Effect of different vegetation species traits on channel development in tidal marshes

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By

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Preface

This thesis forms the conclusion of my Master in Marine Sciences at the Faculty of Geosciences at Utrecht University, the Netherlands.

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Abstract

Tidal marshes play an important role in climate change mitigation through natural coastal protection. The effectiveness of the natural coastal defence by tidal marshes is closely related to its channel network which is in turn greatly influenced by the vegetation cover of the marsh. Previous research suggests a dual effect of vegetation on marsh topography; stabilizing sediment on the one hand versus promoting erosion and channel incision on the other hand. This study attempts to link these effects to different vegetation species and species traits, focusing on *Salicornia procumbens, Spartina anglica* and *Puccinellia maritima*. To be able to study the long-term development of a tidal channel network in different scenario's, a modelling study is performed, whereby simulations by an ecological model are coupled to hydro-morphodynamic modelling in Delft3D. The modelling study focussed on the single species and combinations of species, but also on the role of specific species traits. In addition to physical plant properties, the study has looked into the importance of varying spatial and temporal growth strategies.

The results indicate the influence of vegetation on the marsh topography to be highly dependent on the species, but also of a very complex nature. Both the presence of *Spartina* and *Puccinellia* resulted in significant channel development, where *Salicornia* did not induce topographic change at all. The presence of a *Spartina* or *Salicornia* patches obstructs flow, promoting on-site sedimentation and the formation of levees, while this results in off-site flow concentration, acceleration and subsequent channel erosion. Comparison of different species traits emphasized the importance of traits such as maximum age, sensitivity to hydrodynamic stresses, initial fraction and stem height. The total plant cover appeared to be closely related to the rate of channel development. The combination of different species resulted in reduced channel development compared to the most dominant species, although the channel networks were similar in terms of shape. Moreover, the presence and type of vegetation plays an important role in causing tidal asymmetry, which affects the direction of the net sediment transport. This particularly came forward in species shift-scenarios that resulted in increased erosion of the existing channel network, implying reduced protective capacity of the marsh.

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1. Introduction

1.1 Background

Coastal ecosystems are some of the most valued and exploited natural systems across the world (Constanza et al., 1997). They provide various ecosystem services, such as provisional ecosystem services (e.g. life stock and fisheries), regulating ecosystem services (e.g. water cleansing and carbon sequestration), cultural ecosystem services (e.g. recreation) and supporting ecosystem services (e.g. coastal protection) (Morris et al., 2002; Kirwan et al., 2013; Lal et al., 2013; Temmerman et al., 2013). Tidal marshes specifically are an important factor for natural coastal defence. Being located in the upper intertidal zone and therefore subjected to tide and wave driven inundation and sedimentation tidal marshes induce additional friction on hydrodynamics and therefore effectively attenuate storm surges and waves. Moreover, they provide an extra storage area for water and thereby protect the hinterland from flooding in converging estuaries (Temmerman et al., 2013; Leonardi et al., 2017). In respect to global change, tidal marshes are capable to keep up with sea level rise by enhanced sediment deposition induced by vegetation. Since sediment deposition occurs during flooding of the marsh accelerated sea level rise leads to an extended flooding periods and therefore increased sediment deposition (Morris et al., 2002; Kirwan et al., 2013). Therefore, tidal marshes and their provided ecosystem service are not only crucial for present coastal populations but also for generations to come (Leonardi et al., 2017).

The effectiveness of the coastal defence function exerted by tidal marshes is closely related to the characteristics of the ecosystem; e.g. the size, elevation, vegetation density and distribution of the channel network (Leonardi et al., 2018). Predominantly channels are of foundational importance for tidal marshes. For instance, channel dimensions determine the capacity of the marsh to reduce storm energy and inundation. Several studies have shown facilitation of landward flood propagation and thus reduced coastal protection in the case of deep and wide channels (e.g. Schwarz et al., 2016; Leonardi et al., 2018). Furthermore, there is an important feedback between wetland function and channel network. On the one hand is channel mediated distribution of sediment and nutrients fundamental for vegetation development and the ability of the tidal marsh to keep up with sea level rise (Kirwan et al., 2013). On the other hand, is distribution of vegetation closely linked to the density of the channel network (Sanderson et al., 2000; Leonardi et al., 2018).

1.2 Problem description

Although the channel network affects the distribution of vegetation in the marsh, there is in fact an even more complex interaction between the two, since vegetation colonization also influences channel formation. In general, vegetation is believed to predominantly have a stabilizing effect on sediment. The roots stabilize the sediment and the above ground biomass increases flow resistance, resulting in increased deposition and stabilization of already existing channel banks (D’Alpaos et al., 2006; Coco et al., 2013).

However, the presence of vegetation can also have an opposite effect when flow deviation at dense vegetation patches leads to reduced flow velocities across the patches, but flow acceleration around them. This results in increased erosion in between patches that can lead to channel incision (Temmerman et al., 2007; Schwarz et al., 2014). The contrast between these processes is referred to as scale-dependent feedbacks: on-site sedimentation and facilitation of vegetation growth versus off-site hampering due to increased erosion. The balance between the scale-dependent feedback mechanisms and interaction between plant and morphology is related to ecosystem properties such as sediment properties, hydrodynamics and plant characteristics (Schwarz et al., 2014). Moreover, Schwarz et al. (2014) propose this balance to be closely related to the stage of mudflat-tidal marsh transition; the erosional processes being most important in the early mudflat stages and the stabilization effect dominating on well-developed marshes.

Several studies have shown contrasting interactions between vegetation and flow patterns and erosion. Physical plant properties play an important role in the interaction between vegetation and flow patterns and erosion. Physical properties vary significantly amongst species (e.g. stem height, stem density) which results in different effects on patch adjacent velocity acceleration and erosion (Bouma et al., 2013). In addition, Temmerman et al. (2007) showed how temporal increase in spatial extent, plant cover and plant density influenced scale-dependent feedback strength and consequently increased channel density. The latter was shown for one species, but such spatio-temporal variation in growth also varies between species. This suggests that on top of physical properties, both spatial and temporal variation should be considered when comparing species and their influence on channel initiation. Especially in view of climate change, the relation between plant characteristics and channel formation is of great interest. Varying studies show a climate change-induced topographical shift in plant distribution across the globe (e.g. Kelly & Goulden, 2008, Lenoir et al., 2008) which is likely to affect the vegetation and consequently the ecosystem services of tidal marshes as well (Strain et al., 2017). Strain et al. (2017) expects a shift from the dominant marsh grass *Spartina spp.* to the succulent *Salicornia veneta* on the Mediterranean coasts. On the other hand, Gray and Mogg (2001) expect a northward expansion of *S. anglica* and an increased importance in later successional stages of *Puccinellia maritima. S*imilar processes are likely to occur globally and therefore it is relevant to improve understanding of morphologic consequences.

1.3 Objective

The objective of this study is to explore the effects of different vegetation species traits on the initial development of a channel drainage pattern, considering both species-specific physical plant properties as spatial and temporal variation in growth strategies. In addition, different combinations of species-specific traits were studied, indicating two or three species are present at the same time, as well as a transition in species traits representing a species shift. The study focuses on three dominant tidal marsh species in the Netherlands: *Salicornia procumbens, Spartina anglica* and *Puccinellia maritima*. These species widely occur in the pioneer zone and low marsh and play an important role in sediment dynamics (Bouma et al., 2013). To be able to study the long-term development of a tidal channel network for different scenario's, a modelling study is performed.

1.4 Research questions

During the study, the following research questions were addressed:

1. How do physical plant properties, spatial growth strategies and temporal growth strategies vary across the dominant marsh species: *Spartina anglica, Salicornia procumbens* and *Puccinellia maritima*?

2. How do different vegetation species (traits) influence channel morphology in different stages of tidal marsh development?

    a) What is the difference in effect on channel formation between *S. anglica, S. procumbens and P. maritima* (**S1.A**)?

    b) How is channel formation related to respectively physical plant properties, temporal and spatial growth strategies (**S1.B**)?

3. How do different species collectively affect channel morphology in different stages of tidal marsh development?

    a) How are channel morphology and plant distribution influenced by a combination of species (**S2**)?

    b) How does a species shift on developed tidal marshes influence channel morphology and plant distribution (**S3**)?

The indications between brackets refer to scenarios classifications (Table 1).

2. Literature review

2.1 Plant species

To determine appropriate parameter settings for the different species traits, a literature study was performed on *Spartina anglica, Salicornia procumbens* and *Puccinellia maritima*. The following three sections will discuss the main findings concerning the appearance and behaviour of the three species respectively.

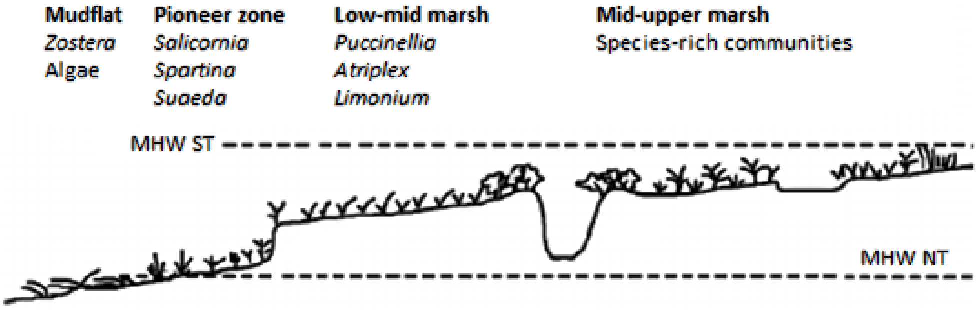


Figure 1. Typical vegetation zonation of a northwest European salt marsh. Dashed lines indicate mean high water during spring tide (MHW ST) and during neap tide (MHW NT). Adapted from Hughes (2004).

2.1.1 Spartina anglica

Spartina anglica, also known as common cordgrass, is a perennial grass that mainly occurs in northwest Europe. The species is a hybrid of *Spartina alterniflora* and *Spartina maritima* (Baumel et al., 2003), that are also abundant grasses in saltmarshes across northwest Europe. In the early 19th century *S. anglica* was actively planted in the Wadden Sea to promote sediment accretion, where after the species rapidly colonized the tidal zone (Nehring & Hesse, 2018).

The grass mainly occurs on the seaward front of salt marshes and on tidal flats where the elevation is between mean neap low water and mean spring high water (Gray et al., 1991; Loebl et al., 2006). *S. anglica* predominantly occurs on gradually sloping shorelines and is adapted to varying substrates, from clay to sand, including organic mixtures (Gray et al., 1991). However, the upper limit is mainly the result of interaction with landward lower marsh vegetation such as *Puccinellia maritima*, while the lower limit is most susceptible to inundation (Gray et al., 1991; Loebl et al., 2006). According to Nehring & Hesse (2018), *S. anglica* tolerates an inundation period of 9 h or more. Observations by Ranwell et al. (1964) had shown that the lower limit of *S. anglica* swards experienced 6 h of inundation on average, but also survived extreme events of more than 9 h submergence. Moreover, the species tolerates a wide range of salinities from ~5 to ~40 PSU (Nehring & Hesse, 2018). There is not much data on the relation between *S. anglica* distribution and current velocities. However, Vuik et al. (2018) showed a relation between orbital velocities and stem breakage of *Spartina anglica* where stems started to break at 0.48 m/s and the majority was broken with velocities higher than 0.95 m/s. Although these are orbital velocities and not flow velocities, it suggests that the species is not very susceptible to high velocities. However, uprooting of seedlings by tide induced currents is said to be very significant (Gray et al., 1991).

Although *Spartina anglica* can grow from seeds, the seeds have a very low survival rate. As a result, the few surviving seeds turn into clearly distinguishable tussocks (Marks & Truscott, 1985). The stem density was measured to be 658 stems/m^2 (Bouma et al., 2013), whereas the coverage can vary from 25% to even 90% (Bouma et al., 2013; Loebl et al., 2006). The grass can become 1.8 m in height (Nehring & Hesse, 2018), but often varies in height. Bouma et al. (2013) measured the average height in the Scheldt estuary to be 0.59 m. The stem diameter is about 4 mm - 5 mm (Nehring & Hesse, 2018; Temmerman et al., 2007; Vuik et al., 2018). *Spartina* has creeping rootstalks (rhizomes) which form a very strong and complex root structure. The initial shoot-root ratio of seedlings is about 1:1 with both being around 1.5 mm after 10 days. Within 40 days the root length increases up to about 10 cm and the shoot length to 15 cm (Poppema, 2017).

Figure 2. *Spartina anglica*

As already mentioned, *Spartina anglica* is a rhizomatous saltmarsh (Nehring & Hesse, 2018). This means that it can reproduce through spread of rhizomes from which new shoots grow. The species can also reproduce via seed dispersion, yet there is a lot of variability in the success of seed dispersal. According to Hubbard (1970), the production, viability and germination of *S. anglica* seeds are very unpredictive, this – was suggested to be related to climate conditions. According to Gray et al. (1991) germination occurs in May or June, whereas Alkemade et al. (1994) already measured an increase in living biomass from March onwards, suggesting germination takes place in March or April. According to Loebl et al. (2006) shoot growth begins in April and May. Maximum biomass is observed around August/September and biomass significantly reduces after October/November (Alkemade et al., 1994; Gray et al., 1991; Loebl et al., 2006). *Spartina anglica* is a perennial species, meaning that it has a minimum life span of more than two years. The plant will reduce in biomass during winter. Both Alkemade et al. (1994) and Gray et al. (1991) suggest that around 35% of the maximum biomass remains during winter.

Several studies have looked into the (expected) consequences of climate change for salt mash species. Climate change may impact salt marshes through rising temperatures, sea level rise and increased inundation or reduced precipitation (mainly at lower latitude; Strain et al., 2017) and rising CO_2 levels (Gray & Mogg, 2001). Many studies suggest that rising temperatures will be an advantage for *Spartina* as their potential habitats expands northward (Gray et al., 1991; Gray & Mogg, 2001). Rising temperatures result in the critical temperature for germination being reached sooner and a more competitive position for *S.*

anglica (Loebl et al., 2006). On the contrary, sea level rise will change the shorelines and these will most likely become (temporarily) unstable, resulting in loss of salt marsh vegetation (Gray et al., 1991). In addition, the shores will experience more erosion due to increased storm frequencies that go accompanied with sea level rise (Loebl et al., 2006). Experiments by Strain et al. (2017) showed that increased inundation would lead to significant losses of *Spartina*, however in reality this will probably rather lead to a landward shift of the species. Strain et al. (2017) showed that temperature could also have a negative impact on the production of *Spartina*, especially in combination with reduced precipitation. However, it must be noted that their study was performed with conditions resembling the Mediterranean coast, were the climate is much drier than in northwest Europe. Finally, according to Gray & Mogg (2001), both rising temperature and CO_2 levels are beneficial for growth of *S. anglica*. However, the benefits were predominantly seen in increased below-ground biomass.

2.1.2 Salicornia procumbens

Salicornia procumbens is commonly referred to as glassworth, picklegrass or pickleweed and previously it was called *Salicornia dolichostachya* Moss*. Salicornia* is an annual halophyte that occupies a substantial part of tidal marshes. The particular species is dominant in pioneer zones along the shores of the North Sea and frequently occurs in a mosaic with *Spartina* and *Puccinellia* (Davy et al., 2001). It plays a very important role on tidal marshes, as it is often the first species to colonize (Davy et al., 2001; Wolters et al., 2008).

S. procumbens mainly grows just above and below the mean high water line, where the mudflats evolve in salt marshes. However, this species is highly tolerant of flooding and could span the entire tidal range or occur in areas that are completely waterlogged (Davy et al., 2001). The species generally experiences 600 tidal submergences per year, whereas it is also possible that *Salicornia* occurs higher up in the marsh in depressions or poorly drained areas (Davy et al., 2001). The species favours a silty or clayey substrate, but also grows in sandy environments (Rozema et al., 1987)**.** Often they occur on highly reduced soils with a high sulphite content and a high salinity (Davy et al. 2011). Likewise, as *Salicornia* tolerates extremely low water potentials in the root area, they would very well survive drought conditions (Davy et al., 2001). On the other hand, *Salicornia* is susceptible to high velocities; due to their imbalanced below and above ground biomass ratio, they are very likely to topple under relatively low velocities (Poppema, 2017).

Salicornia procumbens is a succulent plant that has many branches and grows up to 45 cm high (Davy et al., 2001) with an average height of 28 cm (Bouma et al., 2013). Their roots are relatively short, often penetrating no more than 10 – 20 cm into the substrate (Davy et al., 2001). The limited root network makes *S. procumbens* susceptible to erosion (Poppema, 2017). Its average stem diameter is around 1 cm and the stem density is approximately 189 stems/m^2 (Bouma et al., 2013). The area coverage of *Salicornia* is comparatively low and the species is very sparsely distributed (Bouma et al., 2013). Van Duin & Sonneveld (2016) have measured widely divergent cover values for *Salcornia* ranging from < 5% to 80%. As seedling, *Salicornia* has very short roots of only a couple of mm, whereas the shoots can be up to a few cm (Poppema, 2017). The short roots is one of the reasons why the plant favours clayey environments where the topsoil is often reworked by tidal currents, allowing the seeds to be covered (Beeftink, 1985). The root length rapidly increases to about 5 cm after 40 days, similar to the shoot length (Poppema, 2017).

Figure 3. *Salicornia procumbens*

In contrast to *Spartina* and *Puccinellia*, *Salicornia* is an annual species. This means that the plants will die in the winter and new plants will establish in the following spring. Moreover, the species does not have a persistent seed bank, consequently showing no overlaying in seedbank between generations (Jefferies et al., 1981). Furthermore, *Salicornia* only reproduces through seed dispersal. Consequently, the degree of reproduction is closely related to the hydrodynamic conditions through the export and import ratios of seeds by the tides (Beeftink, 1985). According Beeftink (1985), one plant on the mudflat has an average offspring of ~4.3 individuals, whereas this is much lower on the salt marsh. Germination takes place in late April/May and the plants start to die in September (Davy et al., 2001; Jefferies et al., 1981).

In the face of climate change, the survival rate of seeds and seedlings is likely to be negatively affected by extreme weather events such as storms (Beeftink, 1985). Increased temperatures in spring however, would increase growth of seedlings and reduce uprooting and mortality (Beeftink, 1985). Moreover, *Salicornia* is more likely to tolerate increased salinity stresses related to submergence and/or drought compared to the other species (Strain et al., 2017).

2.1.3 Puccinellia maritima

Puccinellia maritima, also known by the name common saltmarsh grass is a very common occupant of the salt marshes that fringe the northwest European coastlines (Gray & Mogg, 2001). *Puccinellia* especially plays an important role in sediment dynamics and is associated with fast deposition rates (Langlois et al., 2003).

Compared to *Spartina* and *Salicornia, Puccinellia* occurs higher up in the marsh (above mean high water) and it favours sandier substrates (Scholten & Rozema, 1990). Very different from *Salicornia, Puccinellia* generally experiences only 50 – 100 tidal submergences per year (Scott & Gray, 1977b). Moreover, *Puccinellia* is susceptible to long periods of inundation. As a response to water logging the species forms lateral roots on the surface which makes the plants more vulnerable to uprooting, particularly in the lower marsh (Scholten & Rozema, 1990). However, in other situations where water logging is not a problem, *P. maritima* is exceptionally well resistant to high velocities, due to its flexible stems, that rather bend than break when velocities reach a certain level. This behaviour was already observed at velocities of 0.2 m/s (Bouma et al., 2013). Rupprecht (2015) found the resistance to bending of *S. anglica* to be about 7 times higher than that of *P. maritima*. *Puccinellia* can even withstand velocities up to 0.9 m/s without significant damage (Rupprecht et al., 2017). Lastly, sediment deposition and resulting burial is beneficial for growth performance of *Puccinellia* with a rate of 4 mm/month, whereas it increases mortality with rates exceeding 12 mm/month (Langlois et al., 2001).

Figure 4. *Puccinellia maritima.*

Because of its flexible stems the shoot height of *P. maritima* is generally only 30 cm (Bouma et al., 2013) with a maximum of 80 cm (Gray & Scott, 1977a). The roots can be up to 1 m in length, yet they often spread laterally and are found mainly in the top 5 cm. However, they could penetrate more than 25 cm deep (Gray & Scott, 1977a). One month after germination the seedling still only has about 1 cm of shoot and even less extensive root development (Gray & Scott, 1977a). *Puccinellia* occurs in relatively high stem densities, with an average number of 6473 stems per square meter (Bouma et al., 2013). The area coverage can vary from 5 – 60 % (Gray & Scott, 1977b) and the species generally occurs in large patches or swards similar to *S. anglica*. Langlois et al. (2003) made a distinction between *P. maritima* on mudflats with an average coverage of 5% and on hummocks where they cover about 95-100% of the surface. However, the mudflats generally take up a larger part of the area than the hummocks.

Just as *Spartina, Puccinellia* is a perennial grass. During winter *P. maritima* ceases growth, but remains green. It begins to grow in April and has maximum growth rates from August till October (Gray & Scott, 1977a). Similar to *Spartina* this species produces seeds that are distributed by the tide, but can also reproduce through dispersion of vegetative fragments. A big difference with *Spartina* is the timing of growth and expansion: *Puccinellia* seedlings are able to start growing at relatively low temperatures of about five degrees Celsius (Langlois et al., 2001) and therefore increases cover and biomass earlier in the year (Scott et al., 1990).

The difference between temporal growth strategies of *Spartina* and *Puccinellia* is mainly due to the different carbon fixation strategies. *Puccinellia* is a C_3 species, whereas *Spartina* relies on C_4 carbon fixation. C_4 carbon fixation is a more efficient way to fix carbon, but also requires extra energy. This is why C_4 plants are more common in dry and warm conditions where there is plenty of energy to be fixed from the sunlight. As a consequence, *Puccinellia* is more adapted to lower temperatures and will benefit less from rising temperatures compared to *Spartina* (Langlois et al., 2001). On the other hand, *Puccinellia* will increase growth if more atmospheric CO_2 becomes available, so that this will not be a limiting factor (Gray & Mogg, 2001). Furthermore, since *Puccinellia* is a species that predominantly occurs later in succession, it is likely that disturbance of the habitat by sea level rise will reduce *Puccinellia* cover (Hughes, 2004).

2.1.4 Biotic interactions

Whereas *Spartina anglica, Salicornia procumbens* and *Puccinellia maritima* could occur in a mosaic at similar elevations, these species generally follow up on each other in subsequent successional stages (Beeftink, 1985; Hughes, 2004). It has already been touched upon that the zonation of *S. anglica, S. procumbens* and *P. maritima* is partly determined by their interaction. Before the introduction of *Spartina* along the north European coasts, *Puccinellia* would generally occupy the salt marshes above the mean high water line, while *Salicornia* would dominate the part below (Scholten & Rozema, 1990). When *Spartina* was introduced this species colonized large parts of areas that were previously dominated by *Salicornia* as well as *Puccinellia* in some places whereas only small isolated tussocks were found in other places.

A study by Scholten & Rozema (1990) has shown that *Puccinellia* is more dominant on sandy soils whereas *Spartina* excels on more clayey environments. Moreover, *Puccinellia* has a significant advantage over *Spartina* since it starts to grow earlier in the year (Gray et al., 1991). However, *Spartina* is more resistant to high salinities, submergence and thus has a greater portion of land it can colonize. According to Loebl et al. (2006) *Spartina* is currently more often replacing *Puccinellia,* possibly due to rising temperatures. However, Gray and Mogg (2001) suggest that the competition between *Puccinellia* and *Spartina* will become more in favour of *Puccinellia* as this species will experience more benefits from rising CO_2 levels, due to their different ways of carbon fixation.

There is not much data on the interaction between *S. procumbens* and the other two species. Along the Mediterranean coast *S. anglica* is increasingly being replaced by the more drought resistant *Salicornia* (Strain et al., 2017), however this might not be relevant along northwest European coastlines. It is likely that due to their very different characteristics, there is not much competition between *Salicornia* and the other species. *Salicornia* can occur much lower on the marsh than the other two, or be sparsely distributed across a *Spartina* or *Puccinellia* sward.

3. Methodology

The effect of varying species traits on channel development is analysed by means of a coupled ecological and hydromorphodynamic model that will be discusses in 3.1 The model. The modelling study consists of three phases: 1) single species modelling, 2) multiple species modelling and 3) species shift modelling. More information on the three phases can be found in 3.2 Different scenarios and the species-specific parameters are listed under 3.3 Species parameters. Lastly, the data was analysed in various ways with the focus on vegetation distribution, hydrodynamics and topography

3.1 The model

The modelling study is based on offline coupling between a vegetation model in MATLAB and hydro-morphological modelling with the Delft3D software suite (Hydraulics, 2006). This enabled to investigate the feedback between plant growth and mortality and sediment distribution.

3.1.2 The hydro-morphodynamics model

The FLOW-module of Delft3D simulates unsteady flow and transport related to tidal or meteorological forcing. For this study the FLOW module was used to simulate ebbing and flooding of intertidal areas, calculate hydrodynamic flow, sediment transport and morphodynamics. Simulations were done in 2D (depth-averaged) for computational efficiency.

Delft3D simulates flow by solving the shallow water equations, horizontal equations of motion and the continuity equation (Hydraulics, 2006). Tidal forcing is applied on the open boundary on the seaward side of the domain, whilst the other three boundaries are closed. The forcing is an harmonic M2-tide that is constant throughout the year, has a period of 745 minutes and an amplitude of 1.75 m. Hydraulic boundary conditions were imported for one year of 372 days and this timescale is coupled to the morphological time scale with a morphological acceleration factor (MorFac) of 30, resulting in a total simulation time of 30 years. A MorFac of 30 was used as it has minimum influence on the model outcome with maximum reduction of computation time (Reyns et al., 2014). The hydrodynamic and morphodynamic time steps were set to respectively 0.2 and 6 minutes. However, data is saved every 18.6 or every 37.2 minutes, depending on the modelling scenario (hydrodynamic timescale). The data is saved less often in the majority of the scenarios to regain some computational efficiency despite of the bigger domain (see 3.1.2 Modelling domain).

In our simulations we made use of 0.5 m thick layer of non-cohesive sand with a median diameter (D_{50}) of 0.1 mm and a specific density of 2650 kg/m^3. This type of fine sand is commonly found on vegetated salt marshes in northwest Europe where the three species are present. Moreover, in general intertidal flats are initially built up from sand and only from finer sediments after vegetation has colonized (Schwarz et al., 2016).

To simulate transport of fine sand there are several transport equations available. We tested two of equations that are commonly used: van Rijn equation(1993) and Engelund-Hansen equation (1967). In contrast to the Engelund-Hansen equation, the van Rijn equation distinguishes between bedload transport and suspended transport and allows to incorporate transport fuelled by wave dynamics. Since we perform depth-averaged simulations and do not incorporate wave action, the simpler Engelund-Hansen equation would suffice. Reference runs showed minimal bed level change with both transport equations (Figure 5). However, incision is more apparent with the van Rijn equation and it is strongly influenced by the grid. In addition, the van Rijn equation has seemingly resulted in more boundary effects. These boundary effects nor bed level change that is not induced by vegetation are the focus of this study. Hence the choice was made for the Engelund-Hansen equation.

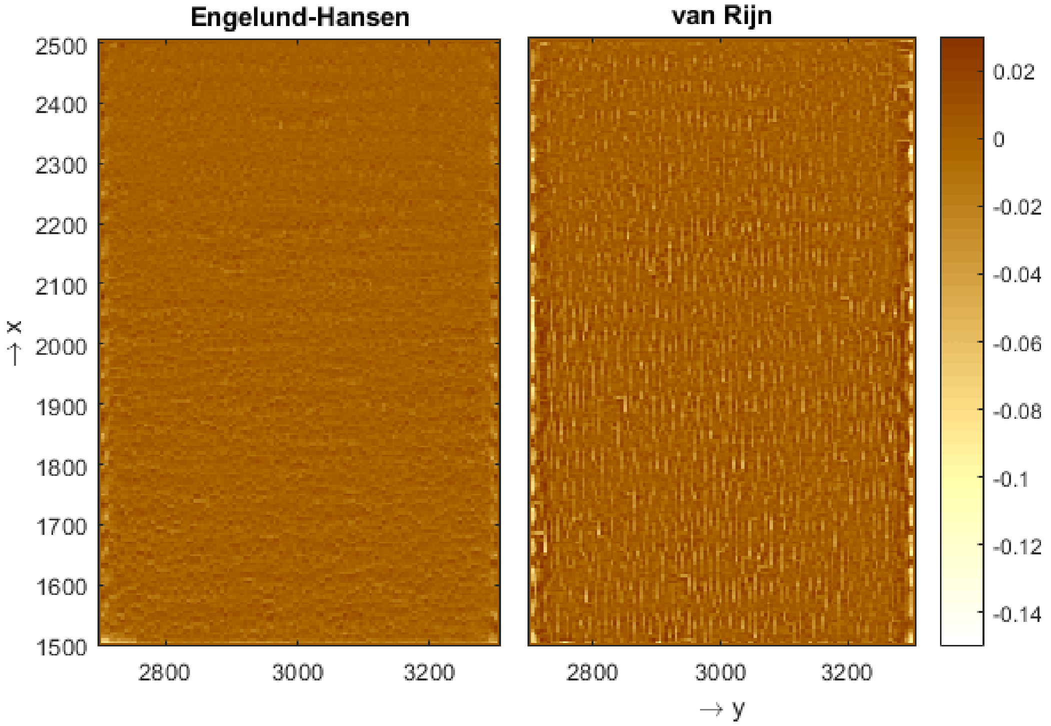


Figure 5. Topography change without vegetation after ~8 years, based on the Engelund-Hansen equation for sediment transport (left) and the van Rijn transport equation (right). Note the direction of the domain: the bottom represents the seaward side of the marsh.

The transport equation by Engelund-Hansen calculates total transport as follows:

$$Total\ transport = \frac{0.05\alpha q^5}{\sqrt{g}C^3\Delta^2 D_{50}} \tag{1}$$

Whereby the median grain size diameter (D_{50}) and the calibration coefficient (α) are to be specified beforehand (D_{50} = 0.1 mm and α = 1), while the flow magnitude (q), the Chézy friction coefficient (C) and the relative density (Δ) are cell-specific and derived from model outcomes. Transport normal to open boundaries is restricted by means of an equilibrium boundary. This way the amount of sediment inflow is limited to the amount required to keep the bed of the boundary at a constant level.

For more details on the conceptual background and the numerical aspects of Delft3D, the reader is directed to the extensive User Manual of Delft3D-FLOW (Hydraulics, 2006).

3.1.2 Modelling domain

Because the focus of the modelling study is predominantly on the relation between vegetation and morpho hydrodynamics, it was sufficient to make use of a hypothetical domain. The domain settings are based on simplified tidal flat topography and hydrodynamic forcing as present in real marsh systems in the Netherlands (Temmerman et al., 2007; Schwarz et al., 2014). As can be seen in Figure 6, the model makes use of three different domains, using the domain decomposition function of Delft3D. The black (filled) rectangle resembles the domain that is used for all of the plotting and will be referred to as SD1. This domain is 1000 m by 600 m with a grid size of 5 m by 5 m and a linear slope of 0.0012 ° and has three open boundaries and one that is closed on the landward side. Including the boundaries, the domain has 122 by 202 grid cells. This domain is used for modelling of the S1.B-scenarios (see 3.2 Different scenarios).

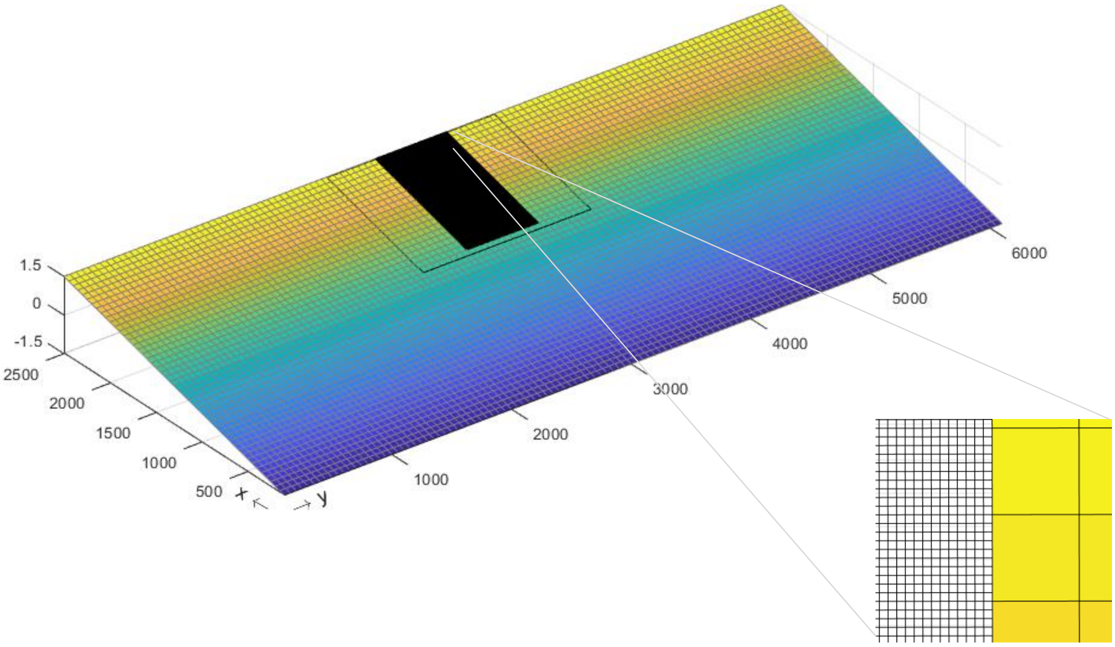


Figure 6. The modelling domain consists of a small domain (black rectangle), inserted in a bigger domain that is forced by a tidal harmonic. The black open rectangle (SD2) indicates the domain for which vegetation dynamics and topography are calculated, the filled rectangle (SD1) is the section that is used to cancel out unwanted boundary effects from the sides.

The open rectangle is the domain (SD2) that is used for all the other scenarios. Although, SD2 was used for the modelling, the extent of SD1 was used for data analyses. This was done to ignore changes in topography induced by the boundaries rather than the vegetation. SD2 has the same properties as SD1, except for its size that is 282 by 212 cells or 1400 m by 1050 m. Both small domains are integrated in a wider domain (2500 m by 6000 m) with a tenfold grid size, for which tidal dynamics were calculated.

3.1.3 The ecological model

This study makes use of an adapted version of the ecological model by Oorschot et al. (2015). This model allows studying both the effect of physical plant properties as spatial or temporal variability in plant growth on flow and sediment dynamics. The effect of vegetation is incorporated in Delft3D by means of hydraulic resistance (Figure 7; Vegetation growth). Delft3D enables to specify bed roughness and consequent hydraulic resistance by defining various roughness/resistance classes (refered to as trachytopes) that are assigned to grid cells (Hydraulics, 2006). The ecological model calculates hydraulic resistance caused by vegetation with the Baptist et al. (2007) relation:

$$C = \frac{1}{\sqrt{\frac{1}{C_b} + \frac{c_d n h_v}{2g}}} + \frac{\sqrt{g}}{\kappa} ln \frac{h}{h_v} \qquad [m^{\frac{1}{2}}/s] \qquad (2)$$

Whereby C is the Chezy coefficient of the vegetation, C_b the Chezy coefficient of the unvegetated area, c_d the drag coefficient, n the vegetation density (no. of stems per square meter multiplied by stem diameter), h_v the height of the vegetation (m), h the water depth (m), κ the Von Karman constant (0.41) and g the gravitational force (9.81 m/s^2). In addition, Delft3D allows multiple trachytope types to be assigned to one cell by means of composite trachytopes (Hydraulics, 2006). This function is used to assign multiple species to one cell or restrict vegetation to only a fraction of the cell.

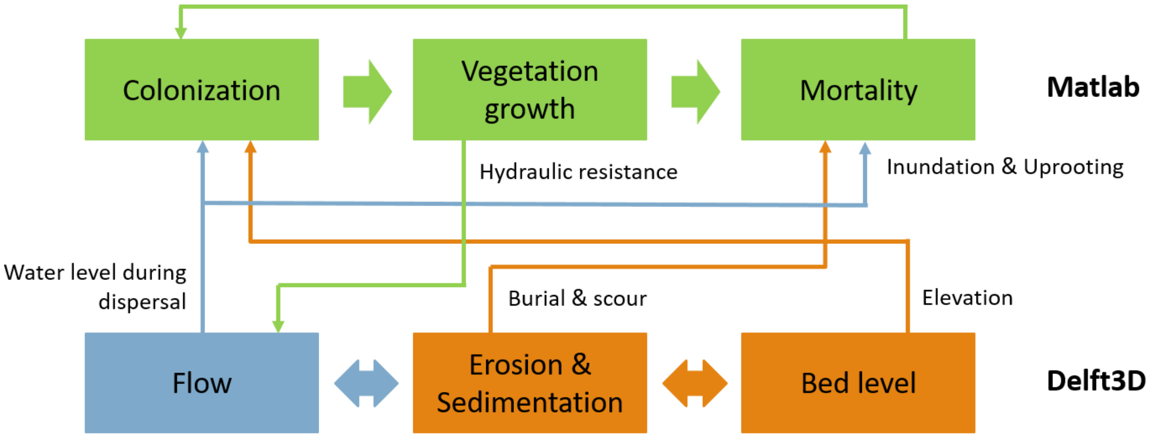


Figure 7. Flow diagram of processes and dynamic interactions between the ecological model and hydro-morphodynamic modelling in Delft3D (Adapted from Oorschot et al., 2015).

Spatial variability in growth is modelled through dose-response relationships related to stress dependent mortality. The model incorporates mortality due to burial and scour, uprooting and inundation (Figure 7; Mortality). Variance in sensitivity to different stresses can be assigned by means of a threshold value and a slope which determines the dose-response curve. A new functionality was added to the model by Oorschot et al. (2015) that allows growth and die-off to be calculated seasonally. This allows differentiating between temporal growth strategies and variation in physical plant features over time. Seasonal variation in growth is dependent on the given start and end of colonization, start and end of growth and the winter time. Additionally, the maximum values for physical characteristics can be set to varying (increasing) values for different life stages as well as for the initial seedling stage. Apart from the parameters that are used to calculate hydraulic resistance, root depth is also incorporated in the model.

Colonization of the domain assumes seedlings are distributed by the tide and is therefore coupled to Delft3D flow outputs (Figure 7; Colonization). Only cells that have been submerged previously, allow vegetation to colonize. However, in order for seedlings to settle, the cell has to be dry during low water. The actual number of cells that will be colonized depends on the species-specific chance of occurrence. Based on this value, a selection of possible cells will be colonized by the initial fraction of the species. If a cell is already populated by an earlier generation or other species the initial fraction depends on the available fraction (Oorschot et al., 2015).

In addition to distinguishing between different species, the ecological model allows to incorporate several species at once. True ecological interactions (e.g. competition) are not considered in the model, hence the main factors determining species presence are survival to stress, timing of colonization (first come first serve) and initial fraction during colonization.

The ecological model has the same time scale as morphology and is coupled to Delft3D every 15.5 days or every 744 minutes in terms of the hydrological timescale. This time step of 15.5 days is referred to as one ecological time step (ETS). The ecological year is defined as 372 days and thus consists of 24 ETS. At this point, vegetation is updated based on hydro- and morphodynamics before computations continue in Delft3D (Figure 7).

3.2 Different scenarios

During the modelling study, various scenarios were simulated. The scenarios are classified as S1.A, S1.B, S2 or S3 (Table 1) in accordance with the research questions.

In the majority of the runs, the complete sets of species traits were used for the three species and SD2 was used because the actual effect of the species on topography and hydrodynamics were of great interest. Runs were performed with only one of the species present (S1.A) and with all possible combinations of the species (S2). One run was performed whereby all species were included, but their sensitivity to inundations were set equally (Multi2; threshold: 0.4, slope: 0.12). This was done to find out the importance of stress tolerance against inundation compared to inundation and currents. Finally, two runs were performed whereby a species shift was simulated (S3). The model outputs of Puccinellia and Spartina (30 years), were used as initial conditions for respectively Spartina and Salicornia. The first case resembles a possible invasion by Spartina of higher latitudes stimulated by rising temperatures (see 2.1.1 Spartina anglica). The second case represents a species shift from perennial grasses to halophytes as a result of sea level rise and increased inundation (see 2.1.2 Salicornia procumbens). At the same time, the second scenario shows how the channel network changes when a vegetated marsh turns into an almost bare mudflat. Species shifts are modelled by using the end topography after 30 years of species 1 as input for runs with species 2.

Table 1. Classification of modelling scenarios and related settings (Fld. th = flooding threshold, ini. fract = initial fraction).

Scenario	*Run name*	*Temporal growth variability*	*Spatial growth variability*	*Physical plant properties*
S1.A	**Single species runs**			
	Spartina	*Spartina*	*Spartina*	*Spartina*
	Salicornia	*Salicornia*	*Salicornia*	*Salicornia*
	Puccinellia	*Puccinellia*	*Puccinellia*	*Puccinellia*
S1.B	**Species traits runs**			
	Temporal1	*Spartina*	Reference	Reference
	Temporal2	*Salicornia*	Reference	Reference
	Temporal3	*Puccinellia*	Reference	Reference
	Spatial1	Reference	*Spartina*	Reference
	Spatial2	Reference	*Salicornia*	Reference
	Spatial3	Reference	*Puccinellia*	Reference
	Physical1	Reference	Reference	*Spartina*
	Physical2	Reference	Reference	*Salicornia*
	Physical3	Reference	Reference	*Puccinellia*
	Physical4	Reference	Reference	*Spartina* (ini. fract=Ref)
	Physical5	Reference	Reference	*Salicornia* (ini. fract=Ref)
	Physical6	Reference	Reference	*Puccinellia* (ini. fract=Ref)
S2	**Multiple species runs**			
	Multi1	*Spartina* *Salicornia* *Puccinellia*	*Spartina* *Salicornia* *Puccinellia*	*Spartina* *Salicornia* *Puccinellia*
	Multi2	*Spartina* *Salicornia* *Puccinellia*	*Spartina* (fld. th=Ref) *Salicornia* (fld. th=Ref) *Puccinellia* (fld. th=Ref)	*Spartina* *Salicornia* *Puccinellia*
	Multi3	*Spartina* *Salicornia*	*Spartina* *Salicornia*	*Spartina* *Salicornia*
	Multi4	*Spartina* *Puccinellia*	*Spartina* *Puccinellia*	*Spartina* *Puccinellia*
	Multi5	*Salicornia* *Puccinellia*	*Salicornia* *Puccinellia*	*Salicornia* *Puccinellia*
S3	**Species shift runs**			
	Shift1	*Spartina*(y0-y30) *Salicornia*(y30-y50)	*Spartina*(y0-y30) *Salicornia*(y30-y50)	*Spartina*(y0-y30) *Salicornia*(y30-y50)
	Shift2	*Puccinellia*(y0-y30) *Spartina*(y30-y50)	*Puccinellia*(y0-y30) *Spartina*(y30-y50)	*Puccinellia*(y0-y30) *Spartina*(y30-y50)

In addition, the species traits part of the modelling (S1.B) comprises thirteen runs on SD1. The aim of these runs is to study the effect of different species on morphology and in particular distinguish between different types of species traits. In these runs, the non-relevant parameters were unchanged, but e.g. the physical plant features were set in accordance with respectively one of the three species of interest. The respective variables that were not of interest, had been set to reference values with no variation among the species. Three additional runs were performed whereby the focus was on the physical features, yet the fraction was set constant (Physical4, Physical5 and Physical6). Because this part of the modelling was focused on the difference between the different species and different subsets of species traits, if was sufficient to use the less computationally expensive SD1. The CPU-time of runs with SD2 is 2.4 times longer than runs with SD1.

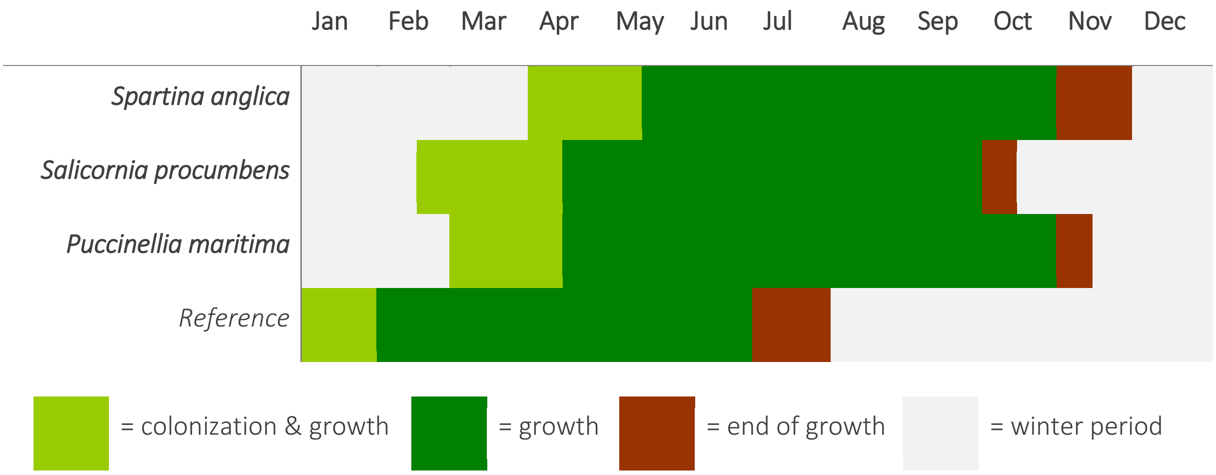
3.3 Species parameters

The following paragraphs give the species specific values that were used for all the runs. The reference values that were used in S1.A-modelling are also displayed.

3.3.1 Temporal growth patterns

The biggest difference between the three species lies in the life cycles. Whereas the grasses *Puccinellia* and *Spartina* are perennial, *Salicornia* is an annual species. This difference may be of significant importance since *Salicornia* has to colonize the domain over and over again every spring and is therefore less fixed to specific locations. The exact age of *Puccinellia* and *Spartina* is not determined but was set to an assumed 20 years. To reproduce natural development, changes in plant properties throughout ontogenesis were incorporated by assigning different properties for seedlings and mature plants (see 3.3.2 Physical plant properties). The first life stage is set to one year and has relatively low maximum values, since the plants evolve from seeds. Furthermore, the species show different seasonal growth patterns. The chosen values based on the literature review are shown in Table 2, as well as the reference settings.

Table 2. Temporal growth patterns of Spartina anglica, Salicornia procumbens and Puccinellia maritima.



	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Spartina anglica	⬜	⬜	⬜	🟨	🟨🟩	🟩	🟩	🟩	🟩	🟩	🟫	⬜
Salicornia procumbens	⬜	⬜🟨	🟨	🟨🟩	🟩	🟩	🟩	🟩	🟩	🟫⬜	⬜	⬜
Puccinellia maritima	⬜	⬜	🟨	🟨🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟫⬜	⬜
Reference	🟨	🟩	🟩	🟩	🟩	🟩	🟫	⬜	⬜	⬜	⬜	⬜

🟨 = colonization & growth 🟩 = growth 🟫 = end of growth ⬜ = winter period

3.3.2 Spatial growth variability

Variability in spatial distribution of the salt marsh species is closely related to mortality due to hydrodynamic stresses. The species have different degrees of susceptibility to several stresses: inundation stress, high velocities, erosion and sedimentation. Naturally, these stresses vary across the domain due to its sloping bottom. The related values are given in Table 3. The threshold value represents the value at which plants start to die due to the related stress. For inundation this is the fraction of the tide that a cell is submerged. The value for which e.g. all plants (100%) die, can be calculated via: 100/slope - threshold.

Table 3. Mortality threshold and slopes related to stresses. In case of a zero-value, the parameter will be ignored. * first life stage. ** second life stage.

	Inundation		Velocity	
	Threshold	**Slope**	**Threshold**	**Slope**
Spartina anglica	0.4	0.25	0.15*/0.25**	3
Salicornia procumbens	0.5	0.12	0.15	3
Puccinellia maritima	0.37	0.4	0.25*/0.5**	3
Reference	0.37	0.4	0.15	3

Mortality due to erosion and sedimentation is modelled in a different way compared to the other stresses as this is based on the plants root length and shoot height. When a sufficient amount of sediment is eroded that the root becomes fully exposed, a plant dies. On the other hand, in the case a plant becomes completely covered by sediment it will die as well. To include the higher susceptibility of *Salicornia* to erosion in the computation, its root length is reduced (see Table 4). Because mortality due to erosion/sedimentation and velocities are inseparably related to the plants physiology, these variables were included in the runs to test the effect of spatial growth variability as well as physical properties.

3.3.2 Physical plant properties

The species vary greatly in physical appearance. Table 4 shows the physical parameter settings of which the majority is based on the literature review. Values that were not found are based on an educative guess. Values for the chance of occurrence are partly based on observed occurrences of 5% of *Puccinellia* patches (Langlois et al., 2003) and the chance of plant establishment of 0.01 (Temmerman et al., 2007) and approximately 0.04 (Schwarz et al., 2014) used in modelling of *Spartina*. The chosen values are slightly higher because our study only considers establishment and potential connection of small patches, whereas the mentioned studies also incorporate lateral diffusion. The difference between *Salicornia* and the other species aims to reflect the different method of reproduction (dispersion of seeds vs. rhizomes). The drag coefficients are calculated based on relations provided by Nepf (1999; see Appendix E). To capture the low resistance of *Salicornia* to erosion due to its toppling mechanism (see 2.1.2 Salicornia procumbens), the root depth of the mature plant was reduced.

Table 4. Physical plant properties. *The model does not work correctly with zero-values for height; 0.05 is the minimum. ** Iinitial fraction represents the part of a grid cell that is covered by a species when it first colonizes.

	Shoot height (m)	**Root length (m)**	**Stem diameter (m)**	**Shoot height in winter (m)**	**Drag coeffi-cient**	**Initial fraction ** (0-1)**	**Stem density m^{-2}**	**Chance of occurrence (0-1)**
SPARTINA ANGLICA								
Initial	0.15	0.05	0.003	-	-	-	-	-
Seedling	0.8	0.2	0.003	0.4	1.1	0.6	700	0.07
Mature plant	1.3	1	0.005	0.4	1.15	0.6	700	0.07
SALICORNIA PROCUMBENS								
Initial	0.05	0.15	0.01	-	-	-	-	-
Mature plant	0.4	0.05	0.015	0.05*	0.9	0.2	190	0.2
PUCCINELIA MARITIMA								
Initial	0.05	0.02	0.004	-	-	-	-	-
Seedling	0.2	0.15	0.004	0.2	0.7	0.3	6500	0.07
Mature plant	0.35	0.15	0.005	0.2	0.7	0.3	6500	0.07
REFERENCE								
Initial	0.15	0.05	0.005	-	-	-	-	-
Seedling	0.5	0.2	0.005	0.4	1	0.5	700	0.07
Mature plant	0.5	0.2	0.005	0.4	1	0.5	700	0.07

3.4 Data analysis

The first step of data analysis was processing the raw data and in particular reduce its size. The data for all of the 41 or 21 time steps within one ETS were averaged to get one data file per ETS. Additionally, only ETS 1, 4, 8, 12, 16, 20 and 24 were saved. This data was then used to analyse vegetation distribution and mortality and topography. Some additional analysis was performed on the hydrodynamics, whereby all of the timesteps within one ETS were incorporated. All data analysis was performed in MATLAB.

One crucial element of data analysis was channel extraction. There are several open access toolboxes available for the extraction of a channel network based on a digital elevation map: e.g. TopoToolbox (Schwanghart & Scherler, 2014) and GeoNet 2.0 (Passalacqua et al. 2010). However, these toolboxes are both based on mountainous areas and did not result in proper extraction of the tidal channel network. For this reason, an alternative tool was created, of which the script is included in Appendix D. This tool relies on the difference between the initial topography and the final topography. Channels were assumed to be present where this difference is significant (standard deviation exceeds 0.02). For this extent of the domain (L_n) channels were extracted based on a negative bed level change ($\Delta Z < -0.03$) and a sufficient amount of neighbouring cells (to ignore isolated depressions). Based on the extracted channel networks, drainage density was calculated as follows:

$$DD = \frac{no.\ channel\ cells * \partial x}{L_n \Delta Y \partial x \partial y} \qquad [m^{-1}] \tag{3}$$

Whereby δx and δy represent the grid cell dimension and ΔY the total length of the domain in the Y direction (in number of cells).

Finally, extracted channel networks were used to classify the shape as either parallel, braided, dendritic, reticulate, complex or superimposed (Hughes, 2012; Figure 8). Furthermore, the shapes of individual channels can be divided into straight, sinuous and meandering.

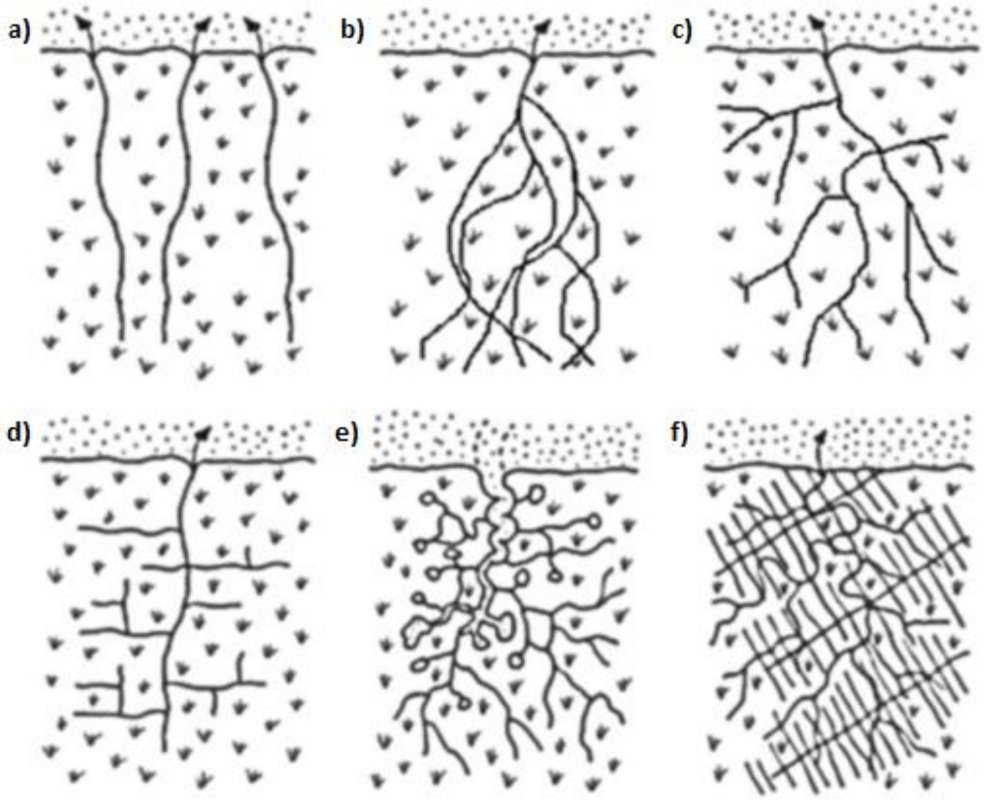


Figure 8. Shape classifications for channel networks on tidal marshes: a) parallel, b) braided, c) dendritic, d) reticulate, e) complex and f) superimposed. Adapted from Hughes (2012).

4. Results

The results are divided in accordance with scenario classifications. Due to the large amount of data, only the most relevant selection will be displayed and discussed here. For more results, the reader is directed to the appendices.

4.1 Single species runs (S1.A)

This section is dedicated to the model outcomes of the single species runs (S1.A). First the vegetation distribution and mortality will be discussed, followed by the species effect on topography and hydrodynamics.

4.1.1 Vegetation

The distribution of vegetation across the marsh appears to be highly dependent on the species, both with respect to marsh elevation and total plant cover. Spatial representations of the vegetation distributions are incorporated in Appendix A (Figure A.1), but descriptive variables are shown in Figure 9, 10, 11. *Salicornia* and *Spartina* are relatively evenly distributed over a wide range of elevations, whereas the convex hypsometric curve for *Puccinellia* indicates it is most dominant in the upper part of the range (Figure 9).

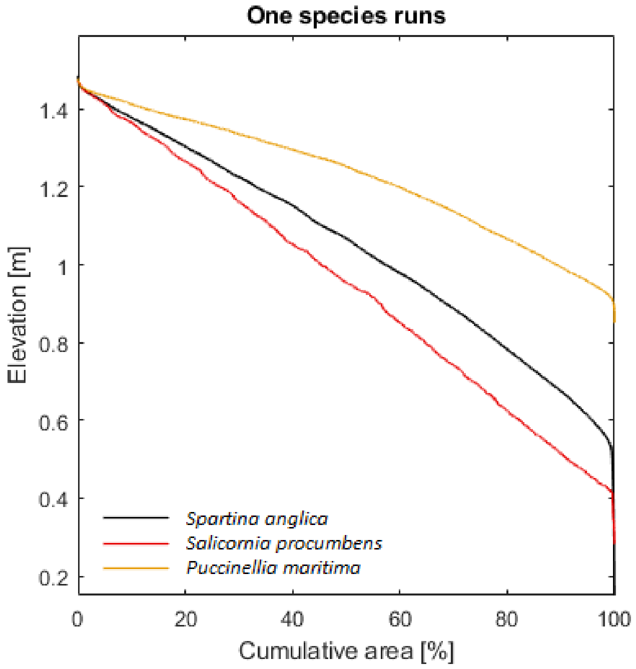


Figure 9. Hypsometric curves for the three species, showing the cumulative distribution of elevations in the area populated by vegetation. The fraction of vegetation cover is not considered.

After 30 years of simulation, *Spartina* covers little above 25% of the domain, while *Puccinellia* covers 11% and *Salicornia* only 1%. Regarding the temporal evolution of total plant cover (Figure 10), the cover of *Spartina* and *Puccinellia* initially increases, reaches a maximum in year 20 and declines afterwards. The cover of *Salicornia* remains constant throughout the years.

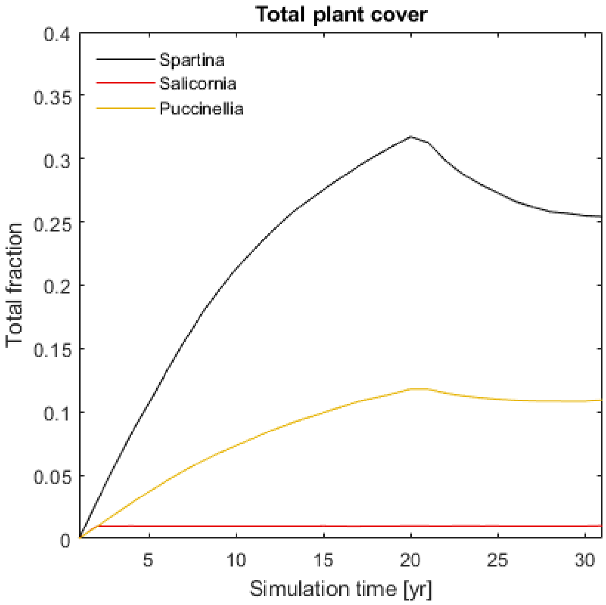


Figure 10. Evolution of total fraction of cover over time. The total fraction is calculated as the sum of all cell-fractions divided by the total number of cells in the domain

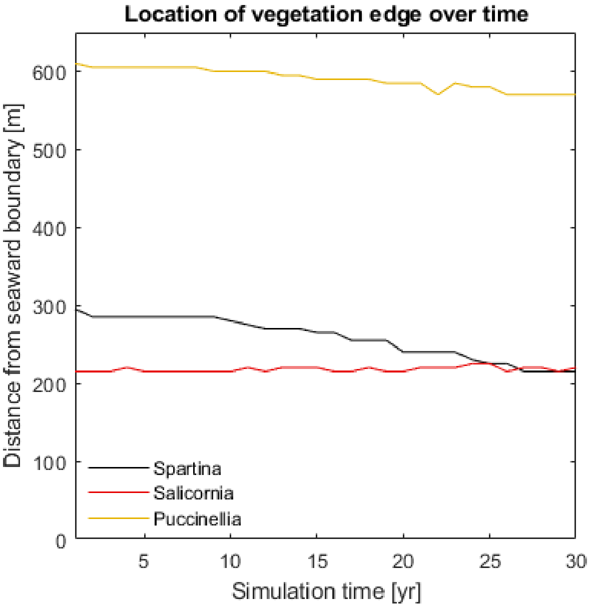


Figure 11. Temporal evolution of vegetation edge with respect to the seaward boundary of the domain. Vegetation edge is defined as location where 5 cells or more have a fraction of cover of at least 0.1.

In terms of temporal evolution of vegetation distribution relative to the sea, a seaward shift is observed for both *Spartina* and *Puccinellia* (Figure 11). The vegetation edge of *Spartina* shifts approximately 80 m over 30 years, where *Puccinellia* shows a shift of about 40 m. In the case of *Salicornia*, no distinct shift is observed.

The distribution of vegetation is highly influenced by hydraulic stress related mortality. Where neither burial and scour have been a cause of death, flooding and uprooting (due to high velocities) have played an important role. The variation in mortality for the three species (based on one species runs) over a time span of eighteen years is displayed in Figure A.3. As expected, *Puccinellia* is especially affected by inundation and *Salicornia* shows the highest mortality rates due to uprooting. For *Salicornia,* mortality stays fairly constant while this is not the case for the other two species. Initially, the percentage of vegetation that dies rapidly decreases for both *Spartina* and *Puccinellia.* However, mortality due to inundation increases again after six years for *Spartina* and after seven years for *Puccinellia*. Mortality of *Spartina* related to uprooting also slightly increases after year six. Spatial analysis showed mortality due to inundation initially being centered seaward of the x-coordinate related to the species inundation threshold. However, after a couple of years increasing mortality numbers were observed on the landward side of this point. Die-off mainly occurs amongst the newest generation. In fact, uprooting was never the cause of death for plants older than a year old. On annual terms, the highest mortality values are observed around the period of colonization.

4.1.2 Topography

Different species are hypothesized to have a different influence on channel formation. In this section the change in topography and the formation of channels are analyzed for the different scenarios.

When comparing the bed level change after 30 years (relative to initial topography) between the three species (Figure 12, 13 and 14), *Salicornia* does not display significant changes in bed level over the simulation period (Figure 13). However, clear channel development can be observed in the other two scenarios. In the case of *Spartina*, a very dense and complex (both dendritic and braided) channel network has developed landward of x = 1750, which coincides with the initial seaward boundary of the vegetation patch (Figure 12). Seaward of this point there are also channels formed, yet with a lower density, a lower complexity and more gradual banks. The planform of the channels in this part is rather parallel as the channels are very linear and not connected to each other.

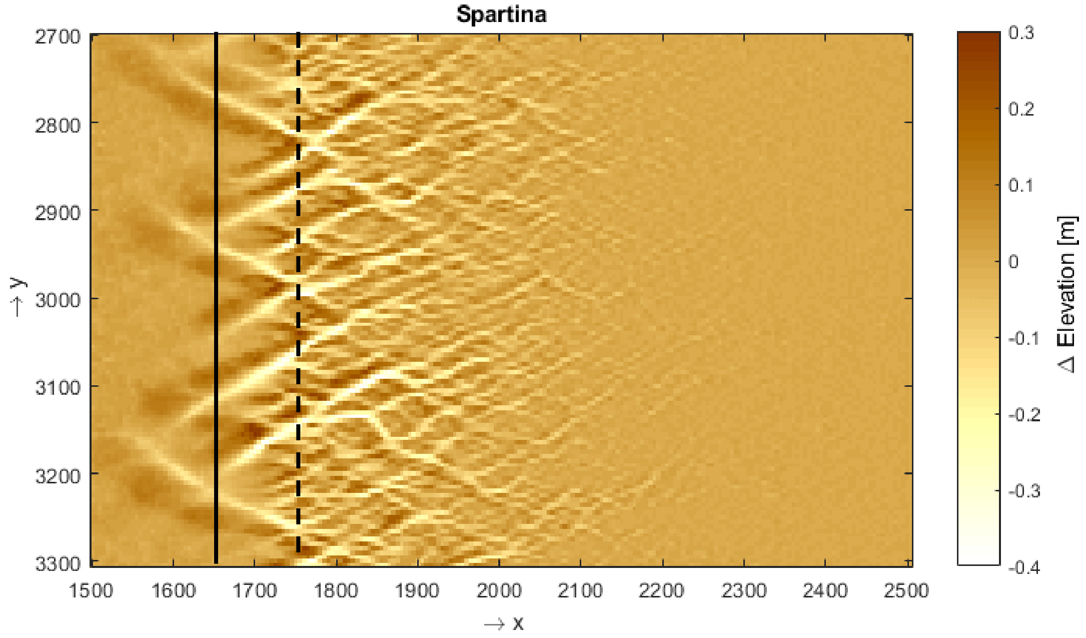


Figure 12. Bed level change over 30 years in the *Spartina*-scenario. The black solid line indicates final vegetation edge (after 30 years) and the dashed line the initial vegetation edge.

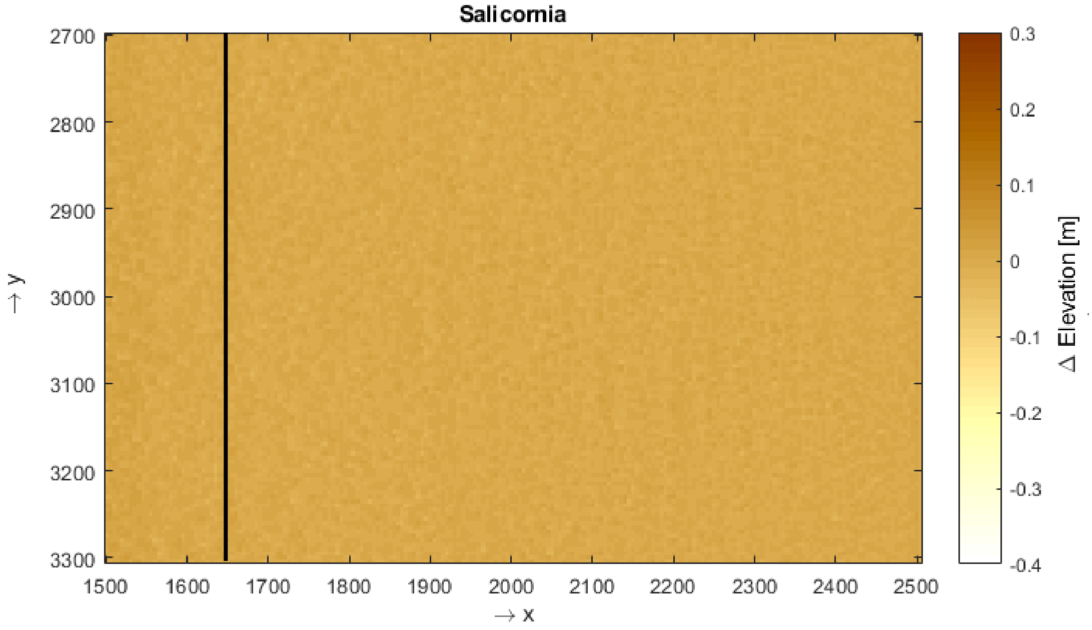


Figure 13. Bed level change over 30 years in the *Salicornia*-scenario. The black solid line indicates initial and final vegetation edge.

The same pattern is visible in Figure 14, with x = 2050 as midpoint. However, in this case the channel network seems to be less developed in terms of its extent (x-direction) and the variation in bed level. The extent of channel development for *Spartina* is about 500 m while it is only 200 m for *Puccinellia*.

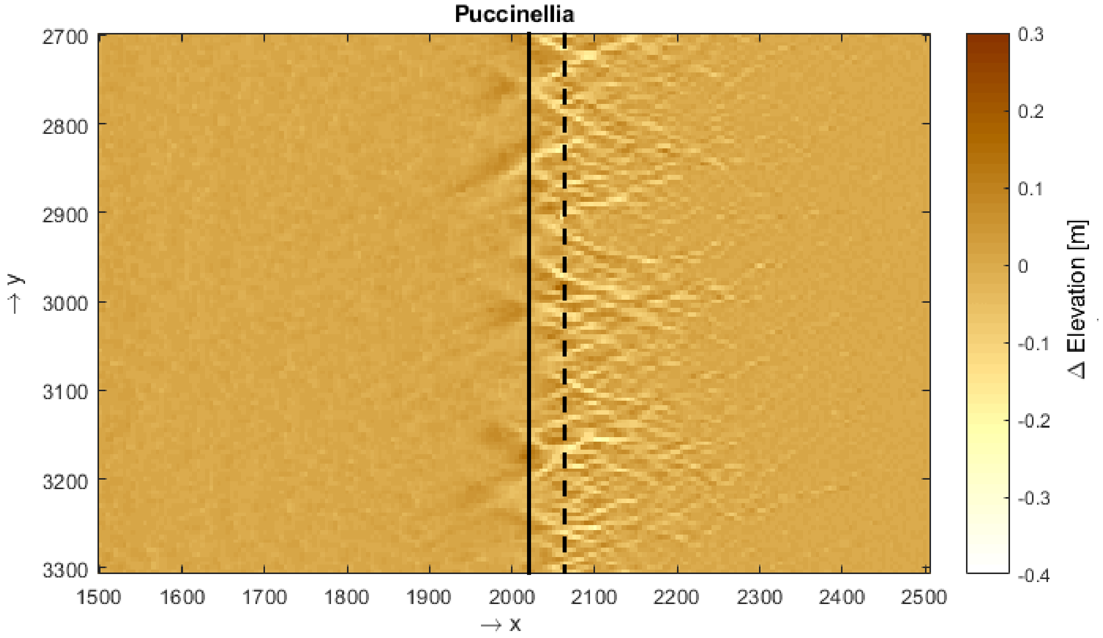


Figure 14. Bed level change over 30 years in the *Puccinellia*-scenario. The black solid line indicates final vegetation edge (after 30 years) and the dashed line the initial vegetation edge.

Figure 15 allows to compare the channel depths and bank heights of the channel networks that were observed in the previous figures. Cross-sections of the bed level change are shown for three different x-locations (Figure 15A, B and C). The cross-sections of *Spartina* highlight the observations mentioned in the previous paragraph: gradually sloping channel(bank)s on the mudflat and much steeper variations on the actual salt marsh. There is no relevant variation in the topography of *Salicornia* and with *Puccinellia* some variation is only visible at x = 2050.

Regarding the cross-sections 50 m into each vegetation patch (Figure 15D), *Spartina* develops much deeper channels (max 0.4 m deep) than *Puccinellia* (~0.15 m). Also the channel banks are higher when *Spartina* is present: ~0.2 m compared to ~ 0.1 m. However, both grasses enable very steep levees to develop, especially compared to the channels on the mudflat.

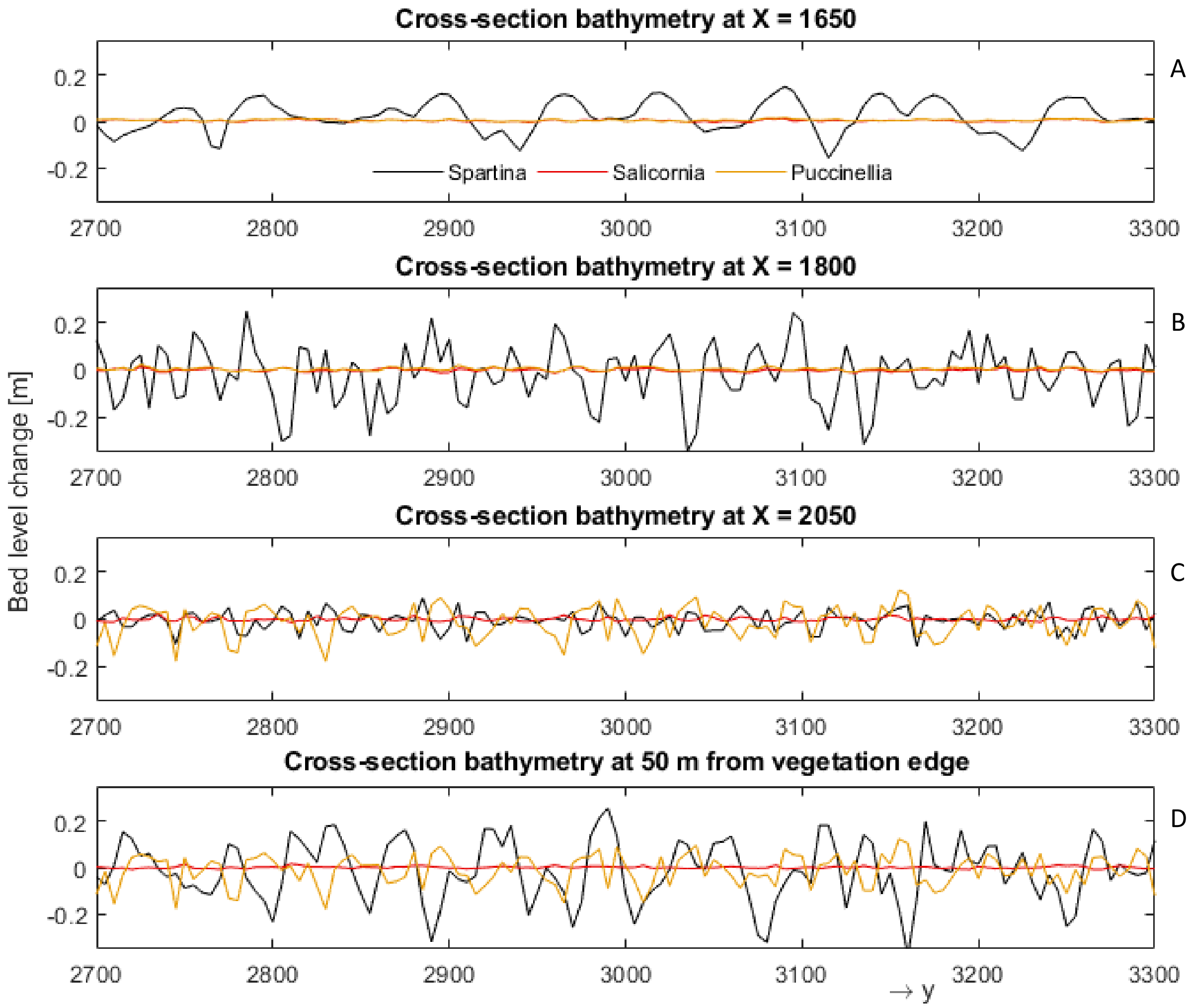


Figure 15. Topography cross-sections after 30 years at different X-locations for three scenarios: *Spartina, Salicornia* and *Puccinellia.* The dashed black line indicates the initial topography. The Y-axis has the same range for all subplots.

When comparing annual rates of erosion and accretion, we see that the maximum amount of erosion is much higher for *Spartina* (850 m^3) than for *Puccinellia* and *Salicornia* (400 m3). In the case of the latter two, the maximal amount of erosion occurred in year 1, while for *Spartina* the amount of erosion increases from year 2 to 20 whereafter it slightly declines (Figure 16A). A similar pattern is present for *Puccinellia,* although the variation is much less. *Salicornia* has a relatively constant annual erosion after seven years have passed. The net erosion (erosion minus accretion) increases over the years (Figure 16B). However, in the case of *Salicornia* sediment accretion subtly prevails over sediment erosion, whereas in the case of *Spartina* erosion exceeds sedimentation from year 5 onwards. In the case of *Puccinellia,* the volume that is eroded remains very close to the accreted volume.

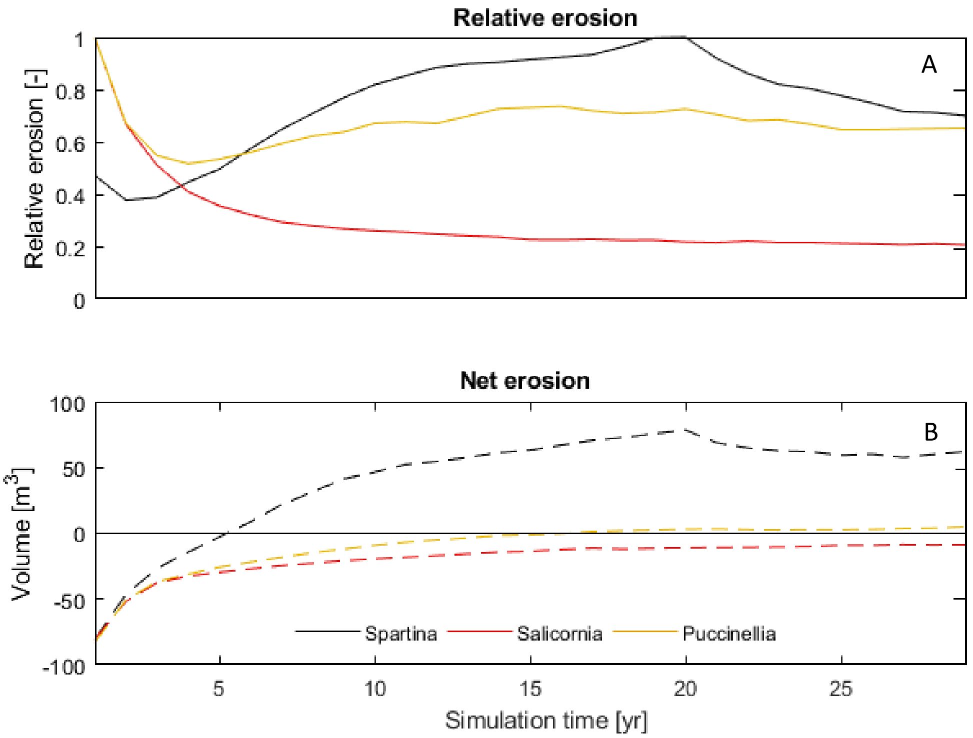


Figure 16. A: Relative erosion is calculated as the annual amount of erosion (sum of domain) divided by the maximum amount of erosion over the entire simulation period (*Spartina:* 850 m^3, *Puccinellia* and *Salicornia*: 400 m^3). B: Net erosion is calculated as the difference between erosion and accretion: negative values indicate accretion dominates, positive values indicate erosion dominates. The values are based on the extent of SD1.

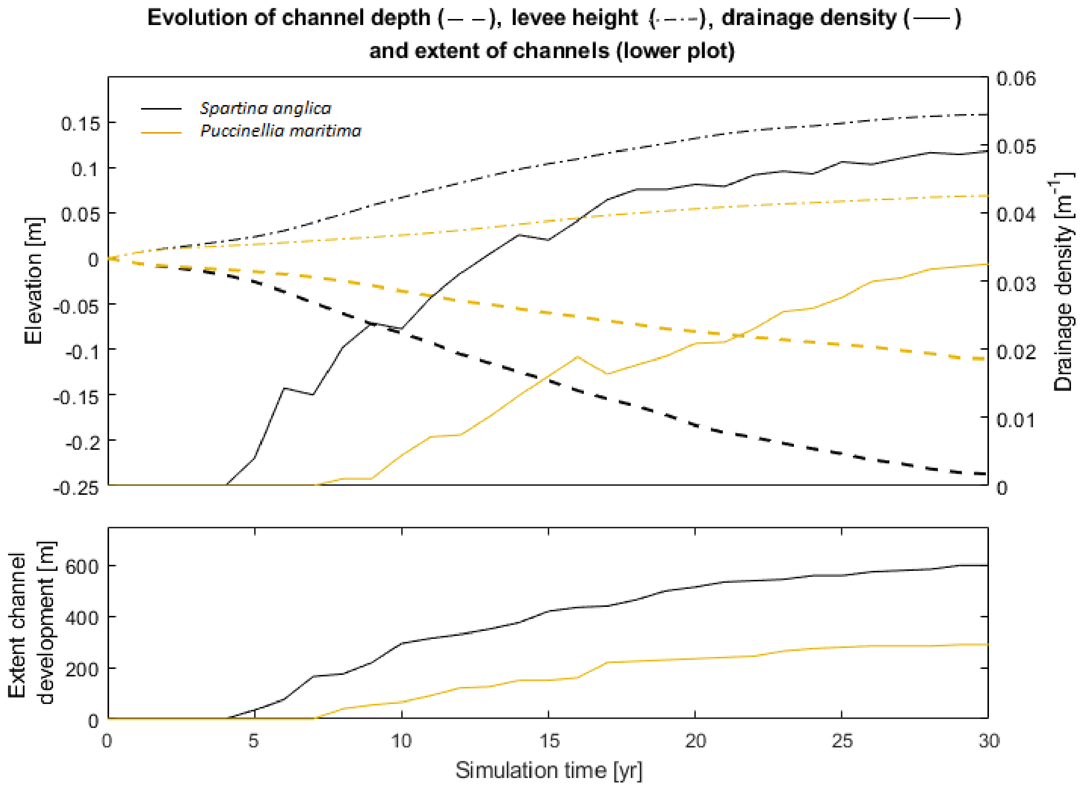


Figure 17. Evolution of channel depth (1st percentile of bed level change), bank height (99th percentile of bed level change), drainage density (length of channels divided by surface area) and channel extent (the distance between the upper and lower boundary of network) over time for two one species runs. The run with Salicornia is not included since no channels were developed.

The temporal evolution of the channel network is quantified by means of the variation in channel depth, levee height, drainage density and network extent (Figure 17). We can see an increase in all parameters over time and a significant difference between *Spartina* (higher values) and *Puccinellia*. Initially, the two species show similar bed level change. The onset of channel formation varies between the two species: year 4 in the case of *Spartina* and year 7 in the case of *Puccinellia*. For both species the channels are deeper than the levees are high. At some point (around year 18 - 20), the rate of change slightly reduces. Since no channel network was present under *Salicornia,* the species was not incorporated in this figure.

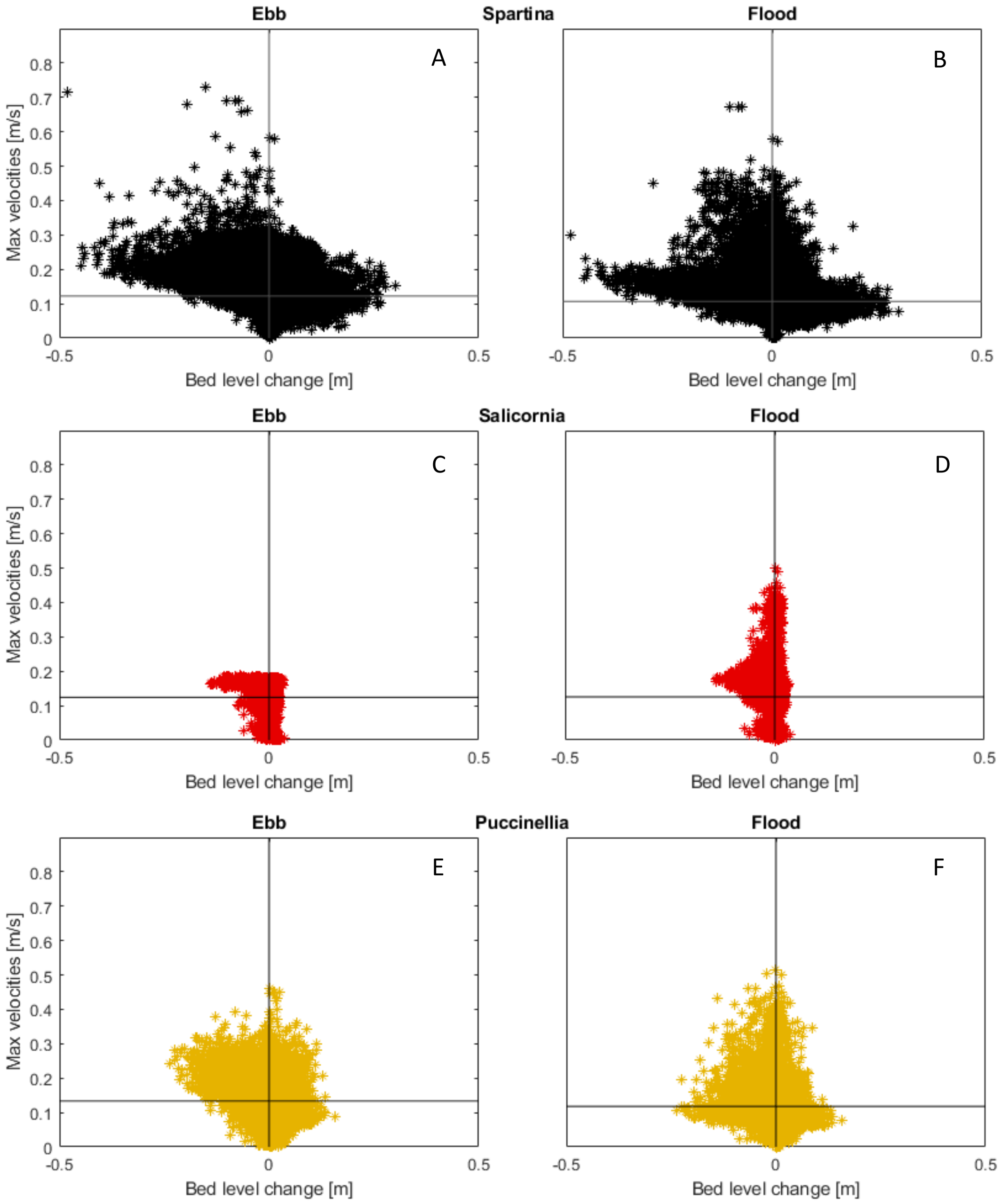


Figure 18. Relation between bed level change after 30 years and maximum flow velocities during ebb (A, C, E) and flood (B, D, F). The horizontal line indicates mean flow velocity of the specific data set. Maximum flow velocities are calculated per cell, based on all time steps related to respectively ebb and flood.

4.1.3 Hydrodynamics

Comparing change in bed elevation with flow velocities we can see a clear coincidence between negative bed level change and higher velocities in all three scenarios (Figure 18). Maximum velocities are much higher for *Spartina* than for the other two species. In the case of *Salicornia*, there is little variation in flow velocities, albeit slightly higher velocities during flood. Especially in the case of *Spartina* high flow velocities are restricted to areas with negative bed level change, which is especially significant during ebb (Figure 18A)

In spatial terms (Figure A.5, A.6 and A.7), overall velocities reduce as the flooding wave propagates landward and increase as the tide pulls back. Velocities are a generally higher at the flooding front and in the case of *Salicornia* there are some slight deviations from a straight line (Figure A.6). However, flow velocities show great spatial variation both under the influence of *Spartina* as well as *Puccinellia* (Figure A.5 and A.7). During flood, some very high velocities are observed in channel-like features. Moreover, these areas appear to be submerged for a longer period than the surrounding marsh. This especially comes forward in the case of *Spartina;* even during the last time step of ebb there is water flowing in narrow streams.

Additionally, maximum velocities are much higher in the *Spartina* scenario, with respect to the other two scenarios. This also comes forward when comparing the temporal evolution of maximum flow magnitude (Figure 19). **E**bb velocities are generally much larger than those during flood in the case of a significant vegetation cover (*Spartina* and *Puccinellia*; after about 5 years). Whereas the flood velocities remain close to constant, the ebb velocities increase over time. This is specifically the case for *Spartina.* In the case of *Salicornia* both flood and ebb velocities stay similar.

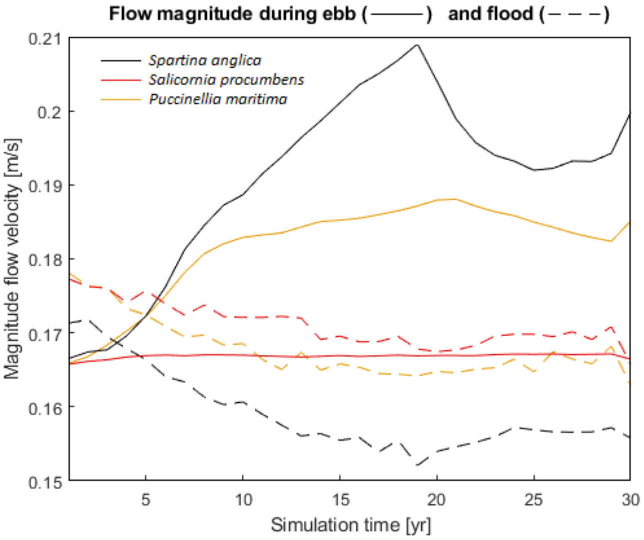


Figure 19. Temporal evolution of 95th percentile of flow magnitudes across the domain, during ebb and flood for the three different species.

The difference in flow velocities between ebb and flood suggests there is tidal asymmetry. This also comes forward from the stage-velocity plots in Figure 20. If the curve is more stretched to either the left or the right, one of the tides dominates over the other. In year 1 flood slightly dominates over ebb, which is most clear for *Puccinellia* and *Salicornia*. In year 6 however, the tides are almost symmetric in the case of *Puccinellia*, whereas ebb dominates for *Spartina*. Finally, in year 16 there is ebb dominance for both *Spartina* and *Puccinellia,* while the *Salicornia*-scenario remains dominated by flood. The moment of the ebb velocity-peak differs between *Spartina* and *Puccinellia: Spartina* experiences peak velocities at a water level of 0.4 m and *Puccinellia* one time step earlier at 0.9 m.

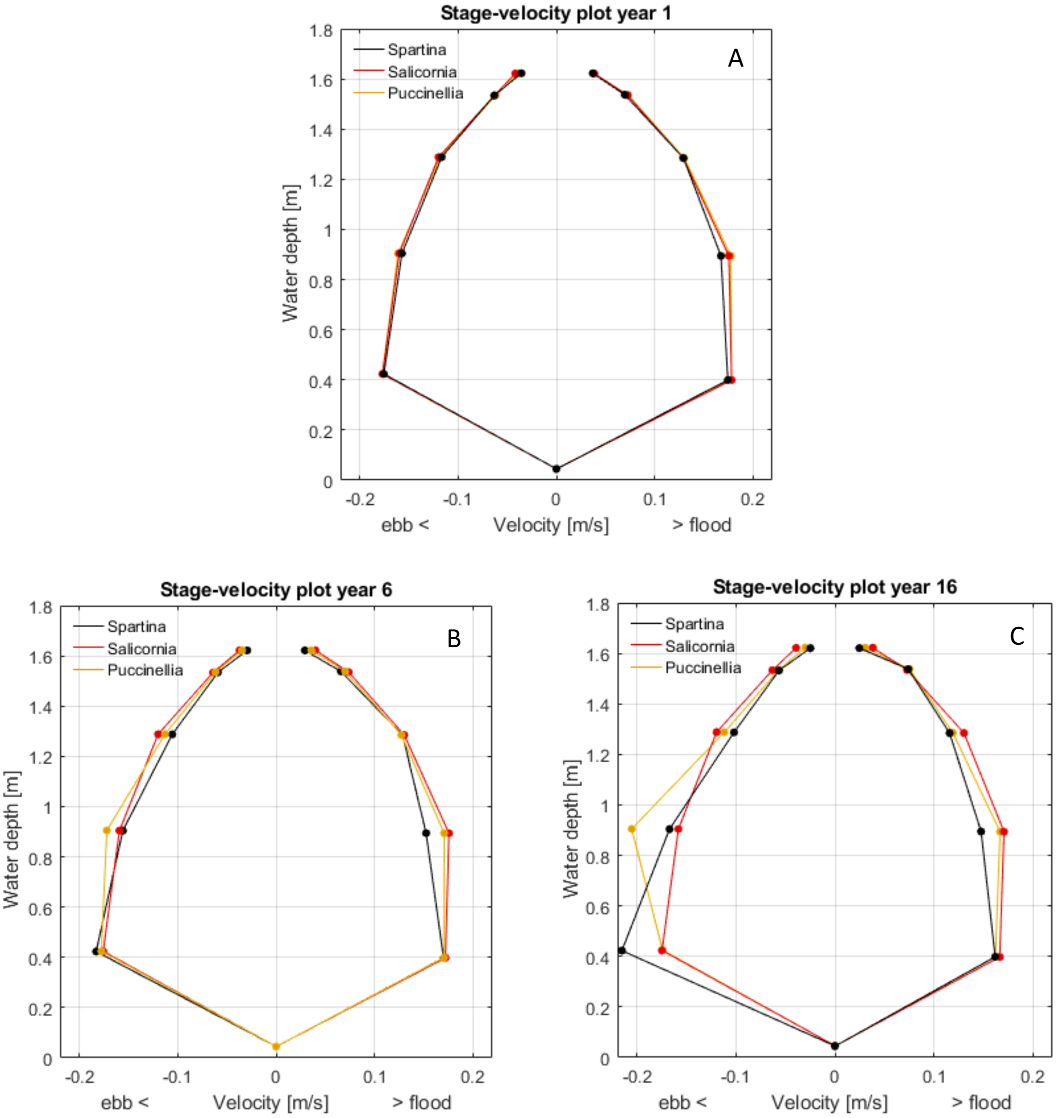


Figure 20. Stage-velocity at three moments in time. For the stage (water level) the average values at the seaward boundary were used. The velocity value is based on the 95th percentile including all cells of the domain.

Lastly, the presence of vegetation has an important effect on the hydroperiod across the domain. Hydroperiod can be described as the fraction of the tide that a domain (marsh) or subdomain (grid cell) is submerged. Shifts in location of cells with a hydroperiod of 37% and 40% are analysed (Figure A.4).

There appears to be a significant landward shift in cells with the specified hydroperiod, when *Spartina* or *Puccinellia* are present. This means that the domain remains submerged for an increasing period. In the case of *Salicornia,* the hydroperiods remain relatively constant. The total shift for *Spartina* and *Puccinellia* is very large for a hydroperiod of 40% (*Spartina:* 500 m, *Puccinellia:* 550 m), compared to that of 37% (*Spartina: 240* m, *Puccinellia:* 260 m). The distance of cells with the respective hydroperiods has reduced to almost a neglectable distance. *Puccinellia* has more effect on the location of both hydroperiods than *Spartina*. In fact, when *Spartina* is present, the inundation regime initially shifts seaward (up to year 7). It is important to note that the hydroperiod is calculated as an average per x-coordinate. This results in an increased hydroperiod when channels are formed as these tend to remain covered by a thin layer of water even during low water.

4.2 Species traits runs (S1.B)

For the species traits runs (S1.B) the most important results are the varying effects of the different subsets of traits on bed level change. For this reason, only the topography will be discussed.

4.2.1 Topography

Changes in topography after 15 years of species traits runs (S1.B) are analysed to compare the effect of different species traits (Figure 21 – 24). From the runs with the focus on temporal growth strategies (Figure 21) we can derive that these species traits of *Salicornia* do not result in channel formation. The results of the runs for *Spartina* and *Puccinellia* are similar: shallow and narrow channels are developed, that span about 150 m. However, the spatial variation in growth does lead to clear difference between the species (Figure 21). The more seaward the vegetation was located (e.g. *Salicornia* vs. *Puccinellia)*, the more extensive the channel development. However, levees are less developed in the case of *Salicornia* compared to *Spartina.* The vegetation distributions related to Figure 22 are included in Figure A.1.

The physical species traits result in neglectable channel development in the case of *Salicornia,* both when its initial fraction is included as when it is excluded. Both the physical features of *Spartina* and *Puccinellia* result in channel development. Compared to *Puccinellia, Spartina* results in a less dense network, but with slightly deeper channels (Figure 23A and 23C). However, when the initial fraction of both species are set equally, *Puccinellia* creates much more defined channels and levees (Figure 24A and 24C).

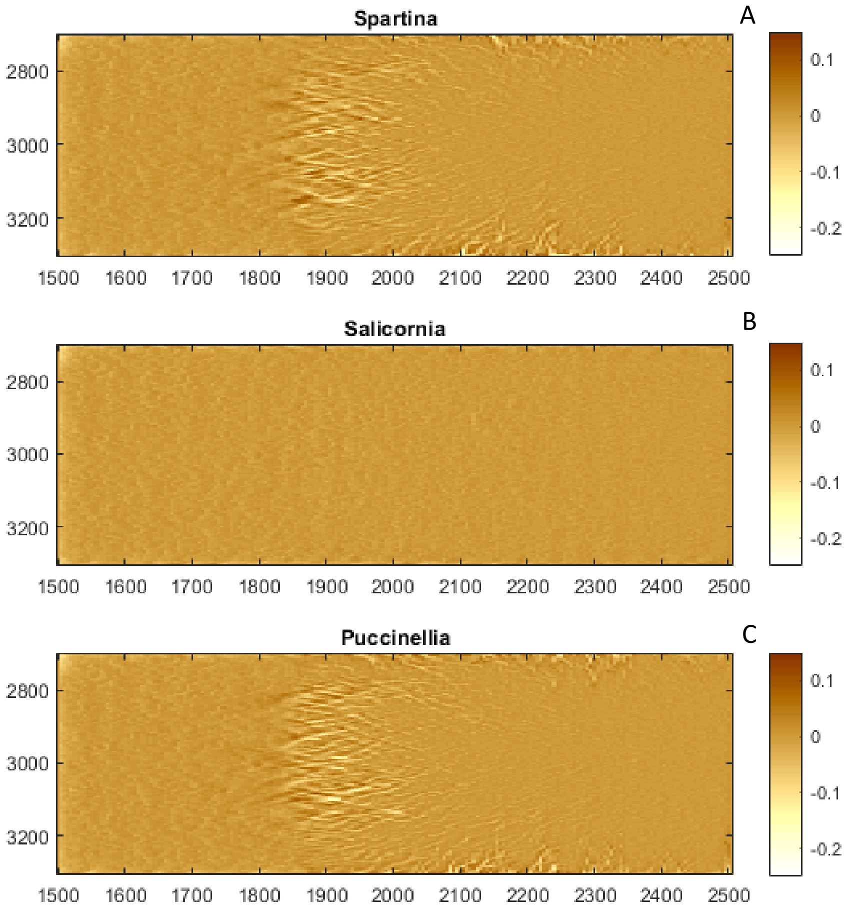


Figure 21. Bed level change after 15 years whereby the temporal growth strategies were set in accordance with respectively one of the three species and the other variables were set to a reference value (Table1; Temporal1, Temporal2 and Temporal3).

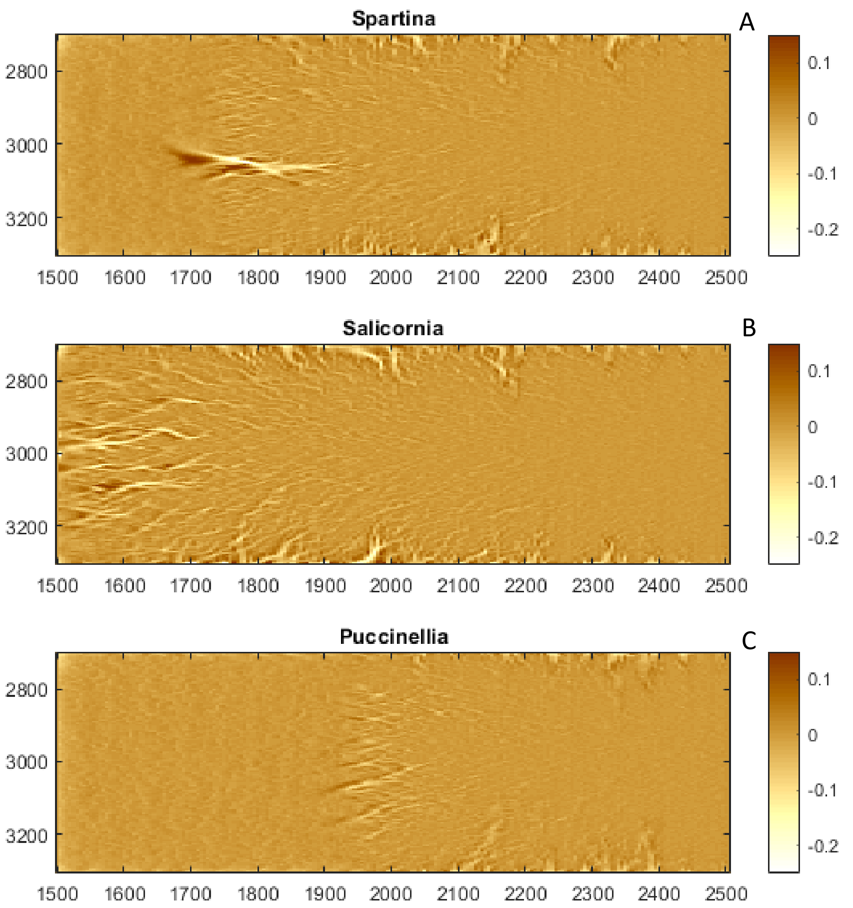


Figure 22. Bed level change after 15 years whereby the spatial growth strategies were set in accordance with respectively one of the three species and the other variables were set to a reference value (Table1; Spatial1, Spatial2 and Spatial3).

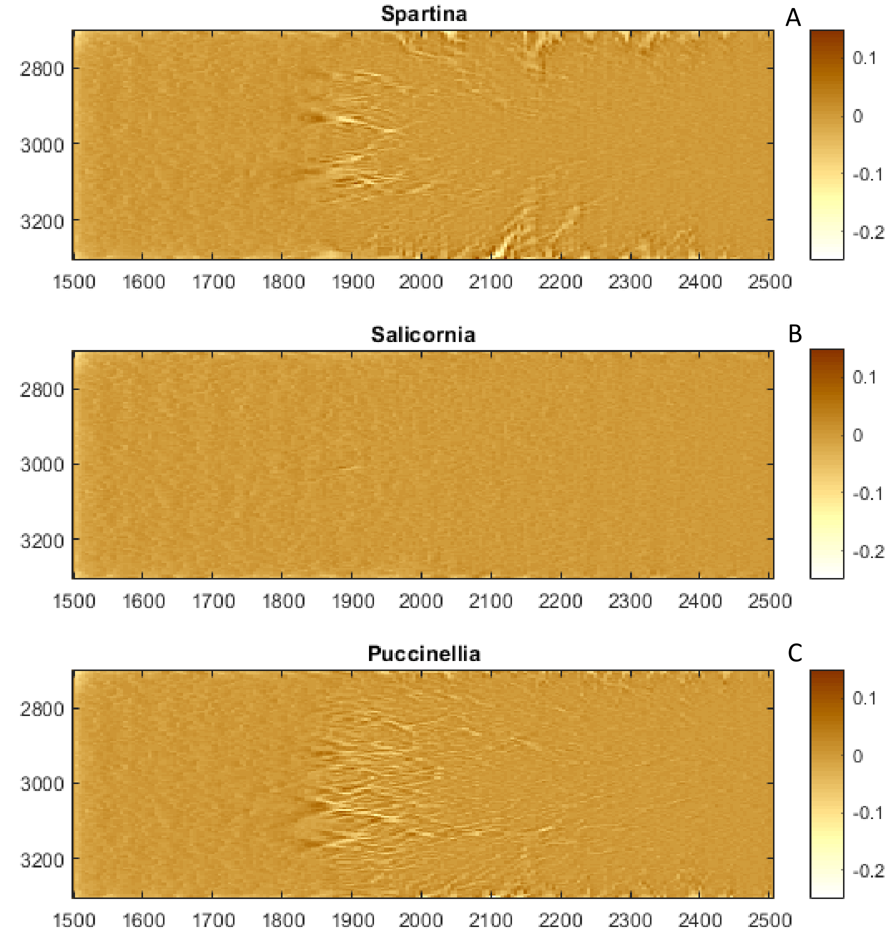


Figure 23. Bed level change after 15 years whereby the physical features (including initial fraction) were set in accordance with respectively one of the three species and the other variables were set to a reference value (Table1; Physical1, Physical2 and Physical3).

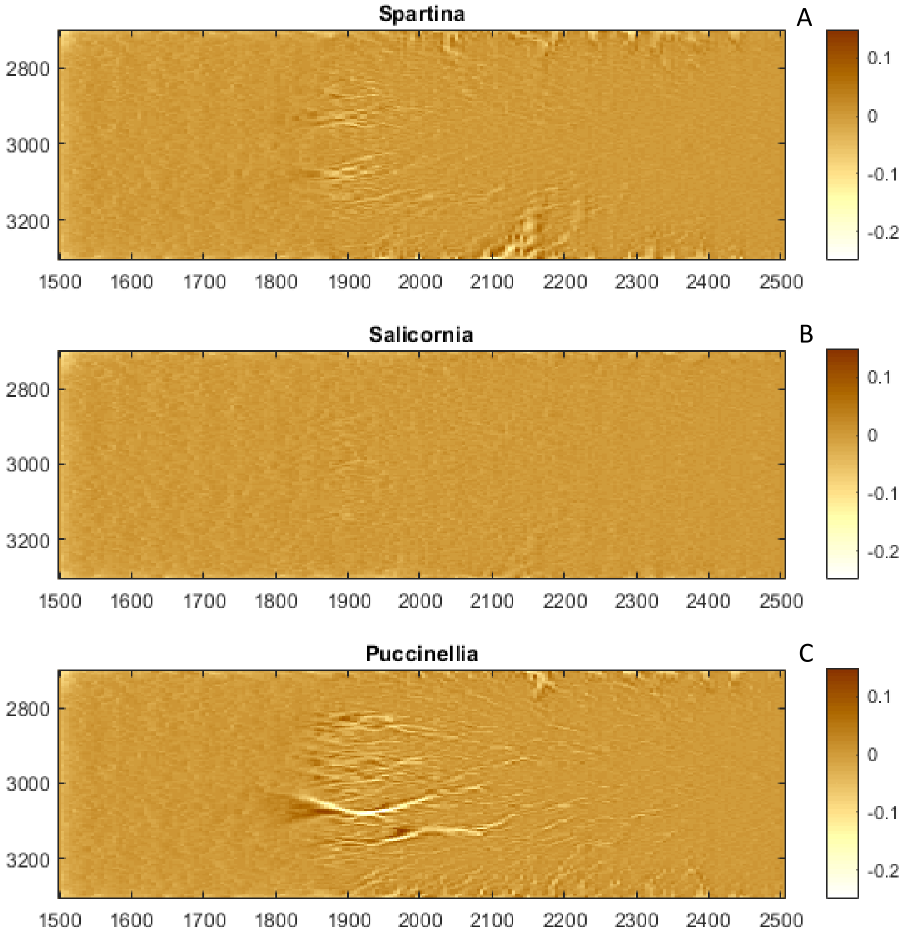


Figure 24. Bed level change after 15 years whereby the physical features (excluding initial fraction) were set in accordance with respectively one of the three species and the other variables were set to a reference value (Table1; Physical4, Physical5 and Physical6).

4.3 Multiple species runs (S2)

The following section gives the most important insights of the multiple species runs (S2) with respect to the results of the S1.A scenarios.

4.3.1 Vegetation

The distribution and mortality of the vegetation are closely related to its spatial growth parameters. However, when two or more species are combined, the variation in their seasonal growth patterns could result in different distributions and numbers. In this case, the species that is first to colonize has an advantage over others. This section will look more into depth in the spatial distribution of the three species in combination with each other.

In all S2-scenarios, there is a visible along-flow zonation in vegetation (Figure 25, 26 and B.1). In the run with all species present at once a clear zonation is observed with a very sparsely populated zone on the seaward side, a densely populated zone on the landward side and an intermediate zone. *Salicornia* is dominantly present in the sparse zone, *Spartina* increasingly prevails landward from x = 1750 and *Puccinellia* landward from x = 2100 (Figure 25; Table 5). Because *Salicornia* has the lowest initial fraction (0.2) it is likely that this species is often suppressed when the other species are present.

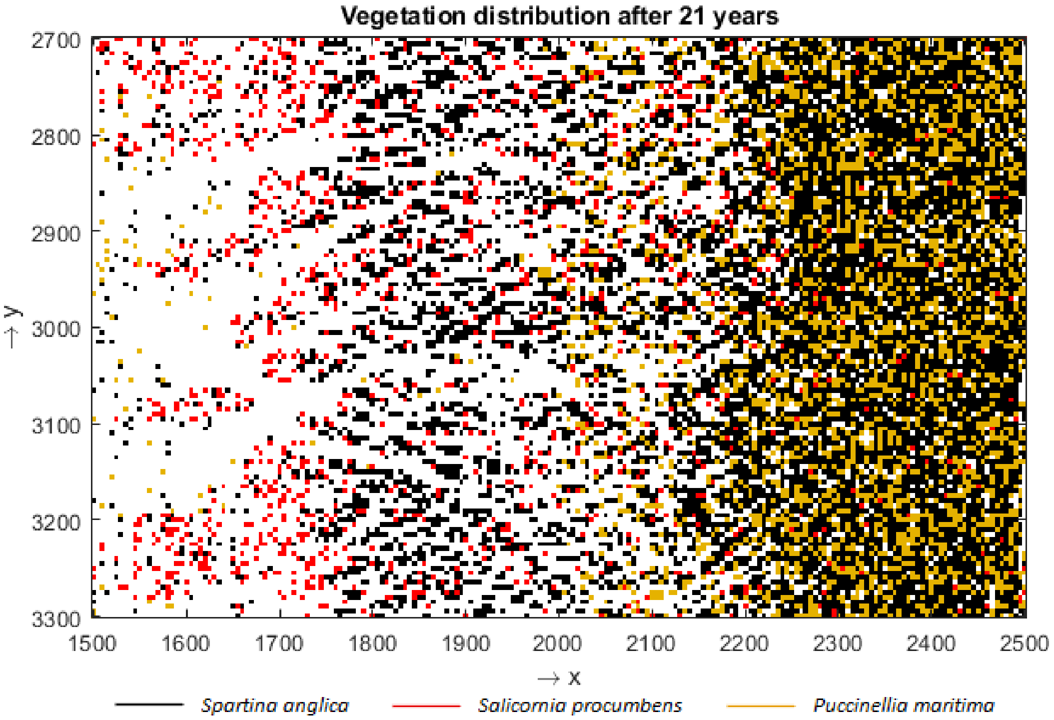


Figure 25. Distribution of Spartina anglica, Salicornia procumbens & Puccinellia maritima after 21 years (Table 1; Multi1). In cells that were colonized by multiple species, the one with the highest fraction prevails. Fractions lower than 0.05 are omitted.

Although for the second run with all species the flooding threshold was set equally for the three species a similar pattern in vegetation cover is visible (Figure 26). However, one big difference is the presence of *Puccinellia* all across the domain in the second run, whereas the occurrences of *Spartina* and *Salicornia* have reduced. In fact, the sparse, seaward zone is now dominated by *Puccinellia* (Table 5). The very dense vegetation patch at the landward sight is of a greater size whereas the middle portion is less dense. Both scenarios result in patches with no vegetation, indicating the probable presence of channels. These patches are bigger in the first scenario (Figure 25), while they are more dispersed in the second (Figure 26).

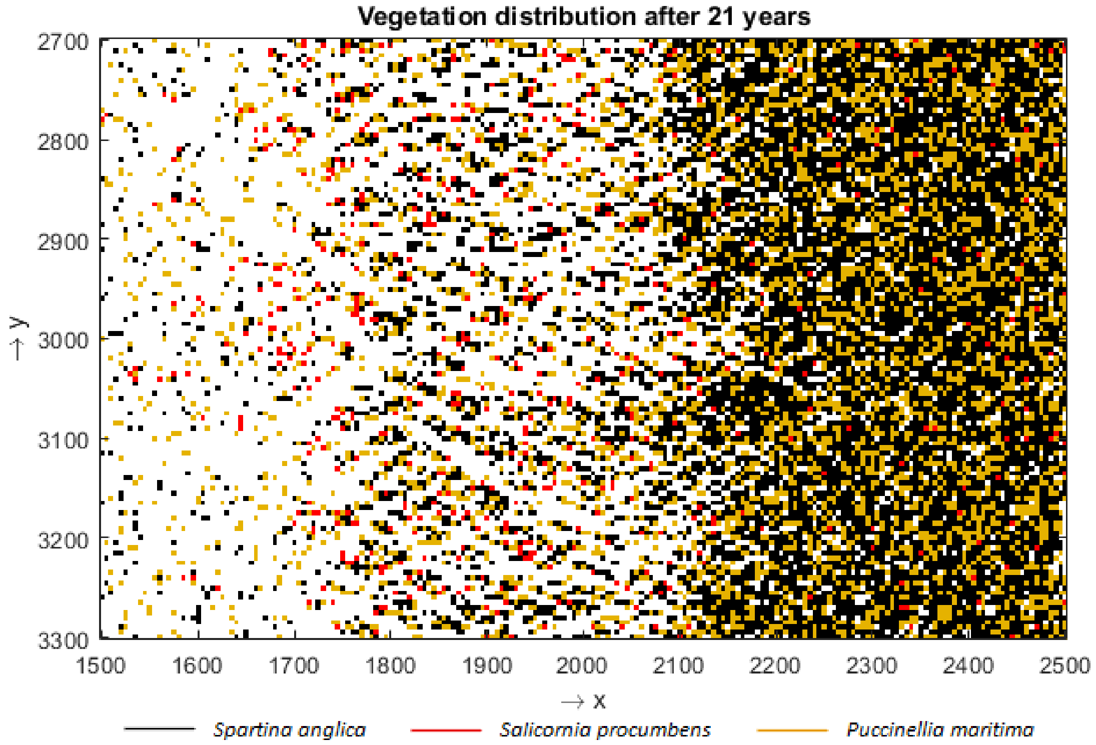


Figure 26. Distribution of Spartina anglica, Salicornia procumbens & Puccinellia maritima after 21 years (Table 1; Multi2). In cells that were colonized by multiple species, the one with the highest fraction prevails. For this run the flooding thresholds of the species were set equally.

Table 5. Share of every species in the total vegetation assemblages per zone for the two all-species runs. Share is calculated as the number of cells dominated by each species (based on highest fraction) divided by the total number of populated cells in every zone respectively. In the first scenarios the boundary coordinates of the zones are defined as respectively: x = 1750 and x = 2100. In the second scenarios the related coordinates are: x = 1750 and x = 2200.

	Multi1: Species-specific flooding resistance			Multi2: Equal flooding resistance		
Zone	**Sparse**	**Intermediate**	**Dense**	**Sparse**	**Intermediate**	**Dense**
Spartina	16.2%	77.8%	66.1%	17.0%	55.4%	65.9%
Salicornia	83.8%	13.2%	1.3%	2.8%	6.7%	1%
Puccinellia	0%	9%	32.6%	80.2%	37.9%	33.1%

To get a better overview of the distributions of the species related to elevation, hypsometric curves are plotted for all the cells were respectively *Spartina, Salicornia* and *Puccinellia* are present (Figure 27). Solid lines are made based on all cells where every species is present and the dashed curves are made based on only the elevation of cells where the species dominates.

In all cases, we can see that *Salicornia* is distributed equally over a wide range of elevations, whereas *Spartina* and especially *Puccinellia* are restricted to higher elevations. The hypsometric curves of *Spartina* and *Puccinellia* are slightly convex, indicating a large part of the population is located at higher elevations. When including only the cells where *Puccinellia* is dominant, the species becomes even more restricted to high elevations. *Salicornia* still covers a wide range of elevations, yet its curve is very different when only based on cells where it dominates. Its concave shape suggests that this species is often suppressed by others at higher elevations and mainly prevails in the area with an elevation of about 0.2 - 0.5 m.

In the second scenario (same sensitivity to flooding) *Puccinellia* is less restricted to higher elevations. In fact, the distribution of *Spartina* and *Puccinellia* is similar when all occurrences are included, yet *Puccinellia* is more dominant at lower elevations. The curves of *Salicornia* closely resemble that of subplot A. The species is distributed relatively evenly across the domain, but dominates more between 0.5 - 0.8 m.

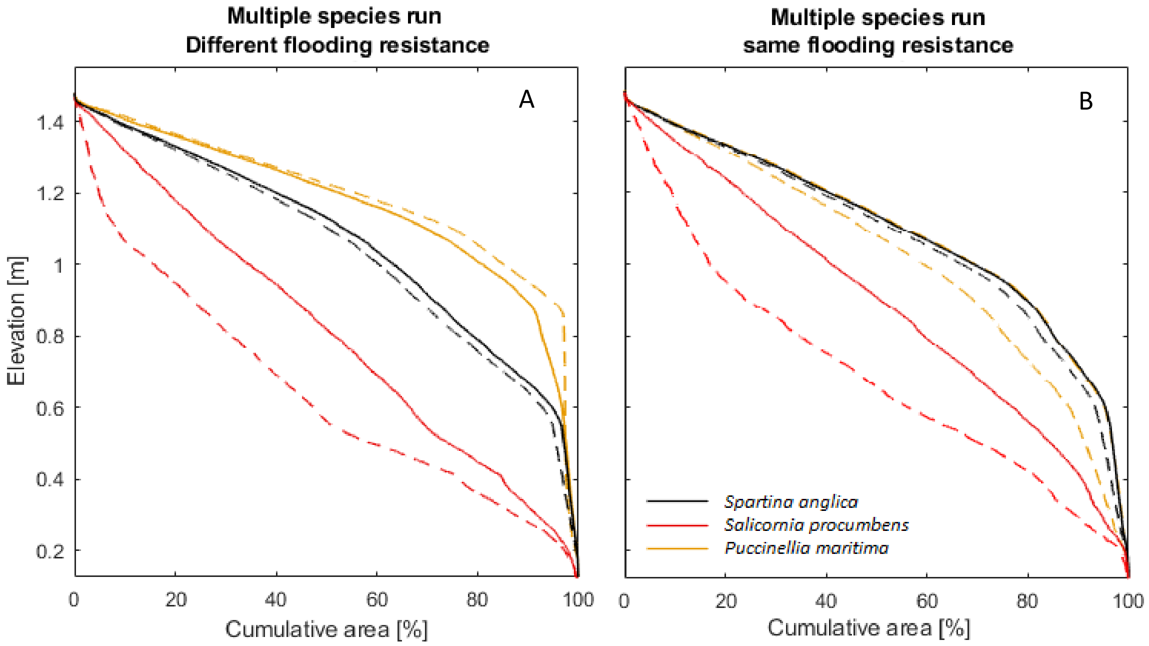


Figure 27. Hypsometric curves for the three species in different scenarios, based on the elevations of cells where the species occurs. Both graphs are based on an all species run. Subplot B is based on the run whereby the flooding resistances of the species were set equally. The solid lines are based on all cells were a species is present, the dashed curves are based on only cells where the species dominates (species with highest fraction prevails). Note: In subplot B, the solid black line (*Spartina)* overlaps with the solid orange line (*Puccinellia).*

The final plant cover of the domain is very similar for the scenarios in which *Spartina* is present with a maximum cover of little above 30%, yet much lower for the scenario of *Puccinellia* and *Salicornia* (Figure 28). In all cases, the plant cover increases up to 20 years and then declines. When both *Spartina* and *Puccinellia* are present, the increase in cover is slightly faster in the first 8 years. The total plant cover in the scenario where species are evenly sensitive to flooding (Figure 28B: All species, no zonation) is about 5% higher than in the other all species-scenario (Figure 28B: All species).

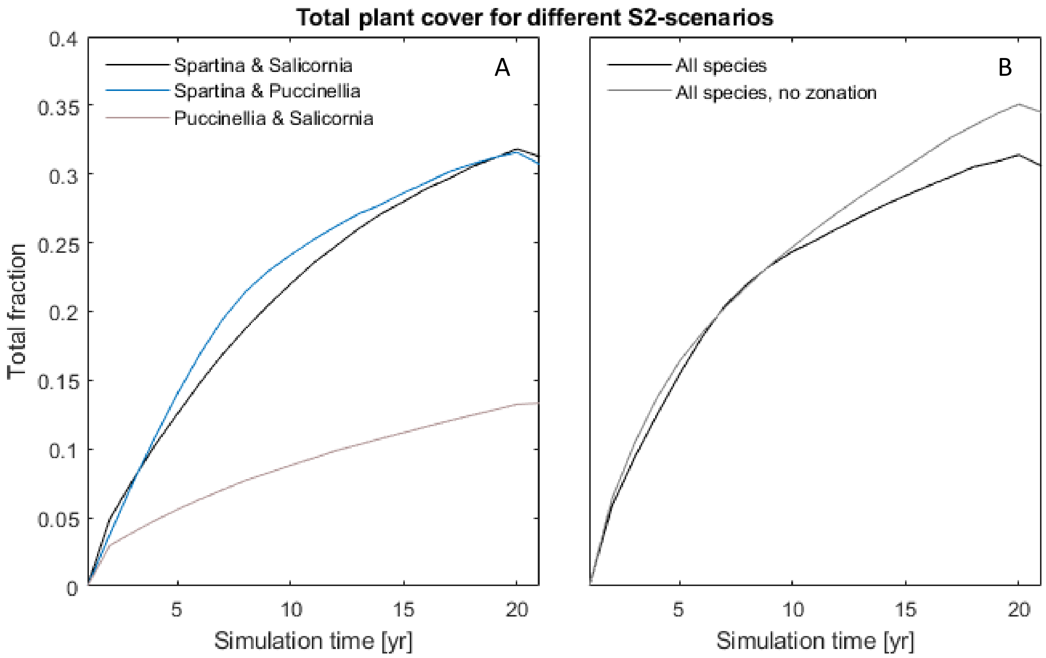


Figure 28. Total plant cover (as fraction of the domain) for different S2-scenarios. The total fraction is calculated as calculated as the sum of all fractions divided by the total number of cells in the domain.

4.3.2 Topography

The two scenarios where all species are present result in similar looking topographies (Figure 29 and 30). However, in the case of a species-specific susceptibility to flooding the channels seaward of x = 1750 are more gradual and shallow than landward of this point (Figure 29), which is not the case when all species are similarly susceptible to flooding (Figure 30). In the latter scenario, the big channels seaward of x = 1750 have similar dimensions compared to the channels landward of x = 1750. In addition, more smaller channels are formed seaward of x = 1750.

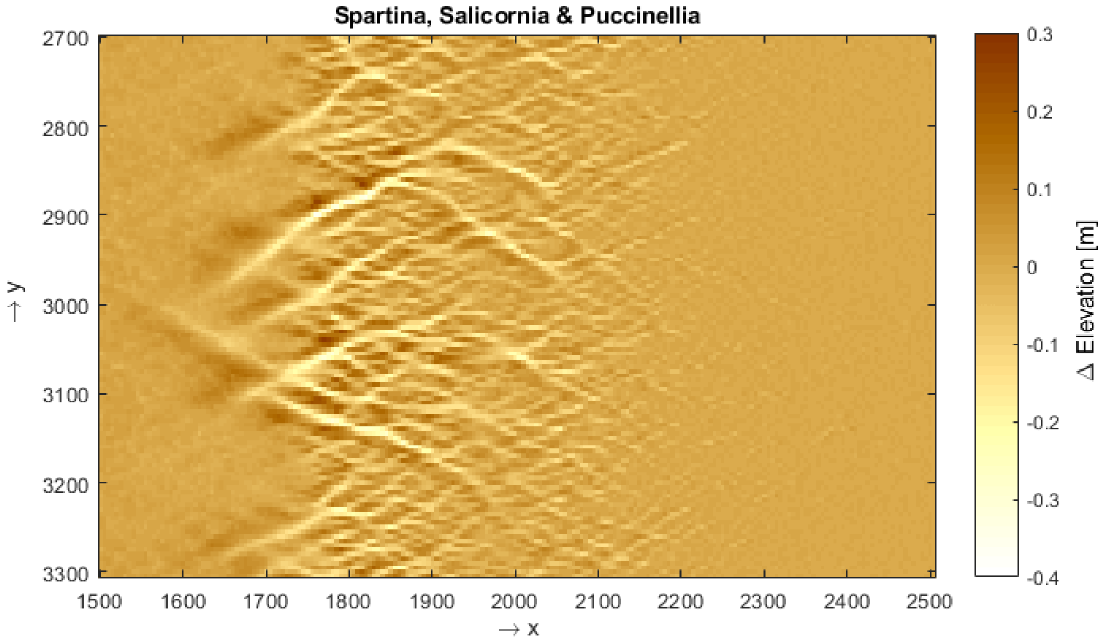


Figure 29. Bed level change over 22 years in the scenario where all species are present (Multi1).

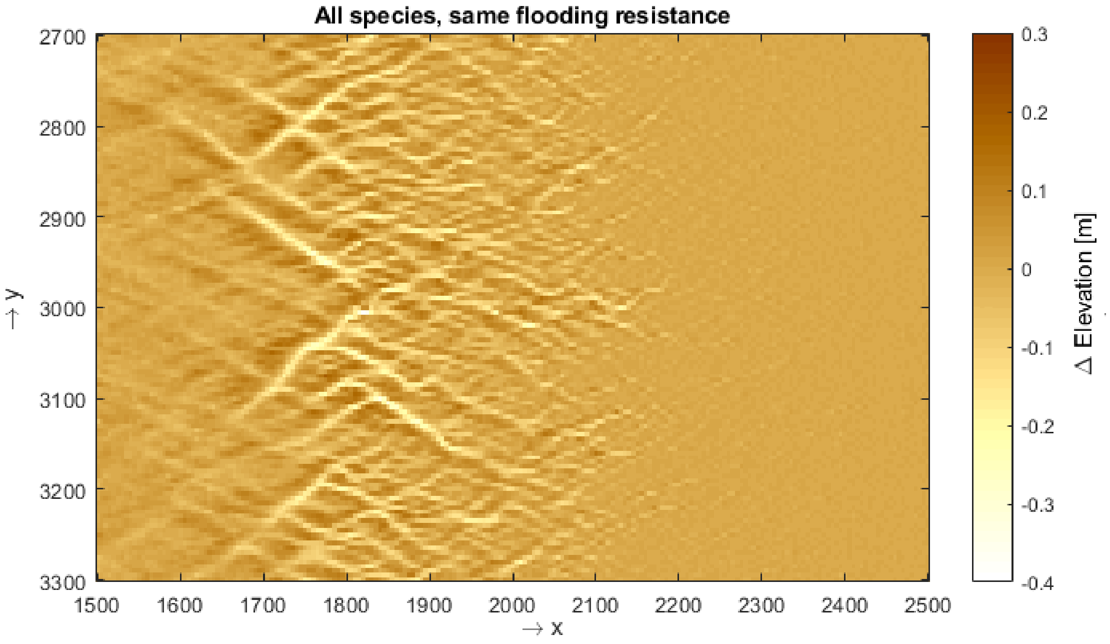


Figure 30. Bed level change in 21 years of the three species-run whereby the species have the same flooding sensitivity (Multi2).

The topography changes related to two-species scenarios are incorporated in the appendices (Figure B.2, B.3 and B.4). Both scenarios that incorporate *Spartina* produce very similar results as the S1.A-scenario with *Spartina*. The topography of the scenario incorporating *Puccinellia* and *Salicornia* looks similar to the S1.A-scenario with *Puccinellia.*

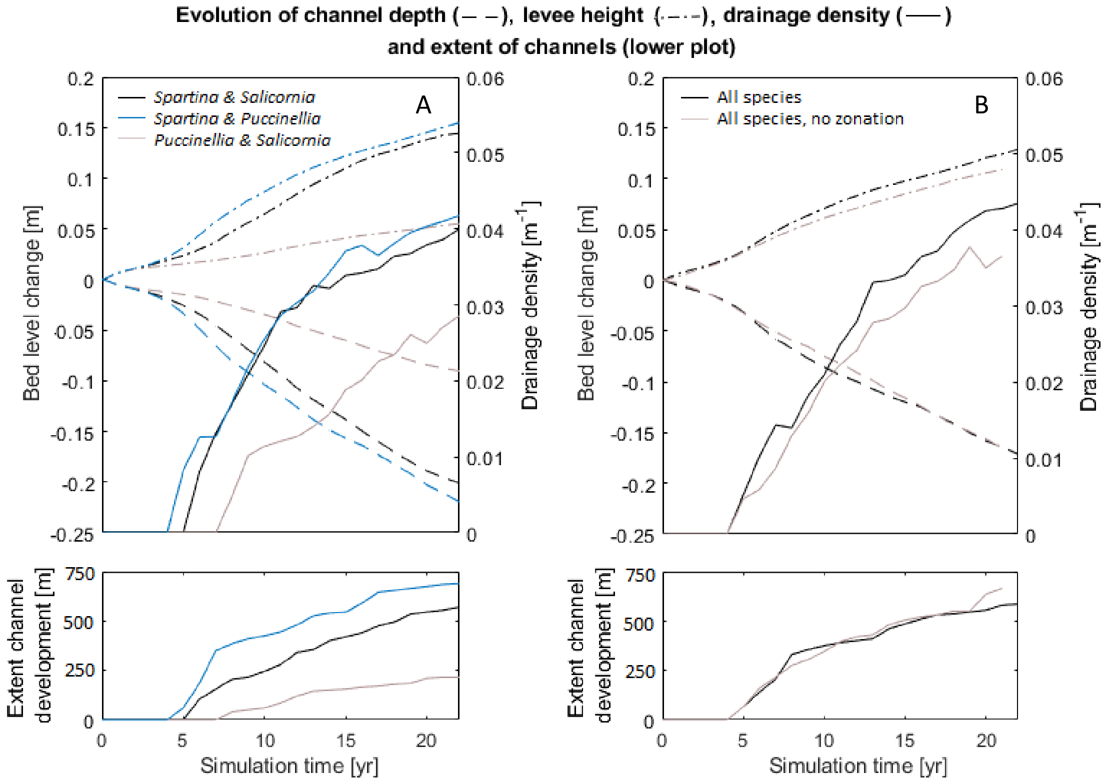


Figure 31. Evolution of channel depth, bank height, drainage density and channel extent over time for S2-scenarios.

The temporal evolution of the channel network is very similar for both two-species scenarios in which *Spartina* is present (Figure 31A). Compared to the S1.A-runs of the most dominant species (in terms of fraction), the combination of species results in (slightly) reduced channel development. The scenario of *Spartina & Puccinellia* results in the largest extent and channel/levee dimensions. The presence of *Salicornia* reduces the overall channel development. In the *Puccinellia & Salicornia*-scenario, all variables remain relatively low and the onset of channel development is delayed.

The two scenarios where all species are present result in very similar channel development (Figure 31B). In both scenarios channel and levee dimensions are lower than in the two-species and in particular the single species scenarios. The extent is slightly higher in the run with equal flooding resistances whereas the drainage density is lower (All species, no zonation).

Based on the hypsometric curves for each of the three species based on the bed level change after 22 years, the majority of plants appears to be located at cells with little bed level change (Figure 32). In addition, a larger number of *Salicornia* plants are located both in depressions and at levees. Both the occurrence of *Spartina* and *Puccinellia* on eroded sites is neglectable, but these species are present on levees. In the first scenario *Spartina* is associated with higher positive bed level changes than *Puccinellia* (Figure 32A). In the case of similar flooding susceptibilities, the hypsometric curves of *Spartina* and *Puccinellia* are similar to each other, whereas *Salicornia* occurs more on levees and in depressions (Figure 32B). Compared to Figure 32A, *Spartina* occurs less on locations with positive bed level change, while *Puccinellia* occurs more on such locations.

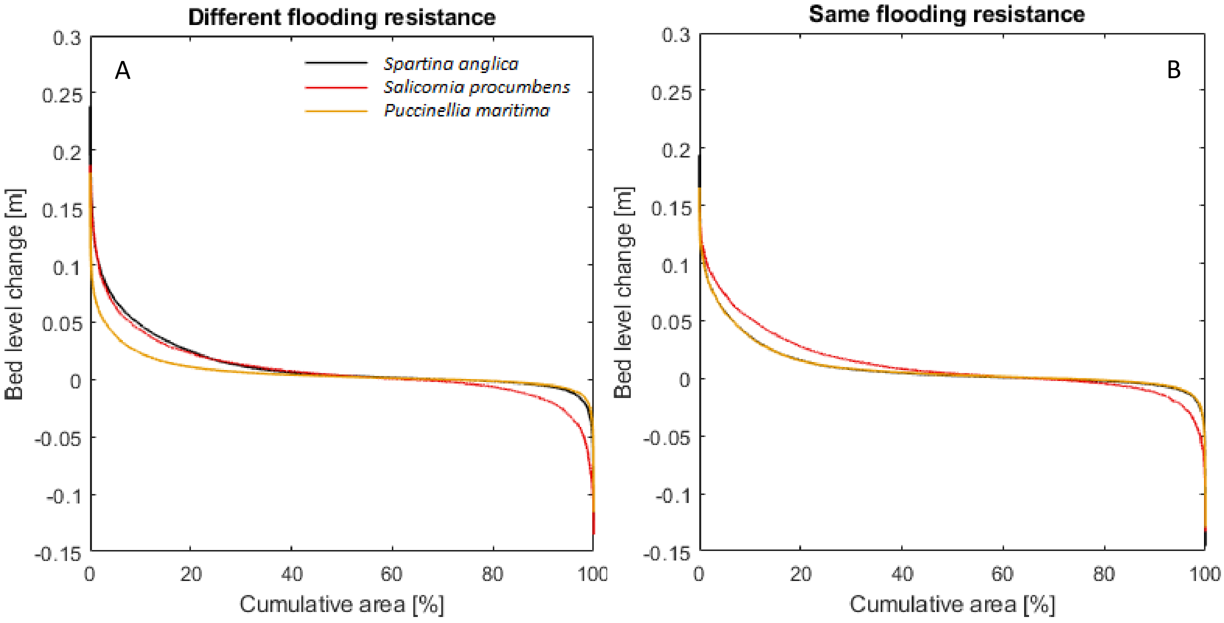


Figure 32. Hypsometry curves for the three species in different scenarios, based on the change in bed level of cells where the species occurs. Plots are based on twomultiple species runs (all species present): Multi1 (A) and Multi2 (B).

4.3.3. Hydrodynamics

Both scenarios in which all species are present, result in increased ebb dominance, already in year 1 (Figure 33). In the case of species-specific flooding sensitivity (black), the stage-velocity curves are very similar to that of S1-results for *Spartina,* with only slightly higher velocities during ebb. However, the all-species scenario where all species were equally susceptible to flooding (grey) caused even higher velocities during ebb, especially close to low water (Figure 33B). The evolution of tidal asymmetry in the two-species runs that incorporate *Salicornia* is very similar to the S1-scenario of the other incorporated species. The combination of *Puccinellia* and *Spartina* produces similar results as the all-species scenario with species-specific flooding resistances.

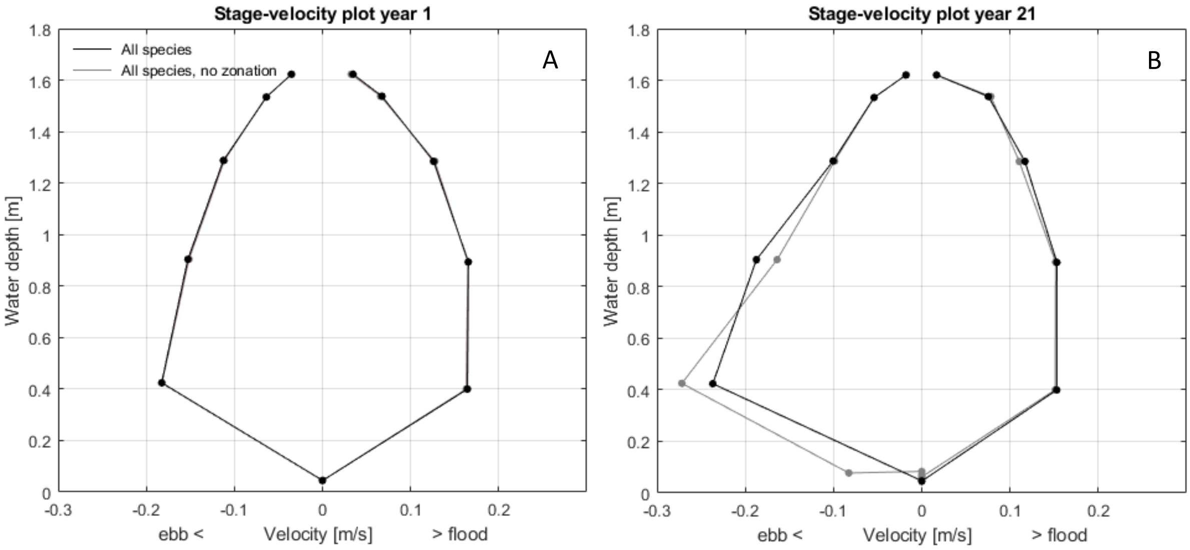


Figure 33. Stage-velocity plots the two S2-scenarios after 1 year (A) and year 21 at the end of simulations (B). Note that the y-limits are different than Figure 19 and Figure 37.

4.4 Species shift scenarios (S3)

This section will discuss the change in topography and hydrodynamics as simulated in the species shift scenarios (S3). Both scenarios have run for a combined time span of 50 years.

4.4.1 Topography

The shift from *Puccinellia* to *Spartina* (Figure 34) resulted in a significant seaward extension of the channel network. After 50 years the channels that were created by *Puccinellia* have branched and are slightly more developed. Additionally, there are small channels formed at the vegetation edge of *Spartina* (between x = 1700 and x = 1800). In between these two groups of channels, three relatively wide and linear, parallel channels have formed and there are two additional wide channels seaward of the vegetation edge of *Spartina.*

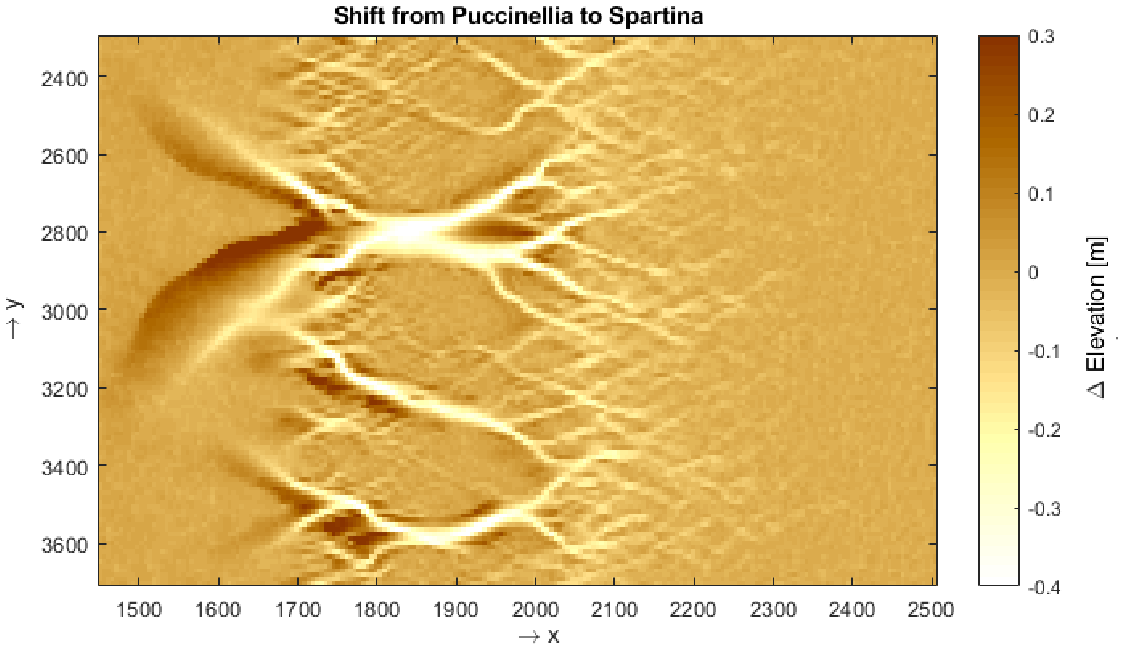


Figure 34. Total change in topography 20 years after the shift from Puccinellia to Spartina (50 years in total).

On the contrary, the shift from *Spartina* to *Salicornia* did not result in a significant change in channels (Figure 35). The shape and the extent of the network have remained very similar. However, the overall domain has eroded further and some unconnected channel segments have become attached. This increase in erosion becomes especially clear when comparing cross-sections from before and after the shift (Figure 36). The shift from *Spartina* to *Salicornia* has resulted in deeper and wider channels as well as erosion of levees.

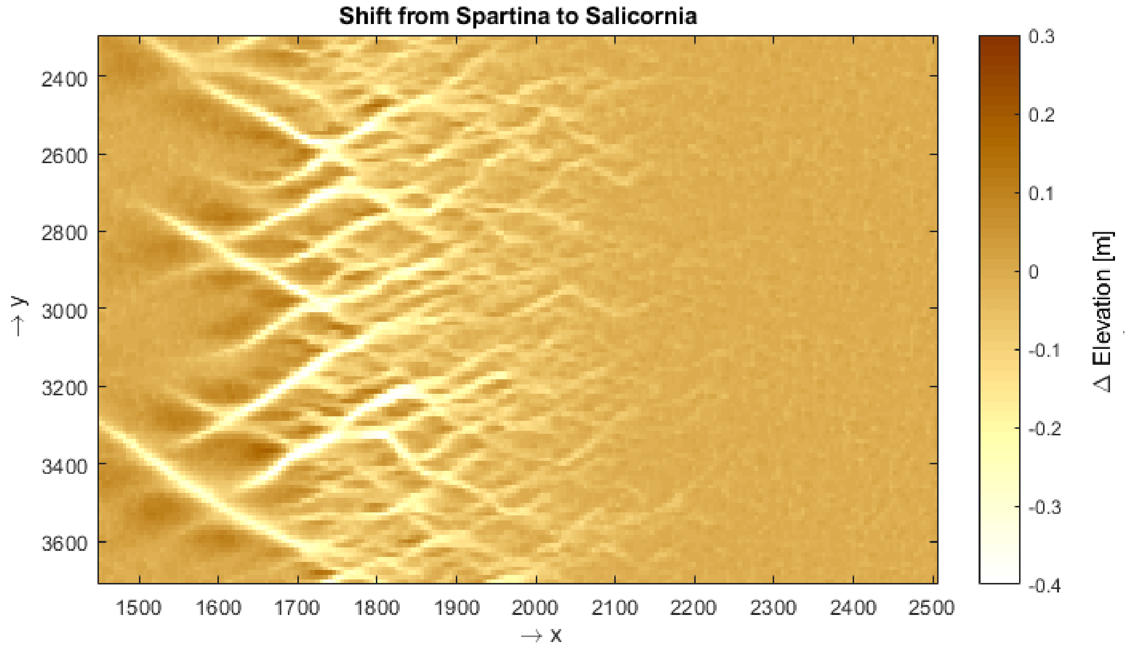


Figure 35. Total change in topography 20 years after the shift from Spartina to Salicornia (50 years in total).

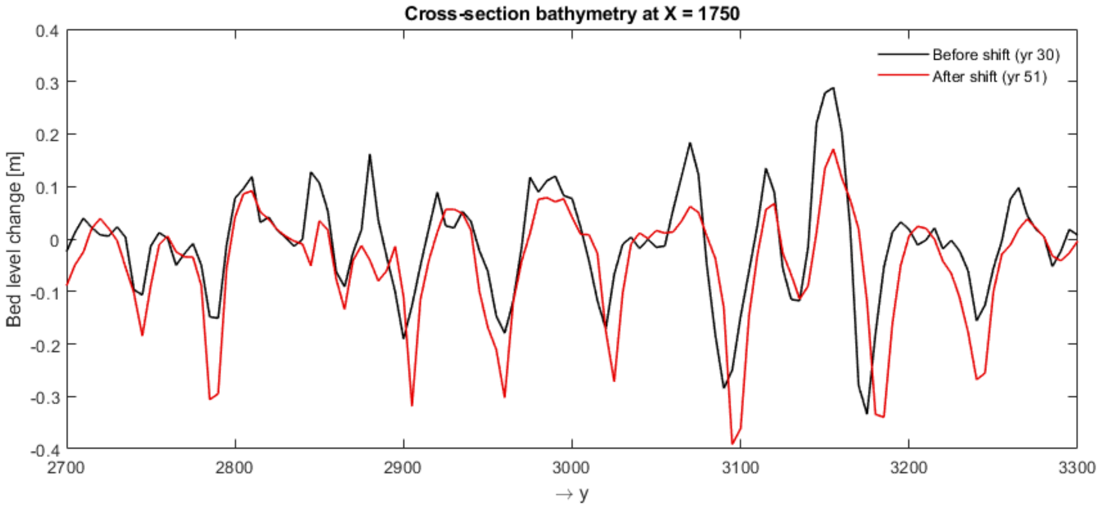


Figure 36. Cross-sections of topography change at x = 1750 just before the shift from *Spartina* to *Salicornia* (black) and 21 years after the shift (red).

Both species shift scenarios result in a rapid increase in drainage density, channel depth and a reduction of levee height just after the shift (Figure 37). In the case of *Salicornia,* the variables remain at this level for the rest of the 20 years. In the case of *Spartina* the levee height and channel depth increase from about 8 years after the shift onwards. The drainage density reduces significantly in the third year after the shift, although it is still more than before the shift. After year 5, the drainage density slightly increases for the following years.

The extent of the channels increases very minimally after the shift from *Spartina* to *Salicornia.* However, in the other scenario the channel extent almost doubles in year 33, whereafter it keeps increasing.

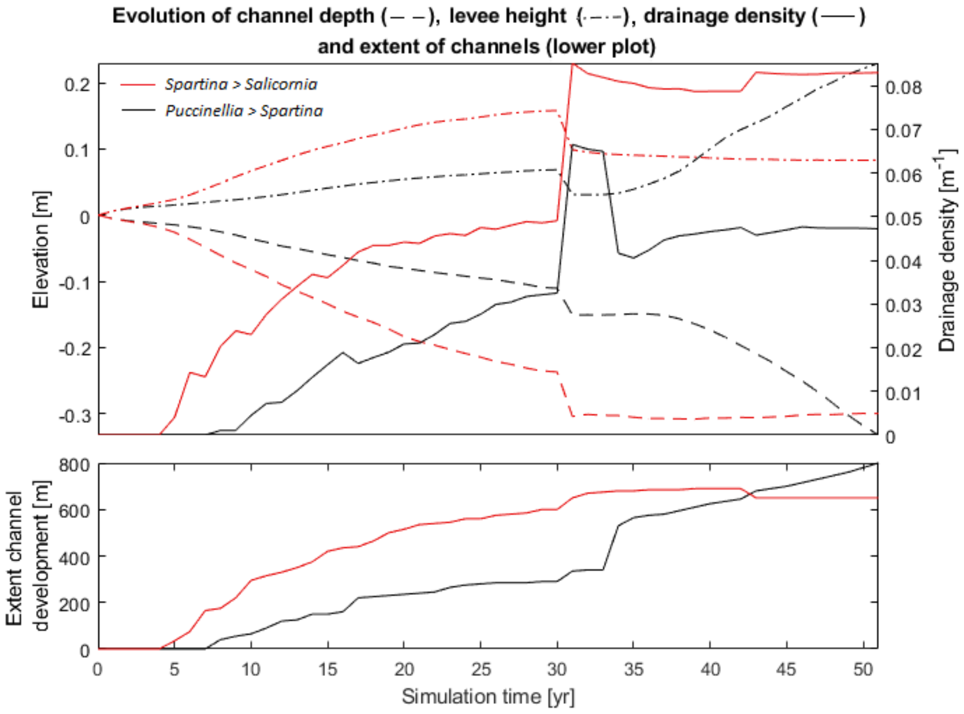


Figure 37. Evolution of channel depth, levee height, drainage density and channel extent over time for two S3-scenarios. The shift occurred after year 30. The rapid increase in drainage density is an artefact of the channel extraction tool (see 7.2 Channel extraction).

4.4.2 Hydrodynamics

In addition, the species shifts alter the tidal asymmetry. The stage-velocity curves in Figure 38A show an increase in ebb-dominance after the shift from Puccinellia to Spartina. The initial peak ebb-flow around a water level of 0.9 m is overruled by even higher velocities around 0.4 m. On the other hand, the shift from *Spartina* to *Salicornia* results in a transition from an ebb-dominant tide to a symmetric situation (Figure 38B).

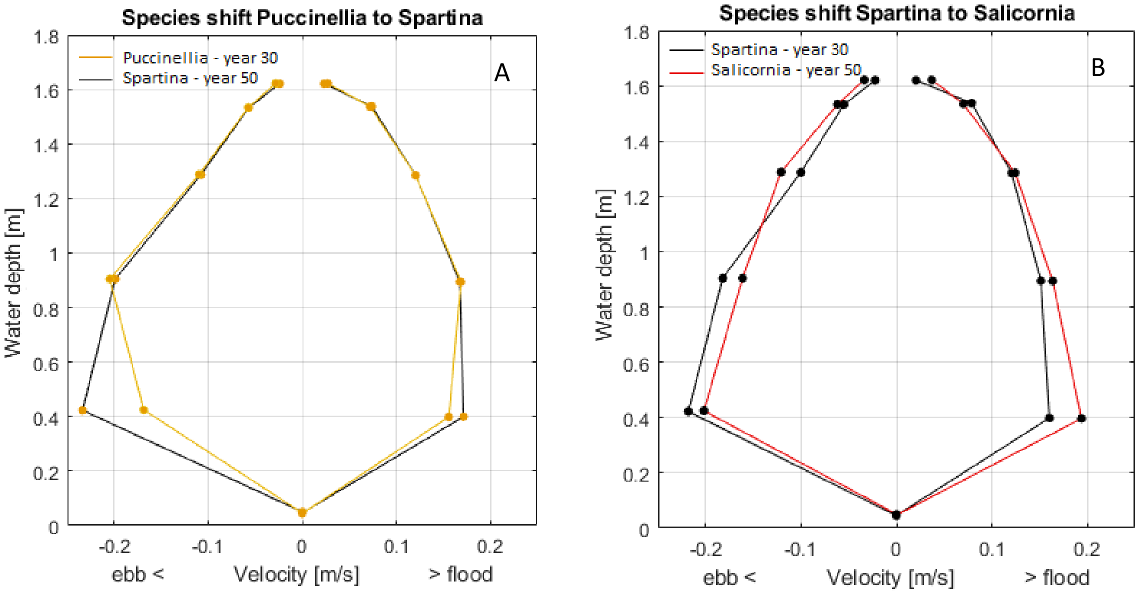


Figure 38. Stage-velocity plots for respectively the shift from *Puccinellia* to *Spartina* (A) and the shift from *Spartina* to *Salicornia* (B). The stage-velocity curves are shown for the moment just before the shift (year 30) and 20 years after the shift (year 50).

5. Discussion

The aim of this study was to investigate the relation between different species and the formation of tidal creeks. In this chapter, the observed changes in bed level and hydrodynamics will be discussed with respect to each group of scenarios.

5.1 Single species scenarios (S1.A)

The results show a significant importance of vegetation for channel formation. In the reference case (bare mudflat) the bed level change was very minimal and restricted to flattening of the initial random variation in topography. While the presence of *Spartina* or *Puccinellia* resulted in the development of a distinct channel network, the presence of only *Salicornia* did not result in channel development.

5.1.1 Two-way interaction between vegetation and morphology

Initially, the presence of the perennial grasses (*Spartina* and *Puccinellia)* resulted in sedimentation dominated system. However, after five years, erosion became exceedingly dominant in the *Spartina*-scenario (Figure 16). This can also be seen in Figure 20 where the *Spartina* scenario is becoming more and more ebb-dominant and therefore sediment exporting. This is also visible in the morphologic development by a faster increase in channel depth compared to a relatively smaller increase in levee height (Figure 17). A similar yet less distinct pattern is observed for *Puccinellia*, but not for *Salicornia*. This effect is directly linked to flow interactions. Of the different species *Spartina* generates highest flow magnitudes potential through flow deviation between patches (Figure 18 and 19). Where *Salicornia* shows very little current acceleration. The differences in flow acceleration between the species are in line with results of Bouma et al. (2013) where *Spartina* results in significant flow deviation, *Salicornia* only slightly and *Puccinellia* a variable amount, depending on the initial flow velocities.

This is not in line with the general view that vegetation has a positive effect on the sediment accretion in the marsh (D'Alpaos et al., 2006). The results of this research suggest that the relation between vegetation and the sediment balance of a marsh is much more nuanced and closely related to the species of vegetation. For instance, *Spartina* creates a very extensive channel network with channels up to 0.25 m deep and a drainage density of 0.05 m^{-1} (Figure 17). On the other hand, the channels of *Puccinellia* are only about 0.1 m deep, the drainage density is just above 0.03 m^{-1} and the extent less than half that of *Spartinas* channels. The average drainage densities as calculated in this study seem reasonable compared to field observations. Marani et al. (2013) analysed several salt marshes located on the northeast coast of Italy and their drainage densities range from 0.1 – 0.025 m^{-1}. Additionally, Kearney & Fagherazzi (2016) analysed several salt marshes with an average drainage density of 0.01 m^{-1}.

However, it would be unjust to say that *Spartina* only promotes erosion of the marsh. In Figure 17 we saw that *Spartina* had created much higher levees than *Puccinellia* had (more than double the height). This implies that the effect of vegetation on topography is two-sided: on one hand plants promote sedimentation, while on the other hand they increase sediment erosion. This is in line with Schwarz et al. (2014) and Temmerman et al. (2007), who state that the effect of vegetation on the topographies is scale-dependent: on-site plants promote sedimentation versus off-site they promote erosion. The results of this study indicate that the balance between these two processes depends on the species-traits, this will be further discussed in 5.1.2 Species traits.

The rate by which the channel network develops (*Spartina*: 23 m/yr, *Puccinellia*: *10* m/yr) is of the same order as field observations in the Venice Lagoon (mean rate of 11 m/yr; D'Alpaos et al., 2007), though on the higher side. However, these observations were done on a microtidal marsh with a tidal range of ~0.7 m and rates could potentially be higher on a meso- or macrotidal marsh. An increase in tidal range is linked to a larger tidal prism which is subsequently associated with a more extensive channel network (Marani et al., 2003).

Apart from channels on the salt marsh, the presence of vegetation up the marsh also resulted in channel formation on the mudflat acting as further drainage pathways. Compared to the marsh channels, these channels are very wide, shallow and have much more gradually sloping channel banks (Figure 15). Also the shape of the channel network is different: whereas the network on the marsh was complex and had both braided and dendritic aspects, the mudflat channels were rather parallel. The mudflat channels are shaped during ebb, when the flow is concentrated in the marsh channels and retains this variation in flow when it reaches the mudflat. The difference in channel cross-section emphasizes the importance of the stabilizing effect of vegetation on channel banks. The seaward expansion of vegetation distribution over time (Figure 11) is associated with channel development on the mudflat. Here, vegetation is restricted to levees where velocities and inundation and consequent mortality are lower. In addition, it is possible that drag exerted by vegetation reduces downstream flow velocities and inundation and facilitates vegetation growth here (Van der Wal et al., 2008).

5.1.2 Total fraction of vegetation cover

Aside from the difference between species, we found a close relation between the total fraction of plant cover and hydro-morphodynamics. However, we will first discuss the evolution of total fraction.

In the runs where either *Spartina* or *Puccinellia* were present, there was a significant increase in total fraction over the years. Since *Salicornia* is an annual species and the probability of seedling establishment remains constant, we did not see any such increase in the *Salicornia*-scenario. After twenty years the total fraction reduced (Figure 10). By year 30, this reduction appears to have stabilized. The total fraction of each species is closely related to its initial colonization fraction. The higher this is, the higher the total fraction will become (*Spartina)*. However, the spatial distribution of the species also plays a role: a species that can only grow on e.g. the upper half of the marsh (*Puccinellia*), automatically has a lower total fraction than if it would be able to grow more seaward as well. The reduction in total fraction after year 20 is related to the maximum age of the grasses. After twenty years, the first generations of plants start to die and the total fraction reduces. A couple of years later, the gaps are filled in by newer generations. The difference in decline between *Spartina* and *Puccinellia* is most likely due to the relatively high fraction by which *Spartina* colonizes. The average colonization fraction reduces as time passes because of space limitation. Therefore, later generations cannot immediately make up for the die off of the first generations.

Although the total fraction is mainly influenced by natural die-off, mortality due to stresses also plays a role. Both average mortality due to inundation and uprooting is highest in year one when all of the species are in life stage one and more vulnerable to stresses (Figure A.3). As the relative share of plants in their first life stage decreases, the mortality also reduces. Additionally, we saw an increase in mortality of *Spartina* and *Puccinellia* due to flooding and in mortality of *Spartina* due to uprooting after year 5. This coincides with the onset of channel development (Figure 17) and can be linked to hydrodynamics. One the one hand, we observed a shift in hydroperiods that started around year 5 (Figure A.4) for both *Spartina* and *Puccinellia.* The domain, and in particular cells (in the vicinity) of channels, remained submerged for a longer period of time. As a result, the velocity or inundation threshold is met more often and further into the domain. On the other hand, in the case of *Spartina*, maximum ebb-velocities vastly increase around year 5 (Figure 19). The increase in mortality due to flooding and uprooting coincides with a reduced incline in total fraction.

The shape of the total fraction-curve recurs in other figures. For instance, Figure 19 showed a similar increase in maximum ebb velocities over the years and the amount of erosion (absolute amount and with respect to sedimentation) in Figure 16 followed the same pattern as well. Moreover, the incline in channel depth, levee height, drainage density and channel extent reduces after 20 years. This is in line with observations by Temmerman et al. (2007), where an increase in plant cover is linked to increased channel development. This suggests that the total coverage of the marsh is closely related to tidal asymmetry, the amount of erosion and plays an important role in influencing the development of the channel network, whereas plant cover is mainly influenced by inundation-driven die-off. The relationship between vegetation and hydrodynamics will be further discussed in the following section.

5.1.3 Vegetation and hydrodynamics

We now know that a higher vegetation fraction goes accompanied with increased development of channels. This became evident when comparing different species with varying initial fractions and regarding the temporal evolution of both total fraction and channel erosion. This can be explained as follows: flow is obstructed by a vegetation patch, flow concentrates in between vegetation patches which subsequently leads to erosion (Bouma et al., 2013; Temmerman et al., 2007). The latter has also come forward in Figure 18 where high velocities are concentrated at the locations with negative bed level change. The density of a vegetation patch is directly linked to its scale-dependent feedback strength (Bouma et al., 2009). A larger or denser vegetation patch leads to more flow deviation and consequently more off-site erosion This explains why the development of the channel network reduces after year 20, when the total vegetation cover reduces. This slowdown in channel development is especially clear for *Spartina* because this species experienced the most decline in total fraction.

However, another relation between plant cover and hydrodynamics has come forward in the previous section. Namely, the temporal variation in ebb velocities follows the change in total plant cover. On the other hand, the velocities during flood show much less variation and even some reduction. This indicates that the more vegetation is present on the marsh, the more the ebb tide dominates over the flood tide. A similar thing comes forward from Figure 20. Although in year 1 the three scenarios are all (slightly) dominated by flood, this is very different in year 16 when ebb dominates both the *Spartina*- as the *Puccinellia*-scenario. *Salicornia* does not alter the flood dominant state of the domain.

Such tidal asymmetry is often observed on tidal marshes. Ebb dominance in channelized marshes is closely related to a difference in delay of the tide propagation within the marsh (Fagherazzi et al., 2008). During flood, the tide fills the marsh relatively evenly and is particularly confined to the channels. However, during ebb there is a significant hydrodynamic gradient (gradient in water level) between the elevated marsh and this incised channels. As a result, there is lateral flow towards the channels and much higher velocities occur (Hughes, 2012; Mariotti & Fagherazzi, 2011). According to Moore et al. (2009), ebb dominance is often restricted to channels, whereas flood dominance is mainly found on banks and marshes. Moreover, Lokhorst et al. (2018) state that the balance between sedimentation and erosion influences the tidal prism and tidal asymmetry: the more net sedimentation, the more flood dominates. This was also observed in our simulations.

Tidal asymmetry plays an important role in residual sediment transport and the morphology of a marsh (Moore et al., 2009). Flood dominance is associated with increased sedimentation rates, infilling of the marsh and thus better coastal protection. Ebb dominance is linked to exceeding erosion of the marsh and loss of protective capacity. This agrees with our results since erosion exceeds accretion in both the *Spartina*- and *Puccinellia*-scenario (Figure 16), whereas accretion dominates in the flood dominated *Salicornia*-scenario. Although, due to the restricted inflow of sediment into the domain, sedimentation was limited, sediment transport rates are higher during ebb than during flood (1.5 times higher on average) for *Spartina* and *Puccinellia*, suggesting morphodynamics are predominantly related to ebb.

5.2 Species traits scenarios (S1.B)

The observed influences of vegetation on the topography and the differences between the species can for a large part be linked to the physical properties and spatial or temporal growth strategies. The lack of channel development in the case of *Salicornia* was also observed in the temporal growth strategies-run (Figure 21). Furthermore, the physical features of *Salicornia* showed very little bed level change (Figure 23). However, when only the species' spatial growth strategies were incorporated *Salicornia* resulted in much more channel development than the other two species (Figure 22). This implies that both the fact that *Salicornia* is an annual species as its physical features results in neglectable channel formation. Because *Salicornia* is an annual species, the plants are not 'fixed' to certain locations like *Spartina* and *Puccinellia* are. Where *Salicornia* establishes is in these simulations not related to where the species was present the year before. As a result, the species would have to start creating channels every year again. On the other hand, *Salicornia* is a relatively small and sparsely distributed species with a low scale-dependent feedback strength as it does not result in much flow deviation nor channel erosion (Bouma et al., 2009; Bouma et al., 2013).

Moreover, it appeared that the closer the species grows to the open sea; the more effect it has on bed level change (Figure 22). This partly explains the difference in channel formation between *Spartina* and *Puccinellia.* There was not much difference between these two species in the runs focusing on temporal growth strategies nor physical features. However, when the fraction was left out of the physical features *Puccinellia* showed greater channel development (Figure 24), indicating that although having only 11% of the stems of *Puccinellia,* the large cover fraction of *Spartina* overall generates more sediment erosion. This suggests that both spatial distribution and initial fraction make the difference between the two grasses, concerning both the extent as well as the amount of bed level change. Initial fraction relates to the size of an initial establishing vegetation patch or tussock. This size mainly influences the drag exerted by the vegetation which determines the scale-dependent feedback strength and channel incision (Temmerman et al., 2007). Spatial distribution is a determining factor in channel formation as it directly influences interaction between vegetation and hydrodynamics. In a sloping tide driven environment species which can tolerate more flooding, grow lower in the intertidal area. These species experience higher velocities and a longer inundation time. Consequently, the flow between vegetation patches will automatically have higher velocities which results in more sediment transport and channel incision.

5.3 Multiple species scenarios (S2)

Up till now, the focus of this chapter was on the effect of single species on salt marsh topography. However, we had also performed runs where by two or more species were in play. This section will focus on the interaction between species and their collective influence on tidal topography.

When multiple species are present this leads to two or three distinct zones in the vegetation distribution, depending on how many species are incorporated. If all species are present, there is a sparsely populated zone at the seaward edge of the domain, followed by an intermediate zone and finally there is a very densely populated zone (Figure 25). Although *Puccinellia* is restricted to higher elevations, *Salicornia* and *Spartina* occur at a wide range of elevations (Figure 27). However, regarding species dominance, the distribution of *Salicornia* is confined to the lowest elevations, *Spartina* dominates the intermediate zone and the upper zone consists of both *Spartina* and *Puccinellia* (Table 5). This is in line with several studies that were mentioned in the literature review (e.g. Beeftink, 1985; Hughes, 2004; Scholten & Rozema, 1990) and also what was expected based on the differences in sensitivity to flooding and uprooting. The fact that *Salicornia* is more supressed at higher elevations is actually not unrealistic. In our case *Salicornia* was often omitted due to its low initial fraction. Proffitt et al. (2005) observed similar situations like this whereby the species was suppressed by *Spartina.* This was the case because the latter reduced light penetration and thus the light availability for smaller species.

On the other hand, the run whereby the three species were given the same flooding resistance, resulted in a similar zonation: one sparsely populated zone, an intermediate zone and a densely populated zone (Figure 26). However, the distribution of the three respective species is not as confined to water depths. Where the sparse seaward zone was initially dominated by *Salicornia*, *Puccinellia* dominates in this scenario (Table 5). This can be explained by the fact that *Puccinellia* is least susceptible to high velocities. On the other hand, we see that *Spartina* and *Puccinellia* are more dominant at higher elevations than *Salicornia* (Figure 27). This can be explained on the basis of the shift in hydroperiod. Based on the initial hydroperiods and the flooding threshold, it is expected that all species occur evenly between x = 1730 and x = 2500. However, due to the shift in hydroperiod, the seaward boundary of this subdomain shifts landward (see Figure A.4). As a result, mortality increases seaward of the new boundaries and the vegetation patch is thinning out. *Salicornia* seems to be less sensitive for this process. This is due to the fact that it is an annual species and the relative mortality is relatively low (compared to surviving fraction). On the other hand, compared to the other species *Salicornia* is more affected by uprooting higher up in the marsh where more channels are formed, resulting in more constant mortality numbers across the marsh.

The channel networks that resulted from a combination of species are very similar to that of the most dominant species. For instance, in all runs were *Spartina* was present, the total fraction was only slightly increased compared to the single species-run with only *Spartina* (Figure 28). On the other hand, channel development was slightly lower (Figure 30). The results of the run with *Puccinellia* and *Salicornia* were very close to the results of only *Puccinellia.* The fact that a combination of species results in reduced channel development, despite the increase in total fraction, suggests that competition for space plays a role. Out of the three species, *Spartina* is the last to colonize (April, versus February; *Salicornia* and March; *Puccinellia*) resulting in a limited space for this species to colonize. Consequently, the species covers less area in the multiple species-runs than in the single species-run and exerts less influence on hydro-morphodynamics.

The channel networks of the two all species-scenarios (with same and different flooding resistances) are very similar. The run whereby the species had the same flooding resistance resulted in slightly more channel development in the sparsely populated zone, with sharper and deeper channels (Figure 30). This suggests that *Salicornia* does not have a sufficient stabilizing effect on channel banks, in contrast to *Spartina* or *Puccinellia.* In addition, from Figure 32 it became clear that *Spartina* and *Puccinellia* mainly occur at locations with a positive bed level change, whereas *Salicornia* also grows in shallow channels (up to 10 cm in depth). This indicates that the distribution of *Salicornia* and the channel network are only slightly related, by means of mortality due to high velocities in deeper channels.

The combination of *Spartina* and *Puccinellia* results in increased tidal asymmetry compared to the S1-scenarios, with significant ebb-dominance (Figure 33). In particular the scenario where all species were equally susceptible to flooding resulted in a strong ebb dominated situation. This can be related to the larger total fraction (Figure 28) symbolizing larger or denser patches of vegetation resulting in strong flow concentration and higher velocities, as was discussed in 5.1.3 Vegetation and hydrodynamics.

From the S2-scenarios it appears that although ecological interactions (e.g. competition) are not considered in the model, indirect hydromorphodynamic-plant interactions do result in a realistic plant assemblages. In particular, varying susceptibilities to inundation causes a typical marsh zonation. On the other hand, we observed that differences in both the initial fraction and the timing of colonization and growth indirectly results in competition between species.

5.4 Species shift scenarios (S3)

Finally, the species shift runs resulted in different channel networks. The species shift from a *Spartina* to *Salicornia* dominated situation resulted in a lot of erosion. There were no new channels developed, only existing channels were widened because banks eroded. Moreover, from the cross-sections it became evident that both *Spartina* had resulted in relatively deep channels (with respect to levees) and steep banks, while the transition from *Spartina* to *Salicornia* resulted in deeper and wider channels and lowered levees (Figure 36). This is in line with the observed differences in channel dimensions between the two S2-scenarios where all species were present. Both results support the theory that vegetation can have a stabilizing effect on channel banks resulting in a reduced width-depth ratio of the channels (D'Alpaos et al., 2006; Schwarz et al., 2014), while the transition from a densely populated marsh to an almost bare mudflat causes channel banks to erode. This suggests that a species shift from a perennial grass to an annual halophyte (or bare mudflat) would be disadvantageous for the ecosystem services of the marsh. The transition goes accompanied with a lot of erosion and a reduced protective capacity. This has also been pointed out by Strain et al. (2017) who state that an increasing dominance of *Salicornia (veneta)* would eventually result in a marsh with a reduced resilience, and a reduced capacity to respond to sea level rise.

On the other hand, the species shift to from *Puccinellia* to *Spartina*, results in rapid extension of the channel network and development of wider and deeper parallel channels. This happens because *Spartina* is less sensitive for inundation and grows much more seaward. After a while the channels that are created by *Spartina* connect to the already existing channels and straight and wide channels are formed. This type of channels allows flood to propagate into the marsh at a quicker pace, reducing the protection of the hinterland (Leonardi et al., 2018). Moreover, the transition resulted in increased ebb-dominated tide (Figure 38).

In terms of temporal evolution of channel development, both shifts initially results in significant erosion of both channels and levees (Figure 37). When species 1 is replaced by species 2, there is a strong reduction in plant cover which results in increased erosion. Consequently, channel depths and levee heights are reduced. The increase in drainage density that goes accompanied with the species shift is an artefact of the way drainage density is calculated and should be omitted (see 7.2 Channel extraction). In the shift from *Puccinellia* to *Spartina* channel depth and levee height increase and the drainage density reduces again after 3 years because channels start to form at the edge of the *Spartina* patch. Because this is much more seaward than the initial *Puccinellia* vegetation edge, the extent of the total channel network increases and the drainage density decreases.

Both species-shift scenarios are likely scenarios with the eye on climate change. Rising temperatures benefit *Spartina* at the expense of other marsh species such as *Puccinellia,* increased drought benefits *Salicornia.* However, the most crucial implication of climate change for salt marshes might be the rising sea level. Generally, marshes are believed to naturally response to an increase in sea level by means of increased sedimentation (Morris et al., 2002; Kirwan et al., 2013). However, on the long term, sea level rise goes accompanied with transgression. In many cases, humans restrict transgression of the marsh (by e.g. urban development along the coast) and instead the marsh is reduced in size (Kirwan et al., 2013). Upper marsh species are replaced by lower marsh or pioneer species that are less susceptible to inundation. As observed in the S3-scenarios, such a species shift results in loss of sediment from the system resulting in a reduction of its protective capacity.

6. Conclusions

The aim of this study was to increase the understanding of the relation between salt marsh vegetation and channel development. By means of various simulations with an ecological model coupled to hydro-morphodynamic modelling in Delft3D, the posed research questions were answered.

The results of the S1.A-scenarios indicate the influence of vegetation on the marsh topography to be highly dependent on the species. In contrast to the perennial grasses *Spartina* and *Puccinellia,* the annual halophyte *Salicornia* did not induce channel formation. Furthermore, the study showed that the relation between vegetation and topography change is very complex. On the one hand, the presence of a vegetation patch obstructs flow, resulting in off-site flow concentration and subsequent channel incision, while on the other hand the plants promoted on-site sedimentation. Moreover, vegetation could (indirectly) cause tidal asymmetry which affects the direction of the net sediment transport of and coastal protective capacity of the marsh. Both *Spartina* and *Puccinellia* resulted in an increasingly ebb-dominant tide whereas the situation remained flood-dominated under *Salicornia.*

Comparison of different species traits (S1.B) emphasized the importance of traits such as maximum age, sensitivity to stresses, initial fraction and the physical appearance. Both the maximum age as the physical appearance of *Salicornia* are responsible for the lack of significant flow deviation and channel incision. The taller grass *Spartina* that is better resistant to flooding and has a higher initial fraction, resulted in a more extensive vegetation cover with denser patches and a better developed channel network than *Puccinellia.* This implies that both temporal and spatial variation in growth and physical features play a role in vegetation induced channel formation.

The combination of different species resulted in reduced channel development compared to the most dominant species (based on total fraction; *Spartina*). In all S2-scenarios the drainage densities were significantly lower, as well as levee height and channel depth. The channel network that was created closely resembled that of the most dominant species in terms of shape. From the run where all species had the same flooding resistance, it came forward that although ecological interactions are not simulated, indirect hydromorphodynamic-plant interactions result in a typical zonation in marsh vegetation.

Both species shift-runs (S3) resulted in increased erosion of the existing channel network, implying reduced resilience of the ecosystem. In particular the shift from *Spartina* to *Salicornia* resulted increased erosion across the domain due to a reduction in vegetation-exerted stabilization of the sediment.

All in all, the coupling between the ecological model and Delft3D was very successful. In contrast to earlier research, the model allowed to distinguish between different species traits as well as incorporated seasonal and spatial variation in growth. Because of this, the study provided us with new insights in the complex interactions between vegetation and tidal marsh morphology.

7. Suggested model improvements and future research

Although this research has resulted in interesting insights in the relation between vegetation and tidal channel development, it has its limitations. This chapter discusses the most important limitations and poses recommendations for further research.

7.1 Model set-up and validation

The difference in channel development by the three species is in line with what was expected based on earlier studies and can also be explained by means of the hydrodynamics. However, the model did not produce channel formation regardless of vegetation presence. In reality, bare tidal flats often host tidal creeks, albeit less significant than on a vegetated marsh (Vandenbruwaene et al., 2015). The fact that our simulations only included channel development induced by vegetation could be related to the domain set-up, as mudflats do not always develop channels or due to the chosen transport equation. The results from the test runs with different transport equations imply that the choice of transport equation determines to some extent the outcome of the simulations. In addition, the equilibrium boundary restricted the inflow of sediment in the system, causing an automatic tendency to erosive behaviour of the system. These restrictions should be taken into account when interpreting the results.

Another limitation of the model set-up is the frequency by which output files are written. For reasons of computational efficiency, runs that are performed with SD2 write results every 37.2 minutes (hydrological time scale). Therefore, only two time steps per tide capture the flow (and other hydrodynamic variables) through channels. Consequently, the model output does not allow significant correlation tests between velocity and topography or vegetation. If time would not be a limiting factor, it is recommended to reduce the output interval.

Furthermore, the S3-scenarios show an interesting evolution of the topography after one dominant species has been replaced by another. However, with the current state of the ecological model it was not possible to simulate a gradual shift from one species to another. We could only use the topography that was shaped by species 1 as initial topography for species 2. This implies that species 1 disappeared from the domain all at once, while species 2 just started to colonize. This is a realistic scenario, an entire population could die at once, yet it is not a probable scenario. For further research it would be interesting to study the effect of a gradual change in species dominance on the topography.

Finally, an important step in the development of the ecological model is model validation. Although the outcomes of this study can be supported by earlier studies and literature, for further research it would be beneficial to compare model outcomes to real systems or experimental set ups. Drainage densities and (the rate of) channel development are of similar order as real systems. However, there is little literature on the difference between marsh species and their effect on channel development. To validate the outcomes of this study, similar experiment could be performed as done by Bouma et al. (2013), whereby morphodynamics are additionally considered.

7.2 Channel extraction

The rapid increase in drainage density induced by the shift from *Spartina* to *Salicornia*, indicates a disadvantage of the self-made channel extraction tool. Generally, drainage density is calculated as the summed channel length divided by the total area of the catchment. However, our channel-extraction tool assigned cells of a raster to either be a channel or not and based on the total number of these cells, the drainage density was calculated. Consequently, the drainage density increases when a channel becomes longer or more channels are created, but also if a channel becomes wider. This should not be the case, but it explains the rapid increase in drainage density after the species shifts. Follow-up research would benefit from a more advanced tool – such as TopoToolbox (Schwanghart & Scherler, 2014) or GeoNet 2.0 (Passalacqua et al. 2017) – with increased applicability on tidal environments.

7.3 Additional factors

In addition, it would be interesting to study the consequences of a different tidal forcing on the relation between vegetation and channel development. In our simulations we made use of a tidal harmonic that is constant throughout the year, while this is not a realistic scenario. In reality, the tidal signal is often a combination of various components and influenced by the spring-neap cycle and by weather conditions. This could affect channel development in two ways. On the one hand, higher flow velocities during spring tide or in winter (due to a higher frequency of storms) could increase channel incision. On the other hand, increased uprooting or inundation of vegetation would increase mortalities and reduce total plant cover which in turn affects channel development. This asks for further research into the consequences for the topography of the marsh.

Furthermore, model results of the S2-scenarios showed ecological interactions could be simulated indirectly through competition for space and varying susceptibilities to hydrodynamic stresses. However, fur further studies considering multiple species, looking into a way to incorporate true ecological interactions in the model as well, might improve model outcomes.

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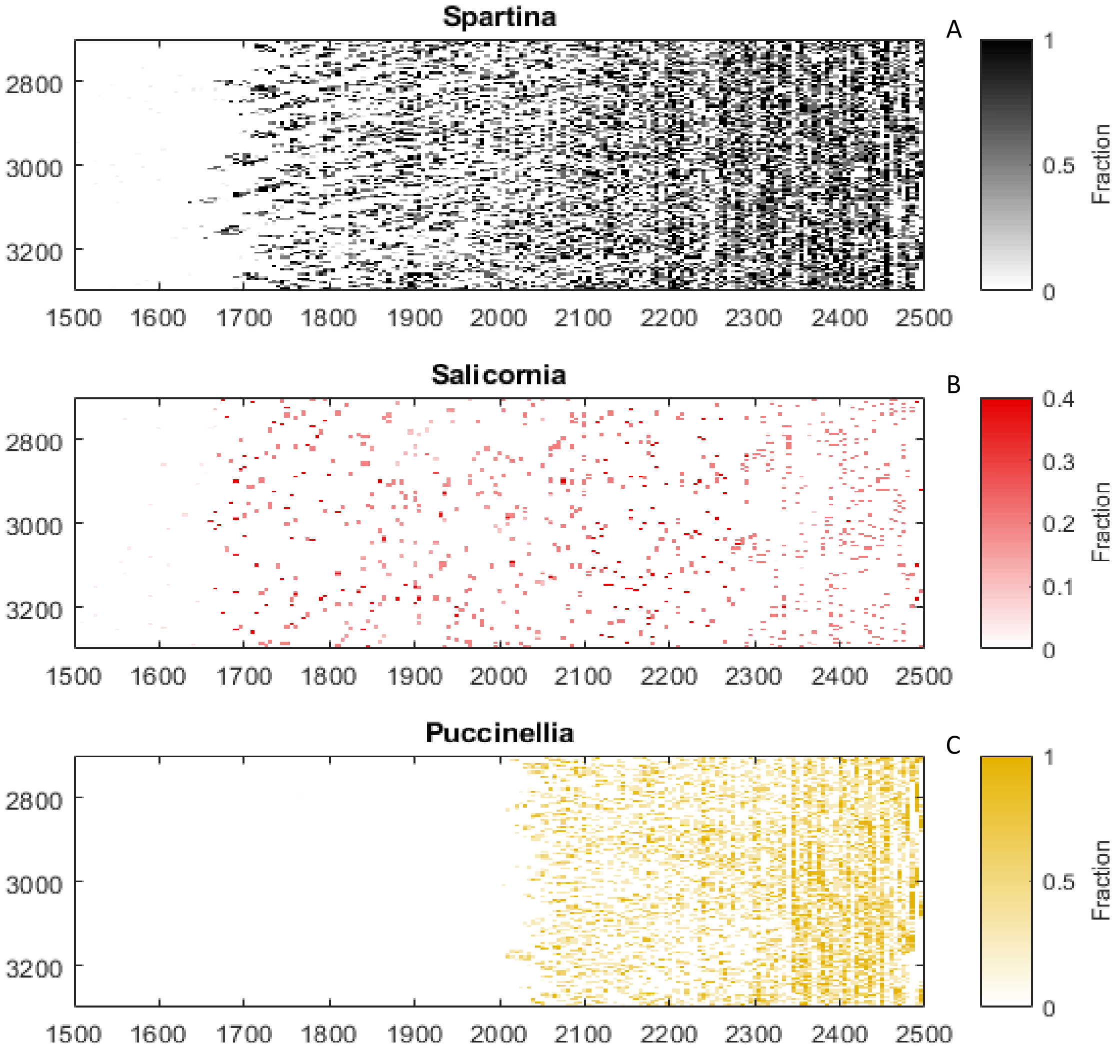

Figure A.1 Vegetation distribution of single species-runs after 30 years

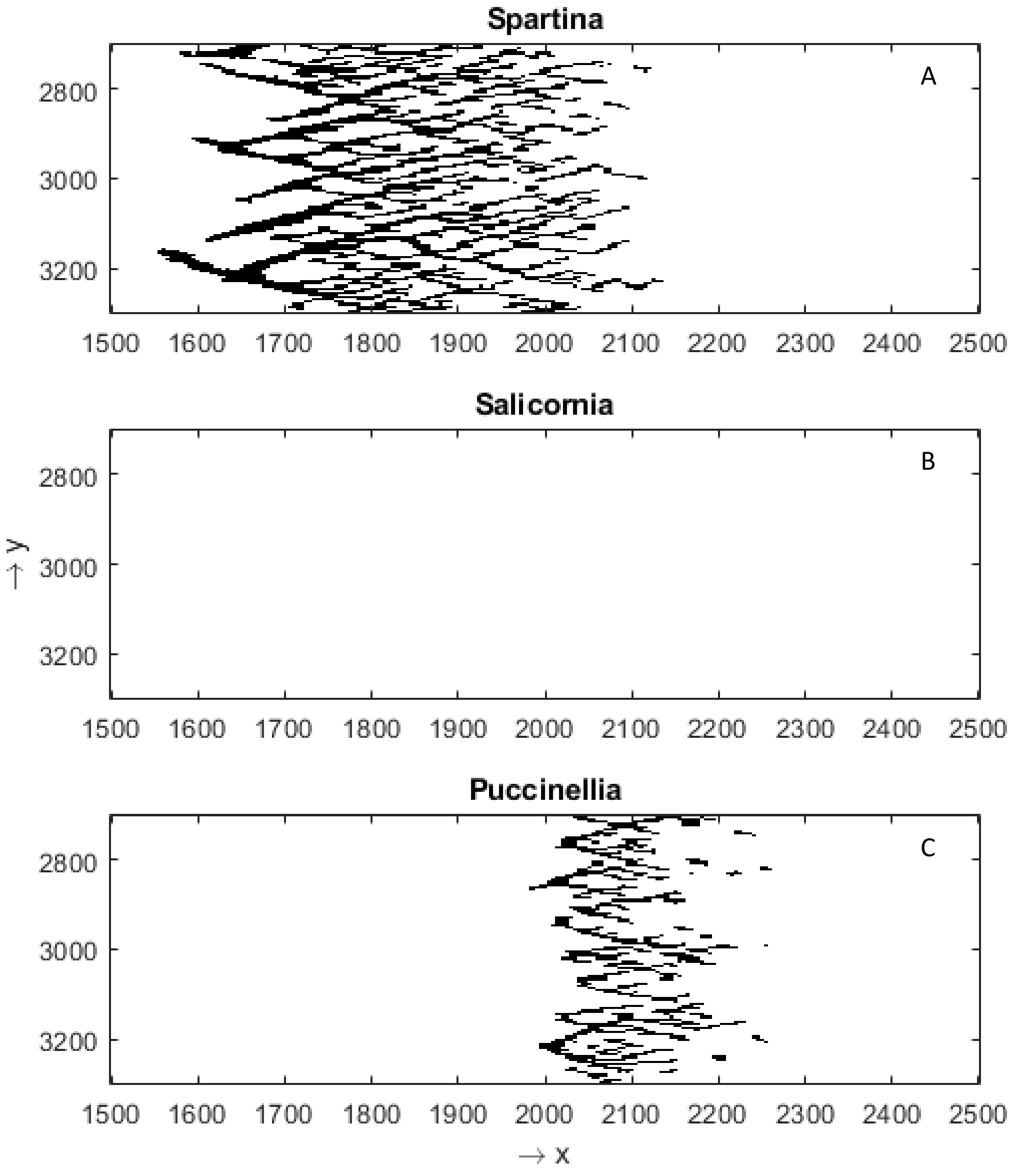

Figure A.2 Extracted channel networks of single species-runs after 30 years

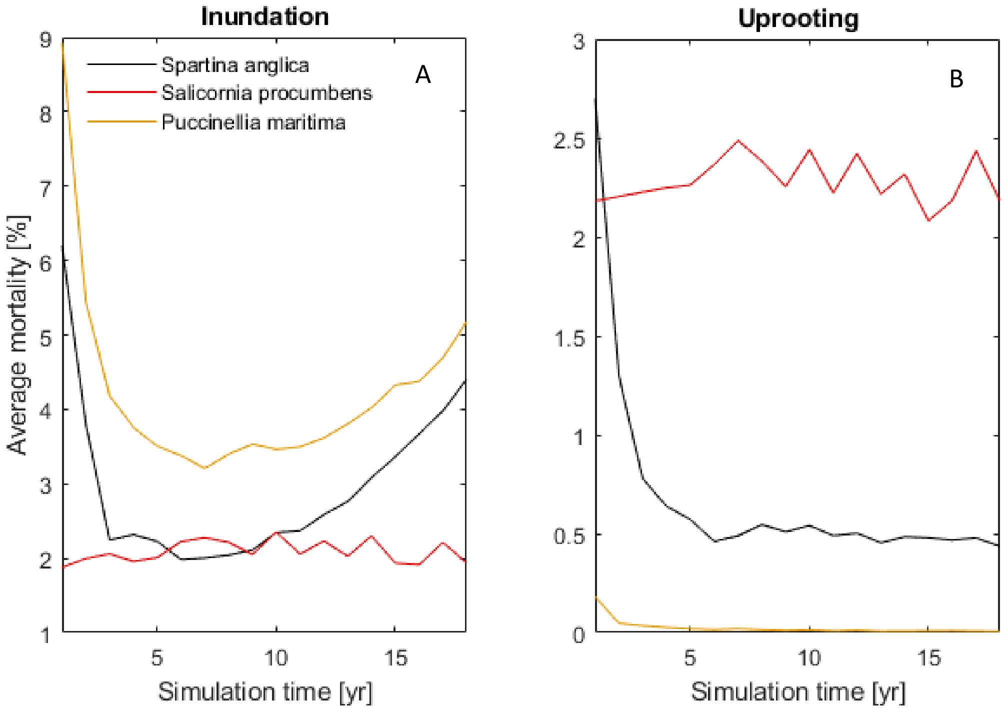

Figure A.3. Average mortality of the three species (single species runs) due to inundation and uprooting (high velocities) per year. The average mortality per year is calculated as the sum of average mortality for each time step. Due to modelling restrictions, mortality can only be plotted for the first 18 years.

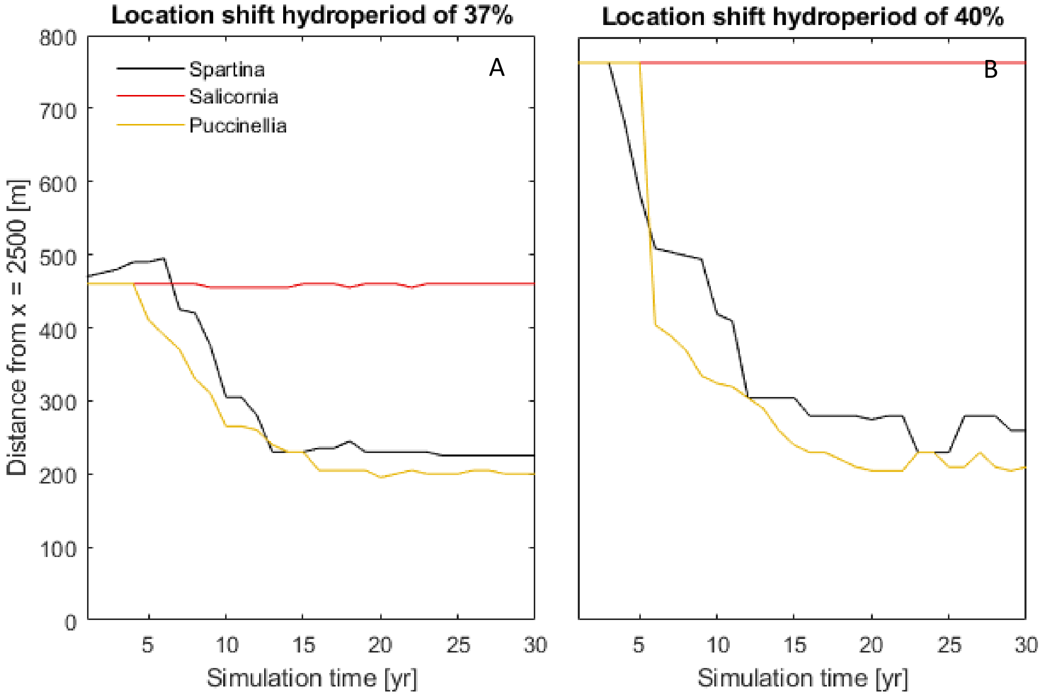

Figure A.4. Location shift of cells with an hydroperiod of 37% (A) and 40% (B). The location is determined as the most landward location in the x-direction, where the average hydroperiod of the column is equal or larger than the respective hydroperiods. These locations are displayed in terms of their distance from the landward boundary of the domain. The values 37% and 40% are chosen because they equal the threshold when respectively *Puccinellia* and *Spartina* start to die as a result from inundation**.**

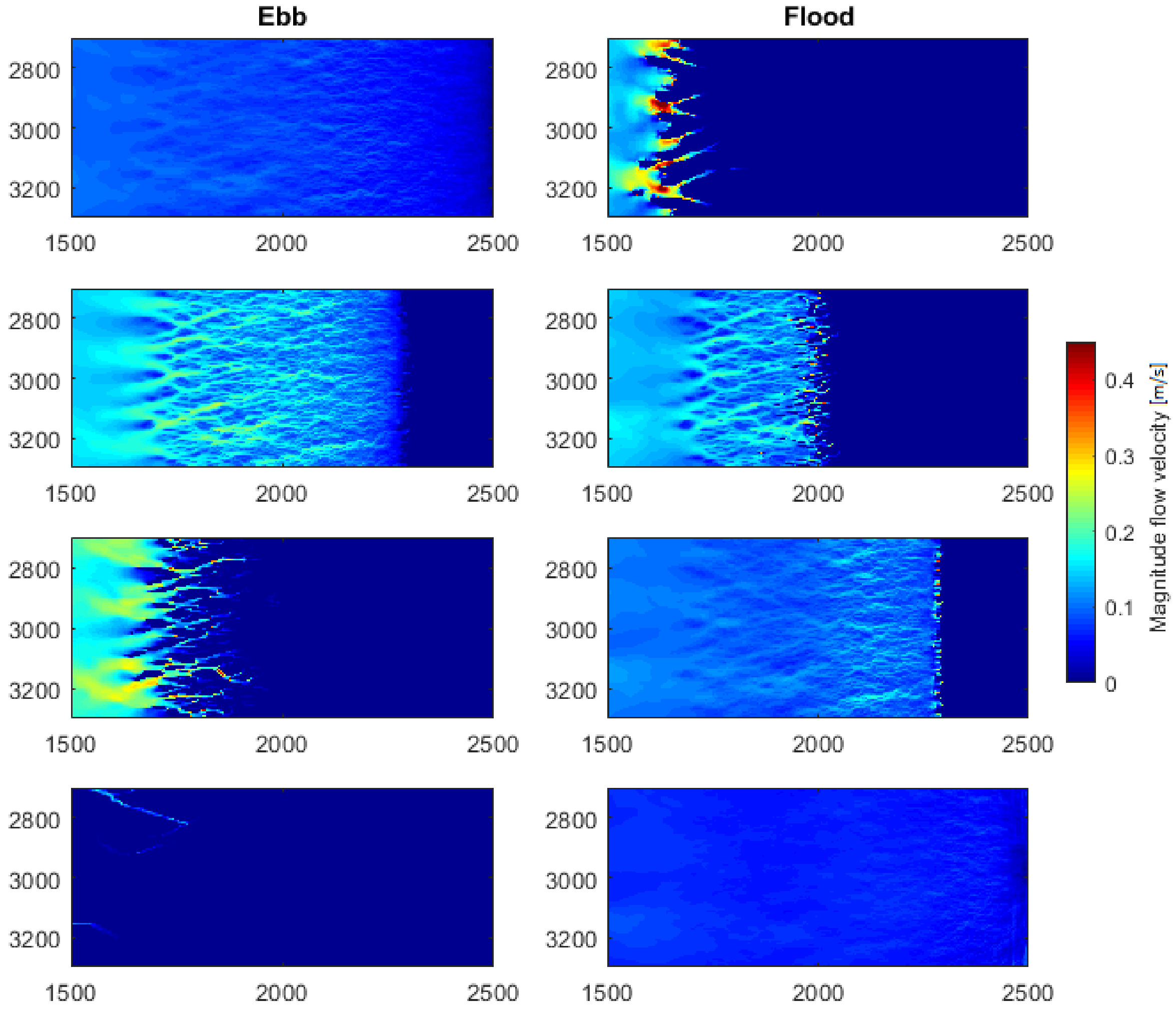

Figure A.5. Flow velocity magnitudes during four successive time steps related to ebb (left) and flood (right) in the presence of *Spartina* after 30 years.

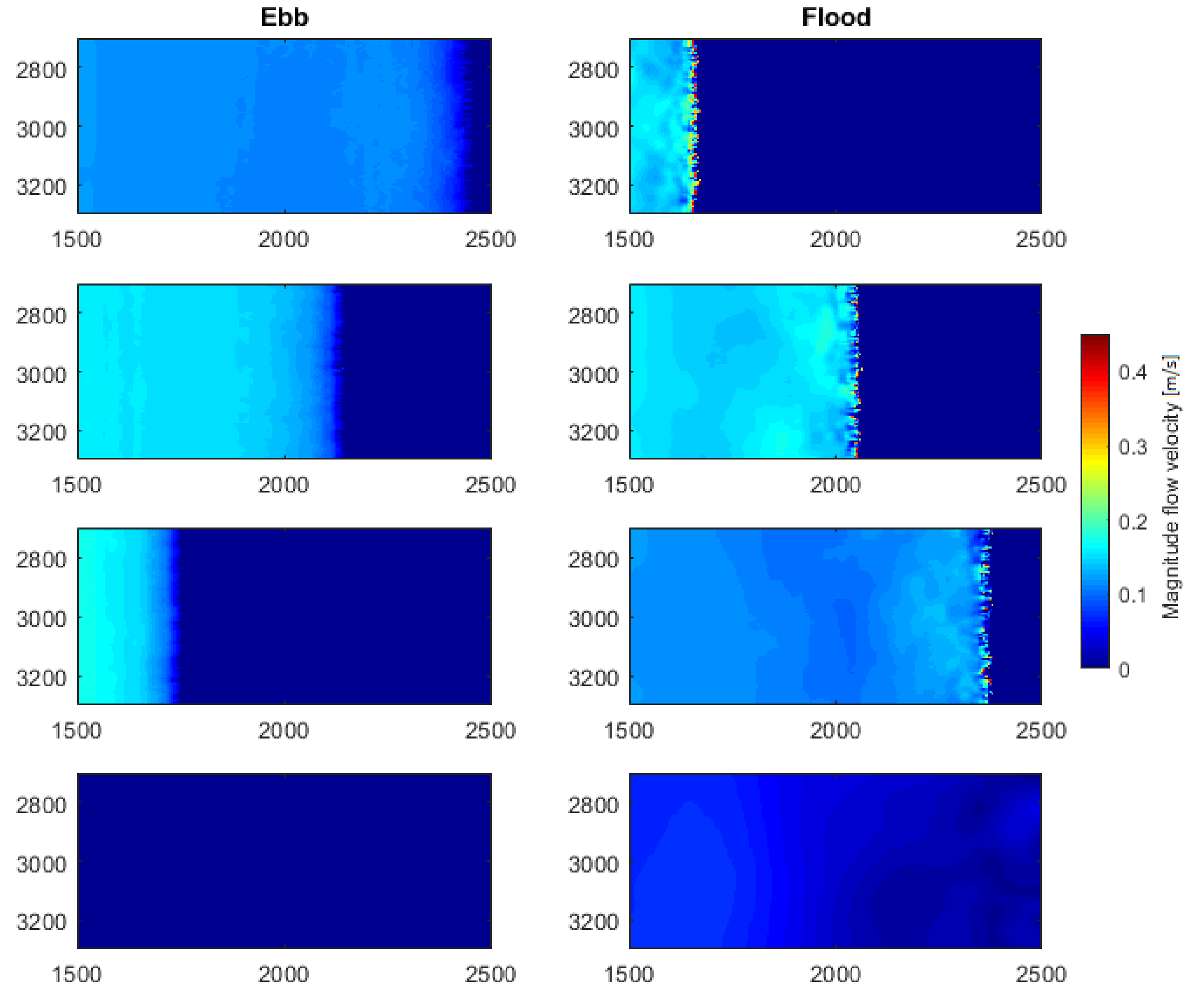

Figure A.6. Flow velocity magnitudes during four successive time steps related to ebb (left) and flood (right) in the presence of *Salicornia* after 30 years. This scenario closely resembles the behaviour of the tides at the initial topography.

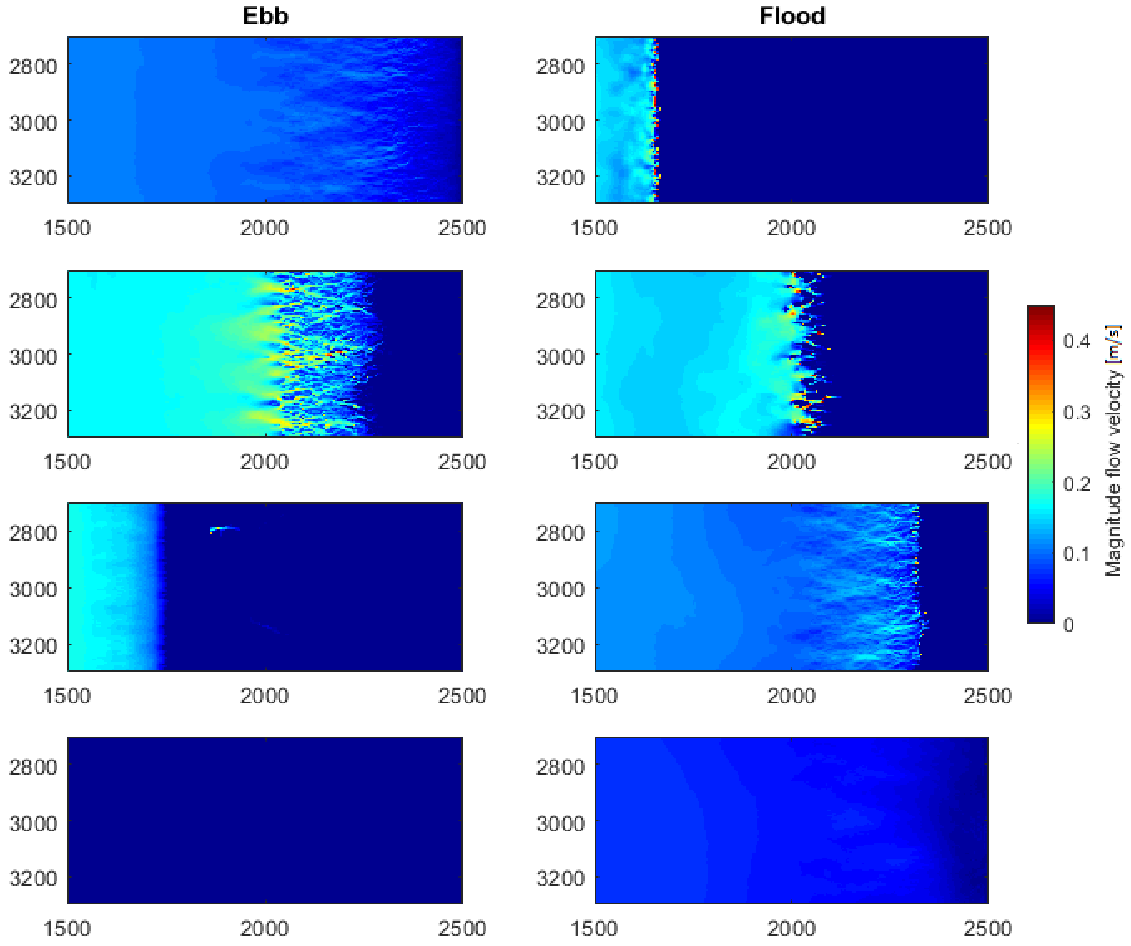

Figure A.7. Flow velocity magnitudes during four successive time steps related to ebb (left) and flood (right) in the presence of *Puccinellia* after 30 years.

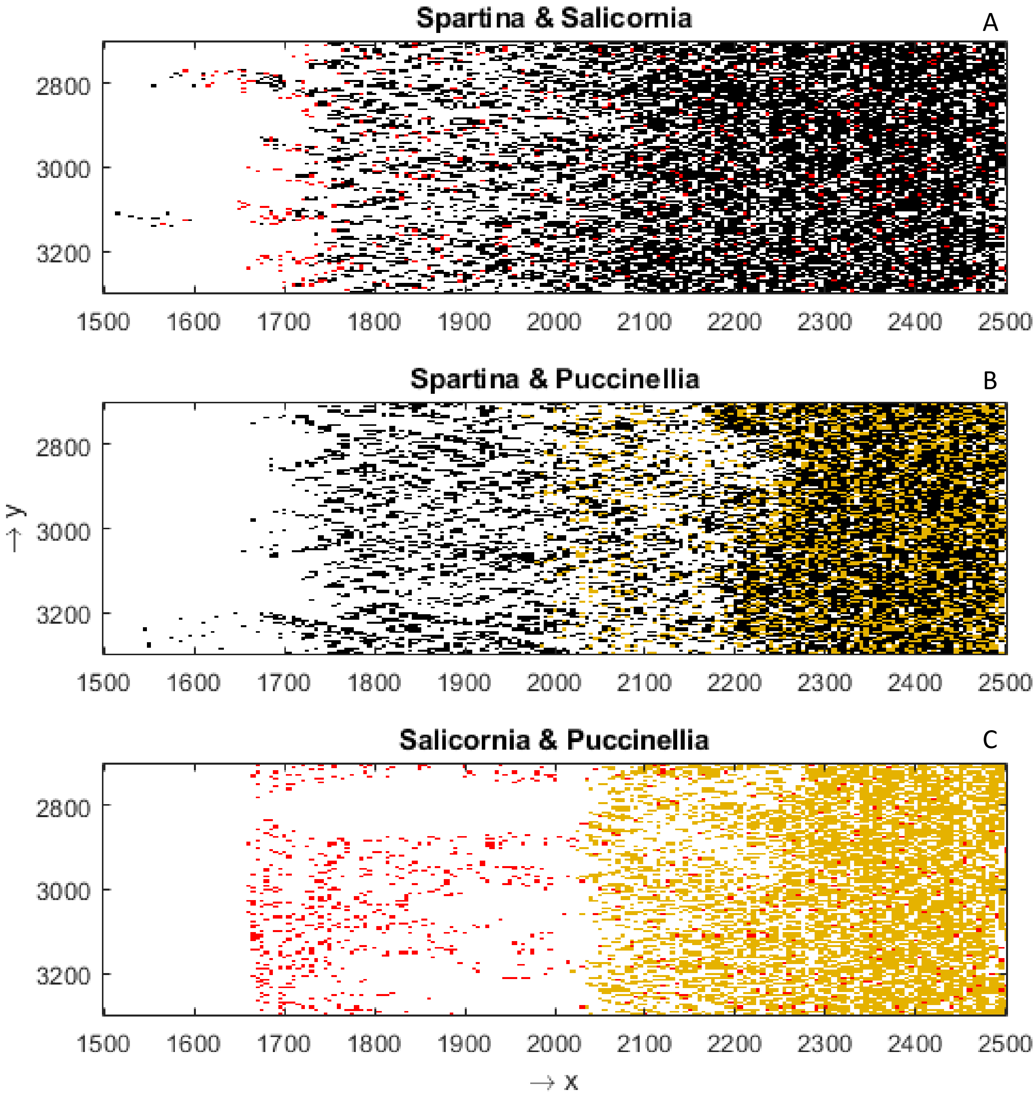

Figure B.1. Vegetation distribution of two-species runs after 20 years.

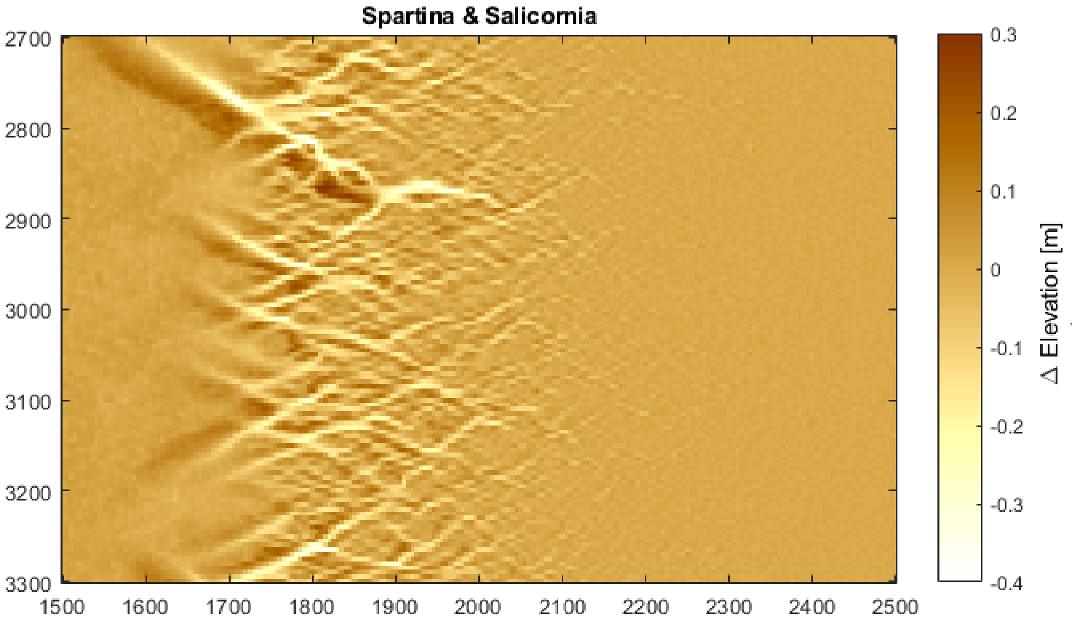

Figure B.2. Bed level change in 21 years of a two species-run with Spartina and Salicornia

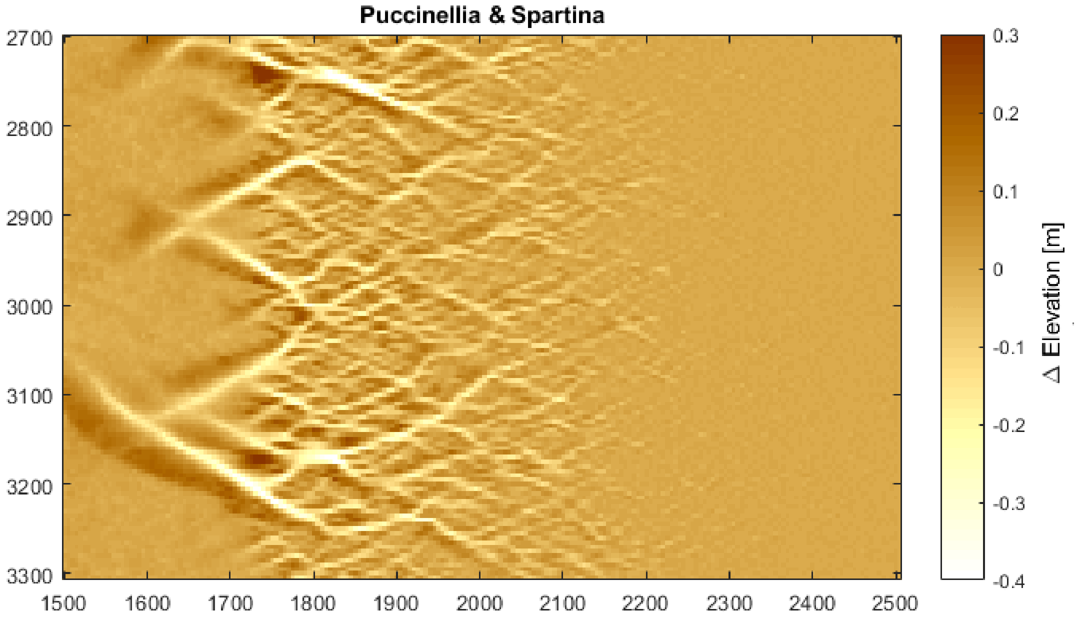

Figure B.3. Bed level change in 21 years of a two species-run with Spartina and Puccinellia

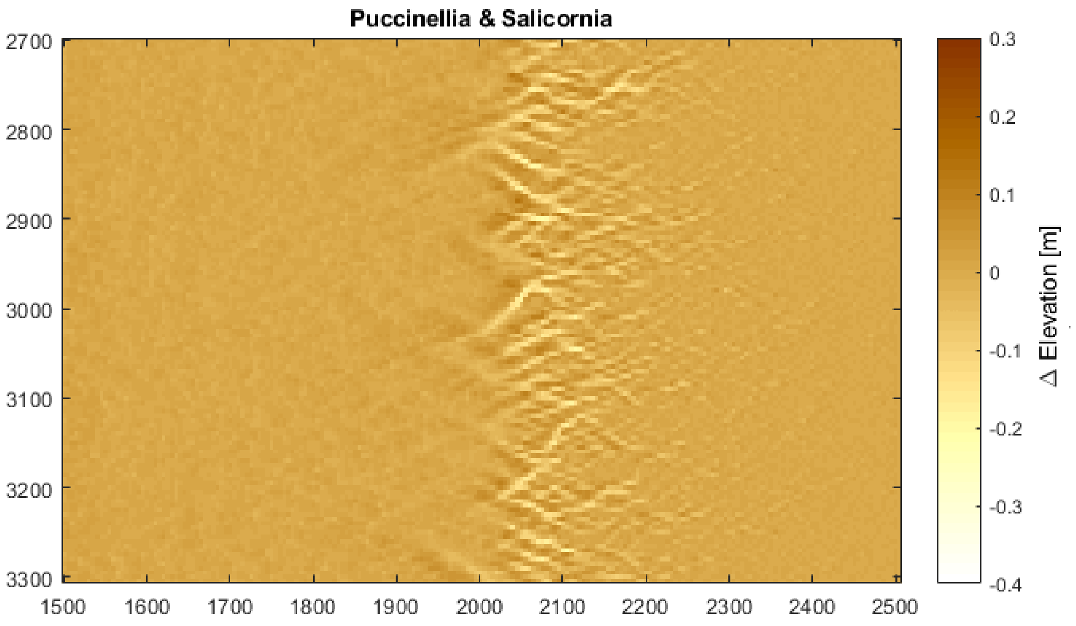

Figure B.4. Bed level change in 21 years of a two species-run with Puccinellia and Salicornia

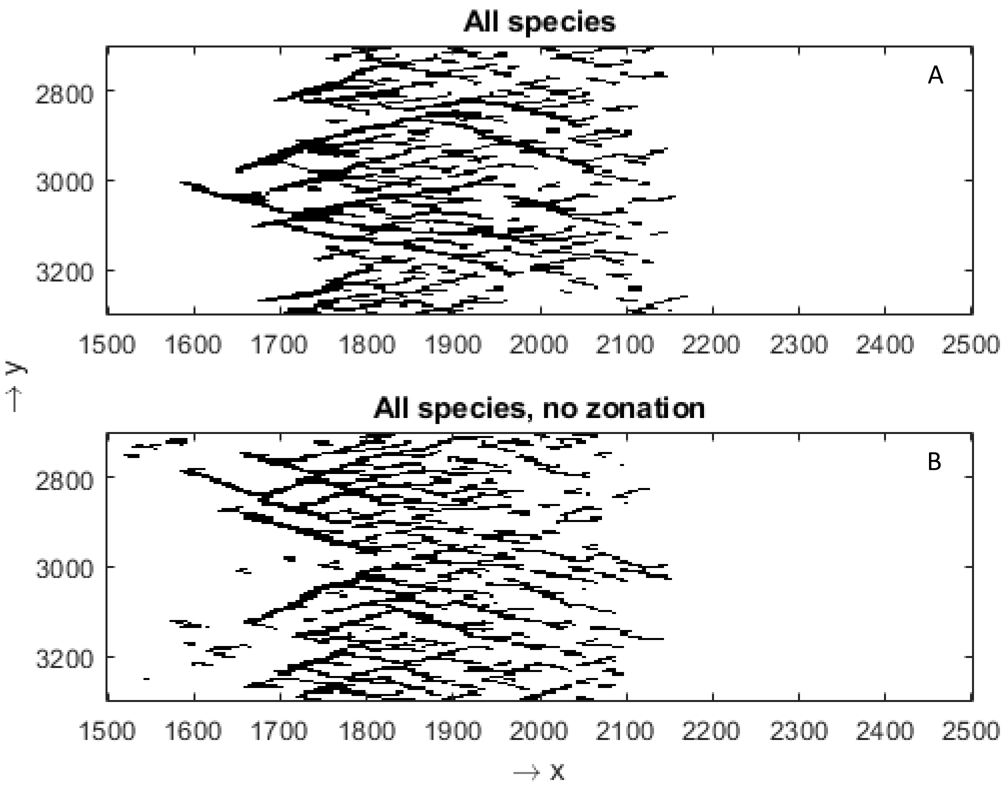

Figure B.5. Channel networks extracted from multiple species-runs with all three species present, whereby the species have a different species-specific flooding sensitivity (A) and an equal flooding resistance (B) after 20 years.

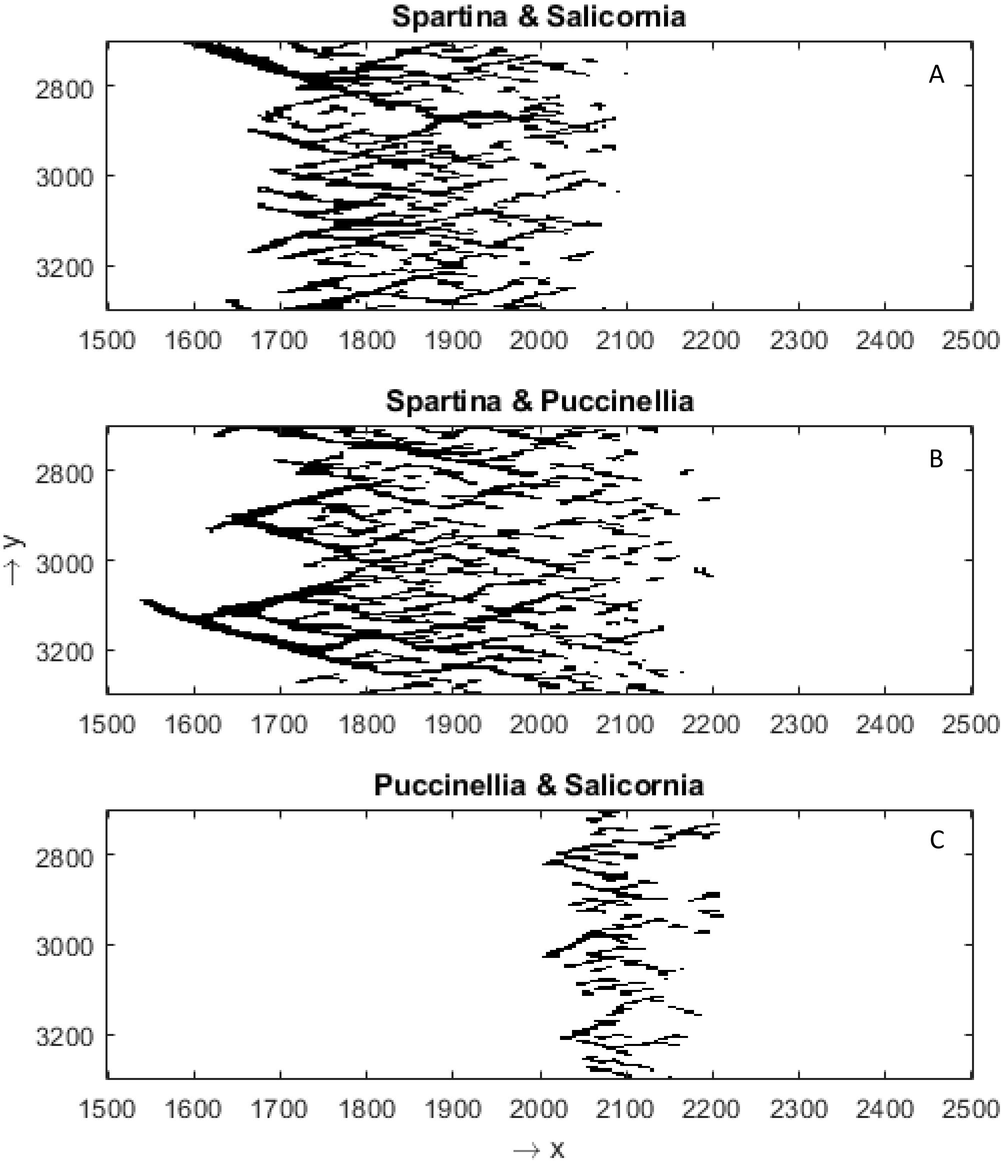

Figure B.6. Channel networks extracted from two species-runs with Spartina and Salicornia (A), Spartina and Puccinellia (B) and Puccinellia and Salicornia (C), after 21 years.

Appendix C: Species shifts (S3- scenarios)

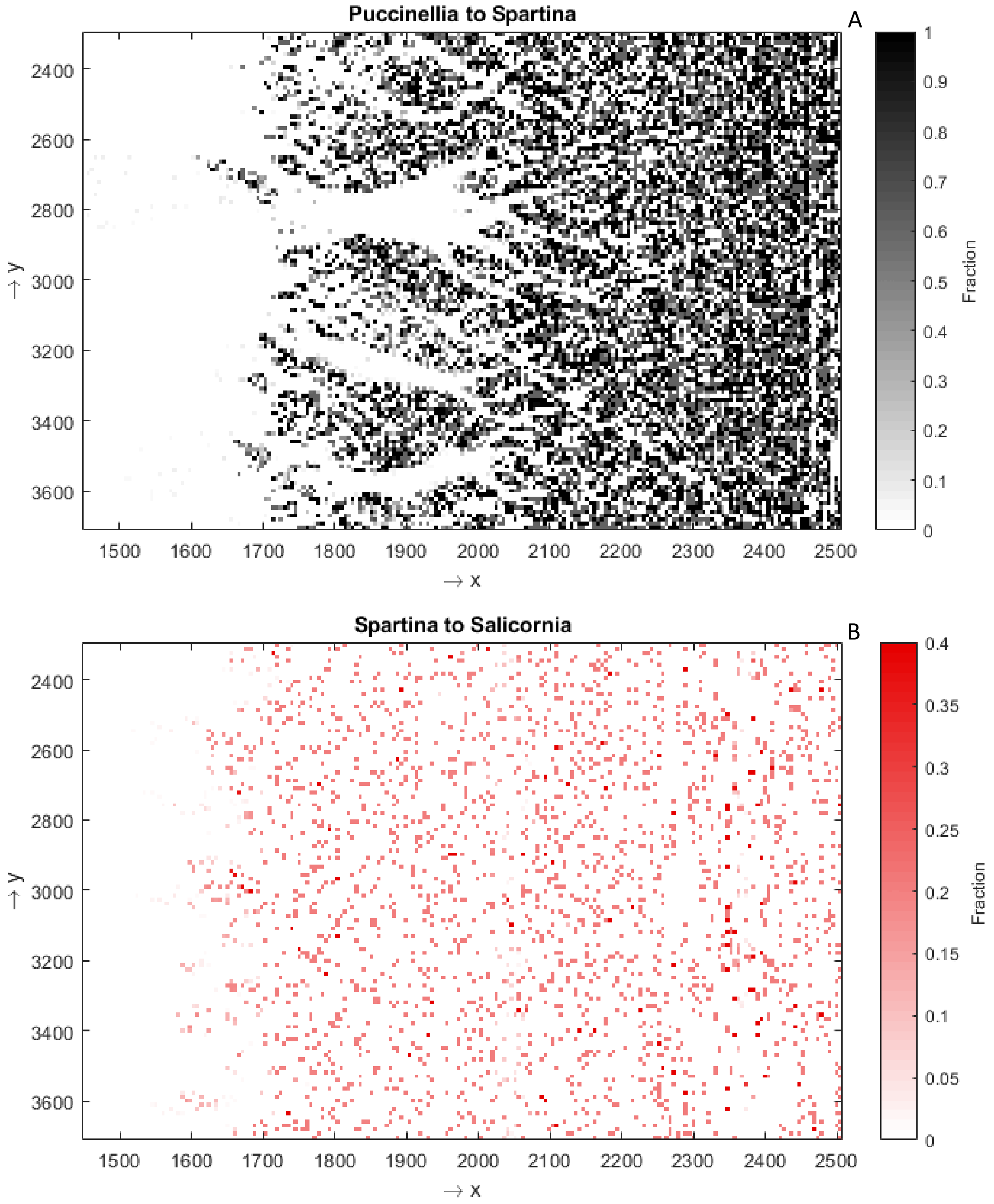

Figure C.1. Vegetation distribution of species shift-runs, 20 year after the shift from Puccinellia to Spartina (A) and from Spartina to Salicornia (B).

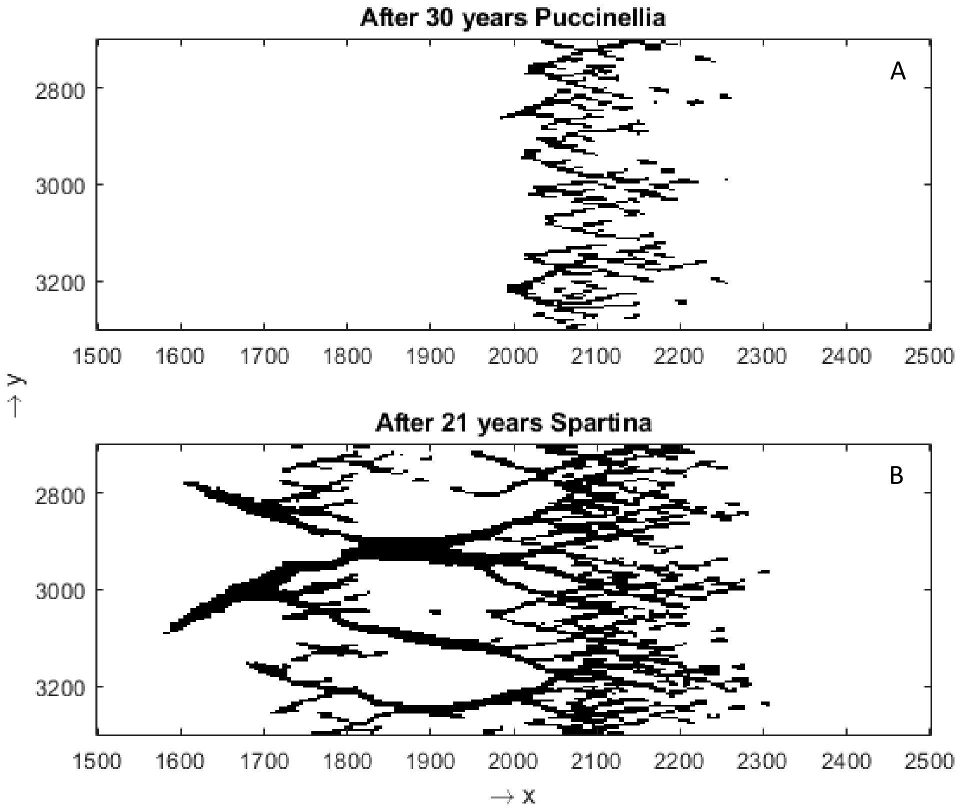

Figure C.2. Extracted channel network just before the shift from *Puccinellia* to *Spartina* (A) and 21 years after the shift (B).

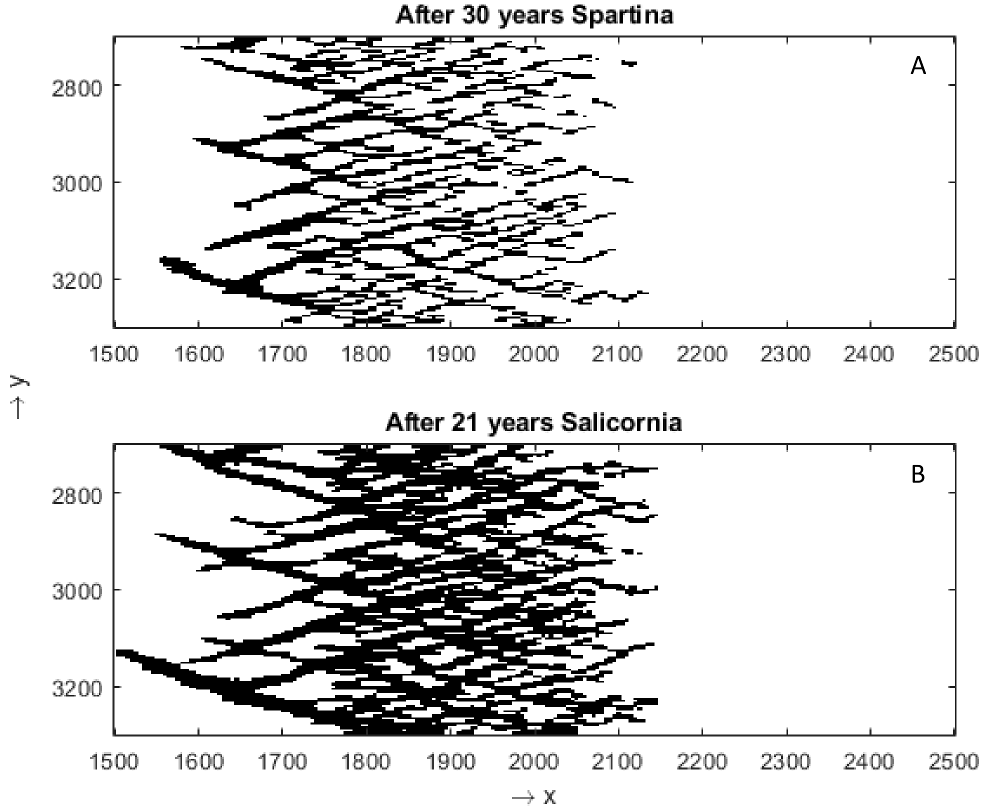

Figure C.3. Extracted channel network just before the shift from *Spartina* to *Salicornia* (A) and 21 years after the shift (B).

Appendix D: Channel extraction tool

```
function Channel = ChannelExtraction(Z, Z0 limit)
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% This function extracts a channel network from a topography, given that
% the initial topography is known, based neighbouring cells with negative
bed level change
%
% INPUT
% Z         matrix of m,n       Final topography
% Z0        matrix of m,n       Initial topography
% limit     value in meters     Amount of cross-stream variation that
defines
%                               the catchment area
%
% OUTPUT
% Channel   matrix of m,n       Channel network with ones at the locations
of channels
%
% I. Bij de Vaate, 2018
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% Calculate bed level change
Sed = Z - Z0;

% Select cells that have a significant negative bed level change
Sed(Sed >= -0.03) = NaN;

% For every remaining location, check if it is not a lonely cell, but has
% neighbouring cells that are also negative
[r,c] = find(~isnan(Sed));
for ix = 1:length(r)
    sumloc = [];

    % Access every location
    for rx = r(ix)-1:r(ix)+1
        for cx = c(ix)-2:c(ix)+2

                % Check neighbouring cells
                % In this case, a subset of 3 by 5 is used because the
                % dominant direction of channels is along stream,
                % this way e.g. circular depressions are excluded
                if rx >= 1 && cx >= 2 && rx <= 121 && cx <= 200
                    if ~isnan(Sed(rx,cx))
                        check = 1;
                    else
                        check = 0;
                    end
                else
                    check = 0;
                end
                sumloc = [sumloc,check];
        end
    end

    % Delete standalone features (e.g. depressions)
    if sum(sumloc) < 5
        Sed(r(ix),c(ix)) = NaN;
    end
end
```

```
% Extract remaining values
Channel = ~isnan(Sed);

% Cut off channels where std is below limit
stdev = std(Z);
loc = find(stdev >= limit);
ll = min(loc);
ul = max(loc);
Channel(:,1:ll) = 0;
Channel(:,ul:end) = 0;

end
```

Appendix E: Additional equations

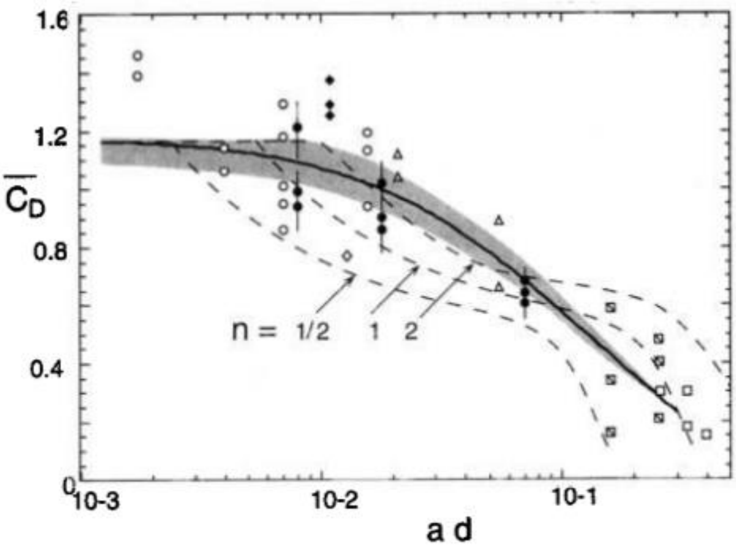

Figure E.1. Relation between drag coefficient and array density (ad) used in a multiple cylinder approach to calculate drag of aquatic plants with a as the vegetation density (calculated with formula E.1) and d the stem diameter (Nepf, 1999).

Equation E.1. Equation to calculate vegetation density (a) based on the number of stems per square meter (n) or relative spacing between stems (S) and stem diameter (d).

$$a = n * d = \frac{d}{S^2} \qquad (E.1)$$