SPATIAL AND TEMPORAL DYNAMICS OF SALT MARSH VEGETATION ACROSS SCALES

A Dissertation

by

DAEHYUN KIM

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2009

Major Subject: Geography

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ABSTRACT

Spatial and Temporal Dynamics of Salt Marsh Vegetation across Scales. (August 2009)

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Chair of Advisory Committee: Dr. David M. Cairns

Biogeographic patterns across a landscape are developed by the interplay of environmental processes operating at different spatial and temporal scales. This research investigated dynamics of salt marsh vegetation on the Skallingen salt marsh in Denmark responding to environmental variations at large, medium, and fine scales along both spatial and temporal spectrums.

At the broad scale, this research addressed the importance of wind-induced rise of the sea surface in such biogeographic changes. A new hypothetical chain was suggested: recent trends in the North Atlantic Oscillation index toward its positive phase have led to increased storminess and wind tides on the ocean surface, resulting in increased frequency, duration, and magnitude of submergence and, hence, waterlogging of marsh soils and plants, which has retarded ecological succession.

At the mid-scale, spatial patterns of vegetation and environmental factors were examined across tidal creeks. Sites closer to tidal creeks, compared to marsh interiors, were characterized by the dominance of later-successional species, higher bulk density, and lower nutrient contents and electrical conductivity. This finding implies that locations near creeks have experienced a better drainage condition than the inner marshes, which eventually facilitated the establishment of later-successional plants that are intolerant to physical stress.

At the micro-scale, this research examined how the extent and mode of facilitation and competition vary for different combinations of plant species along physical gradients. Both positive and negative relationships were spatially manifested to a greater degree on the low marsh than on the mid marsh. This insight extends our current knowledge of scale-dependent interactions beyond pioneer zones to higher zones. On the low marsh, different types of bivariate point pattern (i.e., clustered, random, and regular) were observed for different combinations of species even at similar spatial scales. This finding implies that it is difficult to generalize at which scales competition and facilitation occur.

To conclude, this research stresses the need for a holistic approach in future investigations of salt marsh biogeography. For example, based on results of this current research, it would be meaningful to develop a comprehensive simulation model that incorporates salt marsh ecology, geomorphology, and hydrology observed across scales.

DEDICATION

To my family

ACKNOWLEDGEMENTS

I would like to express my deepest appreciation to my academic advisor, Dr. David Cairns. From the very beginning of my Ph.D. program, he has been my honorable mentor who provided proper guidance and inspirational instruction. Not only this dissertation research but also my general life here at A&M would not have been meaningful without his kind concern, patience, and enthusiasm for what I was interested in. I will forever remember the happy moments when we gathered data together in the field and struggled to write papers.

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My family has been a spiritual home for me. First, I want to thank my beloved wife, Soohyun for her deep love and support. I always miss my brother, his wife, and their baby. Last, my heart is overflowing with gratitude due to the unending love, support, and concern of my mother. I believe that my father is always looking at me from the heaven. This small achievement is humbly dedicated to you, my parents.

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CHAPTER I

INTRODUCTION

1.1 GENERAL OVERVIEW

Biogeographic patterns across a landscape are developed by the interplay of environmental processes operating at different spatial and temporal scales (Delcourt et al. 1983; Malanson 1999). Local scale patterns and processes provide a useful clue to those observed at larger scales that in turn control the former (Wootton 2001; van de Koppel et al. 2006). Key to the success of projecting long-term vegetation dynamics lies in understanding how species behave individually and interactively responding to physical events occurring not only at long-time but also at short-time scales (Delcourt et al. 1983). Although often perceived separately, these multi-spatial and multi-temporal processes are not mutually exclusive. Biogeography is fundamentally concerned with such scale-dependence in which the discipline seeks balanced knowledge on the influence of abiotic processes across spatial and temporal spectrums.

The dynamic nature of hydrologic and geomorphic processes that are the main drivers of plant zonation and vegetation succession in coastal salt marshes makes such locations excellent laboratories for a biogeographic investigation across spatial and temporal scales (Adam 1990). In a broad-scale perspective, long-term sea-level change and subsequent variation in the flooding frequency have conventionally been considered

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This dissertation follows the style of *Annals of the Association of American Geographers*.

the key factor of overall ecological dynamics on salt marsh platforms (Ranwell 1972; Adam 1990; Bakker et al. 1993; Olff et al. 1997; Morris et al. 2002). Zooming in on such platforms finds the presence of tidal creeks, one of the most notable topographic features that create a zonal pattern of plant species across themselves at scales of meters to tens of meters (Adam 1990). The zonation is associated with fluvial-geomorphic tidal creek processes such as sedimentation and cutbank erosion that occur within shorter temporal scales than the gradual, long-term sea-level fluctuation. At a finer scale, rather than abiotic influences (i.e., sea-level variation and tidal creek), species interactions such as competition and facilitation may influence micro-scale patterns in species composition (van de Koppel et al. 2006; van Wesenbeeck et al. 2008). Insights from these various spatial and temporal scales suggest strong scale-dependence in ecological patterns and processes operating in salt marshes.

1.2 RESEARCH OBJECTIVES

In spite of much progress in salt marsh biogeography and ecology at each of these different scales, few attempts have been made to investigate such a multi-scale nature in one single system. Information on scale-dependence in an ecological system is critical if one is to infer reliable pattern-process relationships from ecological data, to extrapolate the relationships to scales beyond which the data were acquired, and to predict how conservation strategies are affected by scale (Wiens 1989; Ludwig et al. 2000). The overall objective of this research is to investigate vegetation dynamics on the Skallingen salt marsh, Denmark responding to environmental variations at broad, medium, and fine scales along both spatial and temporal spectrums.

This research specifically aims to answer the following key questions:

1) At the broad scale, do wind-driven sea-level fluctuations play a significant role in changes of species composition over time?;

2) At the medium scale, does zonal pattern of vegetation across tidal creeks reflect the gradient of cross-streamline edaphic and topographic conditions?; and,

3) At the fine scale, can spatial patterns of vegetation provide insights into interactions among plant species such as competition and facilitation along environmental gradients from outer to inner marshes?

This research attempts to answer the first question using historical data on dynamics of vegetation, sedimentation, and sea level acquired since the early 1930s. Simulation modeling based on these data will illustrate the impact of the wind-driven sea-level change. To answer the second question, floristic, soil, and topographic surveys are performed across various tidal creeks. Ordination techniques (principal component analysis and non-metric multi-dimensional scaling) and Pearson's correlation analysis illustrate how these variables are related. At the fine scale, exhaustive mapping of species, followed by spatial point pattern analysis allows the inference of underlying interactive mechanisms (i.e., competition and facilitation). The results of this research enhance our current understanding of how various ecological patterns and processes are perceived at different spatial and temporal scales. Such a cross-scale insight is of importance to the future scaling attempt on this ecosystem.

1.3 RESEARCH PROCEDURES AND CHAPTER LAYOUT

Figure 1.1 shows the overall research procedures and chapter layout. **Chapter I** contains a general overview of research problems and objectives. **Chapter II** provides a review of the perspectives on previous research and potential knowledge gaps in salt marsh ecology at different spatial and temporal scales. Specifically, the review focuses on a few concepts that are directly related to this research such as succession, environmental gradients, stress, and disturbance. Description of the study area and introduction to methods used are provided in **Chapters III** and **IV**, respectively. In **Chapter III**, the general environmental setting of the Skallingen salt marsh and the history of geomorphic development, sedimentation, sea-level variation, and the North Atlantic Oscillation are explained. In **Chapter IV**, the selection of sampling locations and designs for biotic and abiotic factors at different scales and modeling procedures are discussed, followed by an introduction to subsequent statistical and laboratory analytic techniques.

These introductory parts are followed by chapters of results (**Chapter V**) and discussion (**Chapter VI**). Each of these two chapters consists of three sections for the broad, medium, and fine scale studies, respectively. The last chapter (**Chapter VII**) is a summary of major findings, conclusions, and future research. This chapter is a discussion of how to synthesize insights acquired from the three different scales.

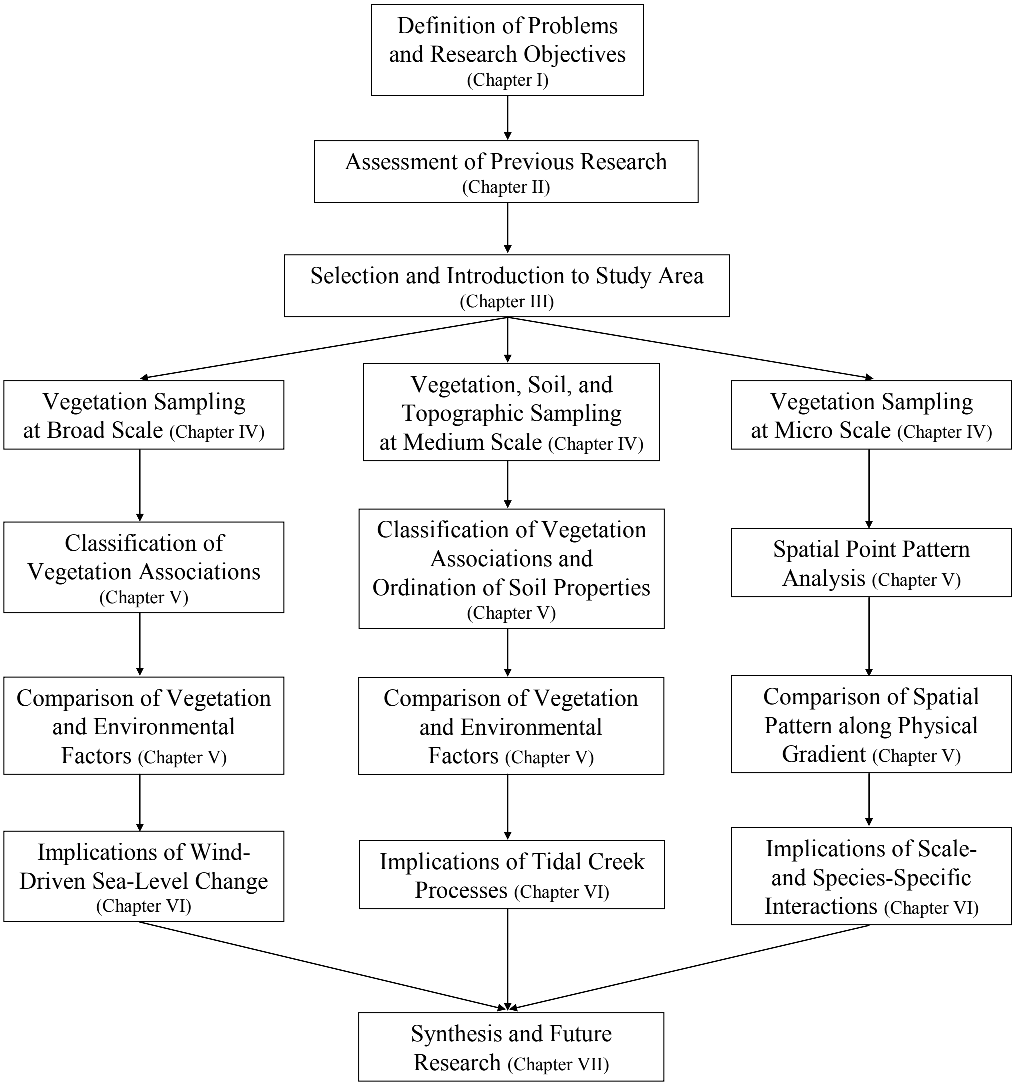


Figure 1.1 Overall research procedures and chapter layout for the study of spatial and temporal dynamics of salt marsh vegetation on the Skallingen salt marsh, Denmark.

CHAPTER II

BACKGROUND: CONCEPTS RELEVANT TO VEGETATION DYNAMICS IN SALT MARSHES

2.1 INTRODUCTION

The biogeography of salt marsh patterns and processes has long been a key focus among coastal ecologists and engineers (Ranwell 1972; Adam 1990). Located at the interface of marine and terrestrial environments, coastal salt marshes show different biotic and physical conditions than those observed in terrestrial ecosystems. The most unique, important condition in salt marshes may be the frequent, direct influence of saline water. This effect is related to a submergence regime that controls the rate of suspended sediment accumulation and the biological success of individual plant species (Ranwell 1972; Adam 1990; Morris et al. 2002). Since the regime of sea water flooding is a function of the surface elevation, there should be spatial heterogeneity, or a gradient of physical and floristic factors across a marsh platform (Bakker et al. 1993; Sánchez et al. 1996; Olff et al. 1997).

This research focuses upon the causal chain between vegetation dynamics and flooding by sea water, and also how their relation plays out over space. This chapter accordingly aims to review previous studies on these foci at different spatial and temporal scales. Section 2.2 provides a background concerning key concepts relevant to this research. Specifically, these are ecological succession, vegetation distributions along environmental gradients, and comparison of stress and disturbance. Section 2.3 then discusses the current state of knowledge on salt marsh biogeography at broad, medium, and fine scales to identify potential knowledge gaps that are the major springboard for this research.

2.2 PREVIOUS VIEWS ON KEY CONCEPTS

2.2.1 Succession in ecological systems

Succession is one of the most frequently used and intensively studied fundamental concepts in biogeography and plant ecology (McIntosh 1981, 1985). Through the 20th century and continuing until today, succession theory has provided a predictive tool and organizational scheme for biogeographers and ecologists (Peet and Christensen 1980). However, due to a variety of perspectives and even definitions of succession proposed, there has been inevitable confusion in the use and application of this concept (Pickett 1976; Huston 1994; McCook 1994). Such confusion may further cause a difficulty in the selection of appropriate traditional perspectives and theories that can be applied to what is observed on coastal salt marshes through time. A thorough, detailed review on ecological succession is beyond the scope of this research. Rather, this section introduces previous views that are potentially applicable to salt marsh biogeography.

A summary of previous literature suggests that, in the broadest sense, ecological succession can be defined as the directional, continuous change in the species composition of natural communities that results from modification of the ambient physical conditions at a given area through time. It has been suggested that there are two major causes of succession (Barbour et al. 1987; Huston 1994): 1) changes in species composition resulting from modified environments that are primarily caused by the activities of the organisms themselves (i.e., autogenic succession; Tansley 1935); and 2) changes in species composition resulting from major environmental transitions beyond the control of the organisms (i.e., allogenic succession).

Three major perspectives are of particular interest in this research (Figure 2.1). First, Clements (1916) argued that ecological communities are equivalent to 'super-organisms' that are capable of self-directed development (i.e., succession) toward an inevitably fixed final, stable stage, or 'climax'. He further proposed that succession proceeded through various discrete stages, a view which was criticized by his contemporaries such as Gleason (1927, 1939) and Egler (1954). The Clementsian view of succession is closely related to the concept of 'relay floristics' (Egler 1954; McCormick 1968). The concept assumes the significance of facilitative effects in which species of an early-seral community modify the ambient physical conditions, such that the habitat becomes more favorable to the growth of plants in the following successional stage. This process often creates quite distinct, sharp zonal patterns of vegetation, for instance, as observed by Sharitz and McCormick (1973) from a study on rock outcrops in the foothills of the southern Appalachians. There was a scattered distribution of small islands of vegetation (3-5 m in diameter) over their study area (Figure 2.2). Each of these islands consisted of concentric zones of different successional communities. From the outermost (bare rocks) to the innermost (deeper soil) parts, the zonal pattern is as follows: mosses and lichens → annuals (*Sedum smallii*)→ herbaceous (*Minuartia uniflora*) and woody perennials.

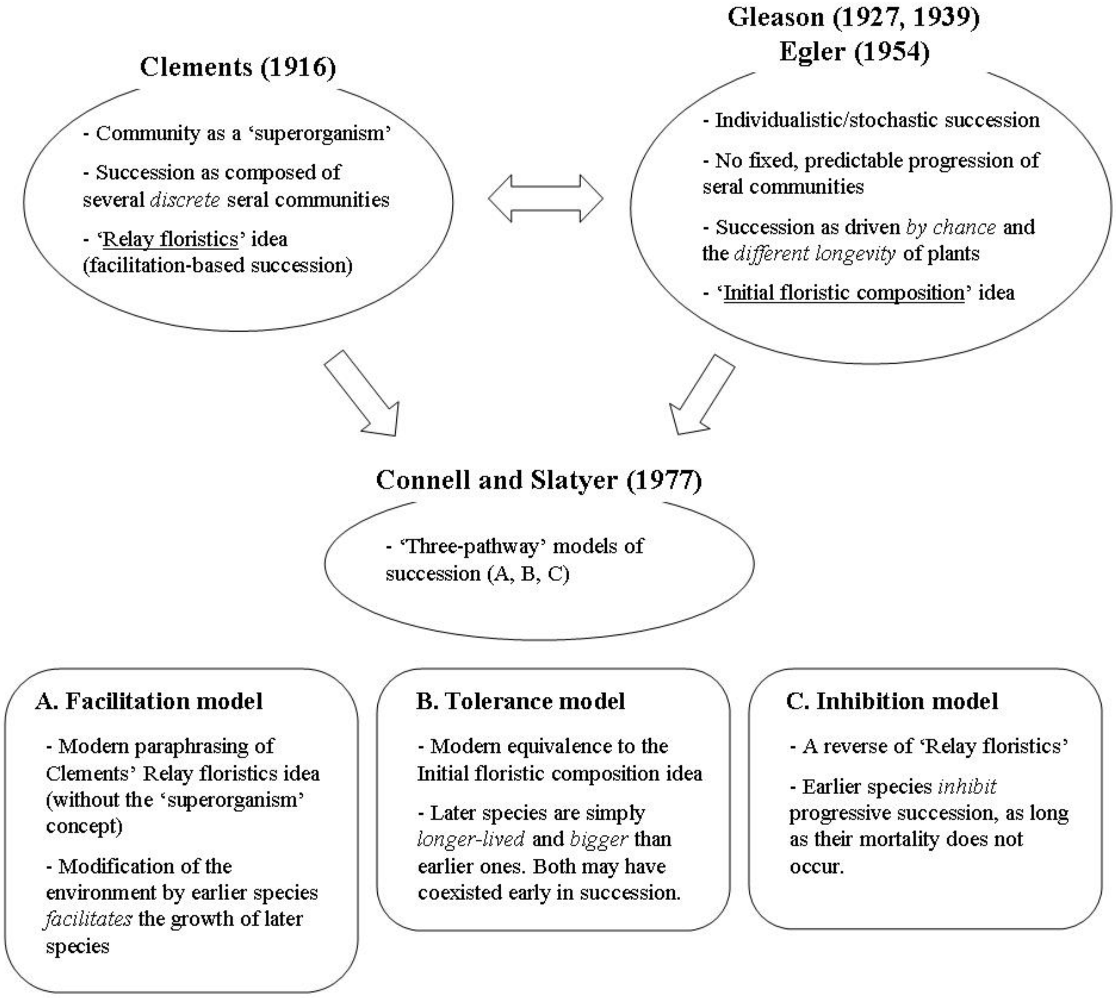


Figure 2.1 Selected major perspectives on ecological succession.

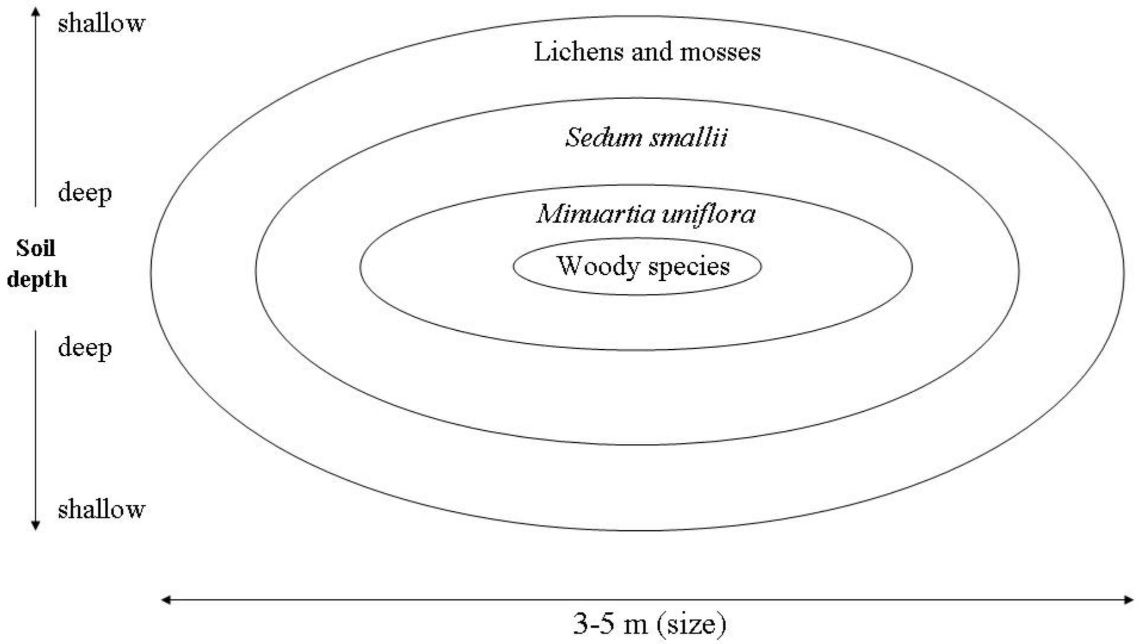
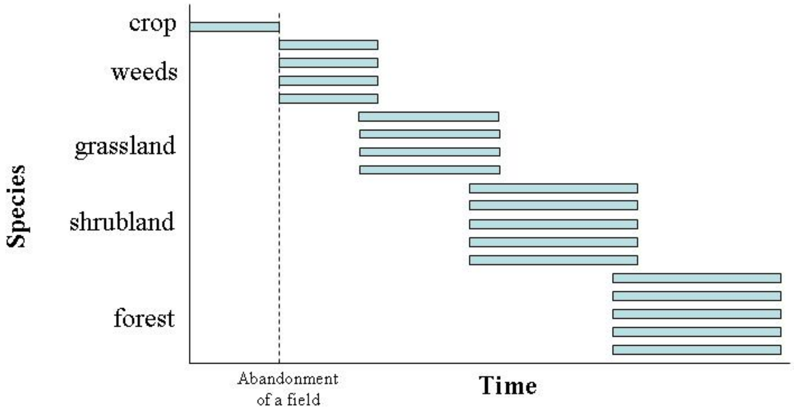


Figure 2.2 A schematic view of zonal pattern of vegetation on the rock outcrops in the southern Appalachians (redrawn from Sharitz and McCormick 1973).

On the other hand, Gleason (1927, 1939) and Egler (1954) argued that groups of species do not appear or disappear together, and that the course of succession cannot always be predictable. Rather, they advocated a view that succession is a stochastic process, or occurring by chance and by the differential growth rate and longevity of plant species. Such a view is based on an assumption that species of all seral stage are present from the initial floristic composition (Figure 2.3). Some of them (i.e., pioneers) may germinate and become dominant rapidly, while others (i.e., intermediate-sere species) also germinate quickly, but grow slowly for a longer period of time. Other late-sere plants become established even later. However, Egler (1954) still implied that any successional pathways may involve both processes of relay floristic and initial floristic composition.

These opposing views on succession of Clements (1916) vs. Gleason (1927, 1939) and Egler (1954) were all accommodated by Connell and Slatyer (1977) who suggested three major modes of ecological succession: facilitation, tolerance, and inhibition (Figure 2.1). The three models imply different mechanisms of vegetation succession, but there is a clear dichotomy that distinguishes the first facilitation model from the others. The facilitation model is similar to the relay floristics of Clements (1916) in that pioneer species invade a disturbed field and gradually make a favorable environment for later-sere species. Both facilitation and relay floristics models dictate that the modification (i.e., amelioration) of environmental conditions is necessary for the establishment of late-successional plants. They also assumed that propagules of intermediate and late-seral species are not present and not recruited in early stages of succession (see also

a. Relay floristics



b. Initial floristic composition

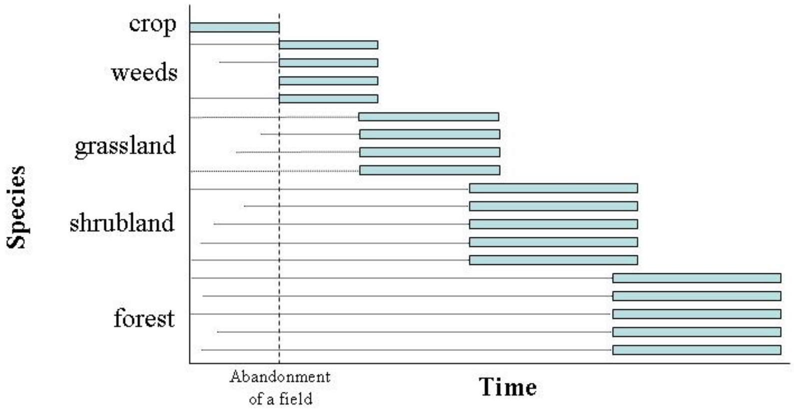


Figure 2.3 A comparison of relay floristics (A) and initial floristic composition (B). Dotted lines imply that seeds of the associated species have been present before the abandonment of the field (redrawn from Egler 1954). Horizontal bars indicate the dominance of associated species.

Figure 2.2A). However, Connell and Slatyer (1977) did not accept the concept of Clementsian ‘super-organism’ in their facilitation model.

Tolerance and inhibition models, on the other hand, assume that propagules of both earlier and later species exist in early years of succession after a system is disturbed as Egler’s initial floristics idea suggested. However, tolerance and inhibition models differ in terms of the growth ability of later successional plants. In the tolerance model, even under the dominance by earlier successional species, later species are able to grow to maturity because they can tolerate and survive in low-resource conditions of the initial stage of succession. Later species, in this regard, are considered superior to earlier ones in terms of the longevity and tolerance. Last, the inhibition model assumes that all species resist the invasion of others. Replacement can occur only when the earlier dominants die or are damaged, releasing space and resources.

On salt marshes, ecological succession is generally associated with a positive feedback in which the presence of vegetation increases sedimentation, which in turn facilitates plant growth due to lowered tidal inundation, salt stress, and edaphic amelioration (Bertness et al. 1992; Srivastava and Jefferies 1995; van de Koppel et al. 2005). As sedimentation and elevation increase, this feedback process facilitates the establishment and growth of later successional species by further reducing the physical stress associated with regular inundation by sea water. Competitive exclusion of earlier species by later competitors would then occur, once the later species begin to establish.

Such a positive feedback suggests that ecological succession on salt marshes can be explained as driven by both autogenic and allogenic processes. Also, I suggest that the facilitation model of Connell and Slatyer (1977) may be relevant to the successional processes on salt marshes, rather than their tolerance and inhibition models. The last two models, as mentioned, assume that both early- and late-successional species coexist from the initial stage of ecosystem development with some doing better than others. On salt marshes, however, late-successional communities hardly occur on low areas with very frequent sea water inundation until pioneers modify physical conditions, while the initial growth of pioneers on high sites is hampered by later-successional species (Pennings and Callaway 1992; Bertness and Shumway 1993; Emery et al. 2001).

However, the attempt of this current research to link the facilitation model and succession on salt marshes does not entirely advocate the idea of relay floristics. There is an overlapping of plant species with different successional phases in a given area with some showing higher cover than others on many salt marshes (e.g., Olff et al. 1988; Adam 1990; Bakker et al. 1993). Such a pattern indicates that there cannot be any fixed or predictable pathway of succession with several discrete seral communities, or 'super-organisms'.

Since the concept of retrogressive succession bears significant implications for the later part of this research, theoretical, but brief background on this term is provided here. Traditionally, beginning from Nilsson (1899), biogeographers and plant ecologists have recognized that both progressive and retrogressive successions are common in many ecosystems (e.g., Cowles 1911; Tansley 1916; Gleason 1927; Phillips 1934). In the simplest manner, retrogression can be understood as a change in species composition toward a phase that characterizes earlier stages of ecosystem development than currently seen. It involves a decline in complexity of structure (e.g., species richness) and ecosystem productivity that is associated with a reduction in soil nutrient availability (Walker and Reddell 2007).

On salt marshes, various causes of retrogressive succession have been investigated such as grazing (Bakker and Ruyter 1981; Bakker 1985), surface undermining by tidal creek processes (Chapman 1940), and mean sea-level rise (Leendertse et al. 1997). It is known that grazers lead to retrogression by selectively suppressing the dominance by later-successional plants, while earlier species tend to be more tolerant to them (Jensen 1985a). Erosion along tidal creeks and mean sea-level rise are believed to increase the frequency of submergence at a given location, thereby facilitating the transition toward an earlier phase than the current state. The later part of this research at the broad scale will be devoted to providing an alternative explanation to the conventional view that this long-term, gradual rise of sea levels has been the key driver of the increased flooding regime and retrogressive (or retarded) succession.

2.2.2 Spatial gradients and zonation of biogeographical patterns and processes

The temporal gradient in physical conditions and the resultant floristic changes was discussed in the previous section (2.2.1). In many ecosystems, on the other hand, there is apparent regularity, or zonation in the spatial arrangement of vegetation, mainly driven by underlying spatial gradients of biotic and abiotic processes. It is noteworthy that both succession and spatial gradients/zonation have been closely related each other, invoking much interest among plant ecologists. For example, Cowles (1899) developed one of the original concept of vegetation dynamics based on the presumed correspondence between spatial zonation in community structure along an environmental gradient and the temporal changes.

Huston (1994) defined a spatial gradient as:

> ‘a change in the value of a particular parameter, such as temperature, soil pH, or species composition, over space and is generally characterized as change along a linear distance’.

In the context of individual-based ecological theory (Whittaker 1975), Huston (1994) also argued that:

> ‘…… zonation is a spatial sequence of species replacements along a spatial gradient of environmental conditions, just as succession is a temporal sequence of species replacements resulting from a temporal gradient in environmental conditions’

In short, concepts of the spatial gradient and zonation cannot be considered separately, but rather should be synthesized in the framework of pattern-process relations. This section introduces major causes of spatial gradients and zonation to assess how traditional perspectives and theories on these concepts provide insights into the understanding of salt marsh biogeography.

In the most general sense, patterns of spatial zonation are divided into two types: 1) zonation caused by temporal asynchrony of biotic processes (i.e., successional zonation); and 2) zonation caused by spatial variation of environmental conditions (see Huston 1994). In the first case, it is considered that different zones in an ecosystem exist simply due to the presence of different temporal phases of the same successional sequence. This view assumes that if a long enough time is guaranteed, all zones would experience the same successional pathways toward the same final state. The final state implies the disappearance of zonal pattern, and consequently the homogeneity in vegetation pattern across the system. However, this process of zonation does not exclude the presence of allogenic effects in the system. Classic examples have been often reported from riparian systems where active meandering of streams causes erosion and accretion of the eroded sediments, which in turn creates a new site for succession at discrete intervals (Weaver 1960; Viereck 1970; Salo et al. 1986; Walker et al. 1986).

In the interior of meander loops of these systems, sequential formation of zones with different stages of succession occurs as sedimentation, and thus the creation of new sites continue. The zones illustrated in Figure 2.4 have been produced by a typical combination of allogenic (fluvial-geomorphic channel processes) and autogenic (temporally different successional phases) processes. However, if enough time and no absence of significant disturbances that reinitiate the succession are conferred, these zones would gradually disappear over time.

Zonation created along spatial gradients of different combinations of environmental factors may be the most common in natural communities. One clear difference between the two types of zonation (i.e., one by temporal asynchrony vs. another by variation of physical conditions) is that, unless such environmental factors become uniform, so the physical gradient disappears, vegetation at different zones would not converge to the homogeneous vegetation cover. Austin (1980) and Austin and Smith (1989) proposed three major types of physical gradients: 1) resource gradients; 2) direct gradients; and 3) indirect gradients.

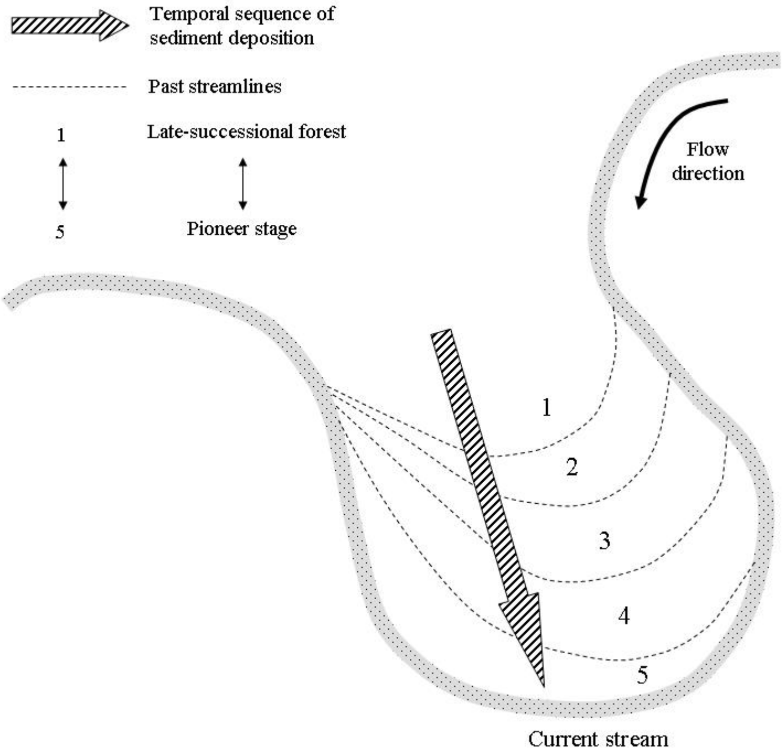


Figure 2.4 A schematic view of zonation driven by temporal asynchrony of biotic processes in riparian ecosystems.

The resource gradients indicate the spatial gradient of properties that are *consumed* and often depleted locally by plants for their growth. These properties include light, water, and mineral nutrients. The direct gradients, on the other hand, are the spatial gradient of properties that regulate physiological processes, but are not consumed or incorporated into the body of plants. Thus the direct gradients are also called regulator gradients (Huston 1994). Air temperature and soil pH are major sources of such a gradient.

In a more general sense, another gradient is considered to influence spatial zonation of vegetation: a complex gradient that is equivalent to a 'factor-complex' gradient (Whittaker 1973) and 'indirect gradient' (Austin 1980; Austin and Smith 1989). Altitude, latitude, and distance from the streamline may be exemplar indicators that do not directly control the growth of plants, but are correlated significantly with various resources and regulators.

Salt marsh platforms are characterized by strong spatial gradients and the resultant zonation of different abiotic and biotic components (Ranwell 1972; Adam 1990). First of all, the gradient of the surface elevation may be the most important physical factor because it directly regulates the frequency and depth of submergence of the system (Sánchez et al. 1996; Olff et al. 1997). Such a major gradient would in turn yield the gradient/zonation of soil properties and plant species. It is therefore considered that in general salt marsh platforms show typical examples of 1) factor-complex gradients of the surface elevation that affect the spatial pattern of edaphic and hydrological conditions, and consequently 2) plant zonation caused by spatial variation of environmental conditions.

However, zooming in on such marsh platforms finds the presence of tidal creeks, often characterized by active meandering that creates point bars and cutbank edges by sedimentation and erosion, respectively. Thus, the formation of a point bar and its gradual expansion over time along tidal creeks on salt marshes can be a good example of the zonation developed by temporal asynchrony of biotic processes as illustrated in Figure 2.4. In short, spatial gradient and zonation of abiotic and biotic factors in the salt marsh ecosystem should be understood in terms of the combination of various types of agents such as the elevation gradient and temporal asynchrony associated with tidal creek processes.

2.2.3 Comparison of stress and disturbance

The terms, stress and disturbance have been widely and frequently used among biogeographers, but it is difficult to define them since most ecological systems are probably always in a non-equilibrium state during their course of continuous adjustment to dynamic physical conditions (Archer and Stokes 2000). In one of the frequently cited definitions, White and Pickett (1985) argued that disturbance is a relatively discrete environmental fluctuation or a destructive event in time that disrupts ecosystem, community, or population structure by modifying resource availability or physical conditions. In a similar perspective, Grime (2001) proposed a short definition of the term as ‘the mechanisms which limit the plant biomass by causing its partial or total destruction’. In addition, Huston (1994) provided a comprehensive definition/explanation as follows:

> ‘Disturbance is any process or condition external to the natural physiology of living organisms that results in the sudden mortality of biomass in a community on a time scale significantly shorter (e.g., several orders of magnitude faster) than that of the accumulation of the biomass. Thus a disturbance may kill a few, many, or all of the organisms in a community, or may simply kill a portion of a single individual, as is often the case with damage to plants.’

In short, it is considered that these definitions commonly stress the importance of ‘abnormality’, ‘externality’, ‘mortality’, and ‘temporal discreteness’. Specifically, partial or complete mortality may be a clearly needed aspect when determining if any phenomenon is a disturbance or not. For example, Huston (1994) suggested that even the gradual invasion of exotic species that we often perceive as disturbance would not be viewed as disturbances, unless they cause sudden mortality in the native community.

Stress, on the other hand, is not directly related to such sudden mortality or selective/complete disruption of natural communities. It is rather defined as ‘the external constraints which limit the *rate* of dry matter production of all or part of the vegetation’ (Grime 2001). However, stress and disturbance are inseparable because disturbances often induce stresses (Rykiel 1985). A stress resulting from a disturbance may be either chronic (i.e., low-level, but continuous) or acute (i.e., high-level, but with a short effect) (Archer and Stokes 2000). In both cases, the function of plants gets impaired, and sometimes there can be gradual mortality.

Salt marsh platforms may be viewed as relatively simple systems with one major, fundamental physical factor that controls soil and floristic conditions: flooding by sea water (Ranwell 1972; Adam 1990). However, it is difficult to make clear distinction between stress and disturbance in such environments, although the flooding events occur in a relatively regular manner. On the one hand, the regular events are often regarded as 'normal' in salt marsh ecosystems, and as a typical cause of *stress* with little controversy (Adam 1990; Bertness 1991; Bertness and Hacker 1994; Emery et al. 2001; Pennings et al. 2005). Normal (either diurnal or semi-diurnal) tidal activities and the associated submergences would bring about a selective limitation of the growth rate and function of salt marsh plants, rather than their sudden mortality.

On the other hand, an abrupt increase of tidal amplitude caused by the construction of dikes (de Leeuw et al. 1994) or ocean storminess (Cramer and Hytteborn 1987; Olff et al. 1988) has been suggested as disturbance (Beeftink 1987). For example, Bartholdy and Aagaard (2001) reported wind-driven submergence of even an entire marsh for up to 24 hours. Such overwhelming events are obviously 1) not occurring on a regular basis, 2) initiated from outside of the plant communities, and 3) the causes of sudden mortality especially of salt- and waterlogging-intolerant species in those communities. Importantly, each abnormal flooding is not simply disturbance at a certain temporal point, but often remains as a source of lingering stress after the event.

I suggest that various hydrologic regimes exist on salt marshes to cause create different types of ecosystem development at different time scales. A perspective is therefore necessary that considers the combined effects of normal, regular inundations (i.e., stress) and abnormal, sudden rises of sea-level (i.e., disturbance) in the study of salt marsh biogeography.

2.3 STATE OF KNOWLEDGE ON SALT MARSH BIOGEOGRAPHY AT VARIOUS SCALES

2.3.1 Influence of sea-level variations on vegetation dynamics – a broad-scale perspective

In salt marshes, sea-level variation plays a key role in shaping vegetation patterns by affecting the biological success of individual plant species and ecological succession through inter-specific interactions (Ranwell 1972; Adam 1990; Bakker et al. 1993; Olff et al. 1997; Morris et al. 2002). Dynamics of salt marsh vegetation can be observed at different time-scales corresponding to the different time-scales of sea-level change (Cramer and Hytteborn 1987; see also Stommel 1963). The most emphasis, however, has been placed upon long-term, gradual rise of sea level rather than their short-term anomalies, in accordance with the world-wide concern about global warming and melting of the polar ice (Hegerl and Bindoff 2005).

In terms of the long-term perspective over decades, the overall behavior of salt marshes depends on the difference between rates of marsh surface accretion and gradual mean sea-level rise (Orson et al. 1985; Stevenson et al. 1986; Reed 1990, 1995). Morris et al. (2002) proposed that, under an optimal rate of relative sea-level rise, a positive feedback between biomass density and sedimentation (e.g., Bertness et al. 1992; Srivastava and Jefferies 1995; van de Koppel et al. 2005) constantly readjusts the marsh surface toward an equilibrium with rising sea levels (see also Redfield 1972; Kirwan and Murray 2007). When sea-level rise exceeds sediment accumulation, there would be a gradual decrease in the relative surface elevation, resulting in increased frequency of tidal inundation. These effects may in turn result in retarded or retrogressive succession toward earlier successional seres dominated by species more tolerant to the physical stress associated with regular inundation by sea water (e.g., Warren and Niering 1993; cf., Bakker et al. 1993).

Compared to this long-time perspective, there has not been much appreciation that short-term fluctuations of the sea surface nested within the long-term, gradual rise can influence the biology and ecology of salt marshes. However, a few exceptions exist. After a 14 year-long data collection at North Inlet, South Carolina, Morris (2000) showed that the net above-ground biomass productivity of *Spartina alterniflora* Loisel. significantly varied, due to changes in the salt balance of intertidal sediments, largely driven by seasonal or monthly anomalies of sea levels. On one of the Frisian Islands, significant positive and negative relationships were reported between annual changes in the cover of major marsh species and fluctuations in the monthly frequency of sea water inundation (Olff et al. 1988). These studies indicate that yearly or shorter-term variations in sea levels can also be the main factor forcing salt marsh vegetation dynamics. Short-term sea-level variations have previously been associated with volume changes in the ocean water due to monthly temperature fluctuations (Pattullo et al. 1955; Morris 2000) and seasonal meteorological storm surges (Beeftink 1987; Cramer and Hytteborn 1987; Olff et al. 1988).

Exposed coasts experience erosion and loss of biomass due to the direct impact of storm waves (e.g., Psuty and Ofiara 2002). However, sheltered backbarrier salt marshes (e.g., Figure 2.5) tend to experience an increase in the duration and depth of over-marsh

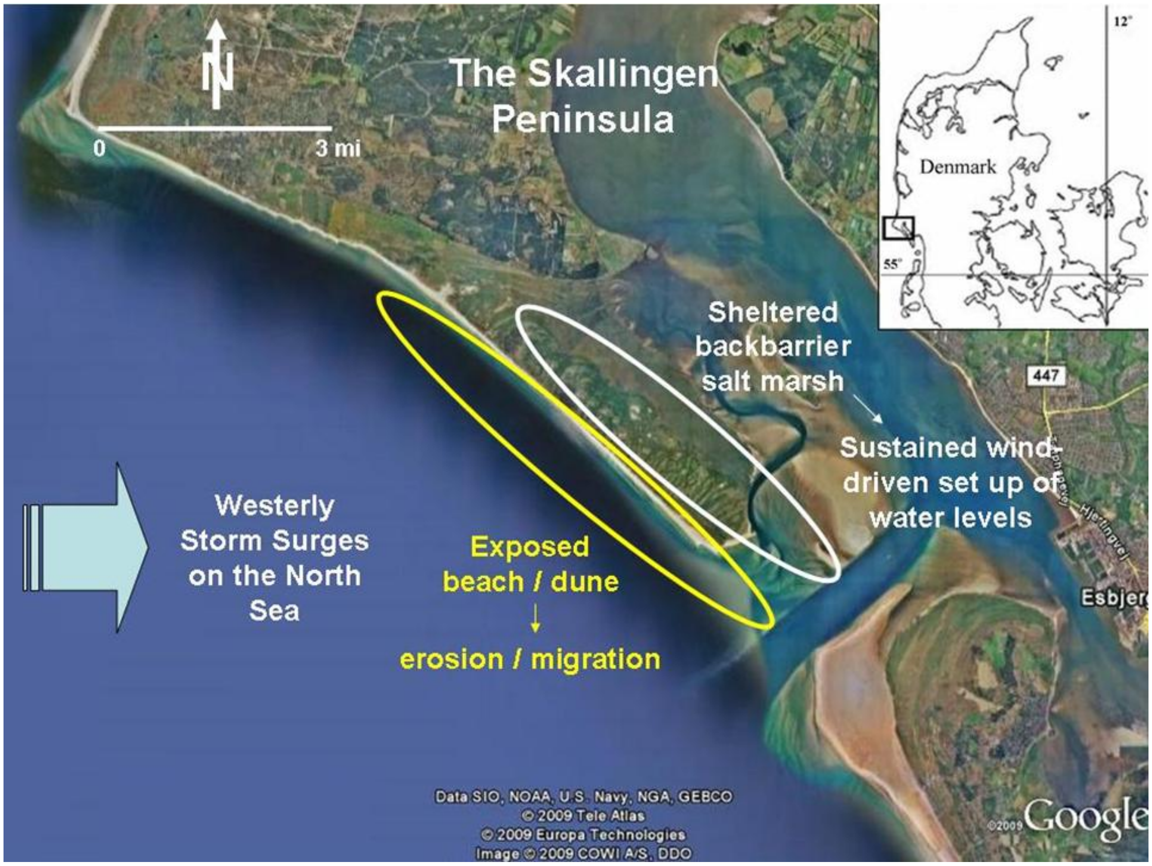


Figure 2.5 The Skallingen Peninsula, Denmark. The study site is a backbarrier salt marsh, sheltered from the direct impact of waves during westerly storm surges on the North Sea.

flooding due to sustained onshore wind-driven set up of water levels. Such an increase occurs regardless of lunar tidal forces and is able to cause a submergence of even an entire salt marsh for up to 24 hours (Bartholdy and Aagaard 2001), thereby affecting the rate of surface accretion (Orson et al. 1985; Stevenson et al. 1986; Reed 1990, 1995) and soil anoxia/salinity (Mitsch and Gosselink 2000). These combined hydrologic, sedimentary, and edaphic alterations can in turn influence the biomass productivity of marsh plants (Bakker et al. 1993; Morris et al. 2002), modes of facilitation/competition between them (Pennings and Callaway 1992; Bertness and Shumway 1993; Emery et al. 2001), and their spatial zonation (Jefferies et al. 1979; Vince and Snow 1984; Armstrong et al. 1985; Pennings et al. 2005).

It is noteworthy that the frequency and magnitude of meteorologically-forced storminess on various ocean surfaces have increased during the 20th century, due to increased anomalies in atmospheric oscillations such as the NAO and the El Niño-Southern Oscillation (ENSO) (Günther et al. 1998; Bromirski et al. 2003). The NAO, for example, enters its positive phase when the Icelandic low-pressure system and the Azores high-pressure system are lower and higher than normal, respectively. This increased pressure difference, indicated by high, positive values of the NAO index, results in frequent and strong westerly gales crossing the eastern Atlantic Ocean on a more northerly track (Serreze et al. 1997; Deser et al. 2000; Figure 2.6).

Reciprocal interactions are believed to exist between global climate warming and increasing anomalies in these oscillation indices (e.g., Schindell et al. 1999; Timmermann et al. 1999; Tsonis et al. 2005; Hurrell and Deser 2009). Also, there is a

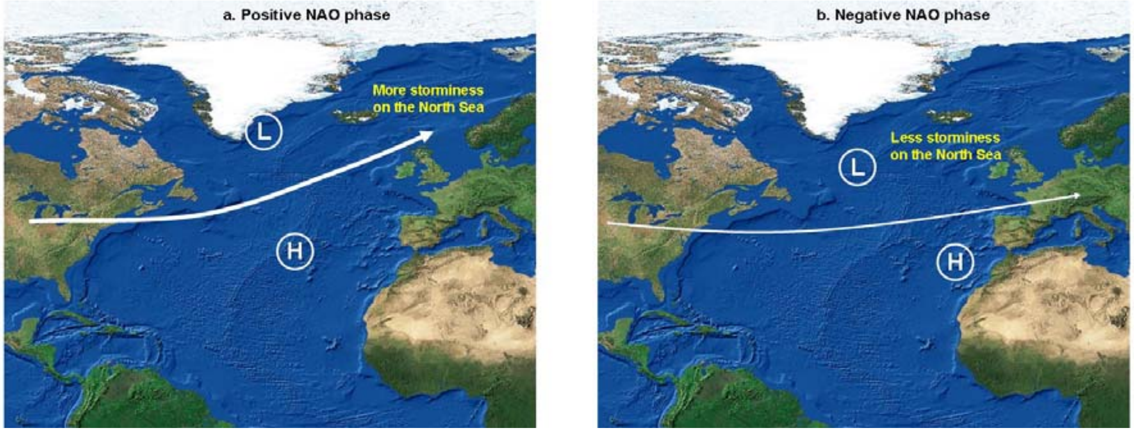


Figure 2.6 Positive (A) and negative (B) phases of the North Atlantic Oscillation (NAO) index. During the positive phase, the Icelandic low-pressure system and the Azores high-pressure system are lower and higher than normal, respectively. This increased pressure difference results in frequent and strong westerly gales crossing the eastern Atlantic Ocean on a more northerly track. When the index is negative, the pressure difference becomes low, so there should be less frequent and less strong storminess around the North Sea.

growing appreciation that these coupled global-scale phenomena profoundly influence a variety of ecological processes in coastal ecosystems with socio-economic impacts for resource users (Stenseth et al. 2003; Wang and Schimel 2003; Miller and Munro 2004). The attempt in this research to link salt marsh dynamics and short-term sea-level variations can be understood in the context of such globally-changing environmental conditions.

2.3.2 Influence of site-specific processes on plant zonation – a medium-scale perspective

Temporal changes in salt marsh vegetation play out over space and result in shifting zonation along an elevation gradient primarily from outer (seaward) to inner (landward) areas of the marsh. This gradient perpendicular to the shoreline has been considered as the key indicator of zonal vegetation change (Sánchez et al. 1996; Olff et al. 1997). Such a conventional focus on the outer-to-inner marsh plant zonation has been useful because, at broad spatial scales, salt marshes in general display little conspicuous topographic relief that may cause spatial variation of vegetation and environmental factors coincident with something other than the gradient from outer to inner marshes. Much of our knowledge about spatial and temporal dynamics of salt marsh vegetation has consequently been derived from studies that inferred successional processes from the underlying elevation gradient at broad spatial scales (e.g., Pielou and Routledge 1976; Snow and Vince 1984; Vince and Snow 1984; Pennings and Callaway 1992; see also Figure 2.7).

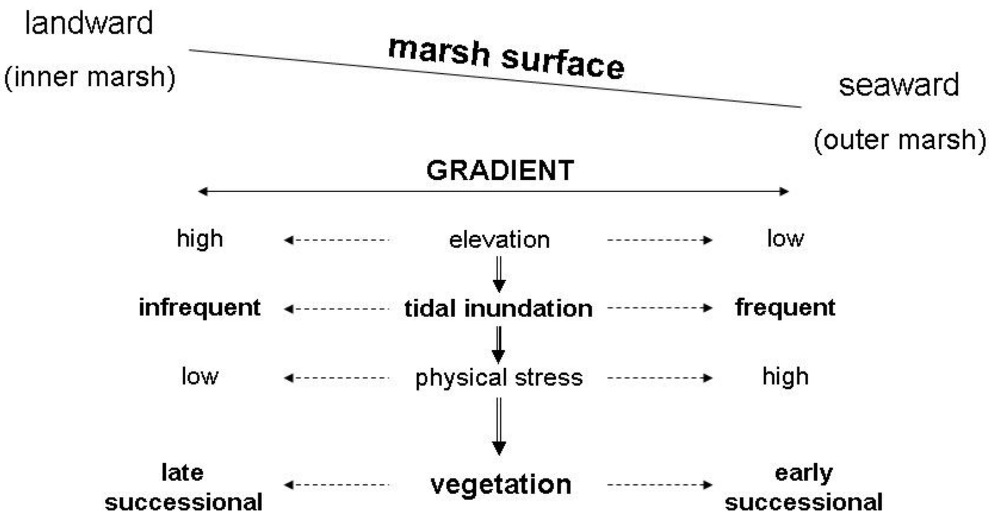


Figure 2.7 A conceptual spatial gradient of physical and floristic factors encompassing outer and inner marshes. This graph provides a brief overview of salt marsh ecology at a broad spatial scale.

Due to this emphasis on salt marsh ecology at broad scales, however, the significance of site-specific processes in creating medium-scale spatial zonation of vegetation has received little attention. Such a lack of attention may be the main reason why there is little integration of macro- and micro-scale processes and patterns in a single study or model (but see D'Alpaos et al. 2007 and Kirwan and Murray 2007). In salt marsh environments, different ecological processes nested within a hierarchy are in operation (cf., Allen and Starr 1982). Tidal creeks, for example, are the most notable salt marsh agents that alter vegetation away from the broad-scale zonal patterns expected when only the cross-shore gradient in elevation is considered. As conduits of tidal flow into inner marsh fields, tidal creeks facilitate the exchange of energy and materials between flooding sea water and the adjacent marsh edges, thereby resulting in physical constraints on plant growth with a small-scale gradient perpendicular to the streamline (Mendelssohn et al. 1981; Adam 1990). This medium-scale effect (meters to tens of meters) explains why the outer-to-inner marsh gradient of surface elevation is a useful but sometimes incomplete proxy when one considers local variations of plant species and environmental factors (Zedler et al. 1999). Consideration of the influence of tidal creeks is an essential step in studies of salt marsh dynamics responding to sea-level rise since their depth and width proved to be significantly affected by variations in sea level (e.g., Kirwan and Murray 2007). These morphological changes should in turn modify patterns (e.g., spatial extent) of medium- and fine-scale species zonation across tidal creeks.

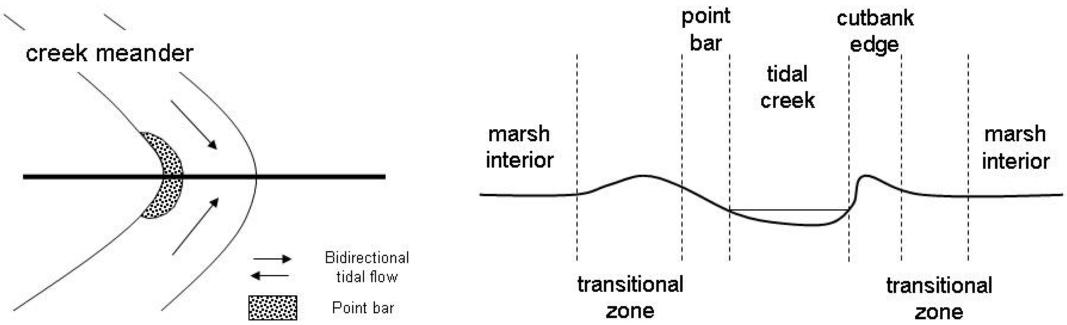


Figure 2.8 Meandering of a tidal creek (A) and the resultant topographic profile across the creek (B).

Lateral migrations of tidal creek meanders create point bars and cutbank edges with hydrologic and edaphic conditions different from those of interior marsh fields (Figure 2.8). In addition, the transitional zone between areas adjacent to and distant from channels is another unique micro-habitat of ecological interest that has not been fully understood in terms of its intermediate fluvial process regime. It is believed that different environmental settings along these topographic sequences (i.e., point bar or cutbank edge-transitional zone-interior) are the key factor that forms different plant communities at mid-spatial and temporal scales.

Although the ecological influence of tidal creeks should be considered in the study of the spatial pattern of salt marsh vegetation and its management (Zedler et al. 1999; Morzaria-Luna et al. 2004), there are fewer studies on the topic compared to those on the cross-shore gradient of vegetation under broader spatial perspectives. On the one hand, previous research explored the localized disturbance pattern *along creeks* (Fischer et al. 2000) and the floristic differences between cells *with and without creeks* (Morzaria-Luna et al. 2004). On the other hand, this dissertation is interested in the mid-scale zonation *across creeks*, encompassing topographic sequences of point bar or cutbank edge-transitional zone-marsh interior.

2.3.3 Influence of species interactions on community structure – a fine-scale perspective

Identification of spatial pattern/structure and the underlying mechanisms that produce it has long been one of the central themes in plant community ecology (Watt 1947;

Rietkerk et al. 2004). Spatial pattern provides a useful proxy for interactive mechanisms such as competition and facilitation among species because they are spatially explicit and also because spatial pattern itself affects process (Silvertown et al. 1992; Cairns et al. 2008).

Competition and facilitation did not receive balanced attention until the 1980s, because of a stronger emphasis on the role of competition, predation, and abiotic factors in creating community structures (see Bruno et al. 2003 for a review). With an increased recognition of facilitative effects among species especially in stressful environments such as salt marshes (Bertness and Shumway 1993), arid ecosystems (Maestre and Cortina 2004), and alpine ecosystems (Callaway et al. 2002), biogeographers and ecologists began to focus on the relative importance of competition and facilitation.

Most recently, a novel theory has emphasized the concept of scale-dependence (Klausmeier 1999; Rietkerk et al. 2004), suggesting that both processes indeed operate simultaneously in a single zone, but at different scales (e.g., van de Koppel et al. 2006; van Wesenbeeck et al. 2008). For example, facilitation at an entire community level occurs along the lower boundary of an intertidal zone where *S. alterniflora* buffers other species behind the zone from intense wave action (Bruno 2000). At smaller scales, inter-specific competition was found to determine the final species sorting in this site (van de Koppel et al. 2006).

While the emerging body of literature of scale-dependence provides a useful conceptual basis for interpreting competitive and facilitative interactions, this research is concerned with additional factors of potential importance: environmental gradients and species-specific interactions. First, recent research on scale-dependence was mostly conducted in spatially limited locations such as pioneer zones of salt marshes. Insights from these low areas may not be fully applicable to processes on higher areas with different edaphic and hydrological conditions. Second, one-to-one relations between various species are worthy of investigation based on a hypothesis that competition and facilitation may occur at different micro-scales depending on which two species are examined.

2.4 SUMMARY OF BACKGROUND AND SCOPE OF THIS RESEARCH

Throughout the background, major concepts relevant to vegetation dynamics were discussed. These concepts were then put into perspective of salt marsh biogeography at three different spatial and temporal scales. At each scale, ecological questions that had been conventionally dominant among salt marsh ecologists were discussed. In the meantime, less appreciated, but still important aspects of ecological patterns and processes were introduced. The focus of this dissertation research will be to reevaluate the implications of these topics that have received a relatively minor emphasis in salt marsh ecology. A summary of such a scope is provided in Table 2.1.

Table 2.1 Major and minor emphases in conventional salt marsh biogeography

Scales studied	Major focus	Minor focus
Large	Long-term sea-level change driven by eustatic effects	Short-term fluctuations of sea level driven by ocean storminess
Medium	Broad-scale spatial gradients of surface elevation and the associated edaphic and floristic patterns	Linkage of fluvial-geomorphic processes along tidal creeks with topographic, edaphic, and vegetation gradients
Fine	Scale-dependence of species interactions	1) Species specific, one-to-one relationships in such scale-dependence 2) Scale-dependence along physical gradients

CHAPTER III

STUDY AREA

3.1 GENERAL ENVIRONMENTAL SETTING AND BIOGEOGRAPHICAL MERITS

The Skallingen salt marsh, located on a peninsula in southwestern Denmark lies at the northern end of the Wadden Sea (Figure 2.5) and is one of the largest undiked coastal salt marshes in Europe. The peninsula is characterized as a barrier spit (Aagaard et al. 1995) which was formed during the last 400 years. It possesses a geomorphological zonation typical to those of other Wadden Sea islands (Bartholdy 1997). From the ocean (west) to the backbarrier lagoon (east), the depositional sequences are as follows: beach, dune, salt marsh, and tidal flat. The study marsh is situated on the backbarrier side of the spit. The marsh started to develop in the beginning of the 20th century along with the formation of tidal creeks (Nielsen 1935). The tidal range is about 1.7 m at spring and 1.3 m at neap tides with a mean of 1.5 m. This area is thus classified as micro-tidal (Davis 1964).

The Skallingen salt marsh provides a good laboratory for a biogeographical investigation across scales. First of all, its natural ecosystem has been well-conserved since the beginning of its development in the early 20th century. Second, such conservation resulted in a wide marsh platform and a complex tidal creek system embedded in the platform. One can therefore not only examine scale-dependent vegetation patterns from micro- to macro-scales across the ample space of the platform, but also decipher how these patterns are constrained by the presence of creeks. Third, historical floristic data have been collected here since the early 1930s (Nielsen 1935; Iversen 1953; Jensen 1985a, 1985b), as well as data on physical factors such as sedimentation and sea-level variation (Bartholdy 1997; Bartholdy et al. 2004). Thus, contemporary ecological patterns can be understood in the light of the past biotic and abiotic dynamics, which is a rare, fortunate situation. The Skallingen salt marsh recently has attracted several geographers and ecologists outside of Denmark, yielding interdisciplinary and international collaborations (e.g., Morris and Jensen 1998; Bos et al. 2002; Kim et al. 2009a; Kim et al. 2009b).

Skallingen often experiences wind-induced sea-level variations. In Esbjerg, a city near Skallingen (Figure 2.5), water levels up to 4.4 m above the Danish Ordnance Datum (DNN) have been measured during storm surges. While the west-facing beach and dune of the Skallingen Peninsula are directly influenced by the westerly storms that cause migration or transformation of swash bars and washover fans (Aagaard et al. 1995; Houser and Greenwood 2007), the sheltered backbarrier salt marsh experiences their indirect effect, or temporary increase of the sea surface. During a wind-driven rise, the entire portion of the marsh area can become submerged by saline water for up to 24 hours (Bartholdy and Aagaard 2001). Considering such long duration and extensive range, these meteorological and subsequent hydrologic phenomena are believed to significantly affect the biology and successional dynamics of the salt marsh vegetation.

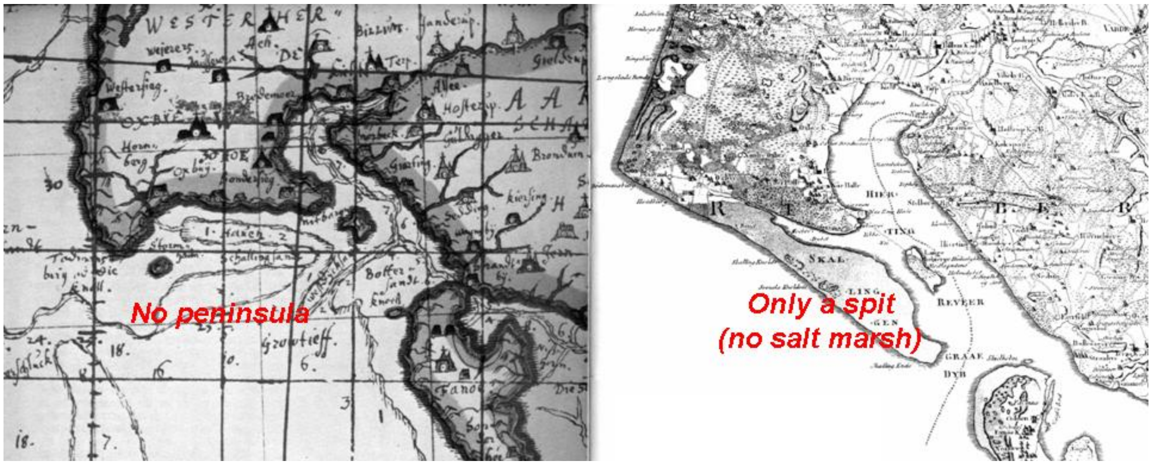


Figure 3.1 Historical maps of the Skallingen Peninsula (taken from Aagaard et al. 1995). Each was drawn by (left) Johannes Meiers (1654) and Videnskabernes Selskabs (1804), respectively.

3.2 HISTORICAL DEVELOPMENT OF THE MARSH

Research on the recent evolution of the Skallingen Peninsula has been mainly conducted based on analysis and interpretation of historical maps and air photos (e.g., Figure 3.1; see also Aagaard et al. 1995). Until the mid-17th century, the peninsula did not exist in southwestern Denmark. It is assumed that Skallingen during this era was characterized by an extensive sandy ridge with little vegetation cover at about 1 m above DNN. In the early 19th century, it appeared that the barrier spit had become significantly larger, along with the development of conspicuous dunes at the ocean-ward (i.e., western) side of the spit. Aagaard et al. (1995) consider that these dune ridges were probably covered by grasses, while the other sandy plain was still absent from vegetation.

At the beginning of the 20th century, the dunefields had become much larger and the initial establishment of salt marsh vegetation at the backbarrier (i.e., eastern) side of the spit had begun (figure not shown here). One important process concomitant to the gradual increase in the marsh surface was the formation of tidal creeks (Nielsen 1935). These creeks were expanded through headward erosion to improve the drainage of the low-lying part of the marsh, thereby leading to permanent vegetation around the mid-20th century (Aagaard et al. 1995).

In 1933, Niels Nielsen (1935) established a monitoring site on the Skallingen salt marsh to record the rate of sediment accretion and vegetation dynamics. Nielsen and Nielsen (1973) reported the texture of the marsh deposits approximately as follows: 40 % clay, 50 % silt, and 10 % fine sand. They further classified their research profile into five characteristic zones:

Zone 1: Dunes and beach ridges located at the level of 1.5-2.0 m DNN. The dominant plant species are common dune grasses such as *Ammophila/Elymus arenaria*, *Calluna vulgaris*, *Empetrum nigrum*, *Carex/Armeria maritima*.

Zone 2: Innermost marsh with a few isolated sand ridges (ca. 1.3 m DNN). *Festuca rubra* dominates here.

Zone 3: Inner part of the marsh dissected by tidal creeks (ca. 0.9 m DNN). There are a few salt pans observed. Some more salt-tolerant plants exist: *Puccinellia maritima*, *Salicornia herbacea*, *Spartina townsendii*, *Limonium vulgare*, *Suaeda maritima*, and *Halimione portulacoies*.

Zone 4: Outer part of the marsh (ca. +1 m DNN). Characteristic species include *Puccinellia maritima*, *Limonium vulgare*, *Aster tripolium*, *Plantago maritima*, *Artemisia maritima*, and *Halimione portulacoies*.

Zone 5: The Wadden Sea intertidal flat (ca. +0.6 m DNN). Salt-tolerant species dominate: *Spartina*, *Puccinellia*, and *Salicornia*.

3.3 HISTORICAL SEA-LEVEL VARIATION AND SURFACE ACCRETION

Long-term and short-term sea-level data (Bartholdy et al. 2004) were derived from a tidal gauge located in Esbjerg. The yearly mean sea-level in Esbjerg has generally been increasing since the early 20th century (Figure 3.2; Table 3.1). The rate of mean sea-level rise has increased through time with the exception of the period, 1961-1976. There has been a rapid mean rise of 5.0 mm yr^{-1} since 1976, while the overall rate since 1931 was 2.3 mm yr^{-1}.

All high water levels (HWL) recorded in Esbjerg were corrected for Skallingen. For the correction, a quadratic regression model was used based on recent differences in HWL between the two locations (see Bartholdy et al. 2004). The frequency of HWL at

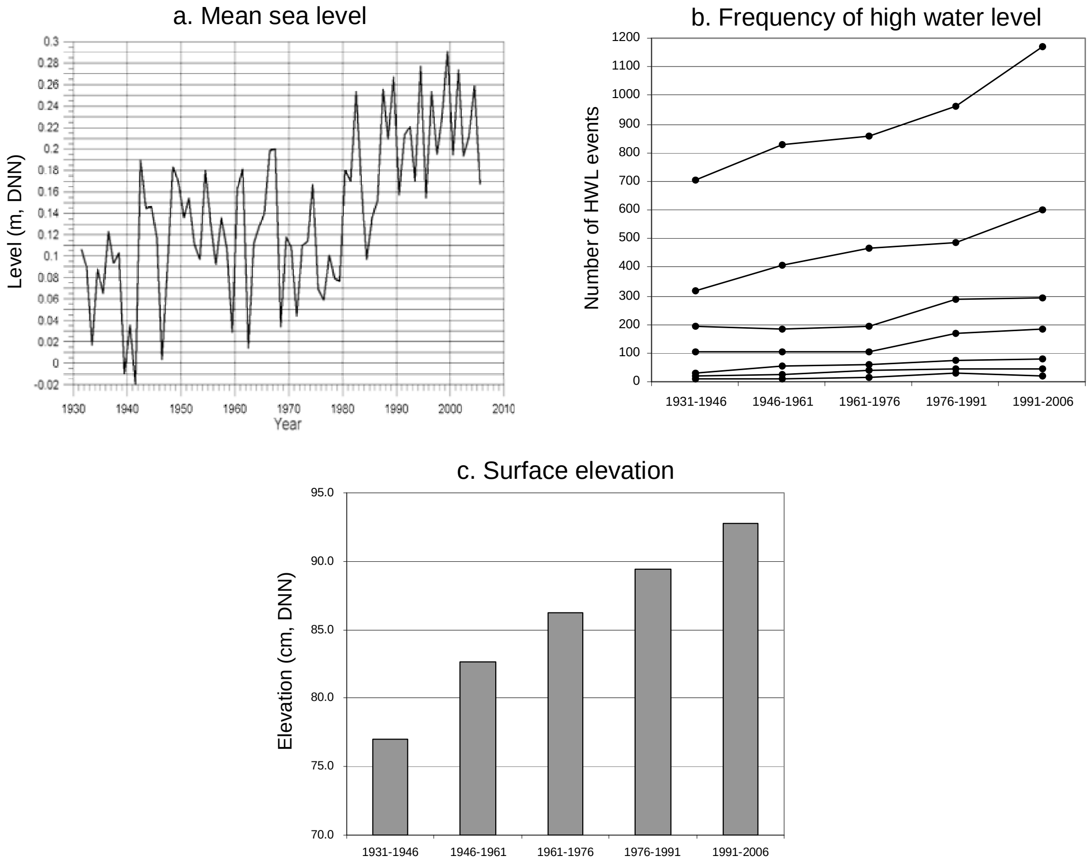


Figure 3.2 Temporal variation of mean sea level (A), frequency of high water levels (HWL) (B), and surface accretion (C), on the Skallingen salt marsh, Denmark. The mean sea-level was based on yearly averages from July to July. In the graph of HWL, the uppermost line through the bottommost line represent 1.0-1.2 m HWL, 1.2-1.4 m HWL, 1.4-1.6 m HWL, 1.6-1.8 m HWL, 1.8-2.0 m HWL, 2.0-2.2 m HWL, and 2.2-2.4 m HWL, respectively (see also Table 3.1). The surface elevation was based on data from a monitoring site in Bartholdy et al. (2004).

Table 3.1 Mean water levels (MWL) and the number of high water levels (HWL) around Skallingen in m DNN, the Danish Ordnance Datum

Period (years)	1931-1946§	1946-1961	1961-1976	1976-1991	1991-2006
MWL†	0.086	0.119	0.116	0.157	0.220
1.0-1.2 m HWL‡	703	826	860	963	1171
1.2-1.4 m HWL	317	405	467	485	600
1.4-1.6 m HWL	193	185	195	289	295
1.6-1.8 m HWL	104	103	102	168	181
1.8-2.0 m HWL	32	57	58	74	79
2.0-2.2 m HWL	19	24	38	45	43
2.2-2.4 m HWL	10	8	17	28	21

† measured at Esbjerg

‡ All HWL were corrected for Skallingen. See Bartholdy et al. (2004) for the procedure for developing a quadratic regression model based on recent differences in HWL between Skallingen and Esbjerg.

§ The fifteen-year periods summarizing MWL and HWL represent half of the official thirty-year periods used in Denmark. This is close to the traditional nineteen-year periods used in normal tidal statistics. Because the location is strongly affected by wind tide, the difference is regarded as insignificant. Since both MWL and the frequency of HWL have increased in general, it is believed that different temporal blocks would not lead to different trends.

Skallingen has generally been increasing since 1931 (Figure 3.2; Table 3.1). In general, the surface elevation has increased by about 0.2 m since 1931 and now an elevation of 0.9 m DNN is considered as the mean level of the Skallingen salt marsh (J. Bartholdy unpublished data). Such an elevation increase up to 0.9 m DNN is minor considering the increased frequency of high water events over 1.0 m DNN and even over 2.0 m DNN. In other words, each HWL in Table 3.1 and Figure 3.2 can be directly regarded as an 'over-marsh' inundation event. The total number of yearly over-marsh HWL has been closely related to the yearly NAO index between 1960 and 1999 (Pearson's $r = 0.62$, $p < 0.01$).

Increases both in mean sea-level and in the frequency of over-marsh high water events have resulted in continuous sedimentation and an increased surface elevation in the marsh since 1933 (Bartholdy et al. 2004). In the outer part of the marsh (close to the tidal flat), the mean accretion rate was about 4.0 mm yr^{-1}, whereas it was about 2.0 mm yr^{-1} in the inner part. Here, 'accretion' refers to the actual elevation change because it was calculated by long-term leveling and measurement of clay thickness (see Bartholdy et al. 2004). In other words, accretion takes into consideration subsurface compaction after sediments accumulated.

Bartholdy et al. (2004) found that the accretion rate had been related to the frequency and magnitude of HWL that was closely associated with the variation in the NAO index. By a graphical comparison, a striking resemblance was detected between the mean accretion rate and the NAO index during the 20th century. A regression analysis, moreover, showed that the index significantly explains 63 percent of the variation in the sedimentation (i.e., $R^2 = 0.63$, $p < 0.01$) between 1970 and 1999.

CHAPTER IV

STUDY METHODS

4.1 RESEARCH OBJECTIVE 1 – SEA-LEVEL CHANGE AND VEGETATION DYNAMICS

4.1.1 Vegetation sampling

In 1933, twenty nine points were established along three transects perpendicular to the coastline on the Skallingen salt marsh (figure not shown here) where Niels Nielsen (1935) and Helge Nielsen (unpublished data) investigated the presence of vascular plant species in 1933 and 1949, respectively. In the summer of 2006, the same locations were visited to acquire the same set of data on species frequency. Finding the previously surveyed locations was possible primarily because the end points of the three historic transects were known (from Bartholdy et al. 2004). The sampling points were located by navigating to their locations using a Global Positioning System (GPS) in conjunction with detailed notes from the 1949 resurvey by H. Nielsen.

In order to replicate the sampling method used by N. Nielsen and H. Nielsen, a 2 m × 1 m rectangular quadrat was used that was sub-divided into 200 subdivisions of 10 cm × 10 cm each to sample the vegetation. Ten of the small subdivisions were randomly chosen and the presence of vascular species in each subdivision was recorded. The frequency of each species in one rectangular quadrat thus varied between 0 and 10. Species nomenclature followed Tind (2003).

At each location, three quadrats were surveyed whereas the previous studies by N.

Nielsen and H. Nielsen were based on only a single quadrat at each point. The number of quadrats sampled was incresaed at each site and the results from the three quadrats were averaged to minimize any effect of having resampled a site that was slightly offset from the originally sampled location. In general, with the combination of GPS and detailed notes from the 1949 survey, it was possible to be within 2 m of each original location.

4.1.2 Identification of vegetation associations

Hierarchical agglomerative cluster analysis was used to classify the samples into ecologically meaningful vegetation associations, aided by indicator species analysis (McCune and Grace 2002). Species occurring in fewer than five quadrats were removed because they could provide little reliability in assigning them to groups. All of the 29 samples from each of the three time periods (1933, 1949, and 2006) were then pooled into one dataset with a total of 87 samples. A sample relativization was followed to make observational units more equitable in species abundance and to enhance the detection of broad compositional similarities among samples.

For the cluster analysis, Ward's method (Ward 1963) was selected. This method minimizes an increase in the sum of the squares of distances from each sample to the centroid of the group it belongs to (McCune and Grace 2002). Due to its nature to look for minimum-variance spherical clusters, it is also considered minimum-variance method, also suggested by Orlóci (1967). Ward's method is known to be an effective, useful tool, as one of the few space-conserving linkage methods. As such, Euclidean squared distance was used for dissimilarity measurement, rather than other measures (especially Sørensen) that are not compatible with Ward's cluster approach. This combination (i.e., Ward's method and Euclidean distance) is one of the approaches recommended for avoiding distortion of a data set and for maximizing defensibility (McCune and Grace 2002).

A combination of graphical and quantitative approaches was used to determine an appropriate number of clusters. A dendrogram was produced from the hierarchical cluster analysis, scaled by Wishart's objective function converted to a percentage of information remaining (Wishart 1969). Such a diagram was expected to provide a qualitative idea of where to prune branches with the appropriate amount of information remaining. Indicator species analysis is a useful, quantitative tool for choosing an optimum number of clusters (Dufrêne and Legendre 1997; McCune and Grace 2002). The technique acquired a final indicator value for each species by multiplying its relative abundance and relative frequency by group. The statistical significance of the highest indicator value for a given species across groups was then evaluated by 5000 runs of Monte Carlo tests. The resulting *p*-values were used as an objective criterion for pruning the dendrogram. The cluster step with the smallest average *p*-value was regarded as the most informative level in the dendrogram (McCune and Grace 2002). All statistical procedures were performed in PC-ORD Version 4.14 (MjM Software Design, Gleneden Beach, OR, USA).

4.1.3 Simulation modeling of floristic and geomorphic dynamics

This section aims to provide methods for simulating past and future dynamics of vegetation and geomorphology on the Skallingen salt marsh based on the field data available and results presented above. Specific objectives of such modeling are 1) to show a close linkage with NAO variation, dynamics of surface elevation, and submergence frequency and 2) to emphasize the significance of short-term wind-induced sea-level variation by comparing baseline and experimental simulation models that respectively assume the absence and presence of such meteorological events.

4.1.3.1 Conceptual model

The conceptual model considered in this research consisted of two major components: physical factors (Figures 4.1A, B, and C) and ecological succession (Figure 4.1D). The abiotic components were divided into three parts: sea-level variation driven by both temporary storminess and normal tides, surface accretion, and frequency of over-marsh inundation. The NAO index variation influenced the total number of HWL per year that was in turn divided into four categories: low HWL (80-100 cm), mid HWL (100-120 cm), high HWL (120-140 cm), and extreme HWL (>140 cm). However, for a baseline simulation where no wind-driven sea-level fluctuation is assumed, the extreme HWL events will not be taken into account because they are not expected to occur under normal tidal conditions.

The rate of sediment deposition per year was dependent upon both the frequency of total HWL and the surface elevation. Specifically, there was a negative feedback between sedimentation and surface elevation because the frequency and duration of submergence should decrease as the elevation increases.

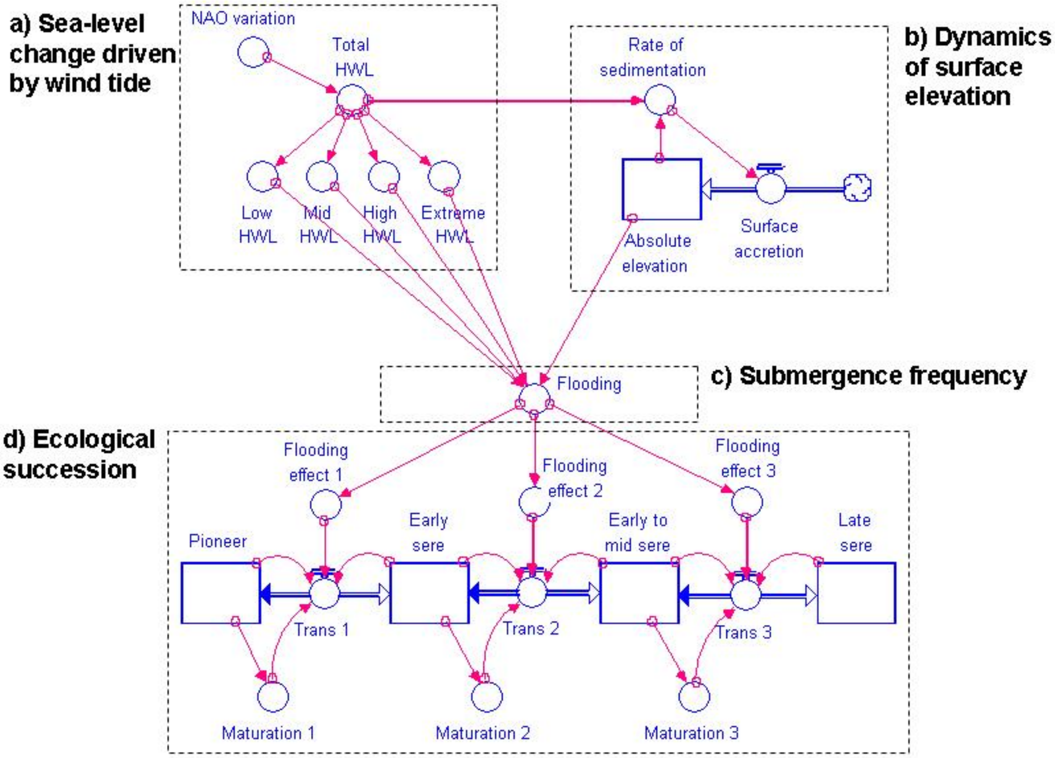


Figure 4.1 Conceptual model of abiotic and biotic dynamics in the study marsh drawn using STELLA® 7.0.1.

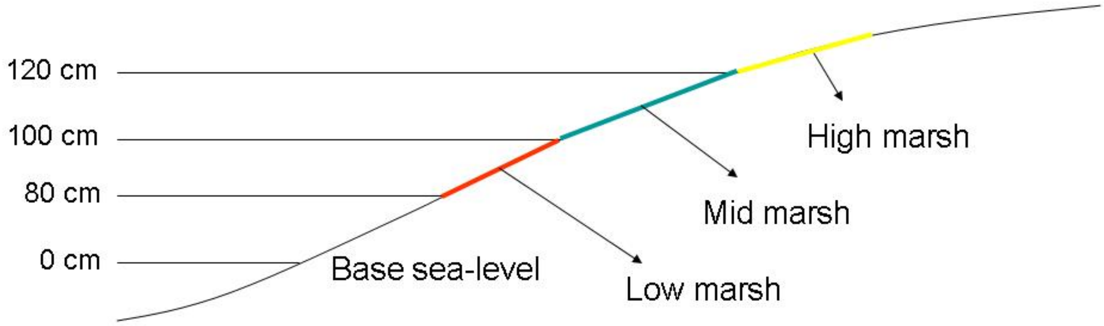


Figure 4.2 Topographic profile with different elevation zones.

The submergence frequency was considered respectively for low (80-100 cm), mid (100-120 cm), and high (120-140 cm) marsh areas (Figure 4.2). Therefore, the frequency should vary depending on which of these three sites is of interest and how its elevation changes over time. For example, a low area with an 80 cm-elevation should experience a flooding frequency of low HWL + mid HWL + high HWL + extreme HWL that is equivalent to total HWL per year. In the case of a 120 cm-high site, only high HWL and extreme HWL were considered as actual *over-marsh* inundation events. In short, every HWL event did not cause a complete submergence of the system.

Ecological succession was significantly influenced by the submergence frequency that controlled 'flooding effects'. The flooding effect was an inverse-linear function in which the effect becomes positive as the frequency of inundation decreases, while entering its negative phase with an increasing submergence frequency. This basic rule, however, varied for different transitions among successional stages, each having different physiological traits: Pioneer species are least sensitive to a certain number of flooding among all stages of species tested. This may also imply that pioneers *benefit* from frequent inundations that restrict the biological and competitive success of later-successional species (i.e., early-sere, early- to mid-sere, and late-sere). Late-successional species, on the contrary, are most negatively influenced by increasing flooding regimes.

Transitions among successional stages explicitly integrated the combined effects of abiotic (i.e., flooding) and biotic dynamics (i.e., competition and facilitation). Because each transition was bidirectional, positive and negative values controlled by 'flooding effects' could in turn result in progressive and retrogressive succession, respectively.

Transitions were also dependent on the density of both earlier and later stages that compete with each other. Last, facilitative interactions were expressed as 'maturation'. Facilitation has been considered an important contribution to (progressive) vegetation succession in salt marshes where the establishment of later-successional species is often hampered by physical stresses imposed by saline water inundation (Pennings and Callaway 1992; Bertness and Shumway 1993; Emery et al. 2001). The biological and ecological success of later species therefore strongly depends on the system maturation facilitated by earlier species that ameliorate edaphic conditions and accumulate organic matters (Bertness et al. 1992; Srivastava and Jefferies 1995; van de Koppel et al. 2005). However, the degree or speed of such maturation should be different among transitions. Specifically, system maturation for allowing the dominance of late-successional species requires a long time since the growth of these perennial, tall-stature species is strongly associated with the progressive accumulation of nutrients (especially nitrogen; Olff et al. 1997; van Wijnen and Bakker 1999).

4.1.3.2 Data

Observed and predicted data for the NAO index variation were combined. They were derived from Bartholdy et al. (2004) and Paeth et al. (1999), respectively. The observed values ran from 1933 through 1999 and the predicted ones encompassed the years from 2000 to 2050. Other than these NAO data, long-term hydrological, sedimentological, and floristic data were acquired from the Skallingen salt marsh.

All HWL events have been recorded by a tidal gauge in Esbjerg. These records were corrected for the study marsh using a quadratic regression model based on recent differences in HWL between Skallingen and Esbjerg (for a detailed procedure, see Bartholdy et al. 2004). After this correction, it was identified that, on average, low HWL, mid HWL, high HWL, and extreme HWL respectively explain 43, 28, 14, and 15% of total HWL each year.

The rate of sedimentation at sites with different surface elevations was determined based on robust long-term field monitoring and simulation modeling approaches by Bartholdy et al. (2004) on the Skallingen salt marsh since the early 1930s. In 1998, these authors revisited locations where Niels Nielsen (1935) spread red sand in 1931. Analyses of sediment cores from these sites and subsequent modeling attempts allowed them to estimate approximate rates of surface accretion as 0.25, 0.16, and 0.07 cm yr^{-1} at low, mid, and high marsh areas, respectively.

Floristic data were acquired and analyzed as shown in section 4.1.1 and 4.1.2. The initial relative occupancy (%) of each group will be determined for the three marshes, based on the results of hierarchical cluster analysis.

4.1.3.3 Experimental simulations – the presence of both wind-driven set up and normal tide assumed

Based on the data available, variables and their relationships in the conceptual model were quantified. Using STELLA® 7.0.1, model simulations were performed with a yearly step interval. Results of the simulation are evaluated with observed data.

4.1.3.3.1 NAO and sea-level variations

The yearly frequency of total HWL varied as a combined function of the NAO index variation (1933-2050), a random variable, and an increase term as follows.

$$\text{Total HWL} = (22.521 \times \text{NAO} + 229.76) \times \text{Random}(0.8,1.2) + \text{Increase term} \qquad (1)$$

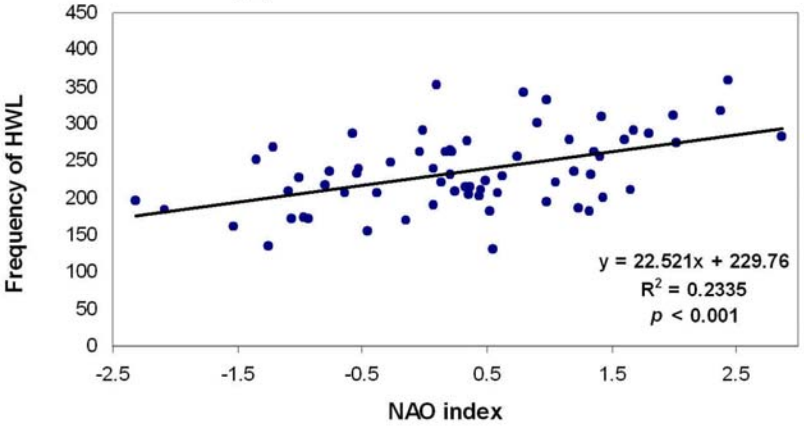
The random variable was multiplied in order to maintain the correlation coefficient between total HWL and NAO as 0.48 (i.e., $R^2=0.23$; see Figure 4.3A). The increase term with a slope, 1.7331 (see Figure 4.3B) was added to realize an increasing number of submergences through time.

4.1.3.3.2 Rate of sedimentation

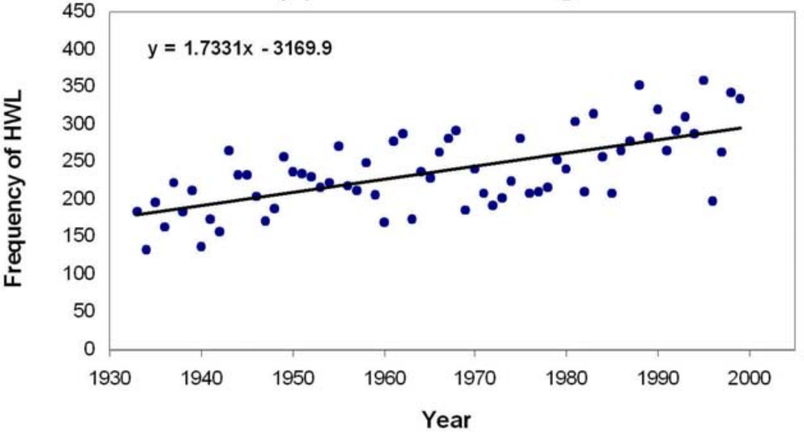
The rate of sediment accretion was parameterized as four categories as follows:

$$\begin{aligned}
&\text{if}(80 \leq \text{Absolute elevation} < 100) \text{ then } 0.25 + (0.25/237.3) \times (\text{total HWL} - 237.3)\\
&\text{else if}(100 \leq \text{Absolute elevation} < 120) \text{ then } 0.16 + (0.16/237.3) \times (\text{total HWL} - 237.3)\\
&\text{else if}(120 \leq \text{Absolute elevation} < 140) \text{ then } 0.07 + (0.07/237.3) \times (\text{total HWL} - 237.3)\\
&\text{else } 0.03 + (0.03/237.3) \times (\text{total HWL} - 237.3) \qquad (2)
\end{aligned}$$

Here, 237.3 represented the average number of HWL per year observed in the field. If total HWL exceeded such an average in a certain year, then the sedimentation rate increased accordingly.



(a) NAO variation vs. Total HWL



(b) Total HWL through time

Figure 4.3 Comparison of the yearly NAO variation and the frequency of total HWL (A) and the frequency of total HWL over time (B).

4.1.3.3.3 Submergence frequency

The frequency of flooding was defined as five categories as follows:

if(Absolute elevation<80) then low HWL+mid HWL×1.1+high HWL×1.2+extreme HWL×1.3
else if(80≤Absolute elevation<100) then (1-(Absolute elevation-80)×0.05)×low HWL+mid HWL×1.1+high HWL×1.2+extreme HWL×1.3
else if(100≤Absolute elevation<120) then (1-(Absolute elevation-100)×0.05)×mid HWL+high HWL×1.1+extreme HWL×1.2
else if(120≤Absolute elevation<140) then (1-(Absolute elevation-120)×0.05)×high HWL+extreme HWL×1.2
else extreme HWL×1.2 (3)

For every case, relatively high HWL (e.g., high HWL or extreme HWL) compared to the current surface elevation were weighted because these events should result in longer and deeper submergences than usual. In this regard, the inundation frequency in the model can also be understood as submergence *intensity*. The equations above assumed that any type of HWL was evenly distributed within the associated vertical spectrum (e.g., the vertical spectrum of low HWL ranges from 80 to 100 cm). Thus, if the surface elevation was 110 cm (i.e., mid marsh) in a certain year, such a site should experience a yearly frequency of *0.5*×mid HWL+high HWL×1.1+extreme HWL×1.2.

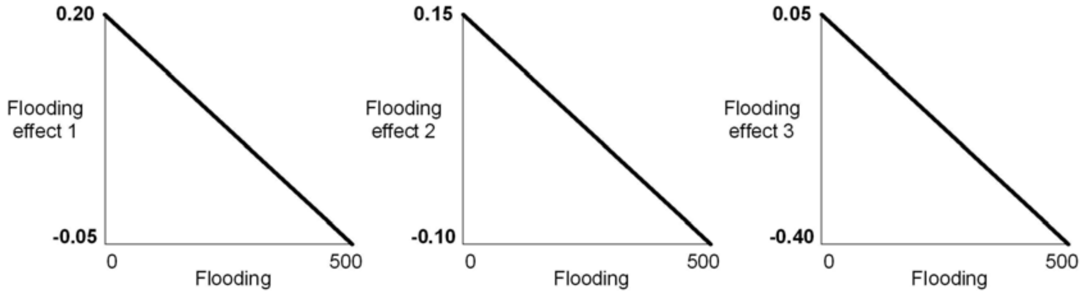


Figure 4.4 Graphical functions for parameterizing flooding effects for different elevation zones.

4.1.3.3.4 Flooding effects

The flooding effect was parameterized as follows (see also Figure 4.4):

$$
\begin{aligned}
&\text{Flooding effect 1} = -(0.25/500)\times\text{Flooding} + 0.20\\
&\text{Flooding effect 2} = -(0.25/500)\times\text{Flooding} + 0.15\\
&\text{Flooding effect 3} = -(0.45/500)\times\text{Flooding} + 0.05 \qquad (4)
\end{aligned}
$$

4.1.3.3.5 Transition between successional stages

A generic equation for transitions between successional phases was as follows:

$$\text{Transition}_{n\rightarrow n+1} = \text{Flooding effect}\times\text{Phase}_{n}\times\text{Phase}_{n+1}\times 0.01 + \text{Maturation}_{n\rightarrow n+1} \qquad (5)$$

Here, system maturation for different successional stages was defined as follows. The constant for maturation 3 (i.e., 0.015) was smallest to ensure that the establishment of late-successional species requires a longer time than other cases.

$$
\begin{aligned}
&\text{Maturation 1} = \text{Pioneer}\times 0.03\\
&\text{Maturation 2} = \text{Early sere}\times 0.02\\
&\text{Maturation 3} = \text{Early to mid sere}\times 0.015 \qquad (6)
\end{aligned}
$$

4.1.3.4 Baseline simulations – the absence of wind-driven set up assumed

A question still remains if wind-driven, short-term sea-level rise does really play a significant role in both ecological and sedimentological dynamics on salt marshes. In addition to experimental simulations above that take into account both wind-driven sea-level change and normal tide, baseline simulations are conducted assuming no such meteorological variations. These baseline simulations therefore do not include extreme HWL (> 140 cm) in the total HWL because such events are hardly expected to occur without wind-driven set up of the sea surface. Now the average frequency of total HWL became 183 each year. However, such a frequency should also be reduced because even some of these 183 occurrences observed in the field may have benefited from the meteorological influence. So it was arbitrarily decided to regard that 80% of the occurrences (i.e., 146) happened due to normal tidal currents only. Because the increasing frequency of total HWL observed in recent years has been strongly caused by the wind-driven sea-level rise, the baseline simulations assumed a constant frequency as 146 through time. All other conditions were the same as defined for the experimental simulations.

4.2 RESEARCH OBJECTIVE 2 – TIDAL CREEK PROCESSES AND PLANT ZONATION

4.2.1 Vegetation, soil, and topographic surveys

In the summer of 2006, 22 transects were selected along four tidal creeks on the Skallingen salt marsh (Figure 4.5). Every transect ran across either part of point bar or cutbank edge sequences (Figure 4.6A). Along each sub-transect, 1 m × 1m square quadrats were established, each of which was sub-divided into 25 cells of 20 cm × 20 cm

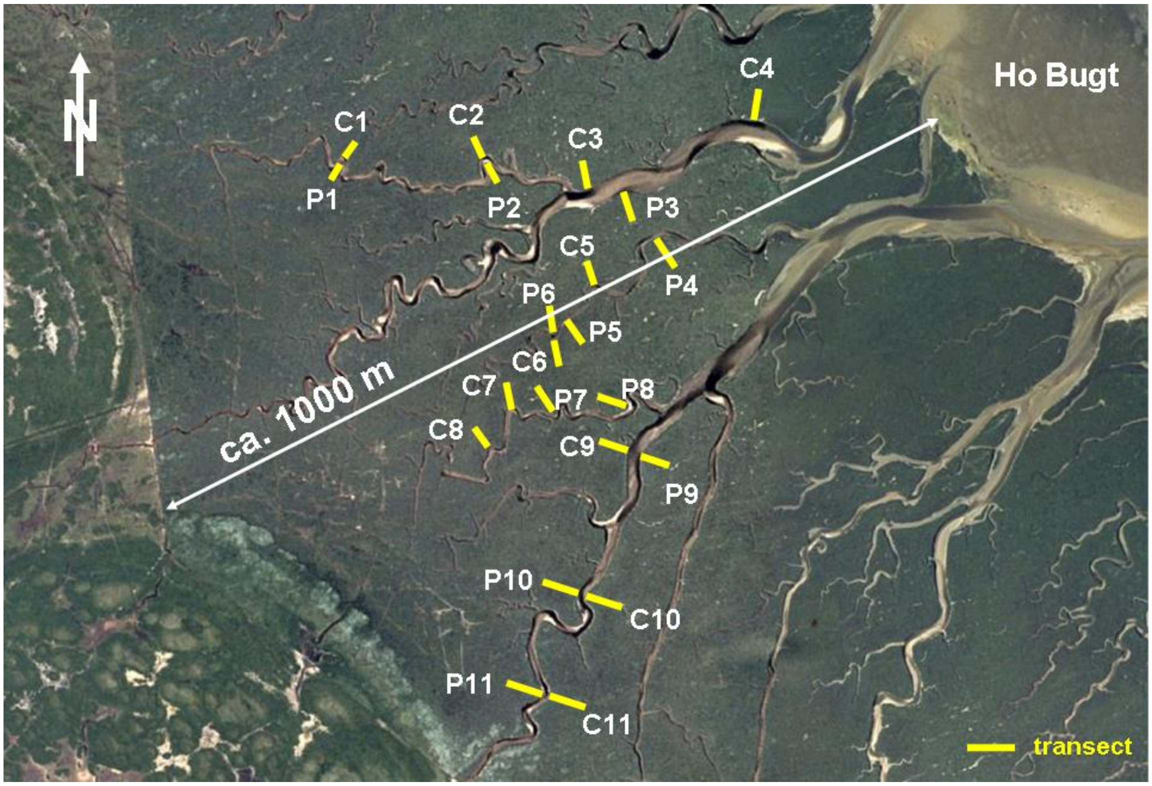


Figure 4.5 Location of medium-scale transects across various tidal creeks. ‘C’ and ‘P’ represent cutbank edge and point bar parts, respectively.

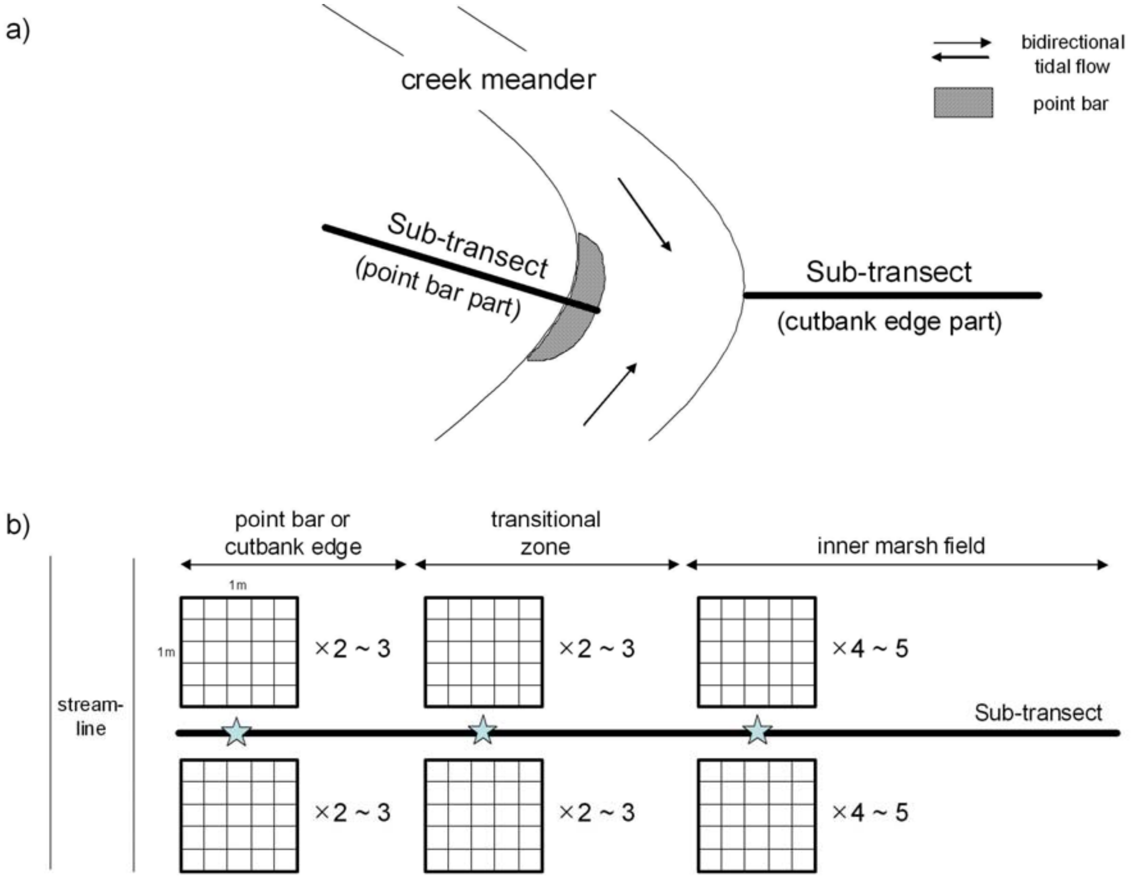


Figure 4.6 A schematic map of point bar and cutbank edge with sub-transects (A) and the establishment of quadrats along each sub-transect (B). The stars represent locations for soil and topographic survey.

(Figure 4.6B). Species composition varied strongly within a narrow zone of sites near the channel, while being relatively more homogeneous at marsh interiors. Accordingly, the number of quadrats and the distance between them were increased as one moved from point bars or cutbank edges toward the marsh interiors: 1) two or three quadrats were separated by 0.5 m in the zones of point bar and cutbank edge; 2) two or three quadrats were separated by 1 m in transitional zones; and 3) four or five quadrats were separated by 2 m - 4 m in marsh interiors. Two replicate quadrats were also established at every site surveyed (Figure 4.6B). In short, 16 to 20 quadrats were established along each sub-transect, encompassing the distance of about 25 m - 30 m from the streamline. The presence of vascular plant species was recorded in each cell (20 cm × 20 cm) so that the frequency of each species in one quadrat varied between 0 and 25. The frequencies from two replicate quadrats were averaged. In this way, information on the frequency of 13 species in a total of 201 quadrats (averaged from 402 quadrats) was acquired.

In the summer of 2007, soil and topographic sampling were also conducted at the middle between the two replicate quadrats (see marks in Figure 4.6B). A cylindrical core was used of which volume was approximately 159.04 cm^3. For the topographic survey, a differential GPS surveying system was used that produced errors in elevation less than 2 cm at each point surveyed.

4.2.2 Soil physical and chemical analyses

First, as preprocessing procedures, all soil samples were autoclaved, dried at 105 ºC for 24 hours. Bulk density (g/cm^3) was estimated by measuring the dry weight of each sample that was then divided by the volume of the cylindrical core used (i.e., 159.04 cm^3) (pages 207-210 in Grossman and Reinsch 2002).

After the determination of bulk density, all samples were ground and sieved to remove any materials with dimensions greater than 2.0 mm. After sieving, visible plant litter was removed. A total of nine soil chemical analyses were then performed including soil pH, electrical conductivity (umhos/cm), phosphorus (mg/kg), sulfur (mg/kg), nitrate (NO_3^-; mg/kg), Na^+ (mg/kg), K^+ (mg/kg), Ca^{2+} (mg/kg), and Mg^{2+} (mg/kg). Soil pH and electrical conductivity were determined in a 1:2 (soil:water) extract of each sample using distilled water. Samples were stirred with an automatic shaker. After 30 minutes, a hydrogen-selective electrode and a conductivity probe were utilized to estimate pH and conductivity values, respectively (Schofield and Talyor 1955; Rhoades 1982). Nitrate was extracted from samples using a 1 M KCl solution. Spectrophotometry was then used to determine nitrate content (Keeney and Nelson 1982). All other nutrients (P and exchangeable cations) were measured by ICPMS (inductively coupled plasma mass spectrometry), after extraction using the Mehlich III extractant (Mehlich 1978, 1984). The extractant was a dilute acid-fluoride-EDTA solution with pH of 2.5. All chemical analyses were performed by Soil, Water, and Forage Testing Laboratory at Texas A&M University.

4.2.3 Identification of vegetation associations and gradient structure

In order to identify vegetation associations across tidal creeks, the same set of hierarchical cluster analysis and indicator species analysis was used as in section, 4.1.2.

With regard to gradient structure in patterns of species composition, nonmetric multidimensional scaling (NMDS) was used (Mather 1976). NMDS is a distance-based ordination technique well suited for non-normal ecological datasets (Clarke 1993; McCune and Grace 2002). It aims to minimize the discrepancy (i.e., 'stress') between ecological dissimilarities among samples calculated from an original data set and those calculated from a new data set created by ordination. After iterative trials to find out a state of the lowest stress, NMDS defines a new configuration of sample units in the ordination space. Because NMDS is a distance-based approach, the distance between sample units can be used as a direct indicator of dissimilarities between them. Samples closer to each other in the ordination diagram exhibit more similar ecological characteristics (e.g., species composition). Sørensen's distance was used to calculate sample dissimilarities with a random starting configuration. The instability criterion was 0.0001 and the maximum number of iterations was 200. To lower the likelihood of local minima, multiple runs of NMDS (n = 40) and a Monte Carlo test (n = 40) were performed. The Monte Carlo (randomization) test determined the minimum number of dimensions necessary to produce the lowest stress. All statistical procedures were performed in PC-ORD Version 4.14 (MjM Software Design, Gleneden Beach, OR, USA).

4.2.4 Identification of gradient structure in soil data

To decipher the gradient structure in the spatial pattern of soil properties, principal component analysis (PCA) was adopted (see ter Braak 1995 and Whittaker 1967). PCA is an ordination technique, widely used in biogeography and soil science to rearrange and simplify complicated data structures (Sondheim et al. 1981; ter Braak 1995). PCA was used to reduce the data into a manageable set of descriptors, because the number of soil attributes considered in this research was large. Such a choice was based on the assumption that a set of identifiable factors should exist as the main environmental controls of soil patterns even in a complex salt marsh soil system. During PCA, components with eigenvalues greater than 1 were only extracted as main factors (cf., Cattell 1978). VARIMAX rotation was then conducted to orthogonally transform the configuration of the PCA plot into new axes to make the components more interpretable (Webster and Oliver 1990). After PCA, new groups of soil variables were created according to their factor loadings. That is, the variables with a large factor loading were sorted and regrouped, which was helpful for investigating the relative contribution of each variable to the principal components. When any soil property showed a non-normal distribution, it was transformed to look like the normal curve of errors before PCA. After PCA, the factors scores of each soil attributes will be correlated with the axis scores of NMDS to investigate the relationship between floristic and edaphic gradients. Analyses were conducted using SPSS® 12.0 for Windows (Norusis and SPSS, Inc. 1993).

4.3 RESEARCH OBJECTIVE 3 – SPECIES INTERACTIONS AND COMMUNITY STRUCTURE

4.3.1 Vegetation sampling and mapping

In the summer of 2008, two 10 m × 10 m square plots were established on the ungrazed, natural zone of the Skallingen salt marsh. One plot was situated on the outer part of the marsh around the interface between the marsh surface and the tidal flat. This site has a low relative elevation below 0.8 m DNN. The other plot was put on an inner part of the marsh platform with a surface elevation being about 1.0 m DNN. This landward, mid-elevation location was distant from the coastline by 367 m. For this research, this site was named as an inner marsh. According to high water statistics from the area (Bartholdy et al. 2004), these low and mid spots are inundated 213 and 111 times a year, respectively.

In each plot, the distribution of individual stems of *Limonium vulgare* and patches of *Triglochin maritima*, *Plantago maritima*, and *Halimione portulacoides* was mapped. Species nomenclature followed Tind (2003). These species are considered early- to mid-successional on northern European salt marshes. They occur at low- to mid-elevation sites where they can have biological and competitive advantages over pioneers and where more competitive, late-successional species such as *Festuca rubra* and *Artemisia maritima* cannot tolerate physical stresses imposed by sea water inundation (see Westhoff 1987; Bakker et al. 1993). In the inner marsh, there were certainly many more species than these four selected ones. However, these species were not selected because their presence rarely occurs in the outer marsh. This research aims to *compare* the spatial pattern of plant species between two plots, each located at the outer and inner plots, respectively. It was therefore needed to maintain consistency in choosing plants to be examined.

The mapping was an exhaustive procedure by which *x* and *y* coordinates/configurations of every stem/patch were recorded with approximately 1 cm-precision. ArcGIS^{TM} 9.2 was then used to digitize the stems and patches, and to estimate the area and centroid of each patch.

4.3.2 Spatial point pattern analyses

Ripley's *K*-function was used to investigate spatial point pattern of each plant species. The function is a second-order spatial analytic technique to describe the tendency of points to be distributed in clustered, random, or regular (hyper-dispersed) patterns at different scales on a two-dimensional plane (Ripley 1981; Diggle 1983; Getis 1984; Haase 1995). Since the centroid of each patch for some species was estimated, the resultant point data may not be based on exact coordinates of rooted stems (except for *L. vulgare*). However, the robustness of such an approximative approach has been reported elsewhere (e.g., Hasse et al. 1996; Moeur 1997; Feagin and Wu 2007).

This study was concerned with both univariate and bivariate point patterns to examine intra-specific and inter-specific interactions, respectively. For detecting univariate patterns of a single species, the function was defined as

$$\hat{K}(t) = \frac{|A|}{n^2} \sum_{i \neq j} \sum w_{ij}^{-1} I_t(u_{ij})$$

where $\hat{K}(t)$ is the univariate sample statistic value at distance, or radius t, A is the area of a plot, n is the number of points (stems or patches) in the plot, w_{ij} is a weighting factor to correct for edge effects, u_{ij} is the distance between points i and j, and I_t is a counter variable (1 if $u_{ij} < t$; 0 otherwise) (see Haase 1995). In bivariate analyses for detecting the point pattern of one variable with respect to the pattern of another variable (i.e., the spatial associations between the two variables), the K-function was as follows:

$$\hat{K}_{12}(t) = \frac{|A|}{n_1 n_2} \sum_{i}^{n_1} \sum_{j}^{n_2} w_{ij}^{-1} I_t(u_{ij})$$

where $\hat{K}_{12}(t)$ is the bivariate sample statistic K at distance t, n_1 and n_2 are the number of points of variables 1 and 2, respectively. The K values were calculated separately for specified range of radius t to examine the pattern of points as a function of spatial scale. A circle of radius t was centered on each point and counted the number of neighbors within the circle (i.e., $u_{ij} < t$). The radius, or spatial scale began from 0 m up to 5 m with 0.2 m increments. To correct points located near one of the borders in the square plot, a toroidal edge correction method described by Getis and Franklin (1987) and modified by Haase (1995) was used. By convention, the resultant K values were converted to a linearized function, $\sqrt{\hat{K}(t)/\pi} - t$ that was plotted against t to facilitate interpretation (Skarpe 1991). The null hypothesis assumes complete spatial randomness (CSR) in which the K-function has an expected value of zero for all radii, t. Positive and negative values imply that points are distributed in clustered and regular patterns, respectively.

A Monte Carlo simulation procedure was then adopted to test the sample statistic K values calculated from the real data for significance. The highest and lowest values of

$\sqrt{\hat{K}(t)/\pi} - t$ were estimated based on 99 randomizations to define the upper and lower bounds of 99% confidence interval (Haase 1995). If a sample statistic *K* value is greater than the upper bound at any given *t*, one can posit that points are clustered significantly. If the value is smaller than the lower bound, points are considered regularly dispersed. If the value remains within an envelope of the confidence limits, the null hypothesis of CSR cannot be rejected. All univariate and bivariate analyses were performed using SPPA 2.0 (Spatial Point Pattern Analysis; Haase 2002).

CHAPTER V

RESULTS

5.1 WIND-DRIVEN SEA-LEVEL VARIATION AND LONG-TERM VEGETATION DYNAMICS

5.1.1 Classification of vegetation associations

Among a total of 17 species investigated on the Skallingen salt marsh, three species (*Glaux maritima* L., *Lolium perenne* L., and *Spergularia media* (L.) C. Presl.) were excluded in the hierarchical cluster analysis because of their low frequency (i.e., occurred in fewer than five quadrats). An examination of the resulting dendrogram led me to decide that a pruning in the zone where information remaining is either greater than 75% or smaller than 50% would not be appropriate (Figure 5.1). This was because there were too many and too few branches in the first and second cases, respectively. Such a conclusion indicated that the number of vegetation associations should be determined between seven and four. Using an indicator species analysis, it was identified that the average *p*-value was smallest at the level of four clusters (i.e., 0.0733). Information remaining was still about 60% at this level. There are therefore vegetation associations on the Skallingen salt marsh that are both ecologically meaningful and statistically significant.

5.1.2 Succession of salt marsh vegetation

In 1933, the study site was dominated by Group A (seventeen samples out of 29; Figure

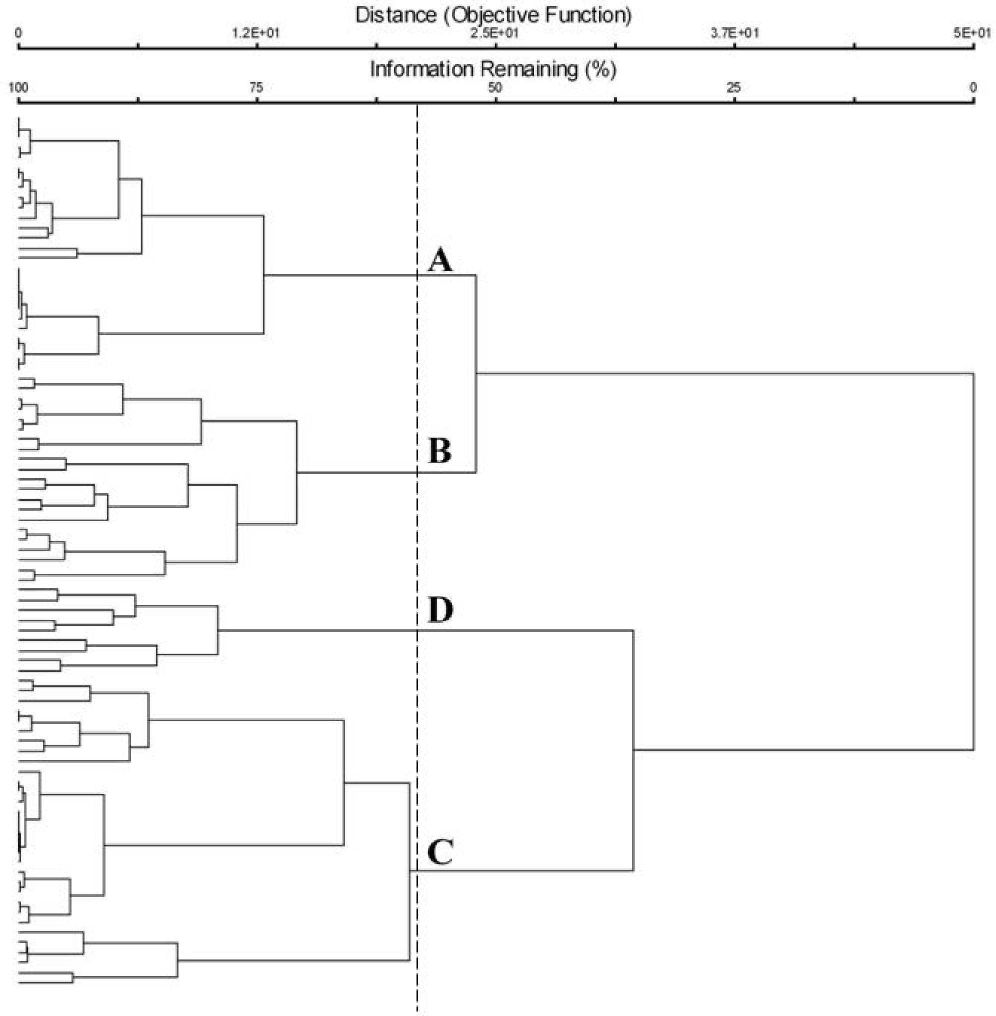


Figure 5.1 Dendrogram produced by a hierarchical cluster analysis on the floristic data. Symbols A, B, C, and D in the graphs represent Groups A, B, C, and D, respectively. The dotted line represents where the dendrogram was pruned.

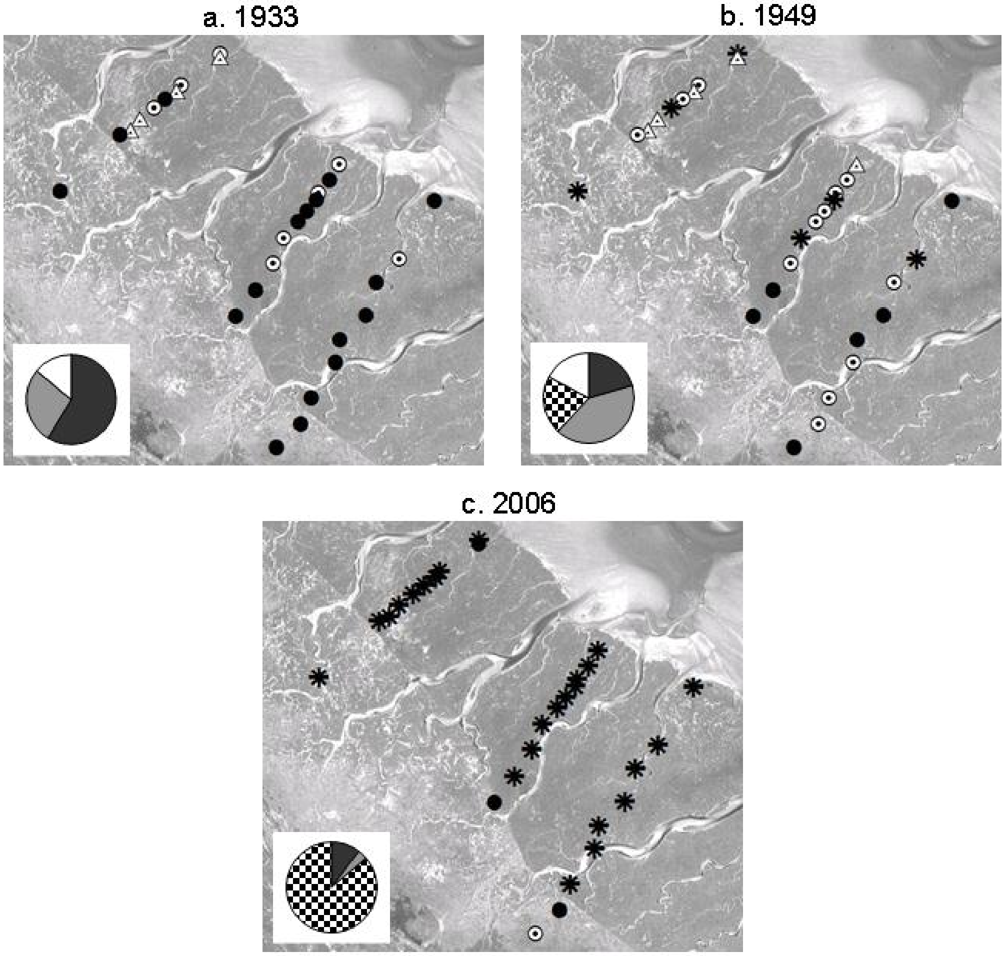


Figure 5.2 Temporal dynamics of spatial pattern of vegetation associations on the Skallingen salt marsh. In the spatial pattern of vegetation, solid circles (●), circles with a dot in the middle (⊙), asterisks (∗), and triangles (△) represent Groups A, B, C, and D, respectively. In each pie chart, areas with black, light gray, dark gray, and white correspond to Groups A, B, C, and D, respectively. G-tests showed that the vegetation cover, or relative group occupancy each year was significantly different from one another ($p < 0.01$). The horizontal length of each photo (taken in 1995) equals about 1.3 km in the real field. In the photo, there is a difference in the vegetation cover between grazed (lower-left side) and ungrazed (upper-right side) parts.

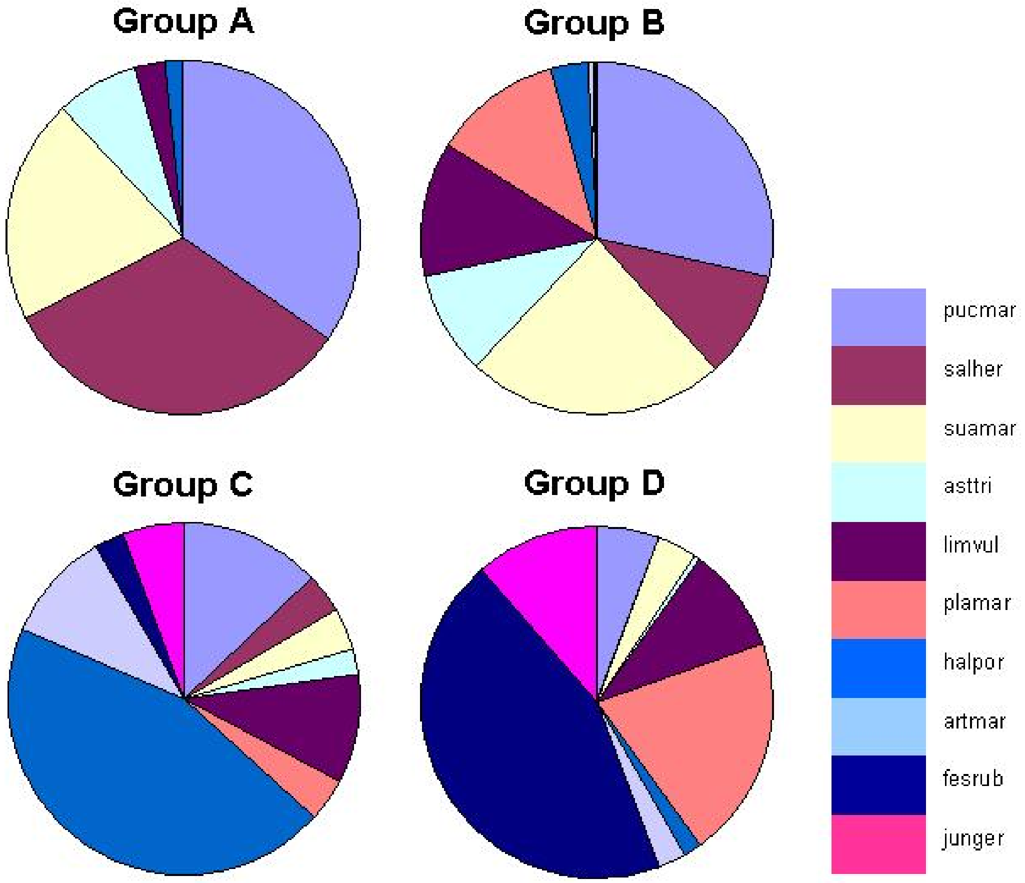


Figure 5.3 Relative abundance of each species for the four groups classified (pucmar – *Puccinellia maritima* (Hudson) Parl., salher – *Salicornia herbacea* L., suamar – *Suaeda maritima* L., asttri – *Aster tripolium* L., limvul – *Limonium vulgare* Mill. and L. humlie Mill., plamar – *Plantago maritima* L., halpor – *Halimione portulacoides* (L.) Aellen, artmar – *Artemisia maritima* L., fesrub – *Festuca rubra* L., junger – *Juncus gerardii* Loisel.).

Table 5.1 Average frequency (0-10) of main plant species† in each group and each year‡

Species§	*pucmar*	*salher*	*suamar*	*asttri*	*limvul*	*plamar*	*halpor*	*artmar*	*fesrub*	*junger*
Group A	9.74	9.13	5.78	2.14	0.72	0.04	0.46	0.00	0.00	0.00
Group B	9.05	3.14	7.43	3.05	3.95	3.76	1.05	0.19	0.10	0.00
Group C	2.55	0.68	0.78	0.41	1.95	0.75	8.70	1.97	0.53	1.09
Group D	1.33	0.00	0.78	0.11	2.22	4.56	0.33	0.56	10.00	2.56
1933	8.79	7.41	5.41	3.10	0.45	2.97	0.03	0.14	1.38	0.28
1949	6.93	2.69	5.59	0.83	4.76	1.34	3.10	0.52	1.83	0.52
2006	2.70	1.08	0.64	0.67	1.07	0.67	7.44	1.76	0.53	1.16

† Species with minor coverage (<1 percent) are not included.

‡ The frequency was averaged from twenty nine sampling locations. The values in the last three rows represent the cover of each species averaged from the 29 sampling locations at each year.

§ pucmar – *Puccinellia maritima* (Hudson) Parl., salher – *Salicornia herbacea* L., suamar – *Suaeda maritima* L., asttri – *Aster tripolium* L., limvul – *Limonium vulgare* Mill. and L. humlie Mill., plamar – *Plantago maritima* L., halpor – *Halimione portulacoides* (L.) Aellen, artmar – *Artemisia maritima* L., fesrub – *Festuca rubra* L., junger – *Juncus gerardii* Loisel.

5.2) that showed high frequency of *Puccinellia maritima*, *Salicornia herbacea*, and *Suaeda maritima* with some presence of *Aster tripolium* (see Table 5.1 and Figure 5.3). This association has been considered typical for a pioneer community on low salt marshes of the Wadden Sea where low species richness results from harsh environmental conditions due to frequent sea water inundation in the early stage of salt marsh development (Westhoff 1987).

Between 1933 and 1949, the study site was characterized by a dramatic decrease of Group A (from 17 samples to six; Figure 5.2). Now, Group B was the most frequent ecological state (12 samples out of 29) that had mainly developed from the stage of Group A through progressive succession. This association showed a general increase of diversity in ecological groups compared to Group A, presumably through continuous sedimentation and ameliorated edaphic conditions. There was a dramatic decrease in *S. herbacea*, and a significant increase in *Limonium vulgare* and *Plantago maritima* which had been minor species in Group A (Table 5.1 and Figure 5.3). Although slight, *Halimione portulacoides*, *Artemisia maritima*, and *Festuca rubra* also showed increased coverage. Because of the lingering, but significant presence of pioneers, Group B should be understood as still representing an early-successional phase. It is noteworthy that six samples of Group C began to emerge with this group.

Transition in species composition between 1949 and 2006 was notable in that 83% (i.e., 19 out of 23) of samples that did not belong to Group C in 1949 became members of Group C (Figure 5.2). Currently, the great majority of total samples (i.e., 25 out of 29) are classified as Group C. This association was dominated by *H. portulacoides* while other species' cover was very low (Table 5.1 and Figure 5.3). The predominance of *H. portulacoides* by its competitive ability and ecophysiological advantages (e.g., tolerance to frequent inundation and high salinity; see Jensen 1985b) has been observed on other low (or sometimes middle) salt marshes in the Wadden Sea (e.g., Beeftink et al. 1978; Beeftink 1987; Erchinger 1985; Westhoff 1987; Bakker et al. 1993). Such dominance is achieved after successional processes beginning with *Puccinellietum maritimae typicum* (an ephemeral stage), followed by a mixed community of *L. vulgare* and *H. portulacoides*. Following Westhoff (1987), it is considered that the ecological state of Group C represents a relatively early- to mid-successional phase of salt marsh vegetation. In this regard, the year of 2006 is attractive because, even after one hundred years of the salt marsh development with a continuous increase in the surface elevation, the major portion of Skallingen is still not late-successional.

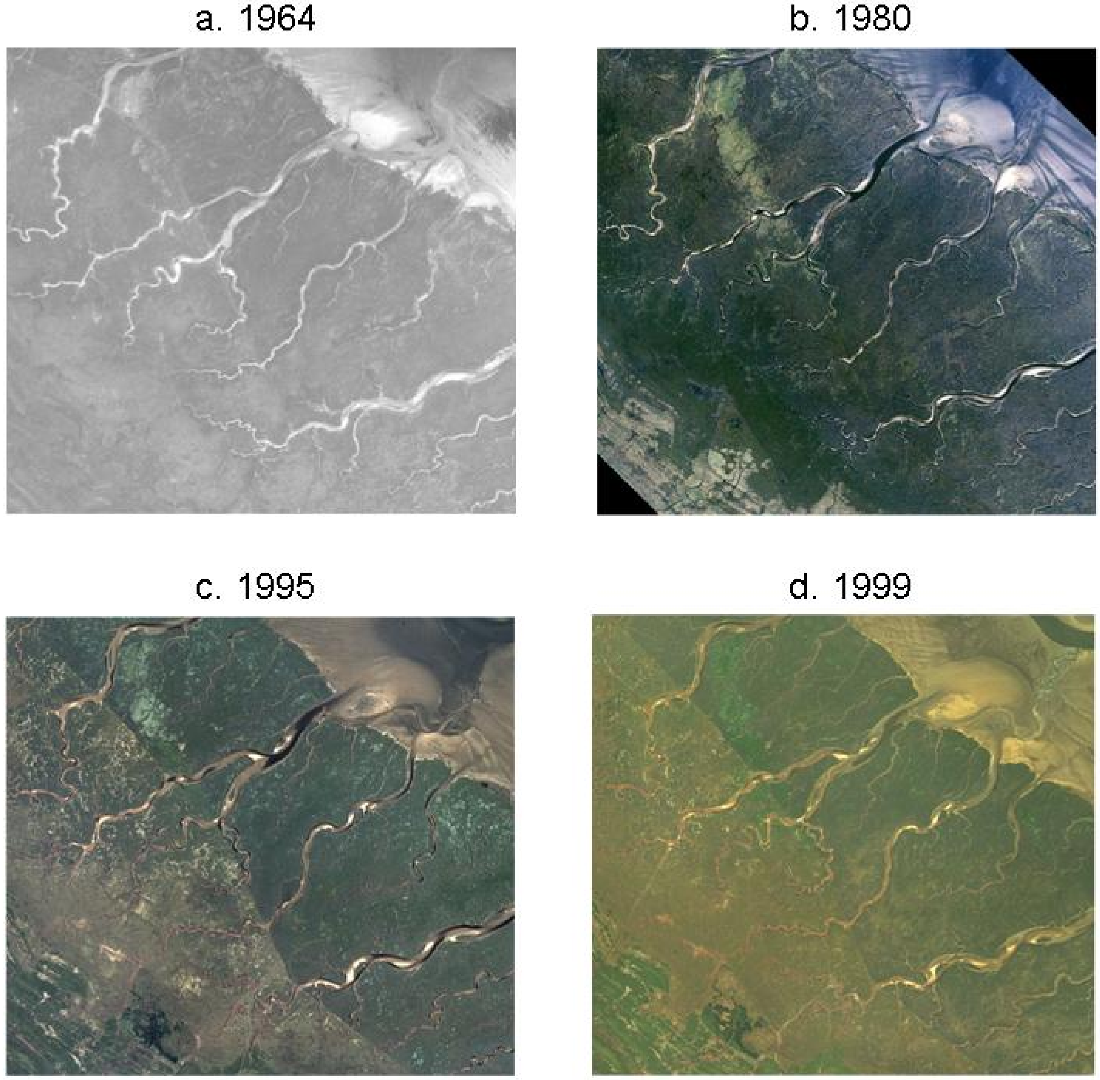
It is also intriguing that Group D has currently disappeared, though some of the ecological type had been present in previous years (i.e., four samples in 1933 and five samples in 1949). Group D was *Festuca*-dominated with *Plantago maritima* and *Juncus gerardii* being secondary dominants (Table 5.1 and Figure 5.3). At other Wadden Sea salt marshes, this association has mainly been observed on high salt marsh areas, representing a late-successional stage (Roozen and Westhoff 1985; Bakker et al. 1993). Considering that the Skallingen salt marsh was still young in the middle of the 20th century, it was unusual that this late-successional group explained 14-17% of total group occurrences (i.e., four-five out of 29). I propose therefore that the disappearance of Group D should therefore be considered as an important ecological change, rather than an incidental event.

The presence of Group D in previous years can be understood in terms of an underlying sand flat beneath the marsh surface. Before the initial development of the Skallingen salt marsh at the beginning of the 20th century, a sand flat had developed for about 400 years (Aagaard et al. 1995). Because locally high sites had already existed on the sand flat (Bartholdy et al. 2004), a late-successional state could be observed on these locations even in the early stage of salt marsh development at Skallingen. A key point here is that even these locally high sites previously characterized by Group D are now dominated by *H. portulacoides* (i.e., Group C). I propose that such an ecological transition may indicate retrogressive succession. Beeftink (1987) also observed a replacement of *F. rubra* by *H. portulacoides* and ascribed such retrogression to increased frequency and depth of tidal inundation.

I acknowledge that results of this research are based on the somewhat limited number of samples (i.e., 29 in each year). Such a constraint in the sampling design may be a main reason why the quadrats established did not capture the coverage of *Spartina townsendii* H. & J. Groves, in spite of its presence on the outermost part of the marsh adjacent to the tidal flat. In addition, there is indeed a patchy distribution of Group D type in the very upper portion (>120 cm) of the marsh. However, except for these two minor limitations, the general pattern of vegetation in both 1933 and 1949 illustrated in this study was confirmed by Iversen (1953) with a descriptive approach at a broad spatial scale. In addition, according to field work for this research, the predominance of *H. portulacoides* in 2006 occurred not only in the 29 sampling locations along the three transects but also on the majority of ungrazed parts of the Skallingen salt marsh.

I also recognize that these conclusions are based on the limited number of snapshots of vegetation (1933, 1949, and 2006), and that there is a gap of fifty seven years between the last two dates. However, according to an interpretation of aerial photographs taken since the 1940s approximately every ten years, a more or less unidirectional change into the dominance of *H. portulacoides* has occurred on the Skallingen salt marsh (see Figure 5.4 for selected images). Specifically, such a change was clearly detected since the 1980s. Focusing on the natural, ungrazed area (i.e., upper-right side in each picture), one can notice the dominant color of dark green which indicates the cover of *H. portulacoides* (i.e., Group C).

An elongated, bright linear feature in the upper part of the system indicates the presence of late-successional plants such as *F. rubra* and *A. maritima*. This area consists of a sand ridge with a surface elevation of approximately 120 cm. It was interpreted by Nielsen (1935) as an aeolian ridge formed on the bare sand flat before the salt marsh accretion started. The area of these species' cover was small in 1964 and increased to a maximum in 1980, after which it decreased again as seen in 1995 and 1999. Thus, in general there have been progressive succession until about 1980 and retrogression of these plants since then. It is noteworthy that this year (i.e., 1980) is in good accordance with the timing of significant environmental changes. First of all, the NAO index has been dominantly under a positive phase since the 1980s (Figure 5.5). Second, accordingly, there were relatively higher rates of the increase in the frequency of HWL (see the last two periods in Table 3.1). The presentation of repeated vegetation samples



a. 1964

b. 1980

c. 1995

d. 1999

Figure 5.4 Selected aerial photographs of the study area taken in 1964 (A), 1980 (B), 1995 (C), and 1999 (D). There is a division into grazed (lower-left side) and ungrazed (upper-right side) parts. The horizontal length of each photo (taken in 1995) equals about 1.3 km in the real field.

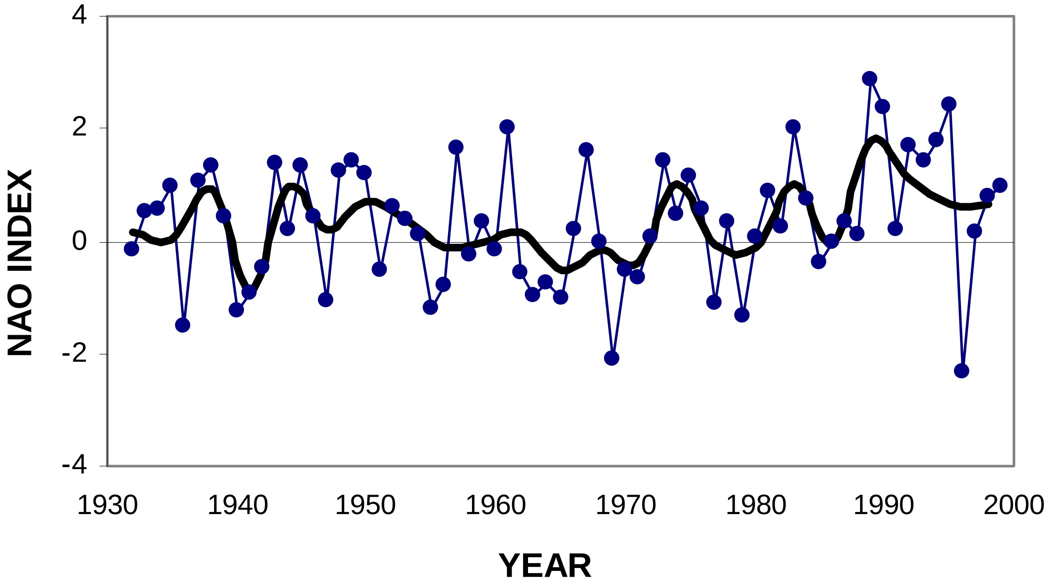


Figure 5.5 Yearly variation of the North Atlantic Oscillation (NAO) index. The smooth, thick line represents the three-year-running mean calculated from the original yearly NAO data. This averaged description indicates that the NAO index has dominantly been under a positive phase since the 1980s, except for the year of 1996.

of the same locations in conjunction with hydrographical, sedimentological, and remotely-sensed data acquired over such a long period is a novel contribution to the salt marsh and biogeographic literature.

5.1.3 Simulation modeling of floristic and geomorphic processes

Table 5.2 provides the initial relative frequency (%) of four different vegetation groups determined based on the results of cluster analysis (see Figure 5.2A). The simulation modeling of this research involved a random variable in the abiotic parts. 10 multiple simulations were thus conducted and the resultant values were then averaged.

5.1.3.1 Abiotic dynamics

There were closely linked dynamic processes among environmental factors. First, the number of simulated inundation occurrences has gradually increased through time (Figure 5.6Aa). The rate of sediment deposition has also increased in the simulation results (Figure 5.6B). The degree of such an increase was highest at the low marsh, while intermediate and lowest at the mid and high sites, respectively. However, there were significant drops of the rate at the low and mid areas around 1995 and 2025, respectively. Correspondingly, the increasing trend of surface elevation slowed down in these times (Figure 5.6C). The difference in the initial surface elevations among the three sites has gradually decreased over time. The yearly number of over-marsh flooding events varied differently among the three sites (Figure 5.6D). There were significantly decreasing and increasing patterns at the low and high marshes, respectively. At the mid

Table 5.2 Initial relative occupancy (%) of each vegetation association at different sites

	Low marsh	Mid marsh	High marsh
Pioneers	70	25	2
Early-sere	25	60	3
Early- to mid-sere	3	10	25
Late-sere	2	5	70

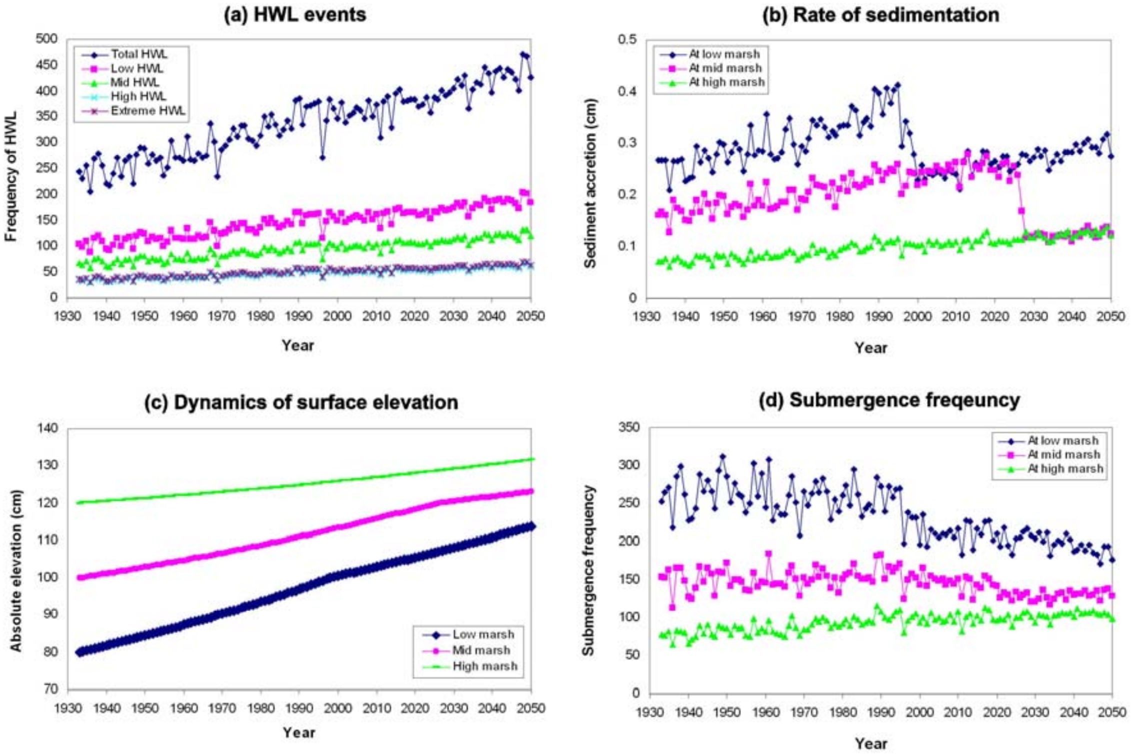


Figure 5.6 Simulated frequency of HWL events per year from 1933 to 2050 (A), rates of sediment deposition (B), dynamics of the absolute elevation (C), and frequency of over-marsh flooding (D). Each value was acquired by averaging results of 10 multiple simulations. Note that sites began as one of low, mid, and high marshes, but owing to the surface accretion over time, each could belong to a different vertical category at any particular temporal point. For example, the site that was initially a low marsh ended as a mid marsh in the simulation.

site, the inundation frequency has been more or less constant during the simulated period.

5.1.3.2 Biotic dynamics

In general, both baseline and experimental simulations showed a gradual replacement of species by others over time very well (Figure 5.7). However, successional patterns were significantly different with regard to the surface elevations tested and whether wind-driven sea-level set up was considered or not. At low marshes in both simulations, the dominance of pioneers and early-successional species was maintained for a relatively long time compared to mid- and high-elevation sites. The performance of these species, however, was very poor on the higher areas.

The difference in results from the baseline and experimental simulations was most notable in terms of the dominance of the late-successional association. Such (pre)dominance was clearly achieved in the baseline simulations regardless of the surface elevation with the fastest speed at the high sites. Due to this dominance, the temporal range in which the other three successional stages dominate became narrower than that produced by the experimental simulations. The high relative occupancy of the late-sere group was suppressed in the experimental modeling due to the dominance of early- to mid-successional associations through time. Even at the high marsh, a conversion of dominance from late-phase to early- to mid-phase was simulated around 2030.

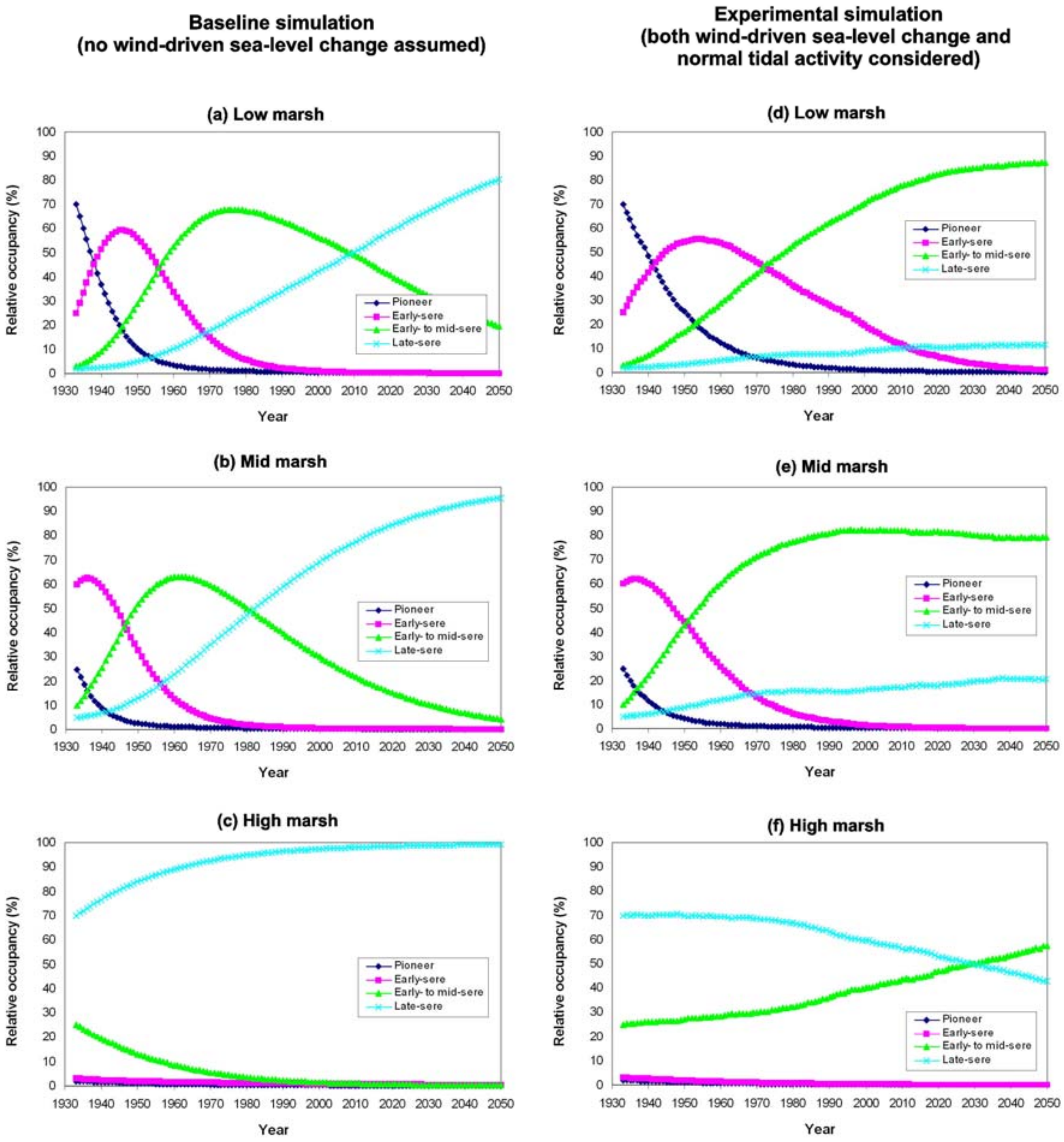


Figure 5.7 Comparison of baseline (A, B, and C) and experimental (D, E, and F) simulations for ecological succession. Each value was acquired by averaging results of 10 multiple simulations.

5.2 FLUVIAL-GEOMORPHIC PROCESSES AND PLANT ZONATION ACROSS TIDAL CREEKS

5.2.1 Classification of vegetation associations

An interpretation of the dendrogram produced by the hierarchical cluster analysis led to determine that the number of groups should be between four and nine (figure not shown here). A pruning outside this criterion would yield too many or too few branches. According to a subsequent indicator species analysis, the average *p*-value was the smallest at the level of nine ($p = 0.0003$) clusters.

The first group was characterized by the high cover of *P. maritima*, *S. herbacea*, *S. maritima*, and *Spartina townsendii* (Table 5.3). These species have been known to comprise typical pioneer, early-sere communities on the low salt marsh area in the Wadden Sea (e.g., Westhoff 1987).

The second, third, fourth, and fifth groups showed a lingering, but significant presence of the pioneer species with an increased frequency of *H. portulacoides*, *L. vulgare*, *Plantago maritima*, and *Aster tripolium*. Such a mixture of various species, or enhanced species richness, indicated a more or less early-successional nature of this association with some degree of progressive succession. In a Dutch salt marsh, a similar community was observed mainly on higher sites of low areas (i.e., '*Puccinellietum maritima* typicum with higher abundance of *Limonium vulgare* and *Halimione portulacoides*' (Roozen and Westhoff 1985)).

In the sixth and seventh groups, there was predominance of *H. portulacoides*, with a difference between them being the degree of the dominance. The dominance by *H.*

Table 5.3 Average frequency of species in vegetation associations across tidal creeks

	puc-mar	*sal-her*	*sua-mar*	*spa-tow*	*hal-por*	*lim-vul*	*pla-mar*	*art-mar*	*fes-rub*	*jun-ger*	*ast-tri*	*tri-mar*
1	16.13	17.21	22.77	5.13	8.02	8.21	0.31	0.13	0.00	0.00	4.52	0.10
2	10.89	3.91	14.32	0.76	24.88	13.20	2.18	0.21	0.00	0.00	6.32	3.20
3	16.34	2.92	5.34	0.71	24.50	13.42	2.50	0.71	0.03	0.03	9.16	1.87
4	13.38	5.42	11.63	0.58	24.46	15.33	15.96	1.50	0.00	0.00	5.13	5.33
5	17.31	18.22	17.61	0.17	23.78	18.39	3.31	0.28	0.00	0.00	8.50	9.39
6	7.23	0.50	3.30	0.05	24.91	6.65	2.78	2.38	0.00	0.01	2.42	0.72
7	1.90	0.28	0.84	0.00	25.00	1.10	0.53	1.36	0.26	0.45	0.64	0.29
8	4.14	0.23	1.93	0.07	24.45	3.45	3.48	16.32	1.89	2.41	1.61	0.16
9	1.21	0.00	0.29	0.00	10.86	3.43	1.64	23.93	21.86	23.86	1.29	0.00

† Species frequency varies between 0 and 25. Because of its fairly minor frequency, *Spergularia media* (L.) C. Presl. were excluded from this table. (*puc-mar – Puccinellia maritima* (Hudson) Parl., *sal-her – Salicornia herbacea* L., *sua-mar – Suaeda maritima* L., *spa-tow – Spartina townsendii* H. and J. Groves, *hal-por – Halimione portulacoides* (L.) Aellen, *lim-vul – Limonium vulgare* Mill. and L. humlie Mill., *pla-mar – Plantago maritima* L., *art-mar – Artemisia maritima* L., *fes-rub – Festuca rubra* L., *jun-ger – Juncus gerardii* Loisel., *ast-tri – Aster tripolium* L., *tri-mar – Triglochin maritima* L.)

portulacoides was considered to result from progressive succession by its competitive ability and ecophysiological advantages (Jensen 1985b). On low salt marshes, it has often been observed that an ephemeral stage dominated by early-sere species (especially *P. maritima*) undergoes successional processes over time to show a *H. portulacoides*-dominated state via an intermediate course characterized by a mixed community of the pioneers, *L. vulgare*, and *H. portulacoides* (Beeftink et al. 1978; Erchinger 1985; Beeftink 1987; Westhoff 1987; Bakker et al. 1993). This research suggests that the associations dominated by *H. portulacoides* are at a transitional phase between the end of early-successional and the beginning of mid- to late-successional stages.

The eighth and ninth associations showed significantly increased cover of *A. maritima*, *F. rubra*, and *J. gerardii*. The high cover of these species that comprise late-successional communities has primarily been observed on areas with high surface elevation at other Wadden Sea salt marshes (Roozen and Westhoff 1985; Bakker et al. 1993).

5.2.2 Spatial pattern of vegetation across tidal creeks

The upper portion of Figure 5.8 provides a clear pattern of relative occupancy among nine groups across tidal creeks, summarizing the 201 points along 22 transects on the marsh. First of all, point bars were dominated by pioneer communities. The transitional zone above point bars was characterized by an increased frequency of late-successional and *H. portulacoides*-dominated groups. In spite of their adjacency, the point bar and the transition possessed two different ecological states, each of which is located at an

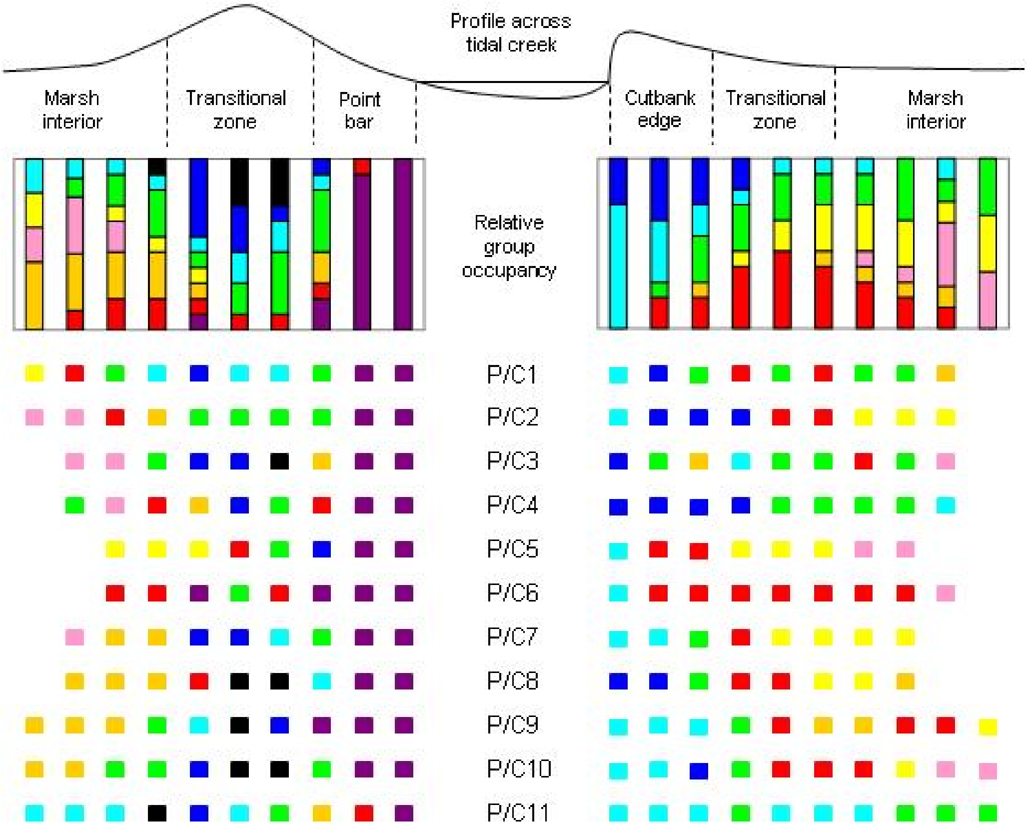


Figure 5.8 Spatial zonation of salt marsh plants across tidal creeks on the Skallingen salt marsh. ‘P’ and ‘C’ represent parts of points bar and cutbank edge, respectively. See Figure 4.5 for the location of each transect.

extreme along a sequence from early- to late-succession. Species composition on cutbank edges was more or less similar to that on the transition of point bar parts, but the edges did not have late-successional assemblages. Inner marshes of both point bar and cutbank sides were under little direct influence of the tidal creeks, and showed a major portion consisting of relatively early-successional communities.

These general patterns were also observed at each of the 22 transects with some degree of variations. Overall, transects located in the southern part of the marsh such as P8, P9, P10, and P11 were characterized by communities with relatively later-successional stages. With an exception at Transect P3, the occurrence of Group 9 was observed only at the transition zone of these transects. It is thus anticipated that such sites would be significantly higher than sampling locations of the other transects. Other than this different between southern and northern transects, it appeared that no visible trend is in operation among transects in the point bar parts. In some cases, the presence of Group 2 occurred in unexpected places such as transitional zone of point bars with a relatively high elevation (P5 and P6).

One of the conspicuous features in the cutbank edge part is that Transect C6 was preoccupied by Group 2 that represents a relatively early-sere phase. This area was composed of islands of small salt pans (figure not shown here). In inner parts of the marsh, other factors than the salt pan hardly allow such dominance by early-successional communities. In this regard, it is considered that the presence of local salt pans may be ubiquitous because approximately 73 % (i.e., 16 out of 22) of the surveyed transects showed the local or sometimes of extensive presence of relatively early-sere species.

5.2.3 Spatial pattern of topography across tidal creeks

In general, point bars showed the lowest surface elevation below 0.7 m DNN at all transects (Figure 5.9). Above point bars, there were transition zones with higher elevations that those of other locations, with an exception at Transect P4. At this transect, the marsh interior and transition zone similarly had intermediate-sere vegetation groups (Figure 5.8). Most transition zones corresponded approximately to the fourth and fifth sampling points from the creeks. However, such a zone occurred in exceptionally inner parts of the marsh at Transect P11, explaining why a late-successional community was observed here (Figure 5.8). The elevation of transition zones at Transects P8, 9, and 10 was conspicuously high, which is accordance with the dominance of late-successional plants on these sites. It appears that Transects P3, 8, 9, and 10 significantly contribute to the averaged elevation gradient in the point bar part. This means that patterns of other transects should also be taken into account in order to comprehensively understand the ecology around tidal creeks on the Skallingen salt marsh.

Compared to the point bar parts, cutbank sides showed less varying elevations across the creeks. However, it was still detectable that the edges possessed relatively higher elevations than the inner marsh fields. Such a trend was specifically visible at Transects C9 and 10. In the previous section, the dominance of mid- to late-sere communities was observed at the cutbank edges (Figure 5.8). Such a floristic pattern implies that even a slight difference in the surface elevation between the edges and the interiors could cause significantly different patterns of vegetation around tidal creeks. It is of interest which factors the micro-scale variation of elevation controls.

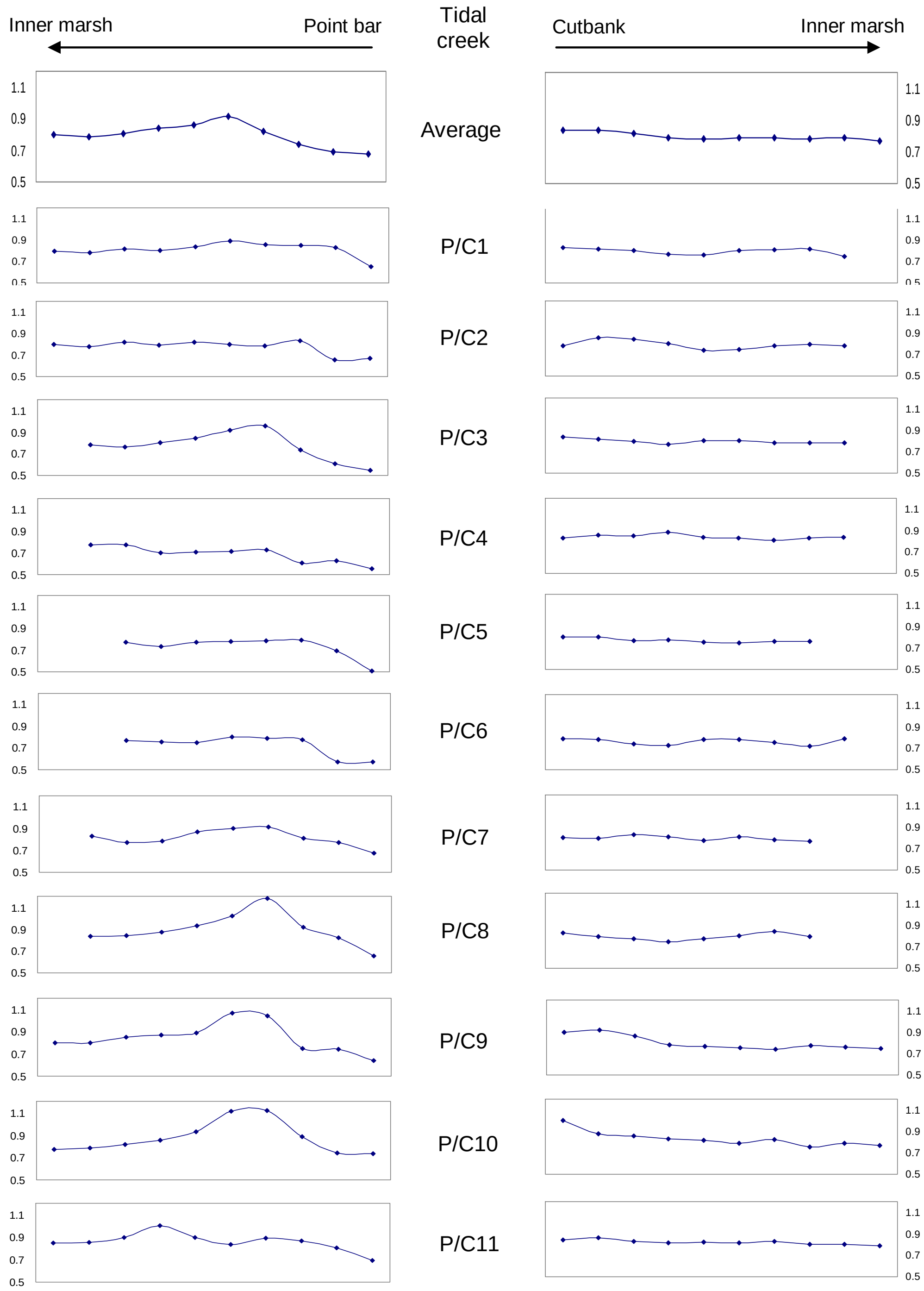


Figure 5.9 Spatial pattern of topography across tidal creeks. 'P' and 'C' represent parts of points bar and cutbank edge, respectively. See Figure 4.5 for the location of each transect. The points represent the location of topographic survey. Units are in meters.

5.2.4 Spatial pattern of soil properties across tidal creeks

There were more or less definable trends in the spatial pattern of soil properties across the tidal creeks (Figure 5.10). First, both bulk density and soil pH gradually decreased with distance from the creek. Electrical conductivity, sulfur, Na^+, Mg^{2+}, and K^+ showed low values at sites adjacent or close to the creeks, but these properties gradually increased with distance from the channels. However, it should be noted that some deviations did exist within these general trends at both sides of the creek. In the point bar side, for example, there were a drop of bulk density and a rise of Electrical conductivity, sulfur, Na^+, Mg^{2+}, and K^+ between point bars and transition zones. On the other hand, Ca^{2+}, nitrate, and phosphorus did not have any consistently increasing or decreasing gradients.

5.2.5 Gradient structure in vegetation patterns

NMDS suggested a two-dimensional solution with two axes explaining over 90 % of total variance (Figure 5.11). Such a suggestion was in good accordance with a careful examination of a scree plot (figure not shown here) that illustrated the relationship between stress and the number of dimensions. The two-dimensional solution dramatically decreased stress into 12.93 (26.42, $p = 0.024$). Values in the parentheses respectively represent the mean stress and significance produced by a Monte Carlo test. The scree plot leveled off to higher dimensional solutions. The final instability was 0.0015, with the stress stabilizing smoothly well before the iteration reached the maximum numbers. On the final configuration of the NMDS plot, the results of the

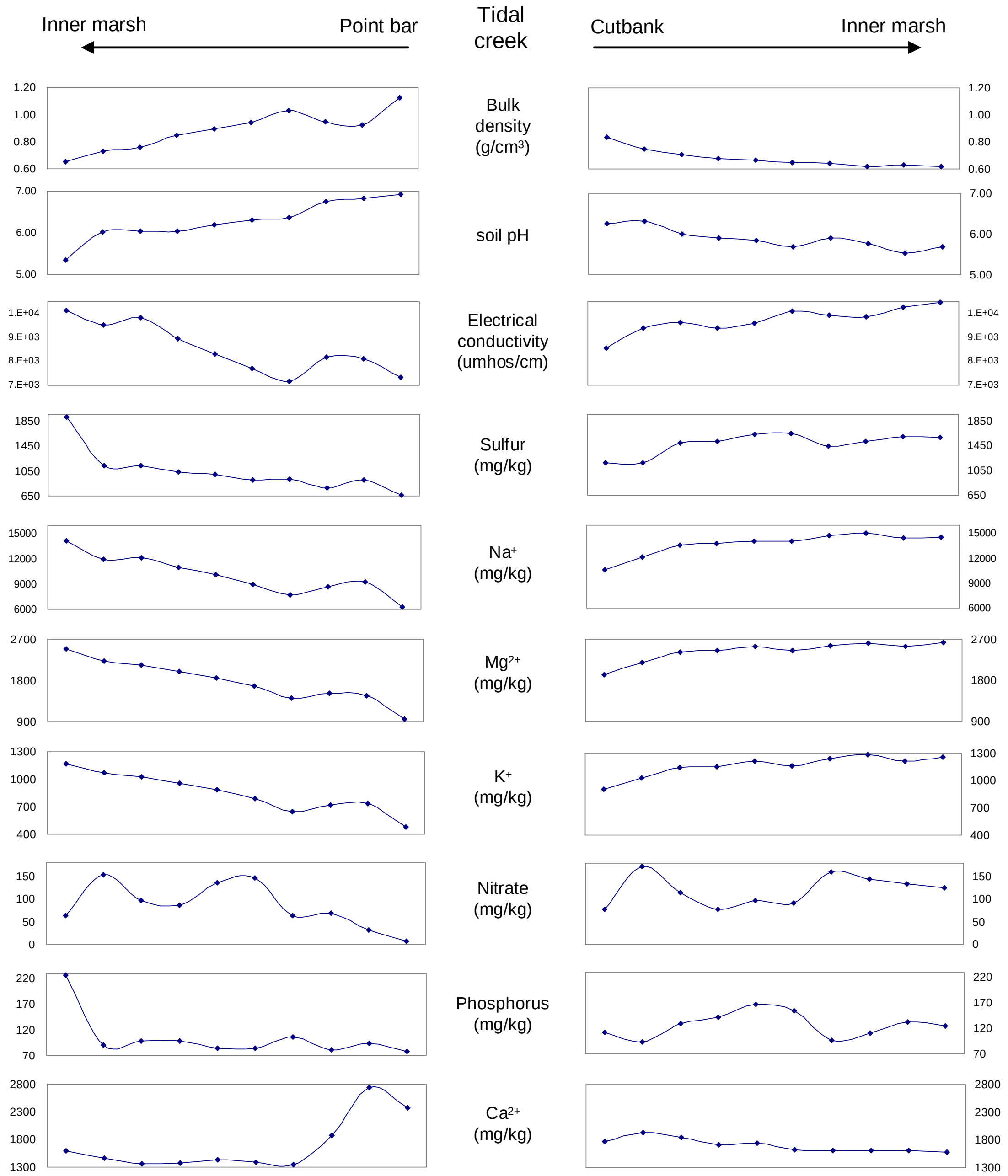


Figure 5.10 Spatial pattern of soil properties across tidal creeks on the Skallingen salt marsh. Each graph contains edaphic information averaged from 11 transects surveyed at point bar and cutbank edge parts, respectively. The points along the line represent the location of soil sampling.

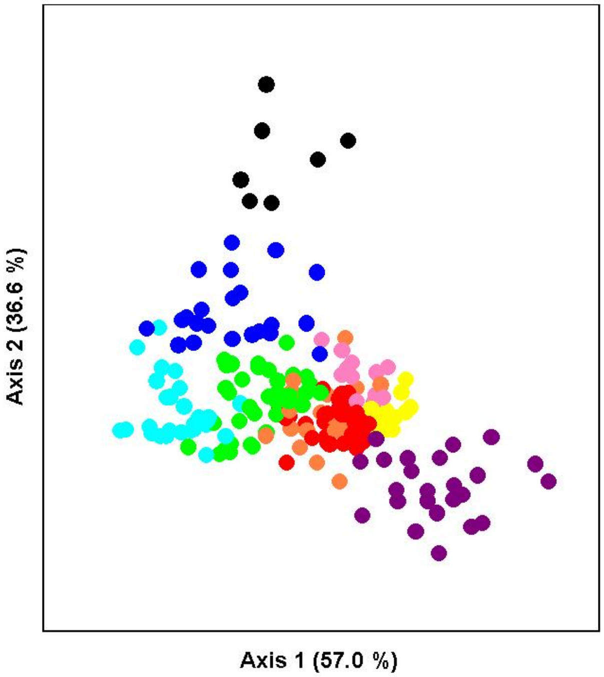


Figure 5.11 Final configuration of non-metric multi-dimensional scaling for the floristic data across tidal creeks. The first through ninth associations in Table 5.3 correspond to purple, red, orange, pink, yellow, green, light blue, dark blue, and black colors, respectively.

cluster analysis, or vegetation associations were superimposed to aid an understanding of potential gradient structure.

5.2.6 Gradient structure of soil properties across tidal creeks

Table 5.4 provided an overview of correlations among soil properties tested. It was noteworthy that only three coefficients were not statistically significant at the 0.05 level (2-tailed): nitrate vs. soil pH, nitrate vs. sulfur, and nitrate vs. Ca^{2+}. Moreover, except for the relation between nitrate and electrical conductivity, all other correlations were significant at the 0.01 level (2-tailed). Such weak or insignificant correlations of nitrate with other soil attributes reflect its fluctuating value across tidal creeks (see Figure 5.10).

A closer look at the correlation matrix suggested that the significant coefficients at the 0.01 level can be further divided into high and low values. Specifically, the first seven soil factors possessed relatively high coefficients one another with a value for soil pH vs. electrical conductivity relationship being the lowest, i.e., Pearson's $r = -0.51$ ($p < 0.01$).

PCA produced three principal components (PC) explaining 90.50 % of total soil variance (Table 5.5). It was noteworthy that a significant portion of all soil properties (i.e., seven out of 10) examined were grouped into the first PC, which is good accordance with results of the correlation analysis (Table 5.4). In this group, except for soil pH, other six attributes showed very high factor loadings for the first component. Nitrate and phosphorus belonged to a group with the highest factor loadings for the second PC. Only Ca^{2+} had a significantly high score for PC 3. A correlation analysis

Table 5.4 Pearson's correlation matrix among soil properties[†] measured in this research

	BD	pH	EC	S	Na^+	Mg^{2+}	K^+	N	P	Ca^{2+}
BD	1.00									
pH	0.61**	1.00								
EC	-0.78**	-0.51**	1.00							
S	-0.83**	-0.79**	0.67**	1.00						
Na^+	-0.97**	-0.58**	0.79**	0.82**	1.00					
Mg^{2+}	-0.96**	-0.60**	0.80**	0.82**	0.98**	1.00				
K^+	-0.96**	-0.54**	0.78**	0.77**	0.98**	0.99**	1.00			
N	-0.19**	0.03	0.14*	-0.09	0.21**	0.29**	0.28**	1.00		
P	-0.40**	-0.70**	0.36**	0.78**	0.35**	0.37**	0.30**	-0.44**	1.00	
Ca^{2+}	-0.27**	0.19**	0.33**	0.27**	0.29**	0.24**	0.27**	-0.08	0.19**	1.00

[†] BD – bulk density, EC – electrical conductivity, S – sulfur, N – nitrate, P – phosphorus

** significant at the 0.01 level (2-tailed)

* significant at the 0.05 level (2-tailed)

Table 5.5 Factor matrix after VARIMAX rotation of the soil attributes measured at the Skallingen salt marsh, Denmark

PC[†]	Variable[‡]	Mean	CV (%)[§]	Factor loadings and communality in PCA			
				PC 1	PC 2	PC 3	communality
PC 1	Mg^{2+}	2061.64	35.00	0.99	0.02	0.02	0.98
	K^+	983.34	35.90	0.98	-0.04	0.06	0.96
	Na^+	11676.05	35.98	0.98	0.04	0.08	0.96
	BD	0.79	100.52[b]	-0.96	-0.09	-0.05	0.94
	EC	9014.24	20.26	0.84	0.09	0.16	0.73
	Sulfur	1222.34	42.34	0.82	0.52	-0.02	0.95
	pH	6.13	9.06	-0.64	-0.50	0.51	0.92
PC 2	Nitrate	101.85	70.88[a]	0.33	-0.80	-0.18	0.79
	Phosphorus	111.45	9.94[b]	0.37	0.87	-0.05	0.90
PC 3	Ca^{2+}	1710.94	17.84[a]	0.25	0.12	0.92	0.93
Eigenvalue				6.152	1.719	1.179	
Variance explained (%)				61.516	17.195	11.793	
Cumulative percentage (%)				61.516	78.711	90.503	

Kaiser-Meyer-Olkin measure of sampling adequacy = 0.792

Barlett test of sphericity = 3416.962, significance = 0.000

[†] PC: principal component

[‡] BD – bulk density (g/cm^3), EC – electrical conductivity (umhos/cm); All other variables are in mg/kg, while pH is unitless.

[§] Coefficient of variation calculated after a transformation (a squared root, b logarithms)

Table 5.6 Pearson's correlation coefficient matrix between principal components and topographical attributes at the Skallingen salt marsh, Denmark

Variables[†]	PC 1	PC 2	PC 3
Elevation	0.45**	-0.04	-0.45**
Distance	-0.28**	-0.07	-0.41**

[†] PC: principal component, Distance: distance from the creek

** significance level less than 0.01 (2-tailed)

Table 5.7 Pearson's correlation coefficient matrix of NMDS axes scores with principal components and soil attributes

	Axis 1	Axis 2
PC 1	-0.02	-0.15*
PC 2	-0.06	-0.15*
PC 3	0.20**	-0.48**
Elevation	-0.59**	0.70**
Distance	0.05	0.12
Bulk density	-0.04	0.20**
pH	0.13	-0.02
EC[†]	-0.04	-0.31**
Sulfur	-0.06	-0.16*
Na^+	0.07	-0.19**
Mg^{2+}	-0.04	-0.12
K^+	0.04	-0.15*
Nitrate	-0.14	0.19**
Phosphorus	-0.20**	-0.12
Ca^{2+}	0.14*	-0.51**

[†] electrical conductivity

** significant at the 0.01 level (2-tailed)

* significant at the 0.05 level (2-tailed)

revealed that both micro-elevation and distance from the creek were significantly correlated with PC 1 and PC 3 ($p < 0.01$; Table 5.6). These topographic parameters, however, showed very low correlation coefficients with PC 2.

5.2.7 Comparison of floristic and edaphic gradients

The two axes of NMDS commonly had a significant correlation with the surface elevation (Table 5.7). However, they were not significantly correlated with distance from the creeks. This is different result from what was observed between principal components and the distance factor (Table 5.6). The second axis showed significant correlations with much more soil properties compared to the first axis. It had significant correlations with all the principal components and soil attributes such as bulk density, electrical conductivity, sulfur, Na^+, K^+, nitrate, and Ca^{2+}. The first axis, however, significantly correlated with only two soil properties: phosphorus and Ca^{2+}.

5.3 FINE-SCALE COMMUNITY STRUCTURE ASSOCIATED WITH COMPETITION AND FACILITATION[*]

5.3.1 Species establishment along environmental gradients

The density and patch size (or diameter) of each species varied significantly along environmental gradients (Table 5.8; Figure 5.12). There were a much greater number of individuals of *L. vulgare* on the outer marsh than on the inner marsh, while the average

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[*] Reprinted with permission from "Scale-dependent interactions and community structure along environmental gradients on a coastal salt marsh" by Kim, D., Cairns, D.M., and Bartholdy, J., 2009. *Journal of Coastal Research*, SI 56, 429-433, Copyright [2009] by Coastal Education and Research Foundation, Inc.

diameter was greater on the inner area ($t = 25.31$, $p < 0.001$). The number of *T. maritima* patches was also smaller in the marsh platform, but there was no significant difference in the average patch size ($t = 0.59$, $p = 0.557$). In the case of *P. maritima*, both the number and the average size of patches were greater on the inner marsh ($t = 8.65$, $p < 0.001$). The establishment pattern of *H. portulacoides* was conspicuous in that the species comprised a matrix on the marsh platform, while there were sporadic occurrences of its small clumps on the outer area.

5.3.2 Univariate spatial point pattern

Except for *H. portulacoides* (figure not shown here), individuals or patches of each species on the outer marsh showed consistently stronger clustering across wider spatial scales than those on the inner marsh (Figure 5.13). In the mid area, stems of *L. vulgare* were slightly clustered around the scale of 0.4 m. A peak, stronger clumping occurred at the same scale on the low marsh, but the significant clustering was maintained until the scale of 2.0 m. Patches of *T. maritima*, with a peak point also at 0.4 m, were clustered within a radius of 2.4 m on the inner marsh. However, in the low site, stronger clustering was observed across the entire range of spatial scales examined (i.e., 5 m). There was a significantly regular pattern of *P. maritima* patches around 0.2 m in the inner marsh. While a slightly regular pattern occurred as well at the similar radius in the outer marsh, the patches were strongly clumped beyond that scale (i.e., 0.2 m).

Table 5.8 The number and size of individuals/patches of each species along environmental gradients, Skallingen, Denmark

		L. vulgare		*T. maritima*		*P. maritima*		*H. portulacoides*	
		Outer	Inner	Outer	Inner	Outer	Inner	Outer	Inner
Number of individuals/ patches		2303	704	421	263	124	307	268	-
Diameter (m) or patch size (m^2)	Min	0.6	0.7	0.0009	0.0011	0.0059	0.0053	0.0051	-
	Max	12.0	25.0	0.0441	0.0526	0.0737	0.0513	0.6650	-
	Mean	7.44	9.83	0.0068	0.0071	0.0235	0.0799	0.0518	-
	Standard deviation	0.83	3.38	0.0056	0.0066	0.0130	0.0720	0.0716	-

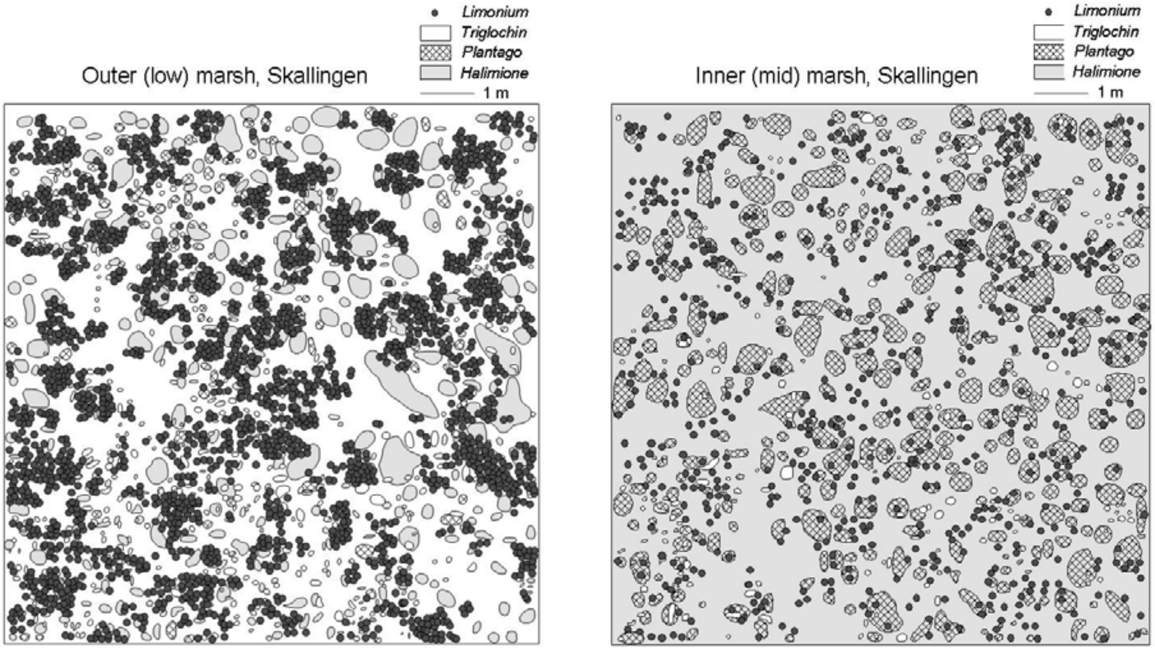

Figure 5.12 Species establishment (10 m × 10 m) along environmental gradients, Skallingen, Denmark.

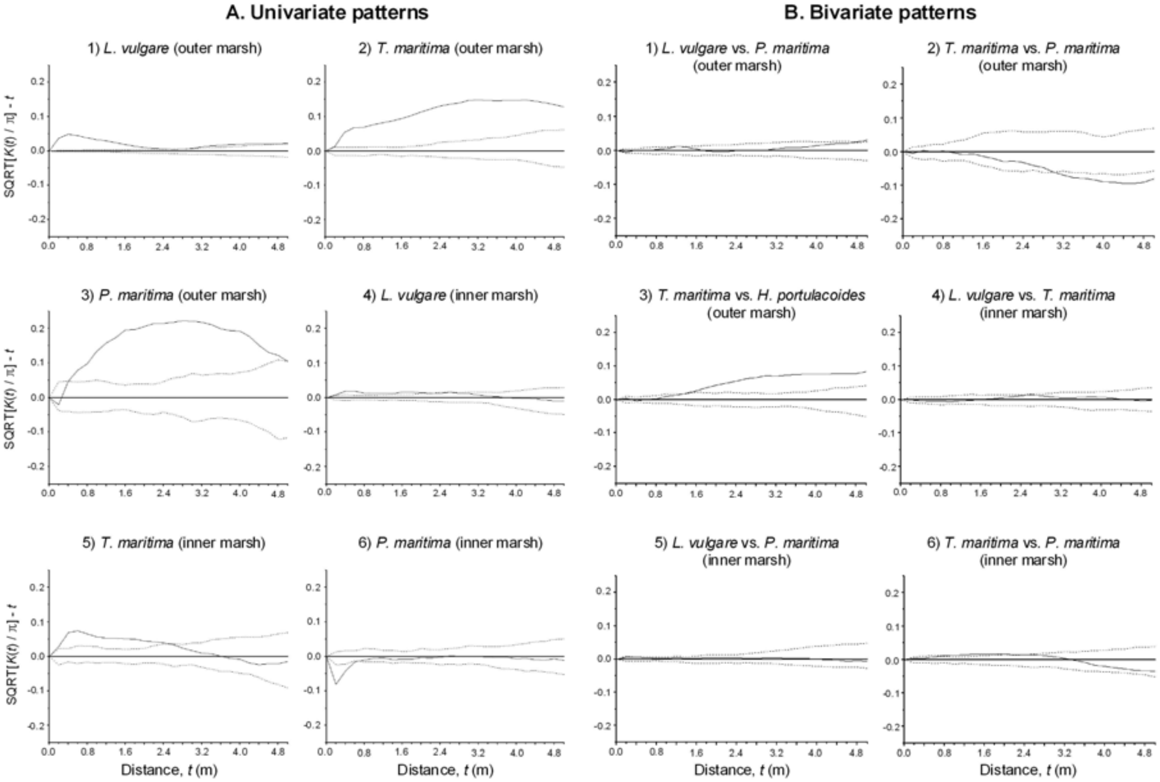

Figure 5.13 Second-order spatial analysis of selected distribution patterns of plant species on the Skallingen salt marsh, Denmark. The solid and dotted lines represent linearized *K* values and simulation envelopes, respectively.

5.3.3 Bivariate spatial point pattern

Bivariate analyses for the inner marsh plot consistently showed that the spatial relationship of any two species was almost random (Figure 5.13). Although the line of Ripley’s *K* for some species was outside of the simulated envelopes in a limited range of spatial scales (e.g., *T. maritima* vs. *P. maritima*), such an escape could not define any strongly positive or negative spatial associations.

In the outer marsh, all three major patterns (i.e., clustered, random, and regular) were identified. Random patterns were mainly observed in the relationships between *L. vulgare* and other species. However, *L. vulgare* had a minor negative spatial association with *H. portulacoides* around the scale of 0.2 m. At the same scale, there was also a weak negative spatial relation between patches of *P. maritima* and *H. portulacoides* (figures not shown here). In addition to these fine-scale observations, significant coarser-scale spatial structures occurred as well in the low area. Patches of *T. maritima* and *P. maritima* made a spatial buffer to each other over the scale greater than 3.0 m. There was a positive spatial association between *T. maritima* and *H. portulacoides* across the scale greater than 1.6 m.

CHAPTER VI

DISCUSSION

6.1 WIND-DRIVEN SEA-LEVEL VARIATION AND LONG-TERM VEGETATION DYNAMICS

6.1.1 Model evaluation

6.1.1.1 Abiotic dynamics

It is considered that the simulation results reflected real patterns and processes observed on the Skallingen salt marsh relatively well. First, the increasing pattern of the simulated total HWL events over time (Figure 4.4A) was very similar to that of the observed ones from 1933 to 1999 (Figure 3.5B). There was a significant positive correlation coefficient between these two variables, i.e., Pearson's $r = 0.76$, $p < 0.01$.

Second, the projected rates of sediment accretion made sense in that, most of all, these rates gradually increased through time (Figure 4.4B), responding to the increase in HWL occurrences per year. Also, as was expected, the low marsh showed the highest rate of accretion due to the longest and deepest submergence regime. Additionally, the high site experienced the slowest sediment deposition because of the relatively lower frequency and intensity of sea water inundation. During the parameterization, it was intended that a decrease in the sedimentation rate would occur when any site tested changes elevation categories after an increase in the surface elevation (see Equation 2). Such an intention was well realized at the low and mid marshes around the end of the 20th century and 2030, respectively. However, it is also recognized that the two drops in the sedimentation rate are so abrupt that they may be regarded as an exaggeration of reality.

Third, the simulated dynamics of surface elevation corresponded well to those observed in the field. Jacobsen (1958) measured clay thickness at several locations on the Skallingen salt marsh in 1949. Bartholdy (2008) revisited these sites to collect the same set of sedimentological data and to conduct topographical surveys in 1999 and 2007. Based on the difference in the clay thickness between the three time periods, he estimated the past and current absolute elevations at each location. This research had a fortunate situation in that two of these monitored locations respectively had surface elevations, 85.83 cm and 102.43 cm in 1949 that were very similar to those simulated for the low and mid marshes in the same year (i.e., 84.17 cm and 102.68 cm; Figure 4.4C). These similarities in surface elevation were maintained in both 1999 and 2007 as presented in Table 6.1. However, the simulated dynamics of the surface elevation for the high marsh could not be evaluated due to the lack of the relevant data in Jacobsen's (1958) and Bartholdy's (2008) research.

Last, variations in the submergence frequency represented the different history of surface dynamics among the three areas. Although the frequency of total HWL itself has constantly increased since 1933 (Figure 4.4A), the actual frequency of submergence at the low marsh has decreased significantly due to the high sedimentation rate and the subsequently rapid increase in its surface elevation (Figure 4.4D). Despite the continuous sedimentation at the high site, the rate of surface accretion was not high enough for the elevation to keep up with the increasing frequency of high and extreme

Table 6.1 Comparison of simulated and observed dynamics of surface elevation

	Low marsh		Mid marsh		High marsh	
	modeled	observed	modeled	observed	modeled	observed[a]
1949	84.17	85.83	102.68	102.43	121.17	-
1999	100.29	99.07	113.10	112.27	125.71	-
2007	102.20	101.00	115.07	115.00	126.55	-

All values are in centimeters. Observed elevations presented in this table are a part of the long-term field data acquired by Jacobsen (1958) and Bartholdy (2008).

[a] There were no field data available to evaluate model predictions for the high marsh.

HWL events. There was no objective field data set to validate these modeled hydrological dynamics at various locations. However, assuming that the simulation results for changes in the surface elevation (Figure 4.4C) are a sound reflection of reality, it is believed that these simulated flooding dynamics can be useful for a further simulation of ecological succession.

In summary, it is of the greatest interest in this research that there has been a *convergence* of environmental patterns and processes in the simulation model presented for the Skallingen salt marsh. Specifically, the difference in the initial surface elevations of the three marsh locations has decreased significantly due to the different rate of sediment accretion (see Figures 4.4B, C). Also, more importantly, the frequency of over-marsh flooding at the three sites became increasingly similar through time (Figure 4.4D). It is considered that such increasing similarity in the abiotic parameters will in turn produce relatively homogeneous or simple vegetation patterns.

6.1.1.2 Biotic dynamics

During the baseline simulation, there was an issue about which percentage of total HWL in a year is considered to occur due to normal tidal activities only (see section 4.1.3.4). This research selected 80% to acquire results presented in Figures 4.5A, B, and C. However, as an attempt at sensitivity analyses, other percentages were tried such as 60, 70, and 90 %, but significantly different results were not encountered.

Considering that the salt marsh ecosystem was still young in 1933, I assume justifiably that most of its portion fell into an elevation between 80 and 100 cm DNN (see also Bartholdy et al. 2004). It is therefore reasonable to use the floristic data (Figure 4.2) to evaluate successional dynamics at the low marsh (Figure 4.5D).

The ecosystem was characterized by extreme spatial heterogeneity due to different land use types (e.g., natural vs. grazed), fluvial-geomorphic processes across tidal creeks, and local mounds that had existed before the initial formation of the marsh surface. It was expected that this inherent complexity would in turn create ecological variability that can hardly be realized using such a simple, non-spatial compartment model as presented in this research. It is thus important to focus upon general model behavior over the landscape rather than zooming in to struggle with site-specific species composition when interpreting and evaluating the simulation results.

At first glance, it appeared that there were significant discrepancies between modeled and observed occupancies (%) of each vegetation association in the low area (Table 6.2). However, there were a few major reasons to consider that the simulation results for the ecological succession are an acceptable representation of reality. First of all, the modeling successfully embodied the (pre)dominance of early- to mid-successional species (i.e., *H. portulacoides*) in the new millennium. This is encouraging since the focus in general was to realize a contemporary stage of retarded succession in which the dominance of late-successional species is suppressed by both frequent submergence and the dominance by early- to mid-successional plants.

Second, the significant difference between simulated and observed values for both pioneer and late-sere was well anticipated. This research set the initial occupancy as 2% only for the late-successional group, despite the observed, much higher percentage,

Table 6.2 Comparison of simulated and observed dynamics of species composition

	Pioneer		Early-sere		Early- to mid-sere		Late-sere	
	modeled	observed	modeled	observed	modeled	observed	modeled	observed
1933	70.00	58.62	25.00	27.59	3.00	0.00	2.00	13.79
1949	26.48	20.69	54.00	41.38	16.17	20.69	3.34	17.24
2006	0.90	10.34	14.40	3.45	75.02	86.21	9.68	0.00

All values are in percentages.

13.79. This setting in turn led to an increase in the initial percentage of pioneer communities up to 70 % that was higher than the observed (i.e., 58.62 %). Such a choice was intentional because the presence of late-successional group at some locations in 1933 was caused not by continuous sedimentation but by the presence of local mounds with high surface elevations around 120 cm that had already existed at Skallingen before the initial development of the marsh surface (Bartholdy et al. 2004). The elevation of these mounds was exceptionally high even in the early 20th century, which would not be expected under normal environmental conditions.

Third, the observed occupancy of the pioneers in 2006 (i.e., 10.34 %) would have been lower, or more similar to the simulated (i.e., 0.90), if there had been no effects of livestock grazing and tidal creeks (see the grazed part and tidal creeks in Figure 4.2). On salt marshes it is generally known that many pioneer species (especially *Puccinellia maritima*) are graze-tolerant more than other later-sere individuals (Ranwell 1972; Westhoff 1987; Jensen 1985a). Lateral migration of tidal creeks can lead some portion of a marsh platform to be exposed to the direct influence of saline water (Adam 1990). These factors, although not included in the simulation model in the current study, explain why a significant percentage of pioneers still exist even in 2006 after a long-term salt marsh development.

6.1.2 Implications and limitations of the experimental model developed

Simulation modeling presented in this research helped answer the fundamental question if wind-driven, short-term sea-level rise does really play a significant role in ecological dynamics of a salt marsh. A comparison of the baseline and experimental models clearly indicated that the presence of such meteorological events is essential for realizing retarded progressive succession: the overall, current situation on the Skallingen salt marsh.

The baseline simulation showed progressive successional dynamics from pioneer to late-sere stages. Such a pattern corresponds to a conventional expectation in coastal biogeography. Traditionally, succession on salt marshes is associated with a positive feedback in which the presence of vegetation increases sedimentation, which in turn facilitates plant growth due to lowered tidal inundation, salt stress, and edaphic amelioration (Bertness et al. 1992; Srivastava and Jefferies 1995; van de Koppel et al. 2005). As sedimentation and elevation increase, this feedback process facilitates the establishment and growth of later successional species by further reducing the physical stress associated with regular inundation by sea water. Under this assumption of the positive feedback, the temporal range of earlier-successional plants became narrower due to their facilitation and the establishment of later-sere species. However, the conventional concept of positive feedback and the consequent progressive succession embodied by the baseline simulation were not in accordance with what has been actually occurring on the Skallingen salt marsh.

Responding to the convergent dynamics in physical factors (Figure 4.4), the experimental simulation produced a relatively simple ecological pattern in which the early- to mid-sere association (pre)dominates the low and mid marshes over time, and eventually even the high site from 2030. It is considered that the modeled inundation regime influenced by ocean storminess represents a level at which pioneers and early-sere species are outcompeted by this dominating group and late-sere plants cannot tolerate. Again, site-specific floristic variations driven by considerable spatial heterogeneity at Skallingen cannot be the focus in the simulation model. Rather, the model is useful in that it successfully simulates the *overall* dominance of early- to mid-sere plants which indicates a significant influence of meteorological tides.

Many salt marshes, regardless of which continents/oceans they belong to, are formed where they can avoid direct effects of waves or storms, and experience relatively mitigated currents to effectively trap fine sediments. However, I acknowledge that there are also exposed marshes where the model and hypothesis of this research may not hold. Such sites exist even at a Danish Wadden Sea coast that is just outside of the Skallingen Peninsula (see Pedersen and Bartholdy 2007). If one intends to simulate ecological and sedimentological dynamics in these marshes, it is recommended that a new factor, *surface erosion* during storm surges, be included.

6.1.3 Implications of wind-driven sea-level change for succession

Succession on salt marshes has conventionally been attributed to the increase of surface elevation relative to the mean high water level and consequently decreased frequency of tidal flooding (Ranwell 1972; Rozema et al. 1988; Adam 1990). This basic notion may lead one to expect that, as sedimentation continues, there would be succession toward a late stage dominated by *F. rubra*, *J. gerardii*, or *Artemisia maritima* at Skallingen, as Roozen (1985) predicted for a salt marsh in the Boschplaat, the Netherlands. Such an expectation is in accordance with that of Olff et al. (1997) who proposed that increasing sedimentation would lead to higher nutrient (especially nitrogen) availability, thereby speeding up successional processes. However, both at Skallingen and at the Boschplaat (Leendertse et al. 1997), the contemporary predominance of *H. portulacoides* rather than such progressive succession was found in spite of the clear increase of surface elevation driven by continuous sedimentation in these sites (see Dijkema et al. 1990; Bartholdy et al. 2004).

Similar to what Leendertse et al. (1997) suggested for the Boschplaat, this research posits that the increased frequency and duration of over-marsh flooding (Table 3.1) were the key factors that have retarded successional dynamics at Skallingen. The magnitude of inundations was often so high in these sites that even upper marsh plots with high elevation have experienced frequent submergence by sea water. These high-magnitude submergence events would easily overwhelm the increased surface elevation that resulted from continuous sediment accumulation. A question is then which process has been augmenting the frequency and depth of over-marsh high water events. One tempting answer has been the effect of long-term sea-level rise. In the Netherlands, Leenderste et al. (1997) proposed this answer based on the correspondence between periods of increased frequency of flooding and sea-level rise during a few recent decades (see Dijkema et al. 1990). Such a proposal could be well accepted until the late 20th century when there was a world-wide concern about the threat of global climate warming, melting of polar ice, and the resultant eustatic sea-level rise (Hegerl and Bindoff 2005).

Although sea-level rise has occurred around the Wadden Sea coasts especially in the late 20th century (e.g., Table 3.1), this research proposes that such a long-term, gradual phenomenon alone may not be enough to explain the increased frequency and magnitude of over-marsh high water events and the retarded successional state (i.e., *Halimione*-dominated) across the Skallingen salt marsh. At Skallingen, the rate of mean sea-level rise was only 2.3 mm yr^{-1} between 1931 and 2006 with a higher rate of 5.0 mm yr^{-1} since 1976. The rate of mean sediment accretion, on the other hand, has been 4.0 mm yr^{-1} in outer marshes since 1933. These data imply that there was 1) a net increase in the relative elevation of the marsh surface until 1976 and 2) more or less equilibrated dynamics between both the marsh and sea surfaces since 1976. The slightly higher rate of sea-level rise than accretion (i.e., 5 mm yr^{-1} vs. 4 mm yr^{-1}) since 1976 cannot explain the increase in the number of extreme HWL (e.g., 1.6-1.8 m DNN or 1.8-2.0 m DNN; see Table 3.1) over the entire marsh. These equilibrated dynamics were possible because not only mean sea-level but also the rate of sedimentation increase due to augmented duration and depth of submergence. In short, this research calls for a change in the conventional belief that long-term, gradual sea-level rise can explain much or even most about coastal biogeography.

I suggest that vegetation dynamics, especially the contemporary dominance of *H. portulacoides* at Skallingen have significantly been influenced by the causal chain of recent variations in the NAO index → increased storminess and meteorological tides on the sea surface → increased frequency, duration, and depth of HWL. The NAO index has been dominantly at a positive phase recently, especially since the 1980s (Osborn

2004; Figure 4.3). Such a phase is the main driving force of frequent westerly gales and consequent short-term wind tides on the North Sea (Serreze et al. 1997; Deser et al. 2000). This association between the NAO and ocean storminess explains the close, positive relationship between the NAO index and the frequency of over-marsh HWL events at Skallingen (Pearson's $r = 0.62$, $p < 0.01$). Based on the same logic, it was also elucidated that the NAO variation significantly explained the rate of sedimentation ($R^2 = 0.63$, $p < 0.01$) (Bartholdy et al. 2004). Mechanisms that control the variability of the NAO index are beyond the scope of this research. Rather, the focus of this research is to extend the connection between the index variation and the increased wind tides to an ecological perspective: retardation of progressive succession. While the *Halimione*-dominated state has been documented to occur mainly on the low (or sometimes middle) part of many salt marshes with frequent influence of sea water inundation (Beeftink 1987; Westhoff 1987; Bakker et al. 1993), it is surprising that such dominance is currently observed in the whole, ungrazed area at Skallingen (Figure 4.2).

6.1.4 Generalization

Although not often addressed explicitly compared to long-term eustatic sea-level variations, the possibility of meteorological storm surges as a driver of vegetation dynamics on salt marshes has indeed been suggested elsewhere (e.g., Beeftink 1987; Cramer and Hytteborn 1987; Olff et al. 1988). For example, the work by Beeftink (1987) provides a good basis for this research by showing how marsh plants respond relatively quickly to the wind-driven yearly variation of waterlogging during the 1960s. Beeftink

(1987) emphasized the need for a longer-term investigation. This study and that of Leendertse et al. (1997) have continued his research line by elucidating how the continuous increase of inundation frequency eventually results in the dominance of *H. portulacoides*. Different from the rapid response of species to the yearly fluctuation of sea levels found by Beeftink (1987), this research anticipates that the contemporary dominance by *H. portulacoides* at both Boschplaat (Leendertse et al. 1997) and Skallingen will persist for the time being unless severe winter frost occurs (e.g., below -15°C, see Beeftink 1987; de Leeuw et al. 1994).

Such an expectation was derived based on the widely-accepted prediction that, linked with global climate warming, both long-term eustatic sea-level rise and short-term wind-induced sea-level rise will continue (e.g., Günther et al. 1998; Bromirski et al. 2003; Hegerl and Bindoff 2005). This expectation therefore does not exclude the importance of long-term gradual sea-level rise, rather than only focusing upon the significance of short-term variation nested within the long-term trend (e.g., Stommel 1963). In other words, one implication of this study is to address the need for a more hierarchical perspective that recognizes and examines sea-level variation at both long- and short-time scales under globally changing environmental conditions (see also Delcourt et al. 1983).

The influence of meteorological tides on biogeographic patterns is also pertinent to coastal ecosystems other than salt marshes in Europe. For example, much attention has been paid to the impact of increased storminess around the Pacific, associated with variations in the ENSO (e.g., Bromirski et al. 2003). Long-term studies on dynamics of coral reef communities reported that areas exposed to storm surges show more limited growth and recovery of corals compared to sheltered areas in Hawaii and Australia (Dollar and Tribble 1993; Connell et al. 1997). Coastal dunes and sand beaches exposed to the storms often experience the migration of swash bars, erosion, and loss of biota (Aagaard et al. 1995; Psuty and Ofiara 2002; Hesp 2007; Houser and Greenwood 2007). Mangroves in the Atlantic and Bangladesh are also susceptible to these meteorological impacts (Smith III et al. 1994; Ali 1999).

The variability in various indices such as the ENSO, the NAO, and the Pacific Decadal Oscillation is widely accepted as the main cause of meteorological/climatic variability from local to global scales. Because of the significant teleconnections among them across continents and oceans (e.g., Elsner et al. 2001; Ineson and Scaife 2007), implications derived from a single study area may provide useful insights to others, rather than remaining as a site-specific introduction to the relationship between the index variation, altered meteorological regime, and ecological dynamics.

6.2 FLUVIAL-GEOMORPHIC PROCESSES AND PLANT ZONATION ACROSS TIDAL CREEKS

6.2.1 Spatial dynamics of vegetation and physical processes

The vegetation pattern across tidal creeks has strongly been influenced by fluvial-geomorphic processes along tidal creeks. First, the high frequency of pioneer species on point bars reflects harsh environmental conditions imposed by frequent inundation of saline water. Competitive, late-successional plants do not dominate such areas (Pennings and Callaway 1992; Bertness and Shumway 1993; Emery et al. 2001).

Second, as illustrated in Figure 5.7, cutbank edges and the transition above point bars had a higher elevation relative to other topographic features. The high elevation resulted from the continuous supply of sediments from channels, which has gradually decreased the frequency of sea water flooding. These topographic and hydrologic changes have in turn ameliorated edaphic conditions and eventually facilitated the establishment of later-successional species that competitively exclude early-sere species. Most importantly, bulk density was highest at these locations and gradually decreased toward the inner marshes. Bulk density is known to closely relate to percolation velocity in salt marshes (e.g., $R^2 = 0.83$, $p < 0.01$ in Bradley and Morris 1990). Such a relation implies that the higher cutbank edges and the transition zone above point bars experience a well-drained condition, while the lower, inner parts have a poor drainage. Accordingly, active leaching of excessive nutrients occurs at these higher sites, thereby lowering the concentration/value of exchangeable cations and electrical conductivity.

Such edaphic amelioration near creeks was also suggested by Zedler et al. (1999) and Morzaria-Luna et al. (2004) in Californian salt marshes. These authors found that creek margins tended to have high species richness presumably due to better drainage, increased tidal deposition of seeds (Hopkins and Parker 1984), and enhanced soil aeration by crabs (Bertness 1985). However, at Skallingen, the average number of species at sites close to creeks (i.e., cutbank edges and the transition above point bars) was significantly smaller than that at other locations (5.3 versus 6.5, $p < 0.01$). This difference in the spatial pattern of species richness between Californian and Danish salt marshes can probably be understood in terms of a different ecological history: I propose that creek margins in the Skallingen salt marsh have experienced more competitive exclusion by later-successional species.

Third, the presence of late-successional assemblages only in the transition zone of point bar parts can be explained in terms of this zone's high elevation relative to other zones. According to the topographic survey carried out in this research, the transition zone where these communities occurred had an average surface elevation of 1.07 m DNN, while the average for cutbank edges was 0.84 m DNN. These average elevations were significantly different from each other ($p < 0.001$). I therefore propose that cutbank edges at Skallingen seldom reach a high enough elevation which can result in a very low frequency of waterlogging, therefore only communities slightly earlier than late-successional can occupy these locations.

Last, the dominance of relatively early-sere species, if not pioneers, in marsh interiors at Skallingen has been caused by infrequent inundation, or an infrequent flushing effect, which led to an accumulation of salts through evaporation of sea water (see also Adam 1990; Mitsch and Gosselink 2000).

6.2.2 Gradient structure in floristic and edaphic patterns

It was originally expected that both micro-elevation and distance from the creeks may be significantly related to spatial gradients of vegetation and soil properties across the creeks. However, only principal components (i.e., PC 1 and PC 2) extracted from soil attributes showed such relationships with both environmental factors (i.e., elevation and distance; see Table 5.6). Although the two axes of NMDS for the medium-scale floristic data did show significant correlations with elevation, their correlation with distance was very weak and insignificant (Table 5.7). In short, spatial structure of edaphic properties was shaped by the interplay of micro-elevation and distance factors, while that of vegetation reflected the prominent effect of *one* strong factor, or elevation. This is why a diagonal gradient was observed in the NMDS plot (Figure 6.1). Stallins and Parker (2003) also reported the same case in which a NMDS diagram for dune species composition at the South Core Banks, North Carolina was characterized by one dominant gradient with a diagonal shape. The diagonal gradient of micro-scale elevation indentified in this research is further explained for each axis as below.

Along the first axis, all samples representing the pioneer stage on point bars are located on the right-hand side (Figure 6.1). So, this axis is largely divided into sites with frequent (right-hand side) and infrequent (left-hand side) submergence, respectively. Such an arrangement of samples caused a significant correlation between the first axis and elevation. However, on the right-hand side, samples from cutbank edges, transitional zones, and marsh interiors are mixed together, which resulted in weak, insignificant correlations with most soil variables (Table 5.7). The influence of surface elevation is more succinctly observed along the second axis.

The second axis of the ordination diagram clearly represents an elevation gradient. Its upper part is characterized by an exclusive presence of points indicating the dominance of late-successional species such as *F. rubra*, *A. maritima*, and *J. gerardii*. Sites with these dominant species corresponded to locally high areas along the transition zone above point bars. A distinct elevation gradient was observed along the second axis. The nine associations across tidal creeks (Table 5.3) were reclassified into four groups as follows: 1) the first association, 2) the second through seventh associations, 3) the eighth association, and 4) the ninth association. Analysis of variance (ANOVA) and a Bonferroni test as a post hoc procedure revealed that the difference in surface elevation among all groups and between any two groups was significant ($F_{3,197} = 92.79$, $p < 0.001$ for ANOVA; $p < 0.001$ for Bonferroni). Moreover, scores of the second axis and the elevation of 201 points showed a high positive correlation (i.e., Pearsons' $r = 0.70$, $p < 0.01$; Table 5.7). In short, such a relatively distinct differentiation of samples along the second axis resulted in significant correlations between this axis and most soil attributes.

The significant control of micro-topography is confirmed by the close relationship between extracted principal components and topographic variables such as elevation and distance from the creeks (Table 5.5). However, it should be noted that PC 2 did not correlate with the topography. The spatial pattern of nitrate and phosphorus is thus understood in terms of other factors that are beyond the scope of this research. It is noteworthy that Ca^{2+} also showed a significant correlation with the elevation and distance factors, but grouped into PC 3, different than other soil properties in PC 1. Such a grouping may indicate that some unidentified controls other than elevation and distance exist in the distribution of Ca^{2+}. Further research is needed to decipher those controls.

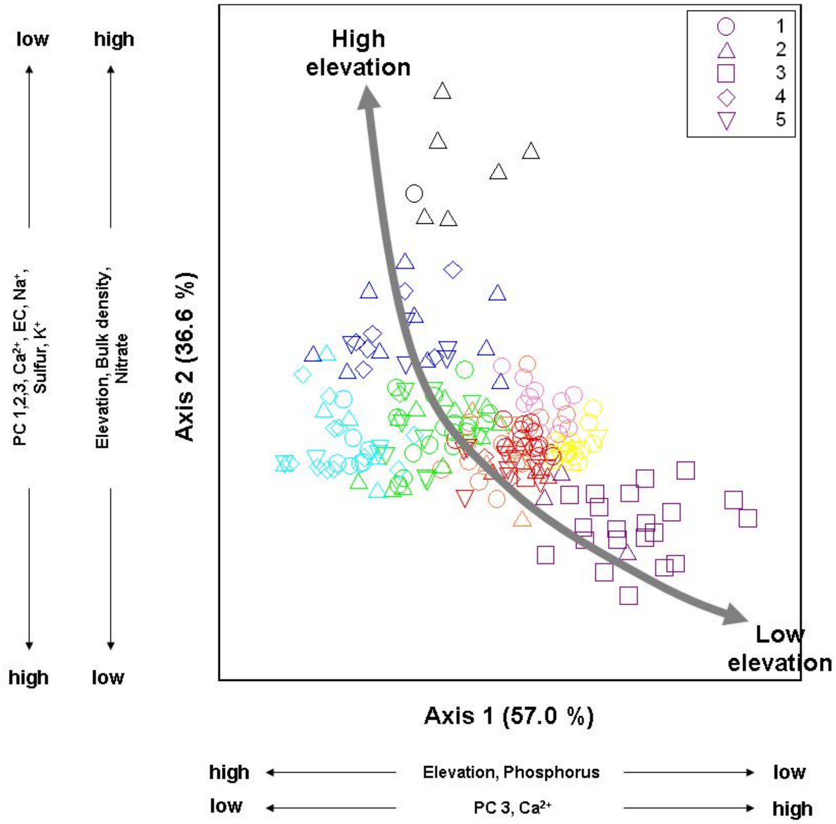

Figure 6.1 Final configuration of non-metric multi-dimensional scaling for the floristic data across tidal creeks. The first through ninth associations in Table 5.3 correspond to purple, red, orange, pink, yellow, green, light blue, dark blue, and black colors, respectively. The diagonal arrow indicates one strong factor, or micro-scale elevation gradient (see also Stallins and Parker 2003). Soil attributes and principal components outside of the ordination diagram represent their relationships with the two axes as reported in Table 5.7). Symbols from 1 through 5 represent marsh interiors, transition of point bar parts, point bars, cutbank edge, and transition of cutbank edge parts, respectively.

6.2.3 Generalization

Results acquired from this research provide similar and different insights into riparian ecology of upland ecosystems. As shown it Figure 5.6, point bars were dominated by early-successional communities. Such dominance reflects the formation process of zonation driven by temporal asynchrony of biotic processes (see section 2.2.2). This process indicates that different zones in an ecosystem exist simply due to the presence of different temporal phases of the same successional sequence (Huston 1994). Upland riparian systems have shown classic examples in which active meandering of streams causes accretion of sediments, which in turn creates a new site for succession at discrete intervals (Weaver 1960; Viereck 1970; Salo et al. 1986; Walker et al. 1986).

However, the dominance of mid- to late-sere species at cutbank edges does not correspond to what occurs at these sites of upland riparian, floodplain systems. Kupfer and Malanson (1993) reported a process of retrogression driven by continuous erosion of cutbank edges, which in turn causes the collapse of overstory tree species on such locations. Once the canopy of these trees becomes removed, light availability for understory herbaceous species increases, so these early-successional plants can dominate the edges. However, such retrogressive succession did not occur at cutbank edges of salt marsh creeks. It is intriguing that, in spite of very similar fluvial-geomorphic processes, cutbank edges of the upland riparian system and the salt marsh creek do show a completely opposite direction of successional processes.

One factor may explain such a successional discrepancy between the two systems: the difference in original *vertical structure* and *successional stage* before inner parts of the marsh and floodplain get exposed to the channel due to continuous cutbank erosion. Before the exposal, the upland floodplain system is usually characterized by stratified vertical structure in which various types of overstory trees and understory shrubs/grasses as mentioned above. This state is considered as representing a mid- to late- or late-sere phase. Light availability is an important factor that maintains the stratified structure.

The salt marsh interiors, however, do not consist of such stratified structure and represent an early- to mid-successional stage. Once these interiors begin to be exposed to a tidal creek, they would receive more sandy sediments than before, which in turn increases bulk density (see Figure 5.10) and enhances the drainage of inundated sea water. Such changes in sedimentary and hydrological processes are believed to facilitate progressive succession. In short, the succession observed at cutbank edges may be a good example of allogenic succession in which processes beyond the control of plant species play a key role.

6.3 FINE-SCALE COMMUNITY STRUCTURE ASSOCIATED WITH COMPETITION AND FACILITATION

6.3.1 Species establishment along environmental gradients

Patterns of species establishment are considered to reflect different mechanisms of species interaction along environmental gradients. The greater number and size of patches of *P. maritima* and *H. portulacoides* on the mid marsh imply that these species have intra-specific biological and inter-specific competitive advantages in conditions of reduced stresses. The dominance of *H. portulacoides* is often observed on northern

European salt marshes following an increase in silt accumulation that enhances soil aeration (Westhoff 1987). Under this condition, the species can have ecophysiological advantages (e.g., tolerance to inundation and high salinity). *P. maritima* develops a strong turf morphology that may provide it with a competitive advantage over *L. vulgare* and *T. maritima* which do not form dense turfs. Similar effects of growth morphologies on plant competition have been documented in other salt marshes (e.g., Bertness 1991) and inland ecosystems (e.g., Schmid and Harper 1985).

On the outer, low marsh, many juveniles of *L. vulgare* and *T. maritima* could occur because *P. maritima* and *H. portulacoides* are less competitive under stressful conditions. On the mid marsh, significantly small portion of the juveniles could survive to become mature due to the competitive exclusion by *P. maritima* and *H. portulacoides*.

6.3.2 Univariate and bivariate spatial point pattern

The stronger clustering of each species over a wider range of spatial scales on the low marsh is believed to support a hypothesis that *intra*-specific facilitation is an important mode of species interaction under harsh environmental conditions. There is indeed an example that can support this hypothesis. van Wesenbeeck et al. (2008) reported that there was a reduction of erosion and thus enhancement of sedimentation and plant growth within the clump of *Spartina anglica* tussock which diverts tidal energy. Outside of this clump, however, erosion was intensified because of no vegetation cover.

The importance of facilitation during secondary succession has widely been recognized in biologically and physically stressful habitats (e.g., Bertness 1991; Bertness and Shumway 1993; Callaway et al. 2002; Bruno et al. 2003), in contrast to ecologists' early preoccupation with competitive processes until the 1980s (Strong et al. 1984). Patterns of facilitation observed in these previous studies were mainly at inter-specific, or community-level, implying that a stress-tolerant species colonizes and ameliorates (disturbed) bare ground, thereby creating a favorable site for the establishment of more competitive species. One potential contribution of this research to the issue of facilitation is to suggest that the process also occurs at the species-level. A similar intra-specific process was recently observed in pioneer zones of a Dutch salt marsh where clumps of *Spartina anglica* minimize surface erosion by diverting tidal energy, and so enhance sedimentation and growth within the clumps (van Wesenbeeck et al. 2008).

Until recently, many biogeographers and ecologists have focused upon the relative importance of competition and facilitation when explaining the structure of natural communities (e.g., Callaway et al. 2002; Maestre and Cortina 2004; Rietkerk et al. 2004). Most recently, a body of literature has proposed that scale is key to understanding how competition and facilitation influence community structure, since both processes operate simultaneously in a single system, but at different scales (Klausmeier 1999; Rietkerk et al. 2004). For instance, van de Koppel et al. (2006) demonstrated that the interaction of large-scale facilitation and small-scale competition creates species zonation on New England cobble beaches. Their conclusion employed a hierarchical view (see Stachowicz 2001) where a foundation species provides potential niches for many species (i.e., large-scale facilitation), while local competition determines the final species composition of that community.

This research may contribute to this theory of scale-dependence by demonstrating how modes of competition and facilitation vary depending not only on spatial scale but also on environmental gradients and species. First, positive or negative inter-specific interactions were spatially manifested to a greater degree on the low site than on the mid marsh. On the mid marsh, the absence of such manifestations was evident in the bivariate random patterns. The scope of this research limits the ability to identify detailed mechanisms of species interaction by which various spatial patterns are shaped. However, spatial analyses of this research revealed that the extent and strength of facilitation and competition can vary significantly along physical gradients. This study therefore extends the current knowledge of scale-dependent interactions beyond pioneer zones (e.g., Bruno 2000; van de Koppel et al. 2006; van Wesenbeeck et al. 2008) to higher marsh sites.

In addition, different types of bivariate point pattern (i.e., clustered, random, and regular) were observed for different combinations of species even at similar spatial scales on the outer marsh. There has indeed been no agreement among recent studies of scale-dependent community structure on low salt marshes: Some documented local facilitation and large scale inhibition (e.g., van Wesenbeeck et al. 2008), while others reported local competition and large scale facilitation (e.g., van de Koppel et al. 2006). Based on the different mode of one-to-one relationships between several species, this research stresses that it is difficult to generalize at which spatial scales competition and facilitation occur.

6.3.3 Generalization and future considerations

This research provides three insights for the study of find-scale species interactions on salt marshes as follows:

1) Facilitation may occur at the population level as well as the community level;

2) The spatial extent and strength of facilitation and competition can vary significantly along environmental gradients; and,

3) It is difficult to generalize at which spatial scales competition and facilitation occur.

However, these implications should be understood as hypothetical rather than conclusive. In other words, the spatial point pattern of individual patches or stems identified in this research may serve as a good proxy for the underlying mechanisms of species interaction, but one cannot exclude any possibility that other factors than competition and facilitation may contribute to such a pattern detected. For example, the existence of small salt pans in the plot may have produced the alteration of ground and vegetated sites, thereby forcing different species separated from each other. Such an abiotic agent may cause a strong clustered pattern.

For future research, it is therefore needed to establish additional plots across the marsh surface. First these new plots should have the same distance from the shoreline as the two plots that were already investigated in this research. Based on such a field design, one can test if the patterns identified from the two plots are generalizable alongshore. Second, more plots needed to be established *between* the plots. Currently, these plots only represent two points along the cross-marsh gradients. More plots in between are needed to understand how facilitation and competition may vary along a gradient.

CHAPTER VII

CONCLUSIONS

7.1 SUMMARY OF KEY FINDINGS

This research investigated vegetation dynamics in relation to changes in environmental regimes on the Skallingen salt marsh at three different spatial and temporal scales. At the broad scale, there was contemporary overall dominance by *H. portulacoides* across the marsh, indicating retarded progressive succession presumably since the 1980s. Such dominance was conventionally attributed to the increase in the frequency of sea water inundation driven by long-term, gradual mean sea-level rise in recent years. Recognizing that there were equilibrated dynamics between marsh and sea surfaces, this research proposed an alternative causal chain: recent variations in the NAO index → increased storminess and meteorological tides on the sea surface → increased frequency, duration, and magnitude (i.e., depth) of HWL → retarded progressive succession (i.e., *Halimione*-dominance).

At the medium-scale, there were well corresponding floristic and edaphic gradients across tidal creeks. Sites close or adjacent to tidal creeks were characterized by the dominance of later-successional species, high bulk density, and low nutrient contents and electrical conductivity. These locations are cutbank edges and transition zones above point bars that have undergone active accretion of sediments supplied from the creeks, which in turn increased the relative elevation. With increasing distance from the creeks, the dominance shifted to early-sere species and bulk density gradually decreased, while nutrient content and electrical conductivity increased. These findings collectively imply that cutbank edges and transition zones experience a well-drained condition, which eventually facilitated the establishment of later-successional plants that are intolerant to these physical stresses. The inner marshes are poorly-drained. This and the accumulation of salts favor the high cover of earlier-successional species.

At the fine scale, three major implications were derived. First, compared to the mid marsh, the outer marsh showed a stronger clustering of *each* species over a wider range of spatial scales. It is thus believed that *intra*-specific facilitation is an important mode of species interaction under harsh environmental conditions. Second, positive or negative inter-specific interactions were spatially manifested to a greater degree on the low site than on the mid marsh. On the mid marsh, the absence of such manifestations was evident in the bivariate random patterns. I therefore propose that the extent and strength of facilitation and competition varies significantly along physical gradients. This research therefore extends our current knowledge of scale-dependent interactions beyond pioneer zones to higher marsh sites. Third, on the low marsh, different types of bivariate point pattern (i.e., clustered, random, and regular) were observed for different combinations of species even at similar spatial scales. This finding implies that it is difficult to generalize at which scales competition and facilitation occur. I propose that the novel concept of scale-dependence in community structure may be advanced by including the dependence on both environmental gradients and combinations of species.

7.2 CROSS-SCALE PERSPECTIVES ON SALT MARSH BIOGEOGRAPHY

This research showed that various ecological and environmental patterns and processes are observed at different spatial and temporal scales (Delcourt et al. 1983; Levin 1992; Csillag et al. 2000; Whittaker et al. 2001; Figure 7.1). Based on the results, this research stresses the importance of understanding multi-scale nature of these patterns and processes in a hierarchical perspective (Allen and Starr 1982; O’Neill et al. 1986).

First, in a spatial sense, the study of vegetation patterns in general identified a more or less homogeneous matrix of *H. portulacoides* cover across the marsh (Figure 7.1A). This simple vegetation pattern at the broad scale, however, could not capture the heterogeneous, complex zonal distribution of species across tidal creeks at the mid spatial scale (Figure 7.1B; see also Zedler et al. 1999). Also, such a medium-scale pattern from early- to late-successional species was too coarse to define the mode of intra- and inter-specific interactions such as competition and facilitation at finer spatial scales (Figure 7.1C).

Second, in a temporal view, the large scale, overall vegetation pattern has been shaped by the interplay of hydrological and sedimentological processes over a long-time span. However, this research addresses the importance of short-term, wind-driven variation nested within long-term trends. In other words, sea-level variations at these different time-scales are not necessarily mutually exclusive, but combined together to drive major vegetation dynamics over decades. The medium-spatial pattern has been induced by semi-diurnal, bi-directional fluvial-geomorphic processes across tidal creeks (e.g., sedimentation and erosion) that may occur over a period of several years.

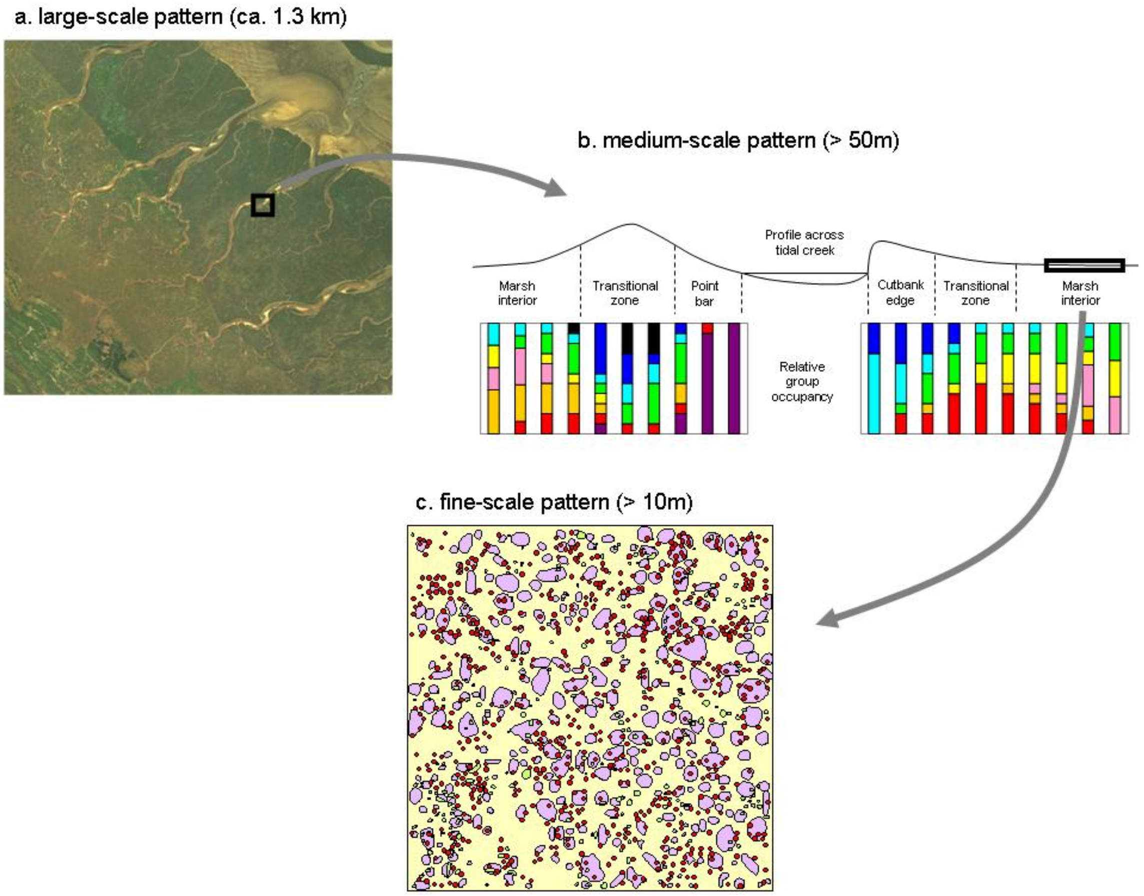

Figure 7.1 Hierarchical relationships among different biogeographical patterns and processes at different scales. Although this graph represents an explicit *spatial* hierarchy, such a representation does also imply a temporal hierarchy. See the text and Figure 7.2. Each figure was derived from Figures 5.4D, 5.8, and 5.12, respectively.

Last, although not proven experimentally or by monitoring, I believe that the micro-scale community structure associated with competition and facilitation can show yearly or even seasonal changes depending on ambient temperature and meteorological conditions (see also Beeftink 1987; Cramer and Hytteborn 1987; Olff et al. 1988; Morris 2000).

Scaling is one of the main components in the study of complex ecosystem patterns and processes (Levin 1992; Malanson 1999). It has been accepted that information acquired at one scale is not necessarily generalizable to others (Haggett 1965). Nevertheless, there have been many attempts to extrapolate fine-scale information across ranges of spatial and temporal scales (e.g., Rastetter et al. 1992; Kunin 1998) and to understand problems generated during the scaling processes (e.g., Mander et al. 2005).

Most academic approaches are confined to a relatively small area or system at a relatively short time period. This kind of reductionism is mainly caused by the practical limitation of time and money available. However, applications of these study results are frequently implemented in larger, administrative spatial and temporal scales (Dalgaard et al. 2003; Miller et al. 2004). Therefore, upscaling is one of the central issues in many academic disciplines.

However, spatial and temporal extrapolation is still quite difficult because of unexpected emergent properties generated during the aggregation of spatial and temporal information, which makes the whole larger than sum of parts (Levin 2005). In addition, there usually exist different ecological processes underlying different spatial and temporal scales. For example, Figure 7.2 illustrates a patch-to-inter patch difference in soil nitrogen concentration as a function of patch size in Australia (Ludwig et al. 2000).

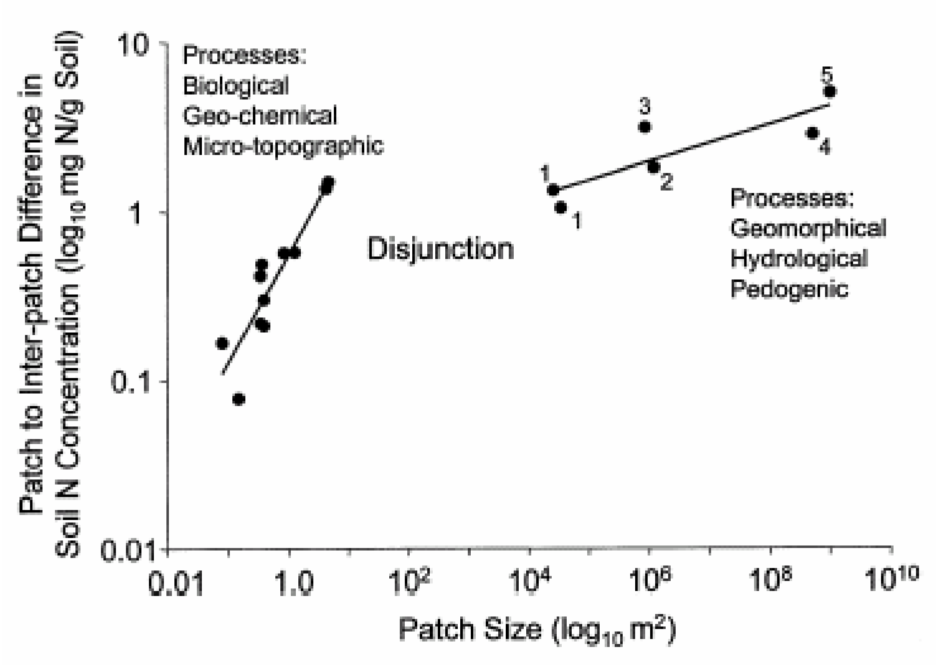

Figure 7.2 Patch to inter-patch differences in soil N concentration in relation to patch size (log10m^2) (Ludwig et al., 2000).

Here, biological, geochemical, and micro-topographic processes are dominant at a small patch scale, while geomorphic, hydrological, and pedogenic processes are dominant at larger spatial scales. The disjunction between the small and large spatial scales is a main source of uncertainties resulting in ecological non-linearity. In the case of this current research, the presence of tidal creeks may be an exemplar of such an uncertainty that would hamper scaling attempts on salt marshes (see also Adam 1990). Detecting the emergence and consequent non-linearity across ranges of spatial scale is still a problem, and will be so into the near future. This is one of the key reasons why our current knowledge on scaling is still theoretical and descriptive rather than empirical and quantitative.

Salt marshes are underrepresented ecosystems in terms of cross-scale perspectives and spatial/temporal extrapolations, while one key research trend of salt marsh biogeography is the connection between vegetation and changes in environmental regimes at broad scales. However, key to the success of projecting long-term vegetation dynamics on a large salt marsh platform lies in understanding how local scale patterns and processes at a short-time scale are embodied through fine-scale species interactions responding to variations in physical factors (Delcourt et al. 1983; Wootton 2001; van de Koppel et al. 2006).

Patterns and processes on salt marshes may be regarded relatively simple compared to those of other terrestrial and marine systems because of their relatively flat topography that is expected to make vegetation-environment relationships uniform and predictable across scales. Nonetheless, no research and generalization have been reported about the possibility of spatial and temporal upscaling of salt marsh ecology.

One implication of this research is to provide a springboard for such an attempt of cross-scale extrapolation. This research has showed what kind of patterns and processes are observed on salt marshes at various spatial and temporal scales. Such results will be a basis for determining biotic and abiotic constraints of future scaling attempts. For example, there may be threshold scales at which biotic interactions, fluvial-geomorphic tidal creek processes, or overall mean high water level variations are dominant constraints both spatially and temporally. Extrapolation approaches beyond these thresholds should cope with theoretical and technical problems that are difficult to unravel (Wiens 1989).

7.3 FUTURE RESEARCH

To conclude, this research stresses the need for a holistic approach in future investigations of salt marsh biogeography. For example, such an approach would involve simultaneous, comprehensive modeling of larger and smaller scale patterns and processes (Figure 7.3). Many conceptual and mathematical models of salt marsh ecology have already been introduced, but most of them focused upon specific spatial and temporal scales. Recently, D'Alpaos et al. (2007) and Kirwan and Murray (2007) attempted to develop integrative models that simulate both marsh platform and tidal channel processes. These authors suggest that a systems approach is necessary to fully understand future changes in vegetation and geomorphology because various marsh components at different scales respond to dynamic coastal environments as a closely-

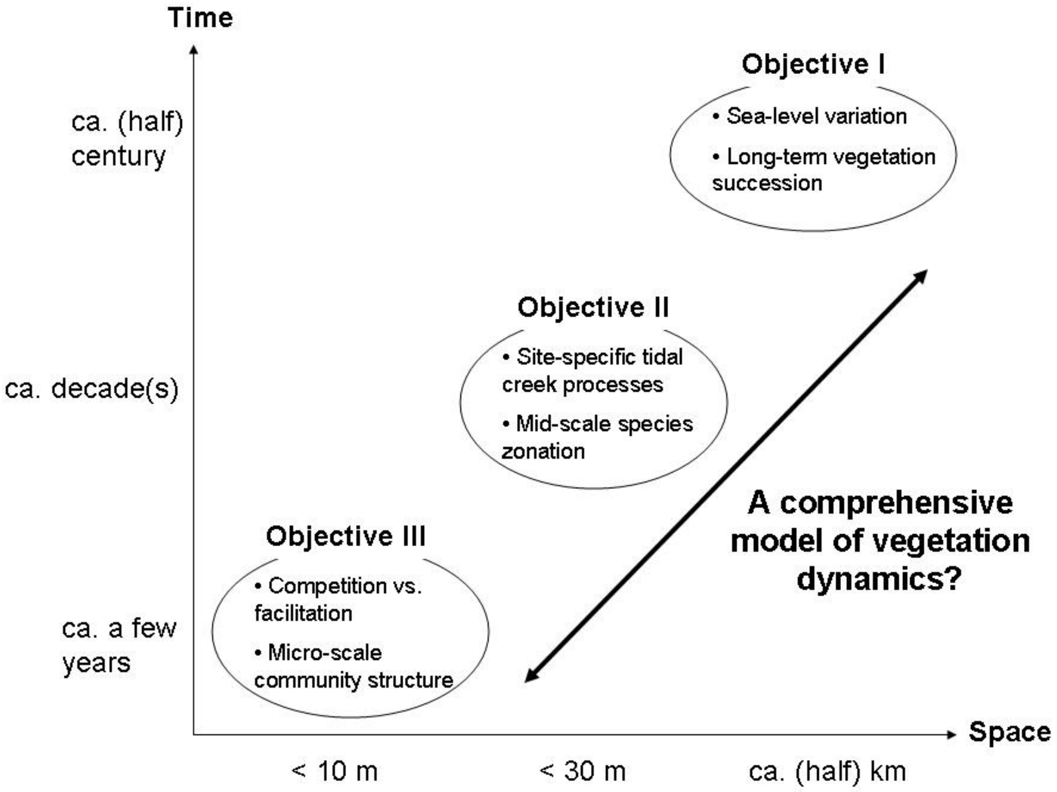

Figure 7.3 Dynamics of ecological and environmental processes and patterns across scales on salt marshes.

linked, holistic entity. Based on results of this current research, it would be meaningful to develop a comprehensive simulation model that incorporates salt marsh ecology, geomorphology, and hydrology observed at a range of spatial and temporal scales (Figure 7.3).

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