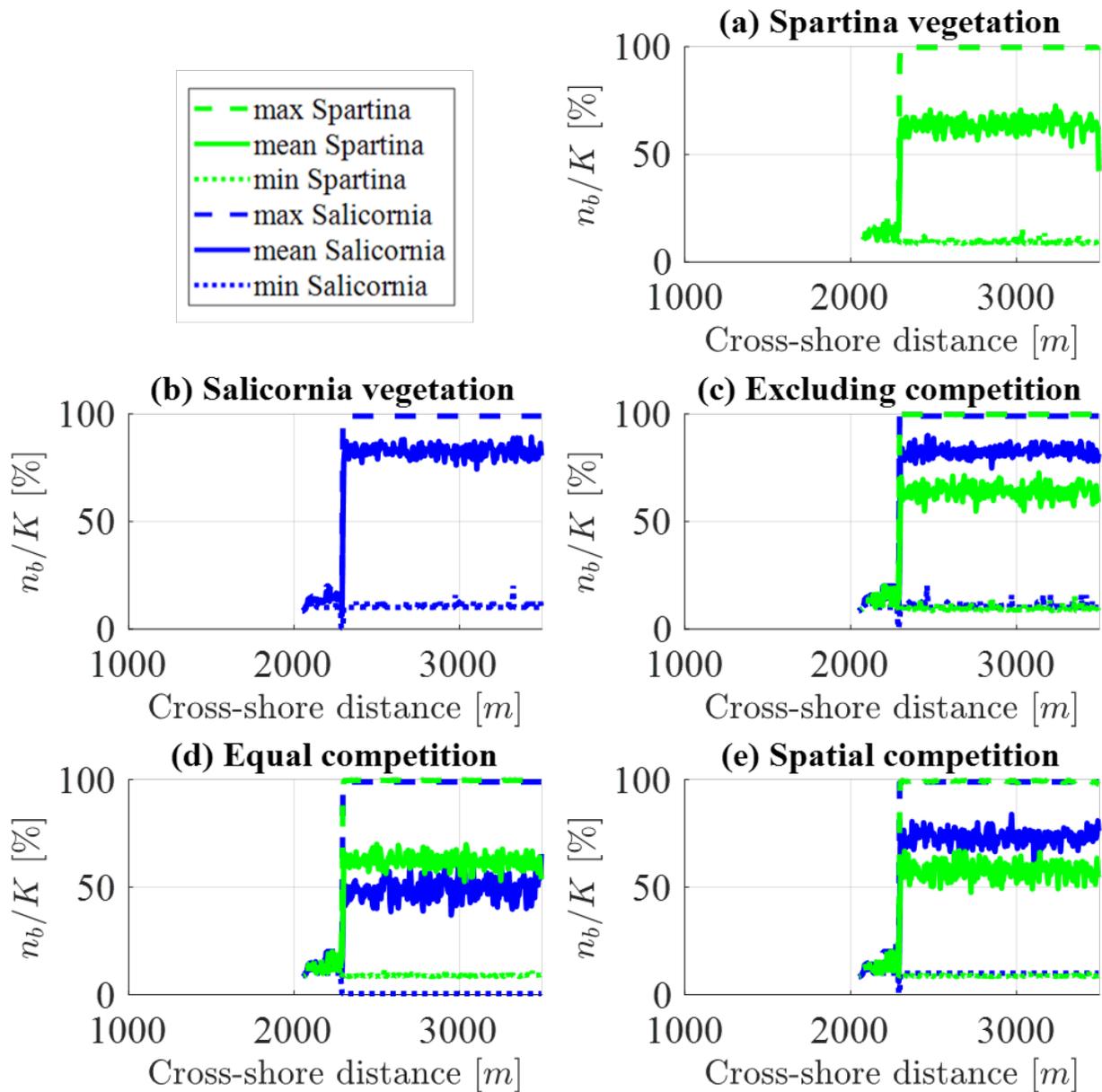


Figure 4.6: The along-shore minimum, mean and maximum vegetation density of *Salicornia* species (blue) and the *Spartina* species (green) at year ten for (a) the mono-species simulation with *Spartina* vegetation, (b) the mono-species simulation with *Salicornia* vegetation, (c) the multi-species simulation excluding competition, (d) the multi-species simulation with equal competition and (e) the multi-species simulation with spatial competition.

Figure 4.6 (c) shows the vegetation density for the *Salicornia* species and the *Spartina* for the multi-species simulation without competition. This results in situation where both salt marsh vegetation species can develop without the interference of the competing species. So, vegetation density of the *Spartina*

species in Figure 4.6 (c) is similar to the vegetation density in Figure 4.6 (a) and the vegetation density of the *Salicornia* species in Figure 4.6 (c) to the vegetation density in Figure 4.6 (b). One could argue that the presence of both salt marsh vegetation species would result in a larger bed roughness and therefore less hydrodynamics. The decrease in hydrodynamics would result in an increase in vegetation density, but no clear increase in the vegetation density of the *Salicornia* species or the *Spartina* species can be noticed when comparing this simulation to the mono-species simulations. This is probably because there is a clear distinction between the vegetated and unvegetated area. So, the hydrodynamics decide where vegetation starts to grow, but after this starting point of the vegetation density, the hydrodynamics does not really influence the vegetation development.

Figure 4.6 (d) shows the vegetation density for the *Salicornia* species and the *Spartina* species for the multi-species simulation with equal competition. In this Figure, it can be seen that the vegetation density of the *Spartina* species is following the same pattern as the vegetation density of the *Spartina* species during the mono-species run. However, the mean vegetation density and the minimum vegetation density of the *Salicornia* species are smaller compared to the mono-species simulation of the *Salicornia* species. This can be explained by the competition and the value of α . In Figure 3.5 can be seen that the isocline of the *Spartina* species is above the isocline of the *Salicornia*. In Section 2.2.3 is already explained that it means that it will result in the extinction of the *Salicornia* species, if only the Lotka-Volterra competition framework is considered for the vegetation development. However, in this research the feedback between hydrodynamics, morphodynamics and vegetation development is considered. For this reason, the *Spartina* species is having an advantage compared to the *Salicornia*. This is why the vegetation density of the *Salicornia* is affected by the *Spartina* species, but the *Spartina* species is less affected by the presence of the *Salicornia* species.

Figure 4.6 (e) shows the multi-species simulation with spatial competition. In this Figure, it can be seen that the vegetation density of both species slightly decrease compared to the mono-species simulations (Figures 4.6 (a) and (b)). This can also be explained with the values for the competition parameter α : In Figure 3.6 can be seen that the isoclines of the *Salicornia* species is on top of the *Spartina* species. This means that the species can coexist. Furthermore, this means that the *Spartina* species is not having an advantage (which is the case at Figure 4.6 (d)). Therefore, the *Salicornia* species is affected by the *Spartina* species and vice versa.

To compare the results of the *Spartina* species and the *Salicornia* species further, Figures 4.7 and 4.8 are included. These Figures show the along-shore average vegetation density relative to the maximum carrying capacity for the *Spartina* species and the *Salicornia* species for the different simulations at year five and year ten. In general it can be seen, that in all cases, the mono-species simulations are quite similar to the multi-species simulation without competition (the blue and red lines in Figures 4.7 and 4.8). In Figure 4.7 (a), it can be seen that the vegetation density of the *Spartina* species is relatively close to each other (between a range of 10%). Hereafter, the vegetation density of the *Spartina* species increases (Figure 4.7 (b)). The difference between Figure 4.7 (a) and (b) can be explained by considering the vegetation density of the species itself and the competing species: if the vegetation density of the *Spartina* species and the *Salicornia* species is small, the competition between the two salt marsh vegetation species is small. Therefore, in Figure 4.7 (a), the vegetation density is small and the differences between the different simulations is small. As the vegetation density increases (Figure 4.7 (b)), the species start to compete and the vegetation density of different simulations differ. In the paragraph above is already explained why these differences between the different simulations occur.

In Figure 4.8 (a) it can be seen that the vegetation density for the *Salicornia* species is also relatively similar during the first five years, all values are between a range of 12%. The average relative vegetation density for the simulation with spatial competition and the simulation with equal competition are only slightly smaller. A larger difference between the different simulations can be seen in Figure 4.8 (b). In this Figure, the vegetation density is smaller for the simulation with spatial competition and the simulation with equal competition. The decrease in vegetation density during the simulation with equal and spatial

competition is again caused by the competition: The increase of both species results in an increase in competition. So, similar to Figure 4.6, it can be seen that the *Spartina* species is less affected by the presence of the *Salicornia* species, compared to the influence of the *Spartina* species on the *Salicornia* species. The vegetation density only decrease with equal competition. While the vegetation density of the *Salicornia* species decreases for both the simulation with equal competition and spatial competition.

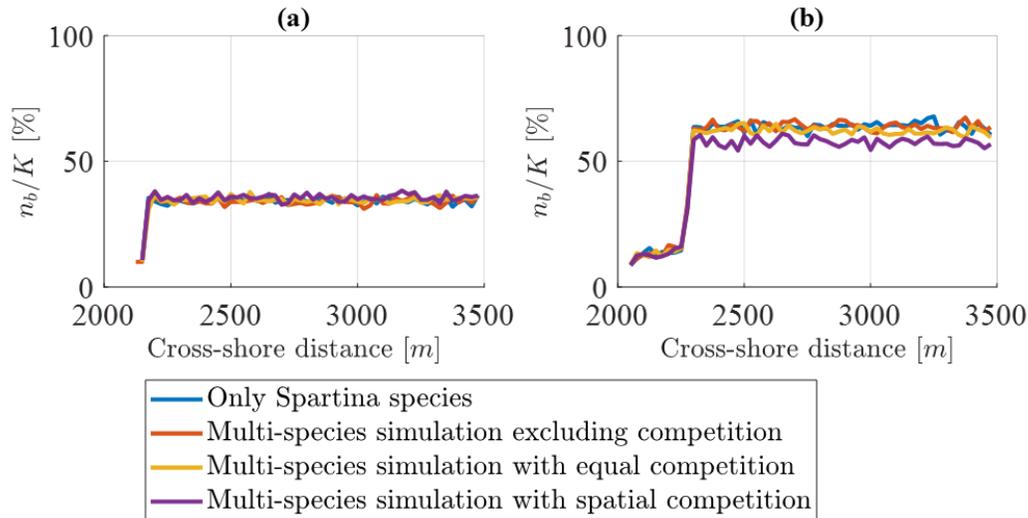


Figure 4.7: The along-shore averaged vegetation density of the *Spartina* species for the four simulations that include the *Salicornia* species at (a) year five and (b) year ten.

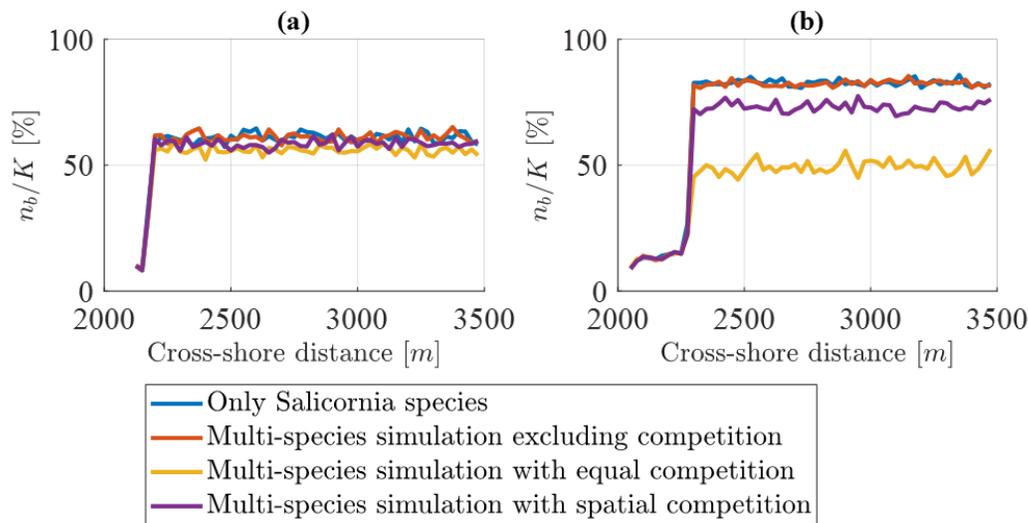


Figure 4.8: The along-shore averaged vegetation density of the *Salicornia* species for the four simulations that include the *Salicornia* species at (a) year 5 and (b) year ten.

Spatial distribution of the vegetation

Figure 4.9 shows the top view of a section of the study area including the percentage of vegetation density in every cell. When considering the whole study area, this area is located in the middle of the along-shore

distance and at three quarters of the cross-shore distance. Figures 4.9 (a) and (b) show the relative vegetation density for the simulations with only the *Spartina* species and only the *Salicornia* species. When zooming into the colonisation behaviour in Figure 4.9 (a) it can be seen that the vegetated cells of the *Spartina* species are connected, which can be explained by the high lateral expansion rate of the *Spartina* species. In Figure 4.9 (b) can be seen that the *Salicornia* species is more present, but the vegetated cells are not connected. This can be explained by the high establishment probability of the *Salicornia* species.

When considering Figure 4.9 (c)-(e) the same patterns can be noted as Figure 4.6 (c)-(e): When equal competition is considered, only the vegetation density of the *Salicornia* species decreases. When spatial competition is considered, the vegetation density of both species decreases and when no competition is considered, the vegetation density of both species is comparable with the vegetation density of the mono-species simulation.

	Spartina			Salicornia		
	Mean nb/k [%]	Mean nb/k relative to mono-species [%]	Vegetation cover [%]	Mean nb/k relative [%]	Mean nb/k to mono-species [%]	Vegetation cover [%]
Only <i>Spartina</i> vegetation	63.7	100	31.8	0	0	0
Only <i>Salicornia</i> vegetation	0.0	0	0	81.0	100.0	28.5
Excluding competition	63.8	100.2	31.7	80.4	99.3	28.5
Equal competition	62.0	97.4	29.8	48.7	60.1	28.2
Spatial competition	57.6	90.5	21.1	71.4	88.2	28.4

Table 4.1: A summary of the development of the *Salicornia* species and the *Spartina* species for the different simulations after ten years.

In Table 4.1, a summary is given on the mean vegetation density and the relative mean vegetation density compared to the mono-species simulation. The Table also shows the vegetation cover, which is the number of vegetated cells divided by the total number of cells. When considering the mean vegetation density relative to the mono-species simulation, one can see similar results as found in the previous Figures: A significant decrease in vegetation density of the *Salicornia* species in simulation four and five and a decrease in vegetation density of the *Spartina* species in simulation five. However, this pattern can not be seen in the vegetation cover: When considering the vegetation cover, one can see that the vegetation cover of the *Salicornia* species is quite stable compared to the *Spartina* species. The vegetation cover of the *Spartina* species decreases significantly during simulation four and five, while the difference in vegetation cover of the *Salicornia* species ranges between 28.2 % and 28.5 %. This is probably caused by the high establishment probability of the *Salicornia* species: When considering the simulation with equal competition, a high vegetation density of the *Salicornia* species would result in a disadvantage for the *Spartina* species. Since the establishment probability of the *Salicornia* species is 8 times higher than the *Spartina* species, it is more likely that *Salicornia* vegetation is already occurring in a cell as the *Spartina* species establishes in that cell.

Next, the distribution of the vegetation density of the vegetated cells will be shown. Figure 4.10 shows how often a certain vegetation density relative to the maximum carrying capacity is occurring for the different simulations with vegetation.

When considering the distribution of the *Spartina* species in general, one can observe the first peak in frequency is occurring around the relative vegetation density of 20%, a second peak in frequency at a relative vegetation density of 35% and thereafter a large peak at a relative vegetation density 90-100%. Between the peak the frequency is smaller. This is also the case for the *Salicornia* species: a larger peak in frequency around 20% and a large peak in frequency at 95-100%. This pattern can be explained by the

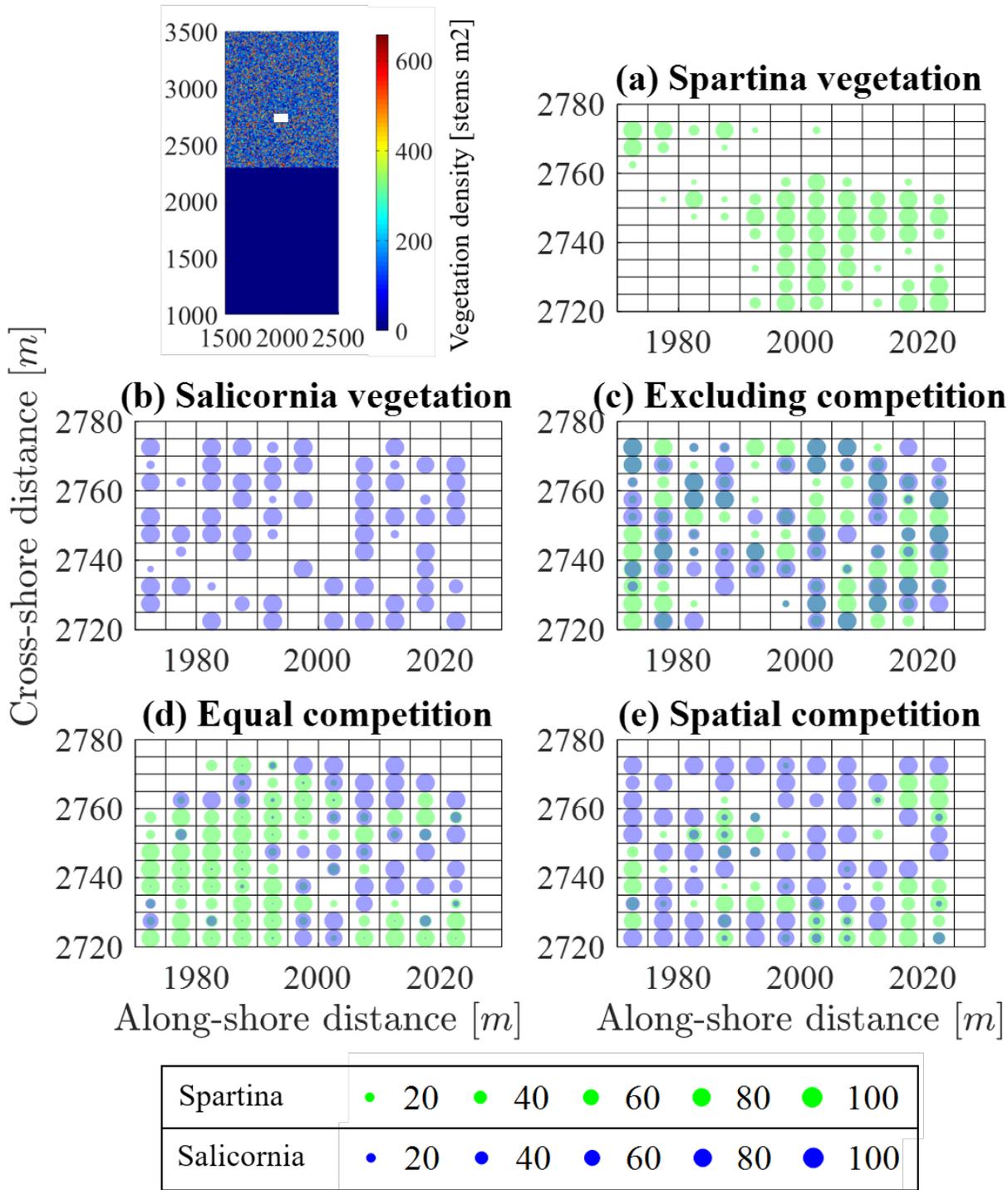


Figure 4.9: A top view of the distribution of the vegetation density of a section in the study area (white square in top left plot). The relative vegetation density of the *Salicornia* species is shown in blue and the *Spartina* species in green after ten years for (a) the mono-species simulation with *Spartina* vegetation, (b) the mono-species simulation with only *Salicornia* vegetation, (c) multi-species simulation excluding competition, (d) multi-species salt marsh with equal competition and (e) multi-species simulation with spatial competition. The dots show the vegetation density relative to the maximum carrying capacity (=189 stems m^{-2} for the *Salicornia* species and 658 stems m^{-2} for the *Spartina* species).

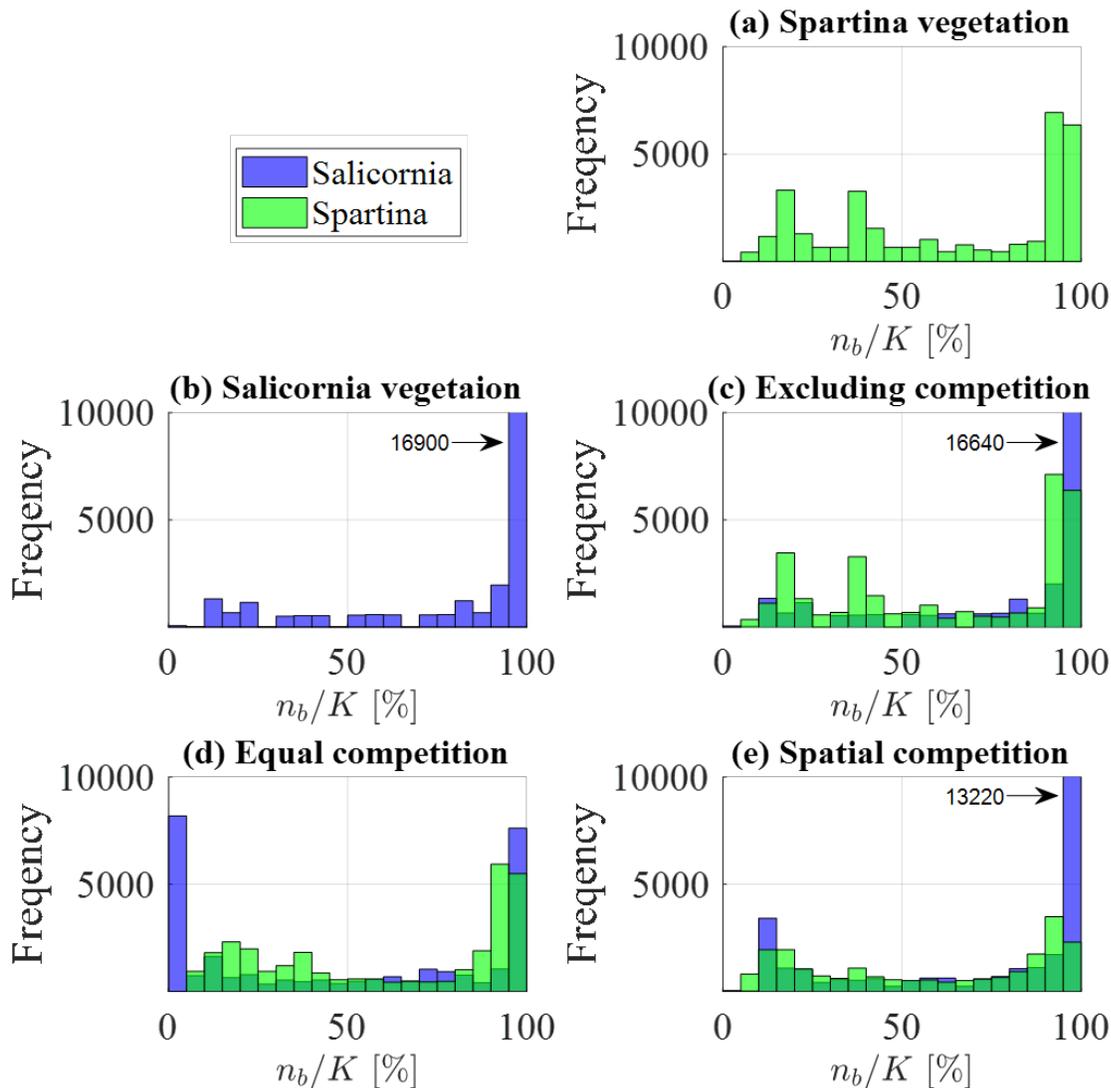


Figure 4.10: The distribution of n_b/K for the *Salicornia* species (in blue) and the *Spartina* species (in green) for the five simulations with vegetation: (a) with only the *Spartina* species, (b) with only the *Salicornia* species, (c) both salt marsh vegetation species excluding competition, (d) both salt marsh vegetation species and the ecological based competition parameter and (e) both salt marsh vegetation species and the spatial based competition parameter.

logistic growth rate: When the vegetation density of the *Spartina* species or *Salicornia* species is around the 40-80%, the growth per vegetation time step is relatively large. Therefore, only a small number of vegetated cells are having a vegetation density around the 40-80%. Likewise, with increasing density, the growth rate declines, and hence the vegetation densities in the last few bins occur more frequently. In general, it can also be seen that in many cases, the vegetation density is smaller than 95%, which means that the vegetation in the cell is still growing towards its maximum carrying capacity.

When comparing the multi-species simulation excluding competition with the mono-species simulations (Figure 4.10 (c) with (a) and (b)), it can be seen that this Figure again represents the summation of the mono-species simulations Figure 4.10 (a) and (b). Figure 4.10 (d) shows the frequency for the multi-species simulation with equal competition. When comparing the vegetation density of the *Salicornia* species of the multi-species simulation with equal competition to the mono-species simulation, one can note that a large peak in frequency at a relative vegetation density of 0-5% is occurring. This peak is smaller than the vegetation density in a new occurring cell (=10%), which means that vegetation is declining caused by competition. The vegetation density of the *Spartina* species of the multi-species run with equal competition is also smaller than the mono-species run, but is less affected by the competition, which agrees with Figure 4.6. When comparing the multi-species simulation with spatial competition with the mono-species simulations, one can again note a larger frequency occurring at a relatively smaller vegetation density for both species. Especially the relative vegetation density of the *Spartina* species is smaller, which also agrees with the Figure 4.6.

Chapter 5

Discussion

In this research, the influence of interspecific competition between the *Salicornia* species and the *Spartina* species is tested on the bio-geomorphological development of salt marshes. This Chapter starts with a discussion of the results and the influence of the competition parameter. Next, the limitations of this research will be discussed. Finally, it will be discussed how the findings in this research can be applied.

5.1 Discussion on bio-geomorphological development

By including the Lotka-Volterra competition framework in the vegetation development module, the vegetation development of a multi-species salt marsh is simulated. In Chapter 4, the results of the mono-species simulations and the multi-species simulation are compared. First, the morphodynamic development will further be discussed. After this, the vegetation development and the influence of the competition parameter α will be explained.

5.1.1 Morphodynamic development

When considering the morphological development, it can be concluded that the bed of the salt marsh is not yet in a morphodynamic equilibrium. In Figure 4.4 it can be seen that the bed level elevation is experiencing a large change between year five and year ten. This indicates that the bed level elevation is still moving toward equilibrium. Since the salt marsh is not in a morphodynamic equilibrium, it difficult to assess the influence of the vegetation development on the morphodynamic development. The changes in the bed can either be caused by the salt marsh vegetation development or by the fact that the bed of the salt marsh is not yet in equilibrium.

5.1.2 Vegetation development

In Chapter 4, the vegetation development of the different simulations are shown. From the Figures (e.g. Figure 4.6 and 4.10) can be concluded that in many cells the vegetation growth is not limited by high inundation depths or bed shear stresses, but has still not reached its maximum carrying capacity. Especially, Figure 4.10 shows that the vegetation density is still small in many cells. So, it can be concluded that the vegetation dynamics is (also) not yet in equilibrium. This also means that a longer simulation duration is needed before conclusions can be drawn whether the two salt marsh vegetation species can coexist or one of the species will become extinct. Besides, in Figure 4.6 one can note a clear distinction between the vegetated area and the unvegetated area. When a cross-shore distance of 2300m is reached, the vegetation density rapidly increases, but remains relatively stable between a cross-shore distance of 2300 m and 3500 m. From this can be concluded that the hydrodynamics and morphodynamics does influence the starting point of the vegetation development, but thereafter not influences the vegetation development. So, when comparing the different simulations, no clear influence of the hydrodynamics and

morphodynamics on/of the vegetation development can be noted.

Competition parameter

In Chapter 4 is explained that the different values of the competition parameter result in differences in vegetation development. To look further into the influence of the competition parameter, the results of the simulations are included in the state-space diagrams, introduced in Section 3.3, see Figures 5.2, 5.3 and 5.1.

In Figure 5.1, the vegetation density of the *Salicornia* species and the *Spartina* species are shown for the multi-species simulation excluding competition. It must be noted that only the competing cells are considered in this Figure. In Figure 5.1, it can be seen that the vegetation density of the *Spartina* species is not below the $66 \text{ stems } m^{-2}$, which is the vegetation density for the *Spartina* species in a new established cell. It can also be seen that only in a few cells, the vegetation density of the *Salicornia* species is below the $19 \text{ stems } m^{-2}$, which is the vegetation density for the *Salicornia* species in a new established cell. So, after the establishment of the salt marsh vegetation species, the vegetation density increases for both species. This process continues until both species reach their maximum carrying capacity.

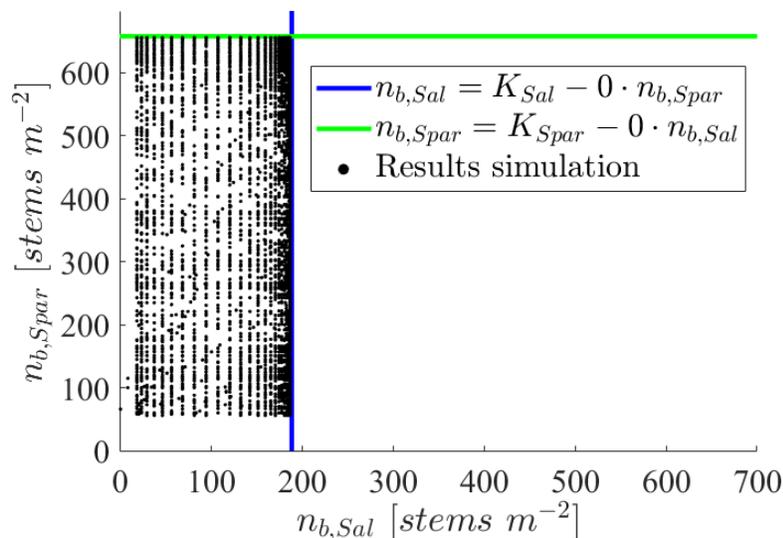


Figure 5.1: The state-space diagram with the isoclines for the *Salicornia* species and the *Spartina* species, with $\alpha_{Spar} = \alpha_{Sal} = 0$ and including the results of the prediction.

Figure 5.2 shows the results in the multi-species simulation with equal competition. In Section 2.2.3 is explained that, in the isolated Lotka-Volterra model, the *Salicornia* species would go extinct since its zero isocline is completely located under the zero isocline of the *Spartina* species. However, in the model which was used, the survival does not only depend on the competition but also the hydrodynamic conditions and the colonisation behaviour of both salt marsh vegetation species. When considering the vegetation density of the *Spartina* species in the competing cells, one can note that the vegetation density starts at $66 \text{ stems } m^{-2}$ and only increases after this. When considering the vegetation density of the *Salicornia* species, one can see a concentration at the vegetation density of $19 \text{ stems } m^{-2}$. However, contrary to the *Spartina* species, the vegetation density of the *Salicornia* decreases in some cases. Especially when the vegetation density of the *Spartina* species increases, the vegetation density of the *Salicornia* species decreases.

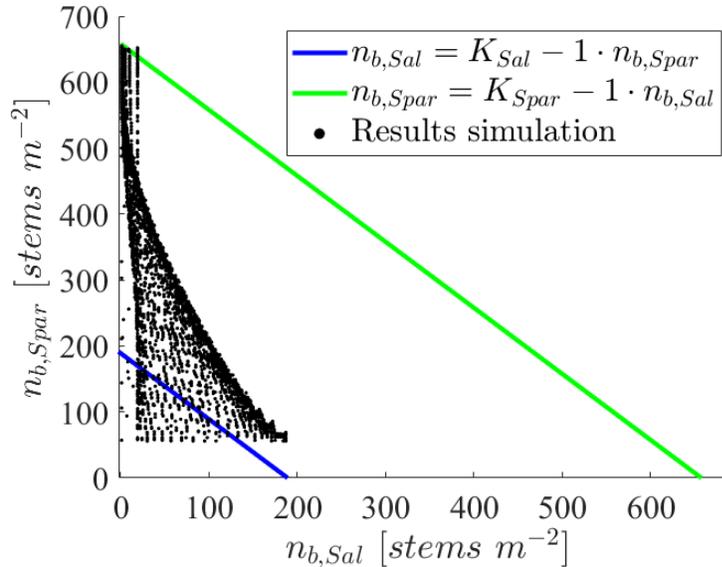


Figure 5.2: The state-space diagram with the isoclines for the *Salicornia* species and the *Spartina* species, with $\alpha_{Spar} = \alpha_{Sal} = 0$ and including the results of the prediction.

Finally, Figure 5.3 shows the zero isoclines of both species in the case with spatial competition ($\alpha_{Sal} = 0.3$ and $\alpha_{Spar} = 3.5$), including the results of the prediction. In Section 5.3 is explained that an equilibrium situation in the vegetation density can occur anywhere on the zero isoclines, since these are located on top of each other. In Figure 5.3 can be seen that, again, the vegetation density of the *Spartina* species starts at 66 stems m^{-2} and the *Salicornia* species at 19 stems m^{-2} . In contrary to Figure 5.2, the vegetation density of the *Salicornia* species does, in general, not decrease. Both species increase in vegetation density until the zero isocline is met. At which point on the zero isocline the equilibrium arises depends on the vegetation density of a species when the competing species start occurring in a cell.

From Figures 5.1, 5.2 and 5.3, it can again be included that the vegetation is still growing and a longer simulation duration is needed before an equilibrium occurs in the vegetation development. Still, one can notice that the evolution of the vegetation density in Figures 5.1, 5.2 and 5.3 quite agree with the equilibrium situations and trajectories shown in Figures 3.4, 3.5 and 3.6: When considering only the Lotka-Volterra competition framework, both species would reach their maximum carrying capacity in the case without competition. In the case with equal competition, the Lotka-Volterra competition framework predicted the extinction of the *Salicornia* species. In Figure 5.2 can be seen that the *Salicornia* species is not (yet) extinct. But, this might be the case, if the simulation duration would be longer, as the vegetation density of the *Spartina* is increasing and the vegetation density of the *Salicornia* decreasing (Figures 4.7 and 4.8). When considering spatial competition, it can be seen that (as expected) everywhere on the zero-isocline an equilibrium situation can occur. Besides, the vegetation density of both species is still increasing and not increasing (Figures 4.7 and 4.8). This means that both species can probably coexist.

5.2 Limitation of this research

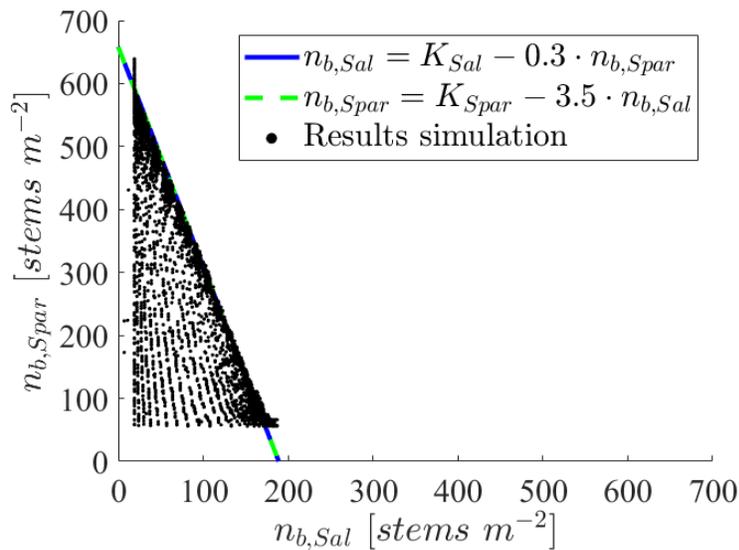


Figure 5.3: The state-space diagram with the isoclines for the *Salicornia* species and the *Spartina* species, with $\alpha_{Spar} = 3.5$ and $\alpha_{Sal} = 0.3$ and including the results of the prediction.

5.2.1 Population dynamics model

The development of salt marsh vegetation is determined with the population dynamics model. This model determines the increase and decrease in salt marsh vegetation density depending on the colonisation behaviour of the salt marsh vegetation species and its resilience to bed shear stress and inundation depth. This also means that several factors were not considered for vegetation development. For example, the presence of nutrients or the salinity concentration is not considered, even though the salinity is known to influence the salt marsh vegetation development (Egan & Ungar, 1999, 2001; Barbour, 1978).

No distinction is made between the vegetation development during the different seasons. In Section 2.1 is concluded that for both the *Salicornia* species and *Spartina* species, the vegetation biomass is larger during the summer compared to during the winter. This increase and decrease of salt marsh vegetation during the different seasons is not included in the population dynamics model: for the input parameters, an average over the year is considered.

The vegetation development is determined in the population dynamics model and depends on several input parameters. In the research of Temmerman et al. (2007) and Van Hulzen et al. (2007), the vegetation development of the *Spartina* species is considered. In the research of Schwarz et al. (2018) both the *Salicornia* species and the *Spartina* species. However, the values for the input parameters for the population dynamics model differ for the different studies. Temmerman et al. (2007) used a carrying capacity of $1200 \text{ stems } m^{-2}$ for the *Spartina* species where Schwarz et al. (2018) used a $658 \text{ stems } m^{-2}$ for the *Spartina* species and $189 \text{ stems } m^{-2}$ for the *Salicornia* species. Besides, Schwarz et al. (2018) made the vegetation density in a new established cell depend on the maximum carrying capacity, which also differs from Temmerman et al. (2007). In this research, the values of Schwarz et al. (2018) are used, since this study also used both the *Spartina* and *Salicornia* species.

In the study of Schwarz et al. (2018), the values for the critical bed shear stress and the critical inundation are similar for the *Spartina* species and the *Salicornia* species, which are also used in this research. This means that the differences in salt marsh vegetation development depend on colonisation behaviour: The establishment probability and the lateral expansion rate. Because of the similar critical inundation

depth and critical bed shear stress, the vegetation starts to develop at the same cross-shore distance.

In the population dynamic model, the increase in biomass by diffusion is described by a diffusion term. The diffusion term states that if the vegetation density is large in a cell, this will distribute with the neighbouring cell. So, if the vegetation density in a cell is large, this vegetation density will decrease as the vegetation density of the surrounding cells will increase. This might not be a good representation of what is occurring in the field: The *Spartina* species does expand in the horizontal direction, but the original vegetation density does not decrease.

5.2.2 Lotka-Volterra competition framework

In this research it is assumed that the interaction between the two salt marsh vegetation species can be described as direct interspecific competition. In the Lotka-Volterra competition model, the competition can also be indirect: E.g. the paper of Wesenbeeck (2007) used environmental conditions to examine the competition on a salt marsh between the *Spartina anglica* and lugworms (*Arenicola marina*). She used the silt content as the environmental condition to determine which species was favoured at a certain location. In Chapter 2 it is concluded that the inundation depth, bed shear stress and net sedimentation rate are important environmental factors when considering the bio-geomorphological development of salt marshes. Besides, the bed level elevation and the bed composition are important conditions that highly influence the inundation depth, bed shear stress and net sedimentation rate. Therefore, (a combination of) these factors could also have been used to determine which salt marsh vegetation species is more favourable at a certain location. But, these factors are already (indirectly) included, when predicting the bio-geomorphological development of salt marshes (Section 2.1.1). In the population dynamics model, the survival of the salt marsh vegetation species already depends on the bed shear stresses caused by flow and the inundation depth. Therefore, it indirectly depends on the bed level elevation, the bed composition and the net erosion rate. Since these processes are already included in the population dynamics model, it would be incorrect to use these factors again for the interaction function. Therefore, the competition between the two salt marsh vegetation species will solely be a function of the population density of the competing species.

In this research, it is assumed that interaction between the *Salicornia* species and the *Spartina* species solely consists of competition. But several studies (e.g. Hernandez (1998); Hernandez and Barradas (2003); Wang and Wu (2011)) found that whether different species positively or negatively interact, depends on the density of the species itself and the competing species. They found that in some cases the species positively interact with each other if the population density is low and the competition starts if the population density is higher. Bertness (1991) also found that the colonisation of a bare mudflat by the *Spartina patens* facilitates the colonisation of the *Juncus gerardi*. However, this changes into an interspecific competition as the vegetation density increases. This facilitation is often caused by the sheltering effect of one salt marsh vegetation species for another salt marsh vegetation species or the reduction of the salinity of a substrate by one vegetation species, which can facilitate the invasion of the competing species (Bertness, 1991). Still, it is assumed that the interspecific interaction between two salt marsh vegetation species solely consists of competition. This because the sheltering from high flow velocities of one species for another species is already included in the population dynamics model (as explained above). Besides, the salinity is not yet included in the population dynamics model.

5.2.3 Hydrodynamic and morphodynamic modelling

In this research, several forcings are considered as constant, which in reality would vary over space and time. E.g. a standard wave with standard wave height and period is used and the bed composition is considered as constant. Besides, the sediment supply of cohesive sediments is set to a uniform and constant value of 0.01 kg/m^3 . The tides are also simplified by two sines, which represent the semi-diurnal tide with the spring-neap variation. In the field, the tides could be larger or smaller, depending on the other

tidal constituents, wind set-up and the season. Since the salt marsh vegetation development directly depends on the inundation depth, a variation in tides and wave would result in different outcomes of the bio-geomorphological development of salt marshes. Still, the ratio between the vegetation density or vegetation cover of the *Salicornia* species and the *Spartina* species would probably not change as a result of a change in tides and wave, since both vegetation species are equally sensitive to the inundation depth.

For the bed profile, a slope of $0.001\ m/m$ is chosen at the bed level elevation on which salt marsh vegetation can occur. Beside the slope of $0.001\ m/m$, a slope of $0.0015\ m/m$ and $0.002\ m/m$ have been tested, of which the results can be found in Appendix A. For the different slopes, the gradient in the vegetation density was examined. But no clear difference in the gradient of salt marsh vegetation density could be noted at the different slopes. Therefore, a slope of $0.001\ m$ is chosen since this agrees most with the literature (see Section 3.2.3).

5.2.4 Vegetation modelling

During the implementation of the Lotka-Volterra competition framework, the decrease in vegetation density due to competition of the *Spartina* species is determined with the current vegetation density of the *Salicornia* species. The decrease in vegetation density due to competition of the *Salicornia* species is determined by the vegetation density of the *Spartina* species of the previous time step. It might be more accurate to use the vegetation density of the current time step. The choice was made not to do so, since this iteration would probably increase the run time. Besides, the difference in the vegetation density between two vegetation time steps is relatively small (mean difference of $\approx 16\ stems\ m^{-2}$ and a maximum of $\approx 45\ stems\ m^{-2}$).

In the population dynamics model, there is no restriction to the maximum height at which salt marshes can occur in the model. The model assumes salt marsh vegetation can grow on the whole bed level, restricted by the inundation depth and bed shear stresses. In reality, the pioneer zone, the zone where the *Salicornia* and *Spartina* species occur, approximately ends at MHWS. These restrictions on the landwards side are not considered.

The Lotka-Volterra competition framework is implemented in the growth term of the population dynamics model. One could argue that the competition between two salt marsh vegetation species would also influence the ability to diffuse or establish and therefore also should be included in the diffusion-term and establishment-term in the population dynamics model. However, the competition only directly influences the growth and in the next vegetation time step, the increase or decrease in growth rate influences the diffusion and establishment of new vegetation.

In this research, the Windows of Opportunity framework is not used to determine the establishment of the salt marsh vegetation species but is accounted for in the establishment term. This is done, because the Windows of opportunity framework requires a small vegetation time step (time step for WoO1 = 2.5 days) (Poppema et al., 2019)). This is far smaller than the morphological time step used in this research (MorFac = 100 days). In Chapter 3 is concluded that the simulation duration should be ten years. This simulation duration would not be achievable without a large MorFac, since a decrease in MorFac increases the run time.

5.3 Applicability

This research provides an insight into how the competition between different salt marsh vegetation species works and how this interspecific competition can be simulated. This research showed that the competition between different salt marsh vegetation species can be simulated by including the Lotka-Volterra

framework in the population dynamics model and coupling this to DFM. From these simulations can be concluded that the competition between different salt marsh vegetation species highly influences the vegetation development. This research also shows that the extent to which the competition influences the vegetation development highly depends on the competition parameter and the maximum carrying capacity.

The inclusion of the Lotka-Volterra framework in the population dynamics model sets the foundation for the inclusion of several (more than 2) salt marsh vegetation species. When several vegetation species are included in the simulation of the bio-geomorphological development of salt marshes, the feedback between vegetation dynamics and morphodynamics can be investigated more thoroughly. This inclusion of several salt marsh vegetation species will eventually lead to more realistic simulations of the bio-geomorphological development of salt marshes since multiple salt marsh vegetation species are often present at a salt marsh.

The next step in this research would be to determine the appropriate value for the competition parameter for salt marsh vegetation species. When the values for the competition parameters are known, several salt marsh vegetation species can be included in the long-term bio-geomorphological development of salt marshes. In this way, it can be determined which (combination of) salt marsh vegetation species proves to be the most resilient. Furthermore, it can be tested whether this multi-species salt marsh can keep up with sea-level rise. Finally, the information on the (long-term) bio-geomorphological development of salt marshes can help with the selection of the combination of the most resilient salt marsh vegetation species and the construction of artificial salt marshes for ecological/recreational purposes and coastal protection.

Chapter 6

Conclusion

Research question 1: What biotic factors are relevant when making predictions of the bio-geomorphological development of salt marshes and what are the timescales of these biotic factors?

First, the establishment characteristics and seasonal change of the *Salicornia* species and the *Spartina* species were determined. Next, conclusions were made that several similarities exist between the two salt marsh vegetation species: For both species, the inundation depth, bed shear stress and net erosion rate are important factors, which influence the bio-geomorphological development of salt marshes. The bed level elevation and bed composition are also important factors that influence the inundation depth and the erosion rate. A difference can be found in the colonisation behaviour: the *Salicornia* species is a fast-colonising species, while the *Spartina* species is a slow-colonising species. Besides, both the *Spartina* and *Salicornia* species experience seasonal change: both species experience a decrease in biomass during autumn and winter, and both species experience an increase in biomass during spring and summer. A large difference between the vegetation species is that the *Salicornia* species dies off during winter and the *Spartina* species only decreases in biomass during the winter, but does not disappear.

The increase and decrease in the salt marsh vegetation density can be calculated with the population dynamics model, developed by Temmerman et al. (2007). In this model, vegetation density can increase through new establishment, diffusion and growth and it can decrease due to high bed shear stresses and high inundation depths.

From the determination of the dominant factors, it has been concluded that both salt marsh vegetation species are sensitive to the inundation depth, bed shear stress, net erosion rate and seasonal change and are dependent on saltwater. So, there is an area in where both salt marsh vegetation species can occur. This also means that the two salt marsh vegetation species interact with each other.

Lastly, the time and space scale of these biotic factors have also been included in the time-space diagram. When considering the interaction between different salt marsh vegetation species, a simulation duration of minimal five years up to several years must be considered, which is the time needed for the *Spartina* species to cover a new area.

Research question 2: How can the interaction between different salt marsh vegetation species in the pioneer zone be included in the prediction of the bio-geomorphological development of salt marshes?

From different studies it has been concluded that the interspecific interaction between salt marsh vegetation species can be described as interspecific competition.

The interspecific competition can be described with the Lotka-Volterra competition framework. In this framework, the growth of a species can be limited by the population density of the competing species, and vice versa. In the vegetation module, the Lotka-Volterra competition framework is included in the population dynamics model, by replacing the logistic growth term of the population dynamics model by the Lotka-Volterra competition framework. This way, the increase in vegetation density is caused by the new establishment, diffusion and growth, and the decrease is caused by high inundation depths, high bed shear stresses and competition.

The extent to which the growth of a species is limited by the competition depends on the competition parameter α and the maximum carrying capacity K . The ratio between the α and K determines whether one of the species will go extinct or if a stable equilibrium will occur. Still, it is unknown what the appropriate α value is for both salt marsh vegetation species.

Research question 3: What is the bio-geomorphological development of mono-species salt marsh versus the bio-geomorphological development of a multi-species salt marsh?

The bio-geomorphological development of salt marshes can be determined by coupling the vegetation module in Python to DFM. By including the Lotka-Volterra competition framework in the vegetation module, the interspecific competition between the *Salicornia* species and the *Spartina* species can be simulated. To test the influence of the interspecific competition on the bio-geomorphological development of salt marshes, the development of a mono-species salt marsh has been compared to the development of a multi-species salt marsh. Since the appropriate values for the competition parameters for the *Salicornia* species and *Spartina* species is not known yet, three multi-species salt marshes are simulated: one without competition, one with equal competition and one with spatial competition.

By comparing the results of the different mono-species simulations with the multi-species simulation, the following conclusions can be drawn: In general, it has been concluded that when considering the morphological development of salt marshes, no clear difference could be noticed between the different simulations. In general, it has also been concluded that both the morphological development and the vegetation development are not yet in equilibrium: The morphological change between five and ten years is larger compared to the change between one and five years. Moreover, it has been shown in Chapter 5 (e.g. Figure 4.10, 5.2, 5.3 and 5.1) that in many cases the vegetation density is smaller than its zero isocline, which indicates that the vegetation development is also not yet in equilibrium. In the different simulations with salt marsh vegetation, a clear difference could be noticed between the vegetated and unvegetated area. From this, it has been concluded that the hydrodynamics and morphodynamics effects the cross-shore distance at which the salt marsh vegetation starts to develop. After this point, the hydrodynamics and morphodynamics do not influence the vegetation development.

For vegetation development, it has been concluded that the interspecific competition strongly influences the vegetation development. The extent to which, however, does depend on the type of competition: When there is no competition between the two salt marsh vegetation species ($\alpha_{Spar} = \alpha_{Sal} = 0$), both species increase to their maximum carrying capacity, without much influence of the competing species. The change in mean vegetation density compared to the mono-species run is minuscule. When considering equal competition ($\alpha_{Spar} = \alpha_{Sal} = 1$), the *Spartina* species experiences an advantage compared to the *Salicornia* species, caused by the larger maximum carrying capacity of the *Spartina* species. In this case, the mean vegetation density of the *Salicornia* species decreases significantly compared to the mono-species run, while the vegetation density of the *Spartina* species decreases slightly. When considering spatial competition ($\alpha_{Spar} = 3.5$ $\alpha_{Sal} = 0.3$), both vegetation species can grow in the same cell until their combined maximum carrying capacity is reached. How much of the *Salicornia* species or the *Spartina* species is present in the cell, when it is in its equilibrium, depends on the vegetation density of

the species when the competing species establishes in the cell. In this case, the mean vegetation density of both species decreases compared to the mono-species run. When considering the vegetation cover, the *Salicornia* species proves to be the more resilient salt marsh vegetation species. The change in vegetation covers is negligibly small for the different simulations. This is not the case for the *Spartina* species. The vegetation cover slightly decreases during the simulation with equal competition and significantly decreases during the simulation with spatial competition.

Main research question: What is the influence of interspecific interaction between different salt marsh vegetation species on the bio-geomorphological development of salt marshes in the pioneer zone?

The interaction between salt marsh vegetation species can be categorised as interspecific competition. When considering the morphological development, no clear influence of the interspecific competition between different salt marsh vegetation species could be found. But, the interspecific competition does influence the vegetation development. The extent to which the interspecific competition influences the vegetation development depends on the competition parameter and the maximum carrying capacity. When there is no competition, both salt marsh vegetation species are able to grow towards their maximum carrying capacity. When the competition between the *Salicornia* species and the *Spartina* species is equal, the *Salicornia* species is affected by the *Spartina* species, but the *Spartina* species is only slightly affected by the *Salicornia* species. When considering spatial competition, the vegetation density of the *Salicornia* species is limited by the *Spartina* species, and vice versa. But, equilibrium situations are occurring on the zero-isoclines, which means that the species can coexist in this scenario.

With the new insights in the interaction between different salt marsh vegetation species and the inclusion of the Lotka-Volterra framework, more realistic simulations of the bio-geomorphological development of salt marshes can be made. This research has shown the importance of the inclusion of the competition in vegetation development and has set the foundation for the (long-term) simulations of a multi-species salt marsh. In the future, these (long-term) simulations of a multi-species salt marsh are expected to contribute to the construction of artificial salt marshes.

Chapter 7

Recommendations

7.1 Recommendations Lotka-Volterra competition framework

In Chapter 2 it is concluded that the differences are large during the different seasons when considering the vegetation establishment and development. Besides, the hydrodynamic conditions are different during the different seasons. Because of this, the inclusion of the different seasons will result in more realistic results.

In Chapter 2 it is also concluded that the smallest time step when considering the vegetation development, depends on the seedling establishment. According to the Windows of Opportunity framework, a period of 2.5 days without inundation is needed for the salt marsh vegetation to establish. In Chapter 5 is already explained that it was not possible to model the Windows of Opportunity framework since a MorFac of 100 is used. But, it would probably lead to more realistic results, when the Windows of Opportunity framework would be included in the determination of the vegetation development.

As mentioned in Chapter 5, the study of Bertness and Ellison (1987) showed that the interspecific interaction between two salt marsh vegetation can be described as mutualism if the vegetation density is small, and as competition, if the vegetation density is large. This mutualism is caused by a decrease in salt concentration in the soil, since the salt concentration decreases as salt marsh vegetation species, with a higher tolerance to salt, start to develop. A next step would be to include this in the bio-geomorphological development of salt marshes. This can be done by either considering mutualism when the vegetation density is small and competition when the vegetation density is large or by including the salinity as environmental factor in the Lotka-Volterra competition framework.

In this research, the value for the competition parameter α is based on different theories. But, the prediction of the bio-geomorphological development of salt marshes will become more realistic, if the values are known for α_{Sal} and α_{Spar} . E.g. the study of Silander and Antonovics (1982) quantified the biotic interaction between different salt marsh vegetation species by perturbation experiments. Such an approach could be used to quantify the interspecific interaction between the *Salicornia* species and the *Spartina* species. Furthermore, one could also consider to translate the species removal response of the study of Silander and Antonovics (1982) to the competition parameter.

7.2 Recommendations bio-geomorphological simulations

In Chapter 2 is concluded that it can take up to several decades for a multi-species salt marsh to develop. In this research is also concluded that both the morphological development and vegetation development are still changing and not yet in equilibrium. Therefore, it is still unsure how salt marshes will develop in the future. Therefore, it would be recommended to predict a longer period (e.g. till the 2100).

When making long-term predictions of the bio-geomorphological development of a multi-species salt marsh, the relative sea-level rise should also be included. In Chapter 1 is explained that the pioneer zone on the salt marsh are among the first to inundate if the relative sea-level rises (Larsen, 2019). Besides, several studies concluded that the survival of salt marshes under different sea-level rise scenarios depends on the sediment supply (Kirwan & Murray, 2007; Best et al., 2018). Therefore, the inclusion of different sea-level rise and sediment supply scenarios would result in more applicable results.

From the paragraph above can be concluded, that the prediction of the bio-geomorphological development of salt marshes is mainly restricted by the run time. Ideally, one wants to make long-term predictions with small vegetation time steps and small run time. But, an increase in simulation duration or a decrease in vegetation time step results in long run times. Therefore, it would be recommended to find a solution for that (e.g. by examining a vegetation speed up factor).

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Appendix A

Bed profile

In Section 3.2.2 is already explained that the bed profile must meet the following requirements:

1. A slope is preferred, which causes a gradient in the vegetation density.
2. For a salt marsh, the slope is generally between the 0.0001 m/m and 0.001 m/m (Larsen, 2019).
3. The minimum bed level elevation is at least -2.3 m and the maximum bed level elevation is at least 2.6 m . Also, the salt marsh vegetation will mainly occur between a bed level elevation of 1.8 m and 2.6 m , which means the slope should be small in these areas.

Requirement 2 and 3 results in a bed profile with a smaller slope (0.001 m/m , 0.0015 m/m and 0.002 m/m) in the area where salt marsh vegetation can occur and a larger slope (0.011 m/m) in front of this area (to reach the minimum bed level elevation). It was still unclear how the different slopes influence the gradient in the vegetation density, therefore three different slopes are tested: 0.001 m/m , 0.0015 m/m and 0.002 m/m . The result of this can be seen in Figures A.1, A.2 and A.3. In the figures can be seen that there is almost no gradient in the vegetation density. Therefore, the bed profile with a slope of 0.001 m/m is chosen, since this slope agrees the most with the literature (see requirement 2).

Bed profile 0.001 m/m

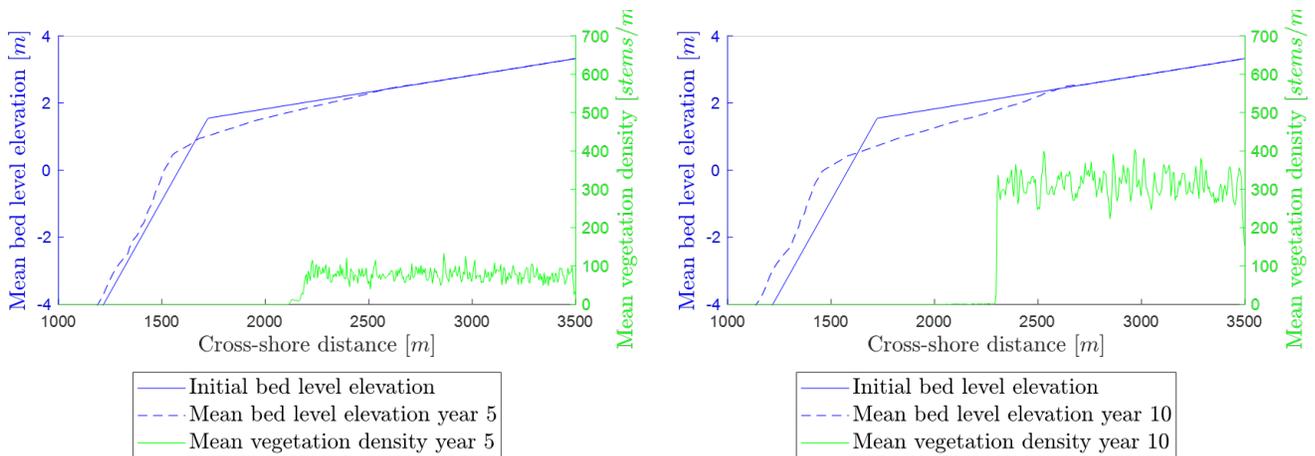


Figure A.1: The vegetation density when considering a slope of 0.001 m/m at the salt marsh. On the left y-axis the mean bed level elevation and on the right y-axis the mean vegetation density for (a) 5 years and (b) 10 years.

Bed profile 0.0015 m/m

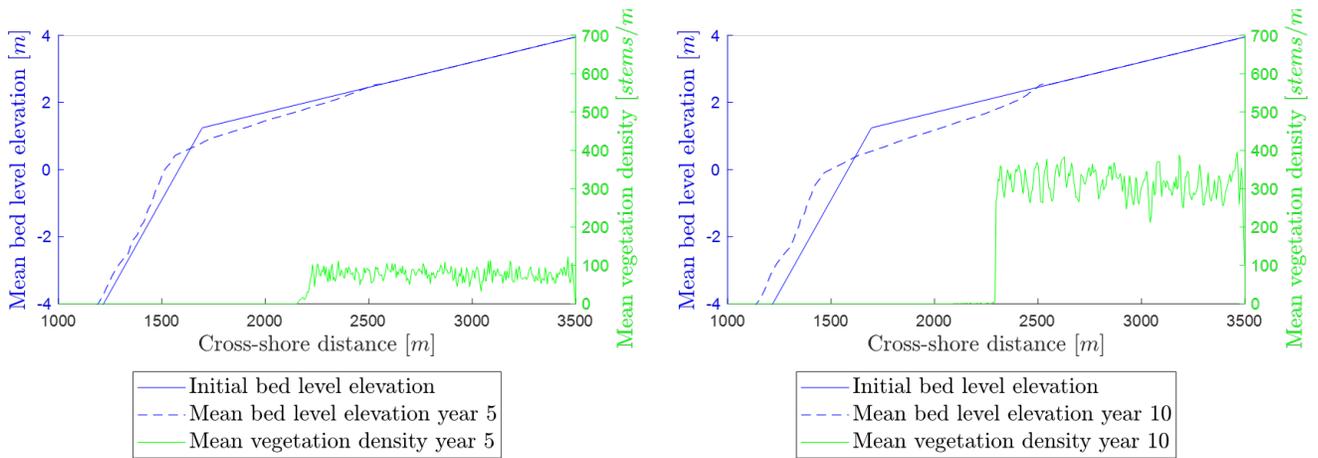


Figure A.2: The vegetation density when considering a slope of 0.0015 m/m at the salt marsh. On the left y-axis the mean bed level elevation and on the right y-axis the mean vegetation density for (a) 5 years and (b) 10 years.

Bed profile 0.002 m/m

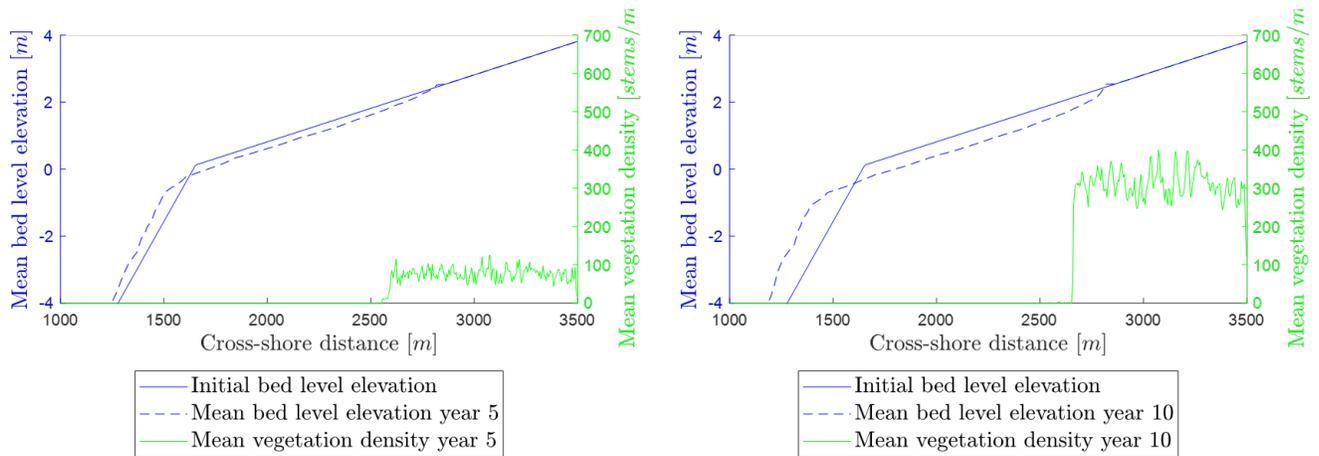


Figure A.3: The vegetation density when considering a slope of 0.002 m/m at the salt marsh. On the left y-axis the mean bed level elevation and on the right y-axis the mean vegetation density for (a) 5 years and (b) 10 years.

Appendix B

Vegetation modelling: Python script

```
# -*- coding: utf-8 -*-
"""
Created on Wed Nov 30 14:43:19 2016

@author: herman
"""
import numpy as np
import matplotlib.tri as tri
import matplotlib.pyplot as plt
import bmi.wrapper
from scipy import integrate
import os
import sys
import datetime

#RC_ini = sys.getrecursionlimit()
#print("initial recursion limit = " + str(RC_ini))
#sys.setrecursionlimit(RC_ini*4)
#print("updated recursion limit = " + str(RC_ini*4))

# define modeling environment
D3D_HOME = r'D:\DFM_veg\code_1709\x64'
#D3D_HOME = r'C:\Software\DFM_veg\Models\DFM\Code1709\x64'
dimr_path = os.path.join(D3D_HOME, 'dimr', 'bin', 'dimr_dll.dll')
dflowfm_path = os.path.join(D3D_HOME, 'dflowfm', 'bin', 'dflowfm.dll')

workdir = r'D:\RiverAndCoastalEngineering\44_beiden_a3\DFM-Veg'
config_file = os.path.join(workdir, 'dimr_config.xml')
mdu_file = os.path.join(workdir, 'fm', 'FlowFM.mdu')

print("D3D_HOME : " + D3D_HOME)
print("dimr_path : " + dimr_path)
print("config_file:" + config_file)

## Add corrects locations to environment variable PATH
os.environ['PATH'] = os.path.join(D3D_HOME, 'share', 'bin') \
+ ";" + os.path.join(D3D_HOME, 'dflowfm', 'bin') \
+ ";" + os.path.join(D3D_HOME, 'dimr', 'bin') \
+ ";" + os.path.join(D3D_HOME, 'dwaves', 'bin') \
+ ";" + os.path.join(D3D_HOME, 'esmf', 'scripts') \
+ ";" + os.path.join(D3D_HOME, 'swan', 'scripts')
#print("PATH:" + os.environ['PATH'])

# define and initialize FlowFM model
#model = bmi.wrapper.BMIWrapper(engine=dll_path, configfile=config_file)
#model.initialize()
```

```

## Define DFM wrapper
model_dfm = bmi.wrapper.BMIWrapper(engine=dflowfm_path, configfile=mdu_file)

## Define and initialise DIMR wrapper
model_dimr = bmi.wrapper.BMIWrapper(engine=dimr_path, configfile=config_file)
model_dimr.initialize()
print ('model initialized')

# get the pointers to important model variables of FlowFM
ndx=model_dfm.get_var('ndx')          # [-] Number of flow nodes (internal + boundary)
ndx1=model_dfm.get_var('ndx1')       # [-] Number of internal flowcells (internal = 2D +
                                     1D )
xzw=model_dfm.get_var('xzw')         # [m] centre of gravity
yzw=model_dfm.get_var('yzw')         # [m] centre of gravity
lnx=model_dfm.get_var('lnx')         # [-] nr of flow links (internal + boundary). First
                                     we have 1D links, next 2D links, next
                                     boundary links (first 1D, then 2D)
lnxi=model_dfm.get_var('lnxi')       # [-] nr of flow links (internal, 1D+2D )
ln=model_dfm.get_var('ln')           # [-] 1D link (2,*) node administration, 1=nd1, 2=
                                     nd2 linker en rechter celnr
dx=model_dfm.get_var('dx')           # [m] link length (m)
wu=model_dfm.get_var('wu')           # [m] link initial width (m), if < 0 pointer to
                                     convtab
ba=model_dfm.get_var('ba')           # [m2] bottom area, if < 0 use table in node type
#sediment1=model.get_var('sediment_1')
#sed1=model.get_var('sed1')
bedlevel=model_dfm.get_var('bl')     # [m] bottom level (m) (positive upward)

# add perturbations
#bedlevel = bedlevel + ((np.random.rand(ndx)*0.04)-0.02)
#model_dfm.set_var('bl',bedlevel)

## initialisation of vegetation variables
rnveg=model_dfm.get_var('rnveg')     # [1/m2] 3D plant density , 2D part is basis input (1
                                     /m2)
diaveg=model_dfm.get_var('diaveg')  # [m] 3D plant diameter, 2D part is basis input (m)
stemheight=model_dfm.get_var('stemheight') # [m] 2D plant heights (m)
rnveg2 = np.zeros(100200,)

# boundaries for vegetation
xbndmin=min(xzw[range(ndx1)])+8.0
xbndmax=max(xzw[range(ndx1)])-8.0
ybndmin=min(yzw[range(ndx1)])+8.0
ybndmax=max(yzw[range(ndx1)])-8.0

### Preparation of graphical output
# prepare location for saving intermediate figures
figsavefolder= os.path.join(workdir, 'figures')
# Create target Directory if don't exist
if not os.path.exists(figsavefolder):
    os.mkdir(figsavefolder)
    print("Directory " , figsavefolder , " Created ")
else:
    print("Directory " , figsavefolder , " already exists")

#triangulate face coordinates for plotting
make_veg_plot = 1
show_veg_plot = 0
face_triang=tri.Triangulation(xzw[range(ndx1)], yzw[range(ndx1)])
#define basic plotting routine for model output
def showfld (fld,face_triang,fsf,i,lvls,ttl ):
    plt.tricontourf(face_triang,fld,levels=lvls)
    plt.title(ttl)
    plt.colorbar(shrink=0.3, extend='both',aspect=10)
    plt.axes().set_aspect('equal')
    figsavepath=os.path.join(figsavefolder, ttl + '_t=' + str(i))

```

```

plt.savefig(figsavepath, dpi = 200, bbox_inches = 'tight')
if show_veg_plot == 1:
    plt.show()
plt.close()

## prepare text file for logging
'''
veg_log_file = os.path.join(workdir, 'veg_log.txt')
f = open(veg_log_file, "w+")
f.close()
with open(veg_log_file, 'a', encoding='utf-8') as file:
    file.write("Vegetation log")
'''

taumn_log_file = os.path.join(workdir, 'taumn_log.txt')
file_f = open(taumn_log_file, "w+")
file_f.close()
with open(taumn_log_file, 'a', encoding='utf-8') as file_f:
    file_f.write("taumn log")
'''

wdmn_log_file = os.path.join(workdir, 'wdmn_log.txt')
file_g = open(wdmn_log_file, "w+")
file_g.close()
with open(wdmn_log_file, 'a', encoding='utf-8') as file_g:
    file_g.write("wdmn log")
'''

### TIME PARAMETERS
# set time parameters for coupled model
#nt=30          # number of vegetation time steps
dt=1.0         # time resolution (years)
mtpervt=86400  # seconds of model time per vegetation step
nt=36 #180     # number of vegetation time steps
ncells = len(rnveg)
#mtpervt=10.0  # seconds of model time per vegetation step
print ('# of vegetation timesteps ' + str(nt))
print ('vegetation timestep length ' + str(mtpervt) + ' seconds')

###
# VEGETATION SPECIES 1: SPARTINA
Seed= 0.00278          # chance of establishment of seedlings in a grid
                      # cell (per year)

inifreq=0.05
r=0.278 # = 1 per jaar # intrinsic growth rate of plant density (per
                      # year)

K=658.0               # carrying capacity of plant density (stems/m2)
P0=0.1*K              # initial plant density of seedlings (stems/m2)
D= 0.0556             # plant diffusion coefficient (m2/year)
Ctau=8.33             # plant erosion coefficient due to bed shear
                      # stress (stems/m2/5min per N/m2 increase of
                      # bed shear stress)

tau_crp=0.25         # critical bed shear stress for plant erosion (N/
                      # m2)

Cinund=833.33        # plant erosion coefficient due to inundation
                      # stress (stems/m2/year per m increase of
                      # inundation height at high tide)

inund_crp=0.21       # critical inundation height at high tide for
                      # plant erosion (m)

diam_spar=0.00304     # default diameter stems
height_spar=0.59     # default height stems
rnveg_cr= 0.1/(diam_spar*height_spar) # critical value for sparse/dense vegetation
alpha = 3.48         # interspecific competition parameter #1 #3.48 #
                      # 0

###

```

```

# VEGETATION SPECIES 2: SALICORNIA
Seed2= 0.0222 # chance of establishment of seedlings in a grid cell
                (per year)

inifreq2=0.05
r2=0.278 # intrinsic growth rate of plant density (per year)
K2=189 # carrying capacity of plant density (stems/m2)
P02=0.1*K2 # initial plant density of seedlings (stems/m2)
D2= 0 # plant diffusion coefficient (m2/year)
Ctau2= 8.33 # plant erosion coefficient due to bed shear stress (
            stems/m2/5min per N/m2 increase of bed shear
            stress)

tau_crp2=0.25 # critical bed shear stress for plant erosion (N/m2)
Cinund2=833.33 # plant erosion coefficient due to inundation stress
              (stems/m2/year per m increase of inundation
              height at high tide)

inund_crp2=0.21 # critical inundation height at high tide for plant
                erosion (m)

diam_sal=0.005 # default diameter stems
height_sal=0.28 # default height stems
rnveg_crp2=0.1/(diam_sal*height_sal) # 71.42 critical value for sparse/dense vegetation
alpha2 = 0.28 # competition parameter 1 #0.28 #0

%% MEAN DIAMETER AND HEIGHT

diam_def_mean=(diam_sal+diam_spar)/2 # default diameter stems
height_def_mean=(height_sal+height_spar)/2 # default height stems

%% DEFINING FUNCTIONS

def makeinirandfield (P):
    rr=np.random.rand(ndxi)
    #Pi=P[range(ndxi)]
    Pi=P0*(rr<=inifreq) # internal cells
    #hier boundaries
    Pi[xzw>xbndmax]=0.0
    Pi[xzw<xbndmin]=0.0
    Pi[yzw>ybndmax]=0.0
    Pi[yzw<ybndmin]=0.0
    # eind boundaries
    P[range(ndxi)]=Pi
    #diaveg.fill(diam_def_mean)
    #stemheight.fill(height_def_mean)
    model_dfm.set_var('rnveg',P)
    return(P)

def makeinirandfield2 (P2):
    rr=np.random.rand(ndxi)
    #Pi=P[range(ndxi)]
    Pi2=P02*(rr<=inifreq2) # internal cells
    #hier boundaries
    Pi2[xzw>xbndmax]=0.0
    Pi2[xzw<xbndmin]=0.0
    Pi2[yzw>ybndmax]=0.0
    Pi2[yzw<ybndmin]=0.0
    # eind boundaries
    P2[range(ndxi)]=Pi2
    #diaveg.fill(diam_def2)
    #stemheight.fill(height_def2)
    #model_dfm.set_var('rnveg2',P2)
    return(P2)

def diffveg2D(P,Dcoeff,ndxi=ndxi,ndx=ndx,lnxi=lnxi,ln=ln,
              dx=dx[range(lnxi)],wu=wu[range(lnxi)],
              ba=ba[range(ndxi)]):
    supq = np.zeros(ndxi)

```

```

qds=Dcoeff/dx*wu
k1=ln[range(lnxi),0]-1
k2=ln[range(lnxi),1]-1
ds2=P[k2]-P[k1]
qsa=qds*ds2
k=np.concatenate((k1,k2),axis=0)
q=np.concatenate((qsa,-qsa),axis=0)
supq=np.bincount(k,weights=q)
supq=supq/ba
return(supq)

#def seedveg(P,bedlev):
def seedveg(P,bedlev,wd_mn,tau_mn,inund_crp,tau_crp,Seed,P0):
    rr=np.random.rand(ndxi)
    dpseed=(bedlev>-2.32)*(P<0.1)*(wd_mn<inund_crp)*(tau_mn<tau_crp)*(rr<=Seed)*P0
    return(dpseed)

def erosveg(P,tau_mn,Ctau,tau_crp):
    dptau=-P*Ctau*(tau_mn-tau_crp)
    dptau[dptau>0.0]=0.0
    dptau[np.isnan(dptau)]=0.0
    return(dptau)

def inundveg(P,wd_mn,Cinund,inund_crp):
    #initial code
    dpinund=-P*Cinund*(wd_mn-inund_crp)
    dpinund[dpinund>0.0]=0.0
    dpinund[np.isnan(dpinund)]=0.0
    return(dpinund)

#i_flag = 0
def vegRoC (t0,P):
    # global i_flag
    dPdt=np.zeros(ndxi)
    # logistic growth
    dPdt=dPdt+growth(P,K,rnveg2[range(ndxi)],alpha,r)#r*P*(1-P/K)
    # Diffusion
    dPdt=dPdt+diffveg2D(P,D)
    # erostau
    dPdt=dPdt+erosveg(P,tau_mn,Ctau,tau_crp)
    # inundation stress
    dPdt=dPdt+inundveg(P,wd_mn,Cinund,inund_crp)
    # return rate of change
    return(dPdt)

#
#salicornia
def vegRoC2 (t0,P):
    # global i_flag
    dPdt=np.zeros(ndxi)
    # logistic growth
    dPdt=dPdt+growth(P,K2,rslt_spartina[(i-1),range(ndxi)],alpha2,r2)#,rnveg[range(ndxi)]
    #r2*P*(1-P/K2-(0.5*(rnveg/K2)))----- (
    # Diffusion
    dPdt=dPdt+diffveg2D(P,D2)
    # erostau
    dPdt=dPdt+erosveg(P,tau_mn,Ctau2,tau_crp2)
    # inundation stress
    dPdt=dPdt+inundveg(P,wd_mn,Cinund2,inund_crp2)
    # return rate of change
    return(dPdt)

def growth(P,K,ncom,alpha,r):
    dPdt=r*P*(1-P/K-alpha*(ncom/K))
    return(dPdt)

```

```

%%% DEFINING INITIAL CONDITIONS

rnveg2 = np.zeros(100200,)
### set initial vegetation field
makeinirandfield(rnveg) # random seeding of plants
makeinirandfield2(rnveg2)

#makeinirandfield2(rnveg2) verplaatst naar forloop
rnveg_pybk = np.zeros(shape=(len(rnveg),))
rnveg_pybk2 = np.zeros(shape=(len(rnveg2),))

rslt_salicornia= np.zeros(shape=(nt+1,len(rnveg)))
rslt_spartina= np.zeros(shape=(nt+1,len(rnveg)))
rnveg_dfm = np.zeros(100200,)
rslt_rnveg_dfm = np.zeros(shape=(nt+1,len(rnveg)))
rslt_diameter = np.zeros(shape=(nt+1,ndx))
rslt_height = np.zeros(shape=(nt+1,ndx))

### couple fixed variables in DFM/Python (i.e. variables without operations in Python)
is_dtint=model_dfm.get_var('is_dtint')
is_sumvalsnd=model_dfm.get_var('is_sumvalsnd')
is_maxvalsnd=model_dfm.get_var('is_maxvalsnd')
bedlvl=model_dfm.get_var('bl')
#wd=model_dfm.get_var('hs')
dPdt_normal=np.zeros(ndxi)
#diameter_dfm = np.ones(ndx)*diam_def_mean
#height_dfm = np.ones(ndx)*height_def_mean

diameter_sal_array = np.ones(ndx)*diam_sal
diameter_spar_array = np.ones(ndx)*diam_spar
height_sal_array = np.ones(ndx)*height_sal
height_spar_array = np.ones(ndx)*height_spar

diameter_dfm2= np.ones(ndx)*diam_def_mean
height_dfm2 = np.ones(ndx)*height_def_mean

%%% RUNNING VEGETATION MODEL FOR NT NUMBER OF STEPS

for i in range(1,nt+1):
    # execute model over length of time step in model time units

    #
    model_dimr.update(mtpervt)
    #time.sleep(60)
    if i!=1: #if i not equal to 1
        rnveg_pybktemp = rnveg_pybk.copy()
        rnveg[rnveg_pybktemp<rnveg_cr] = rnveg_pybktemp[rnveg_pybktemp<rnveg_cr]
        rnveg_pybktemp2 = rnveg_pybk2.copy()
        rnveg2[rnveg_pybktemp2<rnveg_cr2] = rnveg_pybktemp2[rnveg_pybktemp2<rnveg_cr2]
    #
    tau_mn=is_sumvalsnd[range(ndxi),0]/is_dtint
    vel_mn=is_sumvalsnd[range(ndxi),1]/is_dtint
    wd_mn=is_sumvalsnd[range(ndxi),2]/is_dtint
    tau_mn[tau_mn<0]=0
    tau_mn[np.isnan(tau_mn)]=0.0
    vel_mn[vel_mn<0]=0
    vel_mn[np.isnan(vel_mn)]=0.0
    wd_mn[wd_mn<0]=0
    wd_mn[np.isnan(wd_mn)]=0.0

    tau_max=is_maxvalsnd[range(ndxi),0]
    vel_max=is_maxvalsnd[range(ndxi),1]
    wd_max=is_maxvalsnd[range(ndxi),2]
    tau_max[tau_max<0]=0
    tau_max[np.isnan(tau_max)]=0.0

```

```

vel_max[vel_max<0]=0
vel_max[np.isnan(vel_max)]=0.0
wd_max[wd_max<0]=0
wd_max[np.isnan(wd_max)]=0.0

#
### run plant growth model
t=np.array([0.0,1.0])
print('start integrating veg ODE; ' + str(datetime.datetime.now()))
print('is_dtint is: ' + str(is_dtint))

#calculation salicornia
rslt2=integrate.solve_ivp(vegRoC2, t, rnveg2[range(ndxi)])
rslt_rnveg2 = rslt2.y[:,np.size(rslt2.y,1)-1]
rnveg2[range(ndxi)]=rslt_rnveg2+seedveg(rnveg2[range(ndxi)],bedlvl[range(ndxi)],wd_mn[
    range(ndxi)],tau_mn[range(ndxi)],
    inund_crp2,tau_crp2,Seed2,P02)

#calculations spartina
rslt=integrate.solve_ivp(vegRoC, t, rnveg[range(ndxi)]) #,h0=.05,hmax=.1)
rslt_rnveg = rslt.y[:,np.size(rslt.y,1)-1]
rnveg[range(ndxi)]=rslt_rnveg+seedveg(rnveg[range(ndxi)],bedlvl[range(ndxi)],wd_mn[
    range(ndxi)],tau_mn[range(ndxi)],
    inund_crp,tau_crp,Seed,P0)

print('finish integrating veg ODE; ' + str(datetime.datetime.now()))
# take out negative values for rnveg
rnveg[rnveg<0]=0.0
rnveg[np.isnan(rnveg)]=0.0
rnveg = np.round(rnveg)

rnveg2[rnveg2<0]=0.0
rnveg2[np.isnan(rnveg2)]=0.0
rnveg2 = np.round(rnveg2)

print('size before forcing ghostcells rnveg is ' + str(np.size(rnveg)))

# add zeros for veg density at ghost cells open boundary
if np.size(rnveg)==ndxi:
    rnveg_temp = np.append(rnveg, np.zeros(ndx-ndxi))
    rnveg = rnveg_temp
elif np.size(rnveg)==ndx:
    rnveg[ndx:ndx-1] = 0

if np.size(rnveg2)==ndxi:
    rnveg_temp2 = np.append(rnveg2, np.zeros(ndx-ndxi))
    rnveg2 = rnveg_temp2
elif np.size(rnveg2)==ndx:
    rnveg2[ndx:ndx-1] = 0

print('size after forcing ghostcells rnveg is ' + str(np.size(rnveg)))

#
# show model output

if make_veg_plot == 1:
    vegplot2=showfld (rnveg2[range(ndxi)],face_triang, figsavefolder, i , lvls=[1,200,
        400,600,800,1000,1200], ttl="
        Vegetation Salicornia" )

    ## show model output5
    vegplot=showfld (rnveg[range(ndxi)],face_triang, figsavefolder, i , lvls=[1,200,
        400,600,800,1000,1200], ttl="

```

```

                                Vegetation Spartina" )
    Tauplot_max=showfld (tau_max[range(ndxi)],face_triang, figsavefolder, i , lvlsl=[0,
                                0.1,0.25,0.5,1,2,3,5], ttl="Tau_max [
                                Nm-2]" )
    Tauplot_mn=showfld (tau_mn[range(ndxi)],face_triang, figsavefolder, i , lvlsl=[0,0.
                                1,0.25,0.5,1,2,3,5], ttl="Tau_mean [
                                Nm-2]" )
    bedlvlplot=showfld (bedlvl[range(ndxi)],face_triang, figsavefolder, i , lvlsl=[-5,-
                                3,-2,-1,-0.5,-0.1,0,0.1,0.5,1,2,3],
                                ttl="bed level [m]" )

# reset counters, push counters and updated veg field to model
is_sumvalsnd.fill(0.0)
is_maxvalsnd.fill(0.0)
is_dtint.fill(0.0)
#sparse vegetation is set to zero, to prevent small densities in DFM resulting in off
                                roughness values
rnveg_pybk = rnveg.copy()
rnveg[rnveg<rnveg_cr] = 0
rnveg_pybk2 = rnveg2.copy()
#rnveg[rnveg<rnveg_cr] = 0

rnveg_dfm = rnveg+rnveg2

for j in range(ndxi):
    if rnveg_dfm[j] > 0:
        diameter_dfm2[j]= ((diameter_spar_array[j]*rnveg[j])+(diameter_sal_array[j]*
                                rnveg2[j]))/rnveg_dfm[j]
        heigth_dfm2[j] = ((height_spar_array[j]*rnveg[j])+(height_sal_array[j]*rnveg2[
                                j]))/rnveg_dfm[j]
    else:
        diameter_dfm2[j] = diam_def_mean
        heigth_dfm2[j] = height_def_mean

model_dfm.set_var('rnveg',rnveg_dfm)
model_dfm.set_var('diaveg',diameter_dfm2)
model_dfm.set_var('stemheight',heigth_dfm2)

#model_dfm.set_var('rnveg',rnveg)

#dingen opslaan
rslt_diameter[i] = diameter_dfm2
rslt_salicornia[i] = rnveg2
rslt_spartina[i] = rnveg
rslt_rnveg_dfm[i] = rnveg_dfm

# here step to write model results

model_dimr.finalize()
print ('ready')

%% SAVING VEGETATION DENSITY SALICORNIA AND SPARTINA (MODEL ONLY SAVES THE SUMMATION)
np.savetxt('SalicorniaVegDens.txt', rslt_salicornia)
np.savetxt('SpartinaVegDens.txt', rslt_spartina)

```

Appendix C

Results

C.1 Along-shore averaged: extreme years

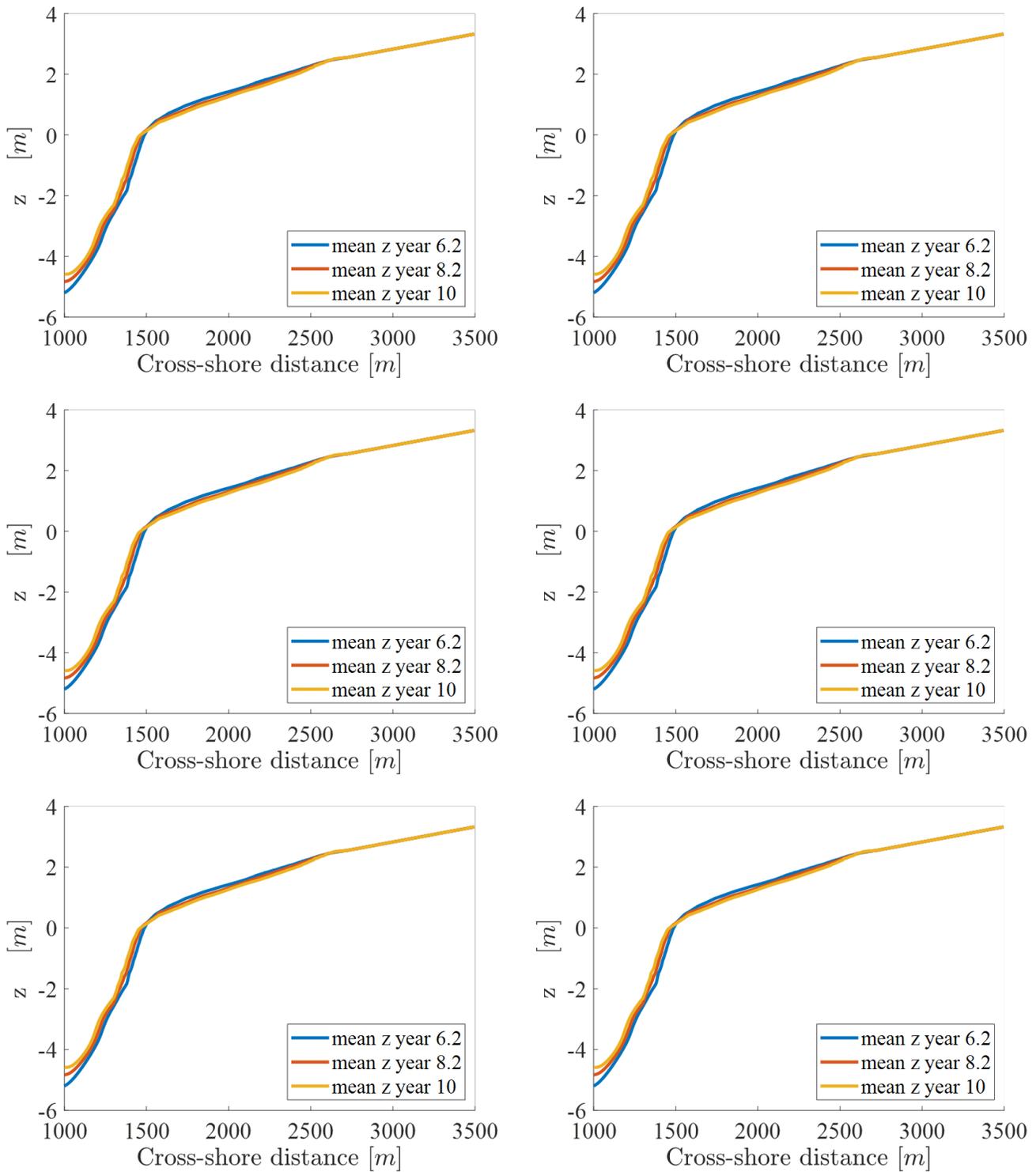


Figure C.1: The along-shore averaged bed level elevation for year 6.2, 8.2 and 10 for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

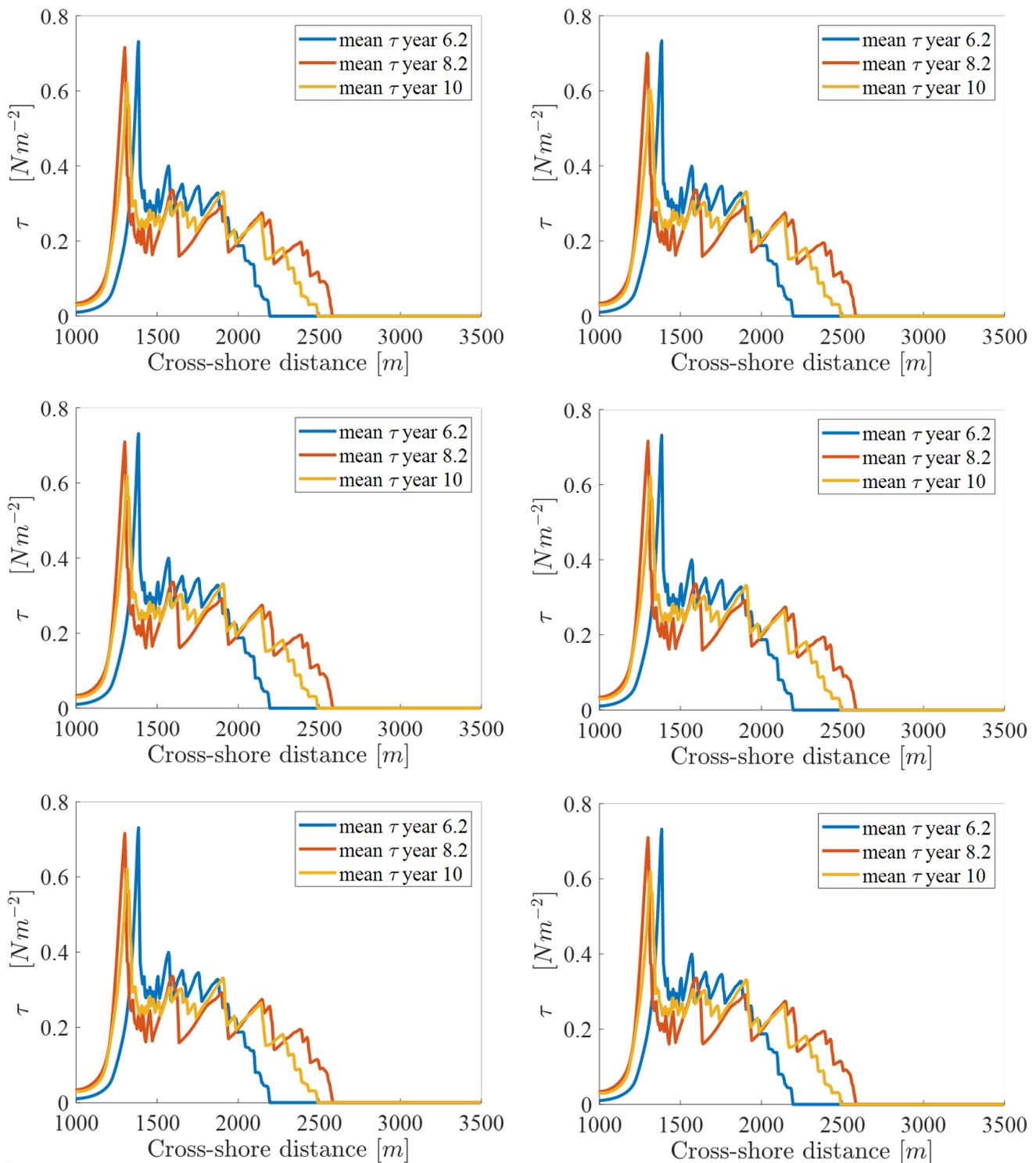


Figure C.2: The along-shore averaged bed shear stress for year 6.2, 8.2 and 10 for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

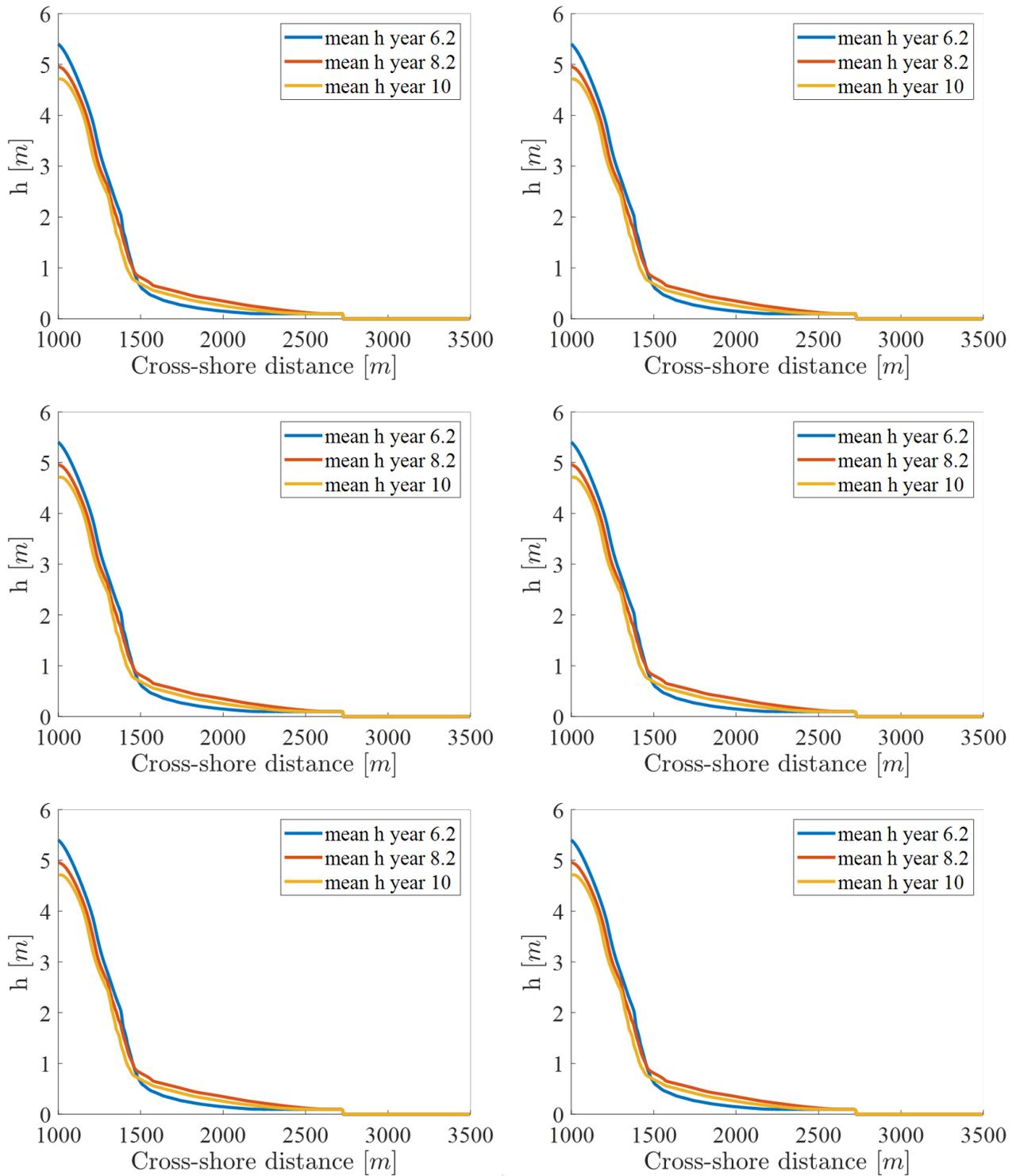


Figure C.3: The along-shore averaged inundation depth for year 6.2, 8.2 and 10 for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

C.2 Overview results year 10

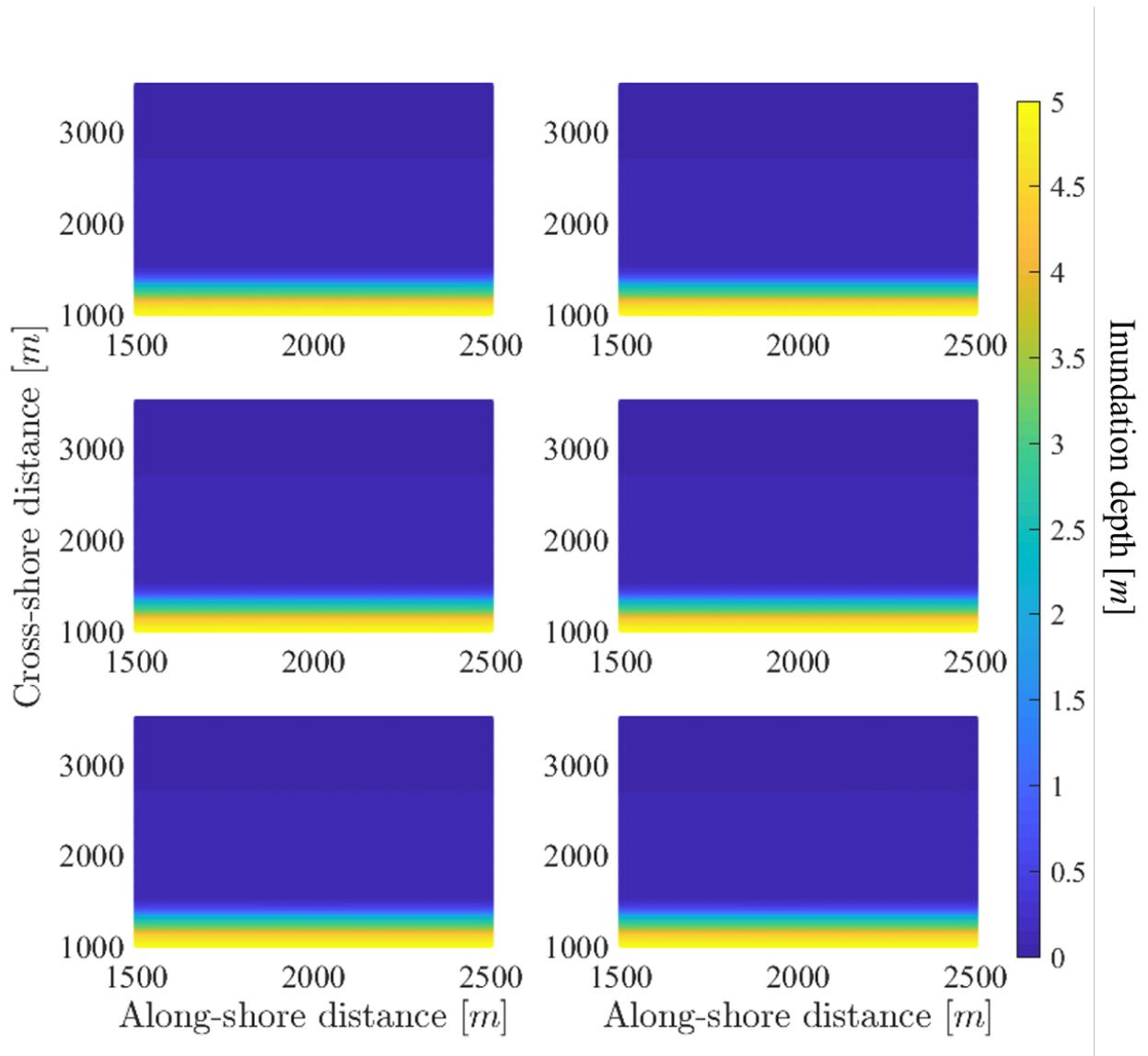


Figure C.4: The inundation depth during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

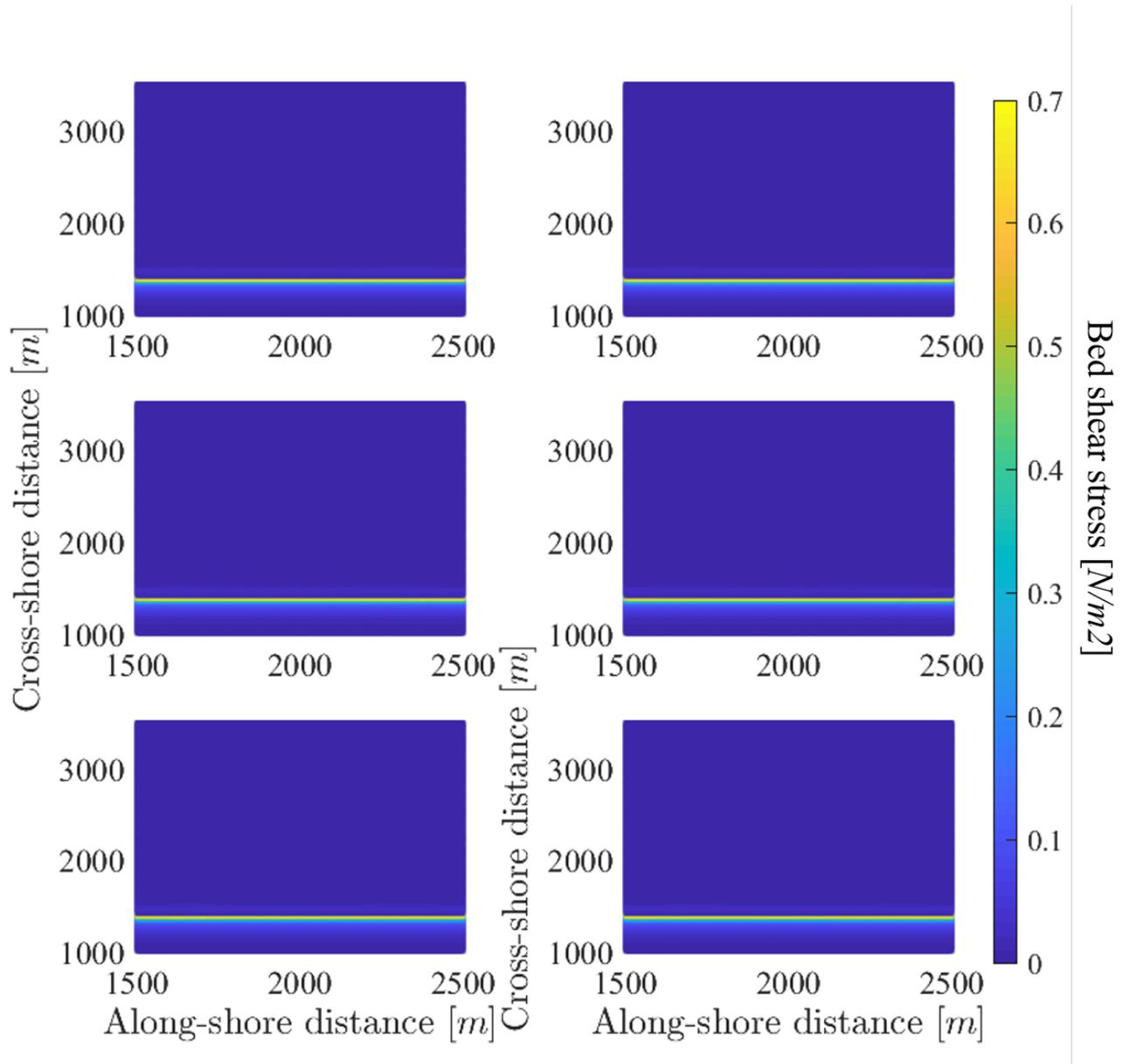


Figure C.5: The bed shear stress during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

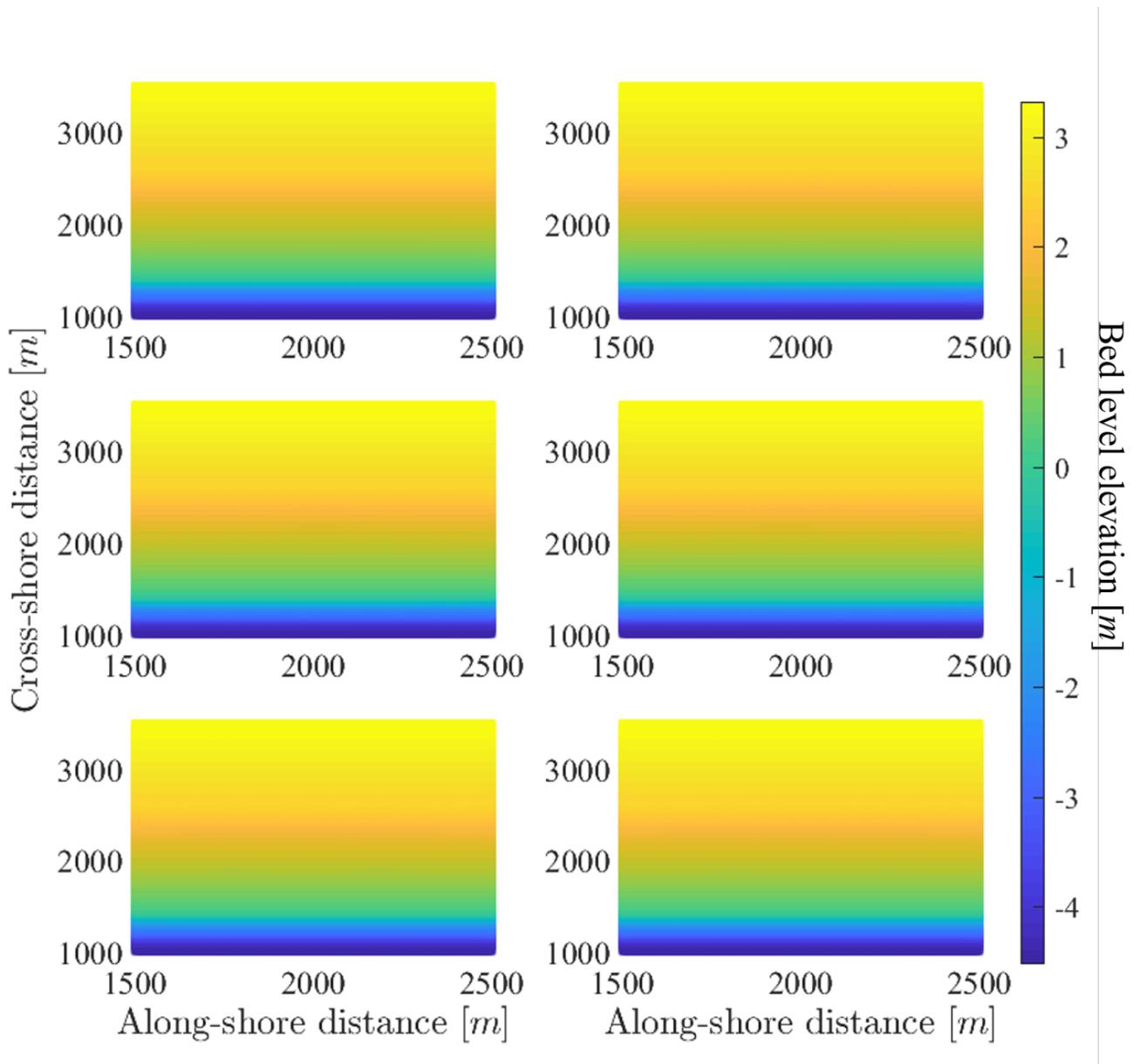


Figure C.6: The bed level elevation during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

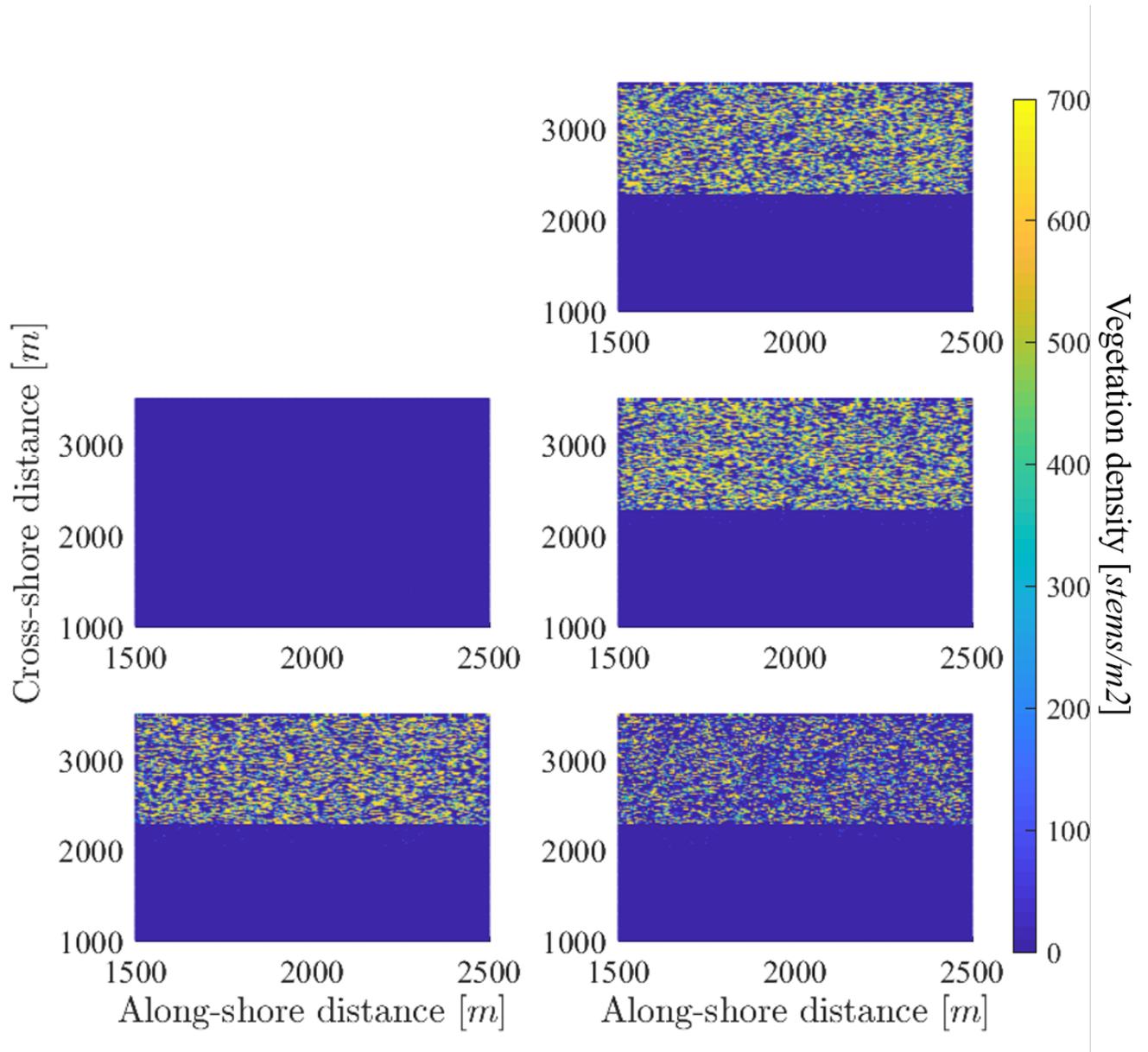


Figure C.7: The vegetation density for the *Spartina* species during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

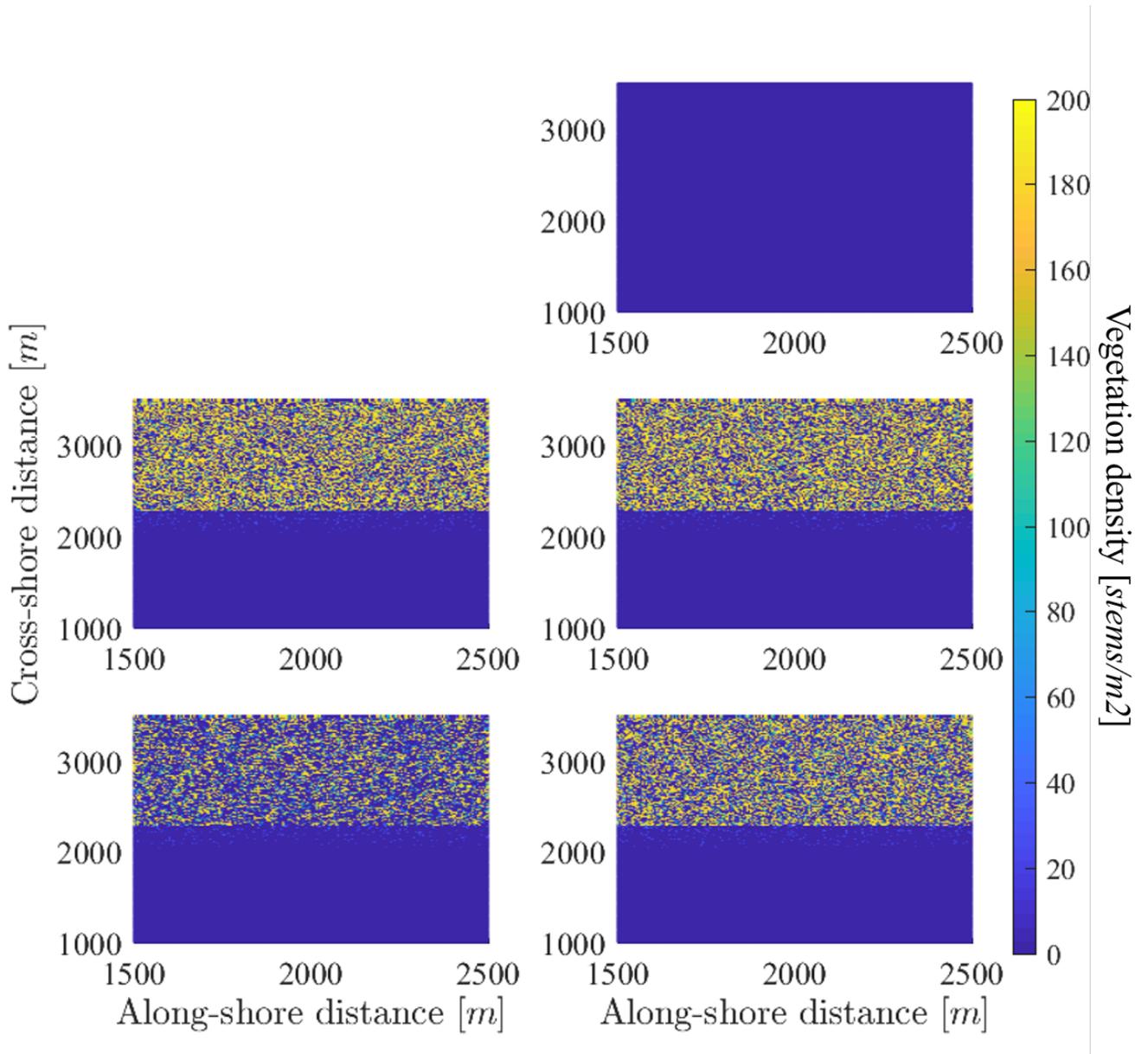


Figure C.8: The vegetation density for the *Salicornia* species during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

C.3 Overview results year 10: Zoomed in

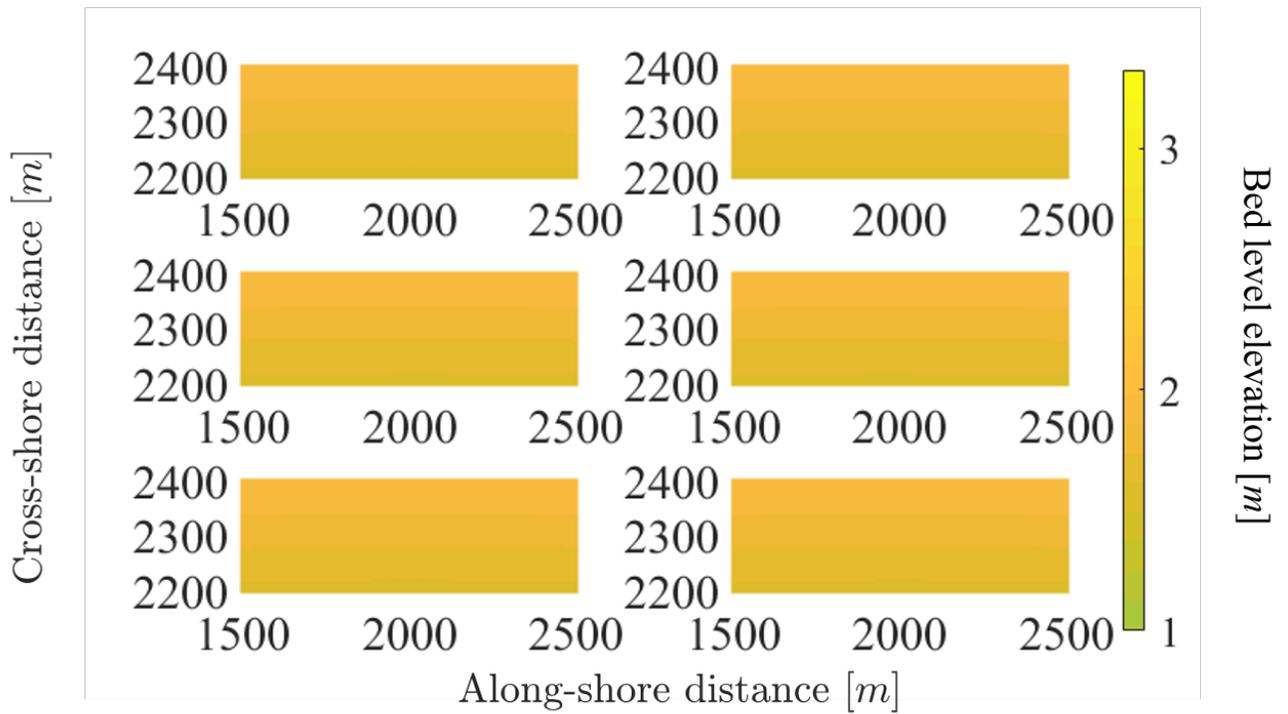


Figure C.9: The bed level elevation during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

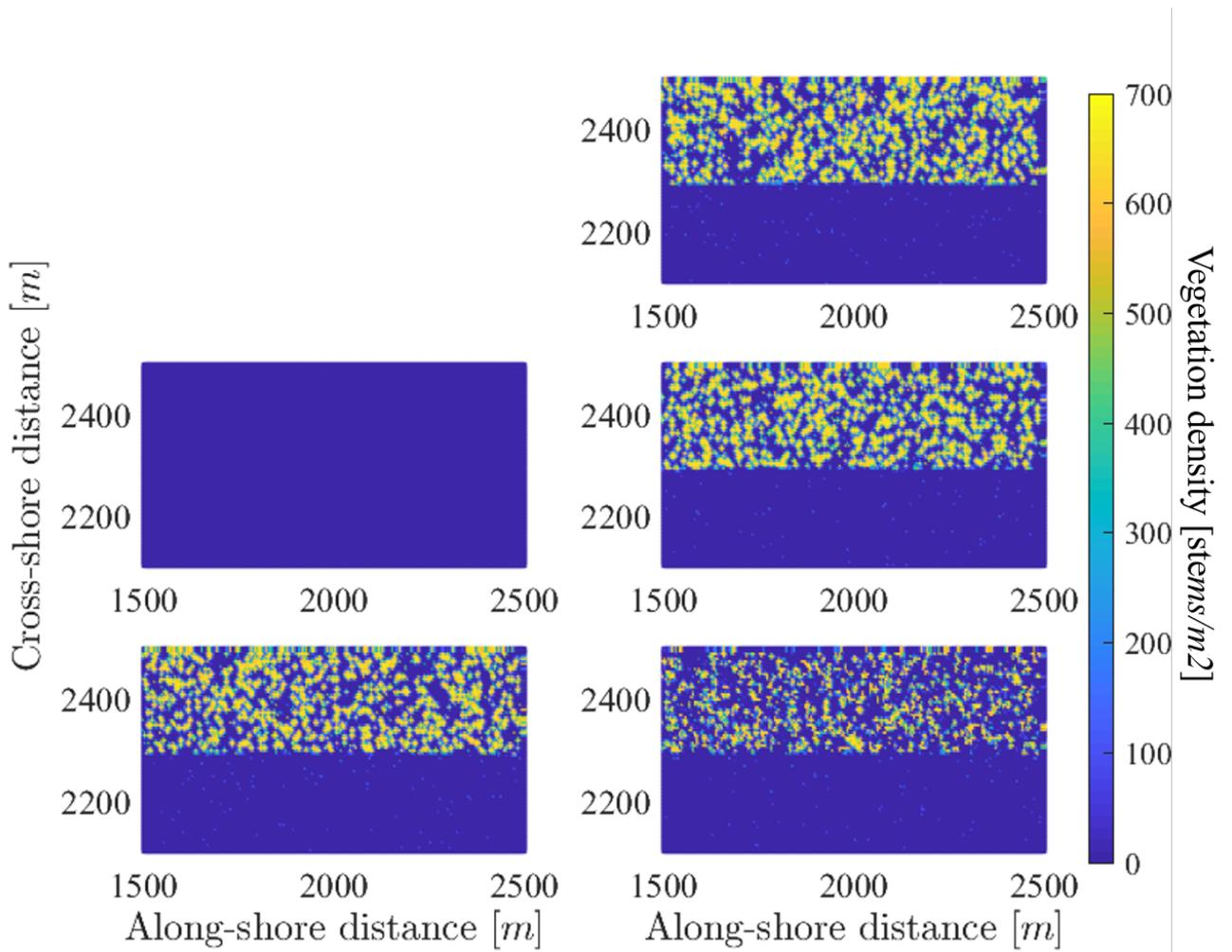


Figure C.10: The vegetation density for the *Spartina* species during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.

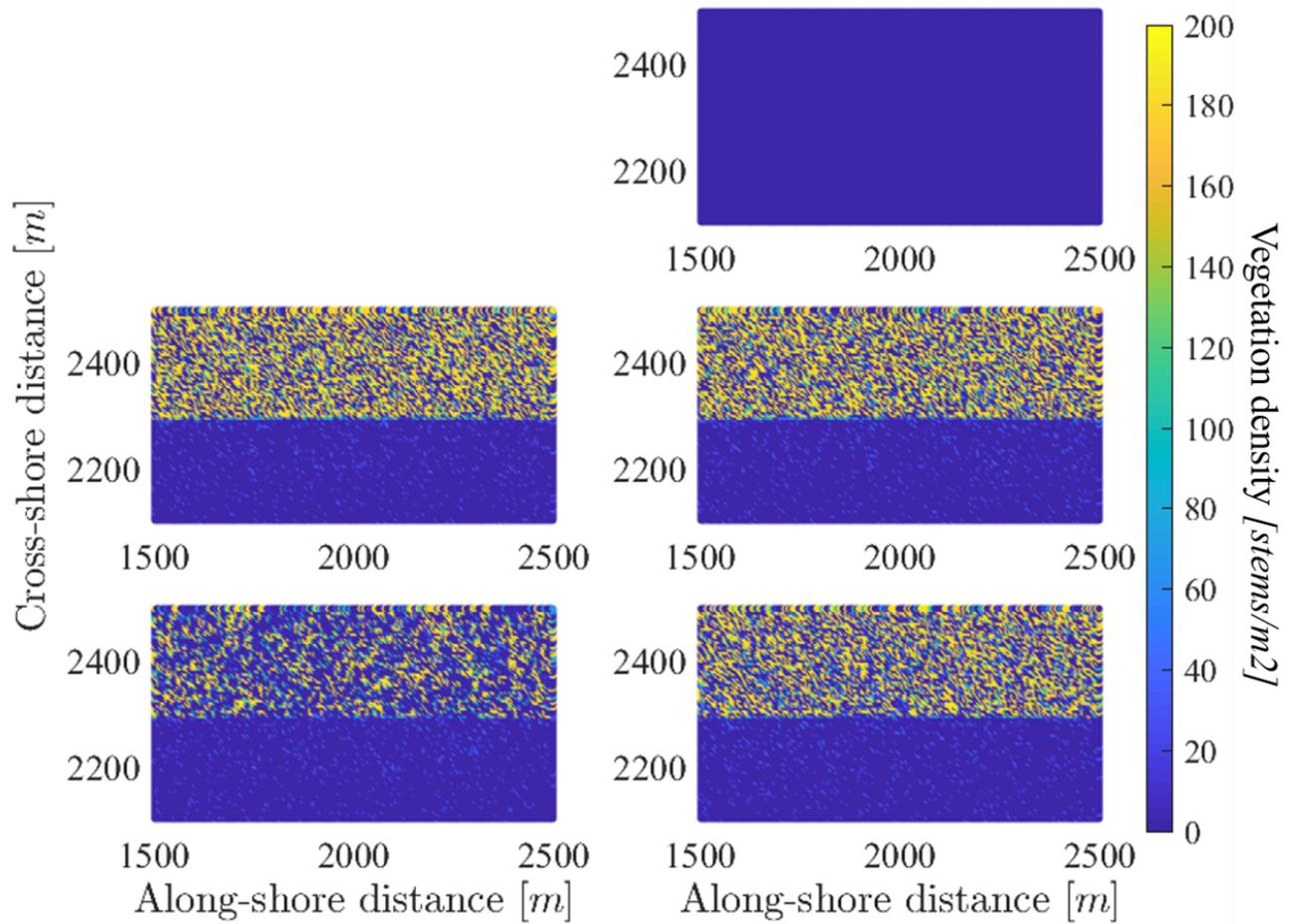


Figure C.11: The vegetation density for the *Salicornia* species during the last time step for the simulation with (a) no vegetation, (b) only *Spartina* vegetation (c) only *Salicornia* vegetation (d) multi-species simulation excluding competition (e) equal competition and (f) spatial competition.