Changing patterns

The influence of stress on vegetation patterns in a salt marsh

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Preface

This thesis is the result of half a year research at salt marshes of Schiermonnikoog for the University of Utrecht and the University of Groningen. I enjoyed producing this thesis because it involved a diversity of activities. The combination of thinking, fieldwork, statistics and writing made it an instructive experience. Many people supported my thesis in one way or another. I would like to thank my supervisors Maarten Eppinga (UU) and Chris Smit (RUG) for their feedback and motivating talks. Furthermore, I would like to thank Maarten Schrama, Kelly Elschot en Elske Koppenaal for sharing their knowledge about salt marshes and equipment for fieldwork. Thanks to Niek Kortooms, Albert Versteegde and Ruth Howison for their assistance during fieldwork. Finally I would like to thank Caroline de Haan and Mareike Erfeling for their thesis-writing-company at the library in Utrecht.

Liesbeth Versteegde
October 27th 2011

Abstract

Biotic and abiotic stress can both be present on salt marshes. Factors as sea level rise and anthropogenic land use may increase stress and thereby influence ecosystems. Many researches involve the consequences of abiotic stress on ecosystems, but little is known about the effects of biotic stress or a combination of the two stress types on ecosystems. The aim of this study was to increase the knowledge about the effects of biotic and abiotic stress on salt marshes. Vegetation patterns are present in salt marshes and patterns are known to shift under influence of stress. Species are the basic elements of plant communities and their interactions influence the formation of vegetation patterns. The effects of biotic and abiotic stress on species growth, species interactions and patch sizes were tested in this research. Grazing history was used as a measure for biotic stress and salinity as a measure of abiotic stress. *Juncus maritimus* is a species that forms vegetation patches in salt marshes at Schiermonnikoog. It was found that *Juncus* cover was not affected by biotic stress, but was negatively influenced by abiotic stress. Species interactions were influenced by a combination of biotic and abiotic stress. Facilitation increased with biotic stress at low abiotic stress, but did not change with biotic stress at high abiotic stress. Patch sizes were influenced by biotic stress. Large patches were more abundant on salt marshes with medium and high biotic stress than on salt marshes with low biotic stress. Abiotic stress also influenced patch sizes, but no trend could be discovered. These results imply that presence of one stress type or both stress types largely influence the plant community in salt marshes.

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1. Introduction

Stress influences the composition and behaviour of plants in communities and is a common feature in ecosystems. Processes as climate change and anthropogenic land use can enhance stress (Rahmstorf, 2007; Rietkerk et al, 2000). Two forms of stress are biotic and abiotic stress. Biotic stress is stress caused by living organisms (Maes and Debergh, 2003). Abiotic stress is defined as "any external condition, apart from the activities of other organisms, that reduces the growth, survival and/or fecundity of a plant" (Maestre et al, 2005: 749). Biotic stress and abiotic stress can both be found in salt marshes. Salt marshes are relatively simple ecosystems with few species (Bertness and Ewanchuk, 2002) located at the border between land and sea. Many salt marshes have been used as cattle grazing area for a long time (Bakker et al, 2003). Herbivores cause stress in plant communities by selective grazing and trampling (Rietkerk et al, 2000; Stahl et al, 2006). Some researches focus on consumer pressure as biotic stress (Graff et al, 2007; Smit et al, 2007; Smit et al, 2009). In this study the focus is on grazing history (grazed years) as measure of biotic stress because the influence of grazing on plant communities is a slow process (Bakker et al, 2003). Salt marshes are characterized by frequent inundation and high salinity (Bakker et al, 2009). Salinity is one of the major causes of abiotic stress in a salt marsh community (Bakker et al, 2009; Bertness et al, 1992; Callaway, 1994). Sea level rise results in enhanced salt stress due to an increased inundation frequency at higher parts of a salt marsh (Olff et al, 1997).

Stress, whether biotic or abiotic can result in spatial pattern formation in ecosystems (Kéfi et al, 2007; Lejeune et al, 2002), because patterned vegetation can persist at a higher amount of stress than homogeneous vegetation (Rietkerk et al, 2002). Spatial patterns are known to change under various amounts of stress and can therefore provide information about the state of an ecosystem (Kéfi et al, 2007). Salt marshes comprise spatial patterns (Bertness and Ellison, 1987). Patches of tall vegetation surrounded by a short sward are present in relatively old (100+ years) cattle grazed salt marshes on Schiermonnikoog. However, it is unknown how these patterns emerge and how they react to biotic and abiotic stress. Species are the basic elements of plant communities and their interactions contribute to the formation of vegetation patterns. Species can interact positively by facilitation and negatively by competition (Bertness and Callaway, 1994; Bertness and Hacker, 1994; Hacker and Bertness, 1999). Some species grow in patches to create a buffer against harsh surroundings. Other species can benefit by growing inside these patches where they are facilitated from these harsh conditions (Bertness and Hacker, 1994). However, the strength and type of interactions are influenced by stress. Competition shifts to facilitation under increasing stress levels (Bertness and Hacker, 1994; Boughton, 2011), but shift back to competition under extreme stress levels (Holmgren and Scheffer, 2010; Maestre and Cortina, 2004). A shift in species interactions influences spatial vegetation patterns (Alados et al, 2006).

Little is known about the influence of a combination of biotic and abiotic stress on vegetation patterns. Three salt marshes at Schiermonnikoog are exposed to a combination of biotic and abiotic stress. Stress and resource availability both influence species growth in a salt marsh community. The inundation frequency influences both salt stress and resource availability (Van Wijnen and Bakker, 1997; Olff, 1997). Stress also affects species interactions and thus species growth and survival. Stress and species interactions have an effect on vegetation patch sizes (Kéfi et al, 2007; Alados et al, 2006). The relations between stress, plant community, species interactions and vegetation patterns are depicted in Figure 1. An increase in land use for cattle grazing poses increasing biotic stress on salt marshes. Sea level rise results in more frequent inundation of salt marshes which causes an increase in salt stress (Olff et al, 1997). It is important to research the consequences of these possible threats on salt marshes because salt marshes are rare ecosystems. Consequences of stress on salt marsh ecosystems can possibly predict changes in stress levels. The influence of biotic and abiotic stress on a salt marsh community will be analyzed in this research. The outcome of this study contributes to the understanding of the response of salt marsh communities to stress. The following research question has been formulated:

How does a combination of biotic and abiotic stress influence spatially patterned vegetation in a salt marsh?

Three sub questions have been formulated to be able to answer the research question:

- *How do biotic and abiotic stress influence the plant community in patches?*
- *How does resource availability influence the plant community in and around patches?*
- *How do biotic and abiotic stress influence patch sizes?*

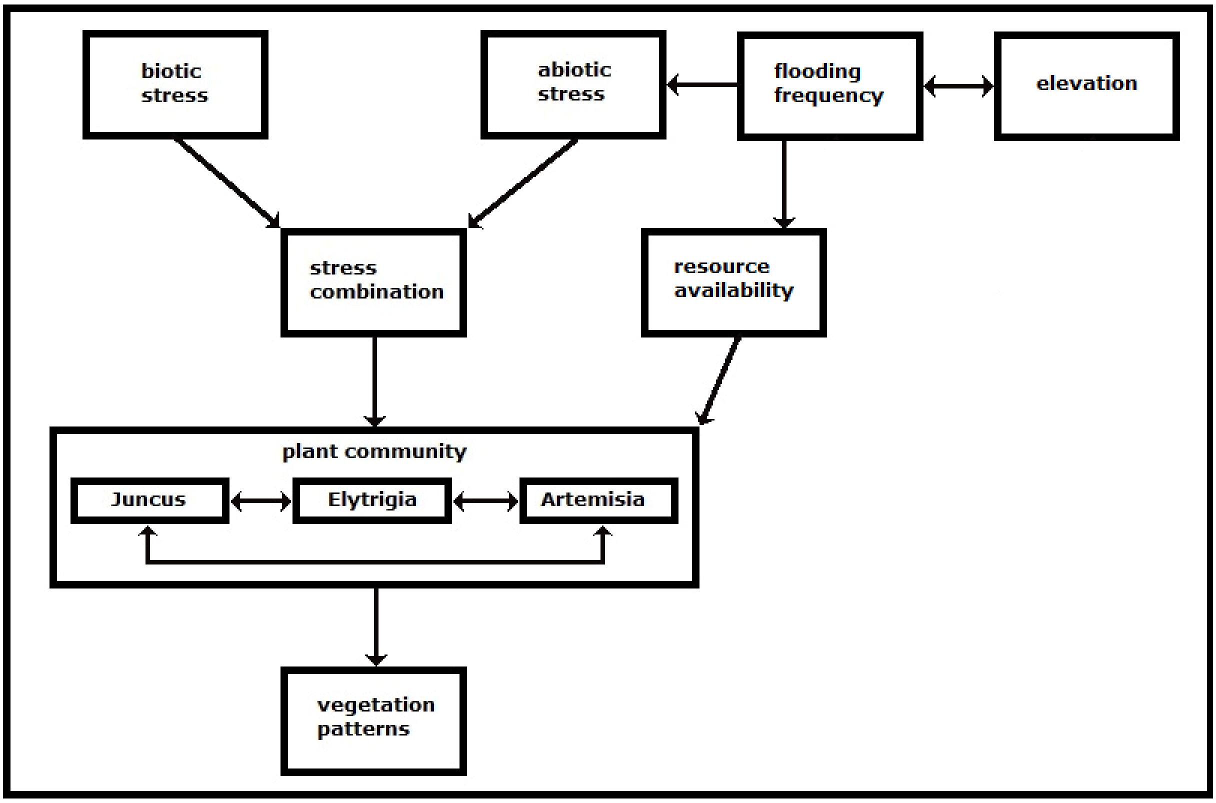

Figure 1. Processes and factors that influence vegetation patterns. Relations are indicated with arrows.

The first sub question concerns the influence of stress on the plant community in patches. Stress influences species growth and survival (Shumway and Bertness, 1992). *Juncus maritimus* is a species that creates patches in grazed salt marshes at Schiermonnikoog. It is an unpalatable rush which expands circular via underground lateral rhizomes (Wetzel and Howe, 1999). Cattle do not graze inside *Juncus* patches due to their unpalatability (Bakker et al, 2003; Boughton, 2011). Other species as *Elytrigia atherica* and *Artemisia maritima* can benefit by growing in ungrazed *Juncus* patches. However, *Elytrigia* is a species that replaces *Juncus* on the long term in ungrazed areas (Bakker et al, 2003). This indicates that on the long term *Elytrigia* will dominate *Juncus* in ungrazed patches. It is hypothesized that the *Juncus* cover in patches declines under increasing biotic stress (H1). *Juncus* is a halophytic species that prefers the higher marsh (Bakker et al, 2003). Halophytic species shift their energy from growth to survival under increasing salt stress (Konisky and Burdick, 2004). Thus it is hypothesized that the *Juncus* cover in patches will decline with increasing abiotic stress (H2).

Juncus facilitates other species in grazed areas. It protects beneficiaries from grazing and trampling; cattle avoid *Juncus* patches due to their unpalatability (Bakker et al, 2003; Boughton, 2011). Growth and survival of facilitated species is higher than unfacilitated species (Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991). *Artemisia* is a species that is facilitated by *Juncus* in grazed areas. It is an unpalatable species that is negatively influenced by trampling and soil compaction (Jensen, 1985). *Artemisia* is present in and outside patches and the facilitating effect of *Juncus* on *Artemisia* can be tested by comparing *Artemisia* height inside to outside patches. When *Juncus* patches appear after introduction of grazing it is expected that facilitation is the most important species interaction. However, when grazing continues it is expected that species in patches behave as in an ungrazed salt marsh where competition is the main species interaction (Bakker et al, 2003). Thus it is hypothesized that facilitating effects of *Juncus* on *Artemisia* decrease with increasing biotic stress (H3). *Juncus* is a high marsh species (Bakker et al, 2003) and *Juncus* cover was expected to decline with increasing abiotic stress. Therefore it is hypothesized that facilitating effects of *Juncus* on *Artemisia* decline with increasing abiotic stress (H4).

The second sub question involves the influence of resource availability on the plant community. Nitrogen is a limiting factor of plant growth in salt marsh ecosystems. It enters the system by sediment deposition as a result of flooding. The flooding frequency decreases as elevation increases. Sediment deposition increases elevation of the marsh (Van Wijnen and Bakker, 1997). Clay thickness is an indicator for the amount of nitrogen which is available for species (Olff et al, 1997). Since plant growth is higher when sufficient nutrients are available than when they are scarce it is hypothesized that *Juncus* and *Artemisia* height increase with increasing clay thickness (H5).

It has been suggested by Kéfi et al (2007b) that vegetation patterns may be an indicator for critical transitions in ecosystems due to shifts in patch size and number under stressful conditions. It is therefore important to research the effects of abiotic and biotic stress on patch sizes. *Juncus* can expand in grazed salt marshes due to its unpalatability (Boughton, 2011). It is therefore hypothesized that *Juncus* patch sizes will increase with increasing biotic stress (H6). Moreover, maximum patch sizes decrease under increasing stress (Kéfi et al, 2007). It is hypothesized that *Juncus* patch sizes will decrease under increasing abiotic stress (H7).

2. Materials and methods

2.1 Study area

Schiermonnikoog is a Frisian island (53°30'N, 6°10'E) in the North East of The Netherlands. The North of the island borders the North Sea and consists of sand dunes. The South of the island borders the Wadden Sea and consists of salt marshes. Various zones which differ in inundation frequency and species composition are found on salt marshes (Bakker et al, 2005). The low marsh and the high marsh are the focus in this research because these zones are cattle grazed. Common species on the low marsh are *Salicornia* spp, *Puccinellia maritima*, *Plantago maritima*, *Spergularia maritima*, *Limonium vulgare* and *Atriplex portulacoides*. Common species on the high marsh are *Puccinellia maritima*, *Festuca rubra, Artemisia maritima* and *Elytrigia athericus* (Olff et al, 1997). Three salt marshes which originated around 1900 were selected as research area. These three salt marshes (Figure 2), the SGS (short grazed salt marsh, low biotic stress), MGS (middle grazed salt marsh, medium biotic stress) and LGS (long grazed salt marsh, high biotic stress) vary in biotic stress. The SGS has been grazed for 24 years (Van Wijnen et al, 1997), the MGS for 39 years and the LGS has always been grazed (Bakker, 1989). Grazing intensity (0,5 cattle/ha) is similar in these salt marshes (Bakker et al, 2003).

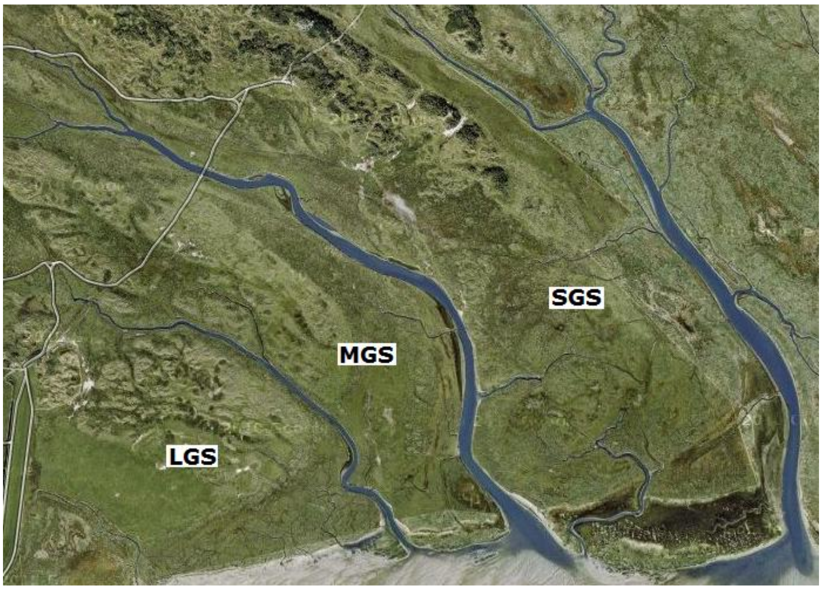

Figure 2. Long grazed (LGS), middle grazed (MGS) and short grazed (SGS) salt marsh on Schiermonnikoog.

2.2 Patches

Vegetation patterns on salt marshes of Schiermonnikoog consist of vegetation patches. The influence of stress on vegetation patches was tested by comparing patches under various gradients of biotic and abiotic stress. The biotic stress gradient was determined by the grazing history of the salt marsh. Patches were selected on the SGS, MGS and LGS. The selection method of the patches differed per salt marsh. The SGS contained many patches and not all patches were selected. Three transects of 2m wide and 300m length were created in the SGS. Every second encountered patch was numbered. All patches with a diameter smaller than 15 metres were selected in the MGS and LGS. Control patches of identical size were selected one metre from every patch in northeast direction where possible. However, due to other vegetation patches, dunes or very obvious height differences the presence or placement of a control patch can vary. Totally, 38 patches and 36 control patches were selected on the SGS, 57 patches and 48 control patches on the MGS and 60 patches and 51 control patches on the LGS.

Abiotic stress was defined by salt concentration in patches. According to Van Oosten (1986) the TDS (Total dissolved solids, measurement of salinity) is >5 g/L on the low marsh and <5 g/L on the high marsh of Schiermonnikoog. Salt measurements were done to divide the patches on the SGS, MGS and LGS into high and low salt stress. In every patch three soil cores of 5 cm depth were taken parallel to the coastline and they were mixed to create a sample. Two similar samples were taken per patch. The TDS in the patches was determined using the method of Davy et al (2011). One of the samples was dried 2 days in an oven on 70°C. The other sample was mixed with 300 ml demineralised water and then filtered after 30 minutes. The electrical conductivity (EC) was measured in the filtered water. The TDS was calculated using the water content and the EC. All patches with TDS>5 g/L were labelled 'high salinity level' and patches with TDS<5 g/L 'low salinity level'. The amount of patches and control patches with low and high salinity at the SGS, MGS and LGS can be found in Table 1.

		SGS	MGS	LGS
Low salinity	Patches	14	10	47
	Control patches	14	6	39
High salinity	Patches	24	47	13
	Control patches	22	42	12

Table 1. Amount of patches and control patches with low and high salinity on the SGS, MGS and LGS.

2.3 Plant community

2.3.1 Measurements

It was hypothesised that the *Juncus* cover in patches declines under increasing biotic stress (H1) and abiotic stress (H2). These hypotheses were tested by comparing the percentage *Juncus* in patches under varying biotic and abiotic stress. The species cover and abundance in patches and control patches were assessed using Londo's decimal scale (Londo, 1976). Vegetation of the whole patch was assessed in patches <$2m^2$. One sample of $1m^2$ per 2 metres was taken parallel to the coastline with a maximum of 4 samples per cross section in patches >$2m^2$. The first and the last sample were always taken at the sides of the patch. Average vegetation cover percentages were calculated per species.

It was also hypothesized that facilitating effects of *Juncus* on *Artemisia* decrease with increasing biotic stress (H3) and abiotic stress (H4). Height differences between *Artemisia* in and outside patches were used as an indicator for facilitation. *Artemisia* height was measured every 2 meters in two cross sections of the patch parallel and perpendicular to the coastline with a minimum of 5 measurements where possible. The average *Artemisia* height was calculated per patch and control patch. Height differences were calculated when *Artemisia* was present in patch and control patch.

2.3.2 Data analysis

The percentage *Juncus* in patches was compared between the SGS, MGS and LGS for low and high salinity level using a Mann-Whitney U test to determine the influence of biotic stress on *Juncus* cover. The alpha level was changed with a Bonferroni correction; α=0,017. Thereafter the percentage *Juncus* between low and high salinity levels was compared on the SGS, MGS and LGS using a Mann-Whitney U test to test the influence of abiotic stress on *Juncus* cover. A Spearman correlation test applied determine the relation between salinity and *Juncus* cover.

Differences in *Artemisia* height between patches and control patches were compared in the same way as the percentage *Juncus*, using the same statistical tests. The influence of stress on the facilitating effects of *Juncus* on *Artemisia* was thereby tested. A Spearman correlation test was applied to determine the relation between salinity and the facilitating effects of *Juncus* on *Artemisia*.

2.4 Resource availability

2.4.1 Measurements

It was hypothesized that *Juncus* and *Artemisia* height increase with increasing clay thickness (H5). Thickness of the clay layer indicates resource availability. Clay thickness in patches and control patches was measured using a soil corer. Measurements were taken in two cross sections, one parallel and the other perpendicular to the coast line. In these cross sections one measurement per two metres was done with a minimum of 5 and a maximum of 8 measurements per patch. At the sides of the patch, soil cores were taken 50 cm from the border where possible. The average clay thickness was calculated per patch.

2.4.2 Data analysis

Spearman correlation tests were performed to determine the relations between clay thickness and salinity, clay thickness and *Juncus* height, clay thickness and *Artemisia* height in patches and between clay thickness and *Artemisia* height in control patches.

2.5 Patch size

2.5.1 Measurements

It was hypothesized that *Juncus* patch sizes increase with increasing biotic stress (H6) and decrease under increasing abiotic stress (H7). Patch diameters were measured in two cross sections; one parallel and the other perpendicular to the coast. The diameters were used to calculate the patch surface using a formula to calculate the surface of an ellipse: surface patch = π x (0,5xdiameter A) x (0,5xdiameter B).

2.5.2 Data analysis

Patch surfaces were compared between the SGS, MGS and LGS for low and high salinity level using a Mann-Whitney U test to test the influence of biotic stress on patch size. A Bonferroni correction was used to correct α; α=0,017. Patch surfaces between the high and low marsh were compared on the SGS, MGS and LGS using a Mann-Whitney U test to test the influence of abiotic stress on patch sizes. Thereafter it was tested whether a correlation could be found between patch size and salinity using a Spearman correlation test.

3. Results

3.1 Plant community

3.1.1 Influence of biotic and abiotic stress on Juncus cover

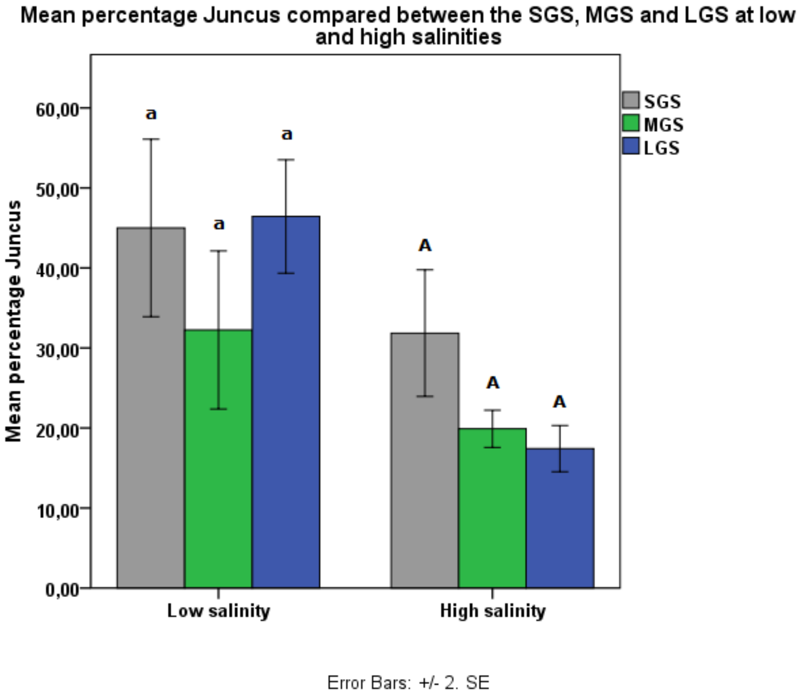

Figure 3. Mean percentage *Juncus* in patches with varying salinity and grazing history. Differences between the grazing regimes at a low salinity level are indicated with different letters and at a high salinity level with different capital letters.

The influence of biotic stress on the *Juncus* cover in patches was tested by comparing *Juncus* cover between the SGS, MGS and LGS at low and high salinity levels. No significant differences in *Juncus* cover were found between the grazing regimes at low or at high salinity levels (Figure 3).Thus biotic stress does not have a significant influence on *Juncus* cover in patches.

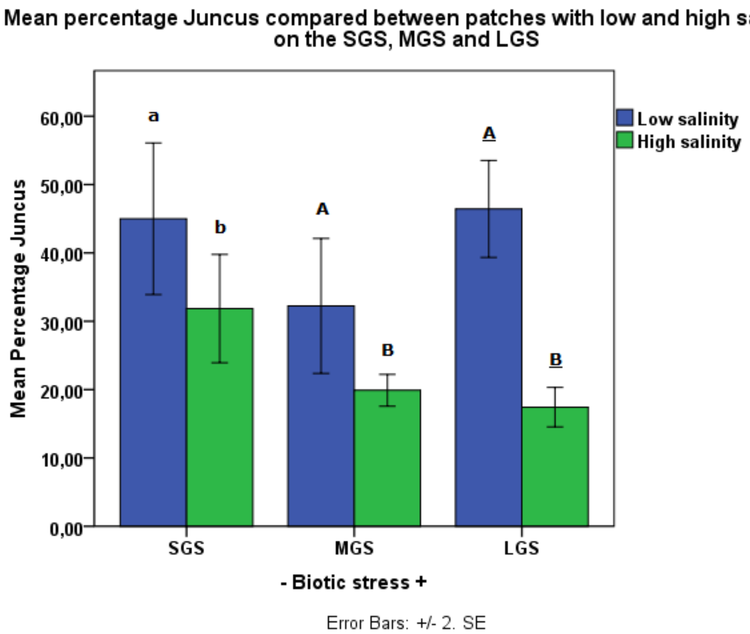

Figure 4. Mean percentage *Juncus* in marshes with varying grazing history at low and high salinity levels. Differences between patches with varying salinity levels for the SGS are indicated with different letters, for the MGS with different capital letters and for the LGS with different underlined capital letters.

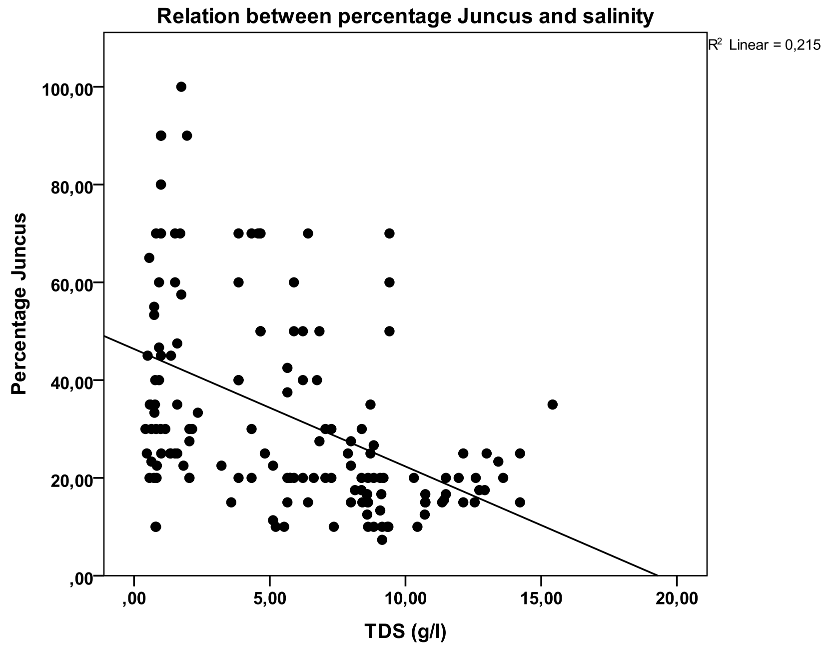

Figure 5. Relation between *Juncus* cover and salinity. A correlation was found (ρ=-0,509, P=0,000).

The influence of abiotic stress on *Juncus* cover in patches was tested by comparing patches with low salinity levels to patches with high salinity levels on the SGS, MGS and LGS. The *Juncus* cover was significantly higher in patches with low salinity levels than in patches with high salinity levels on the SGS, MGS and LGS (Figure 4). Moreover, a negative correlation (ρ=-0,509, P=0,000) was found between *Juncus* cover and salinity (Figure 5). Thus, *Juncus* cover declines with increasing abiotic stress.

3.1.2 Influence of biotic and abiotic stress on facilitation

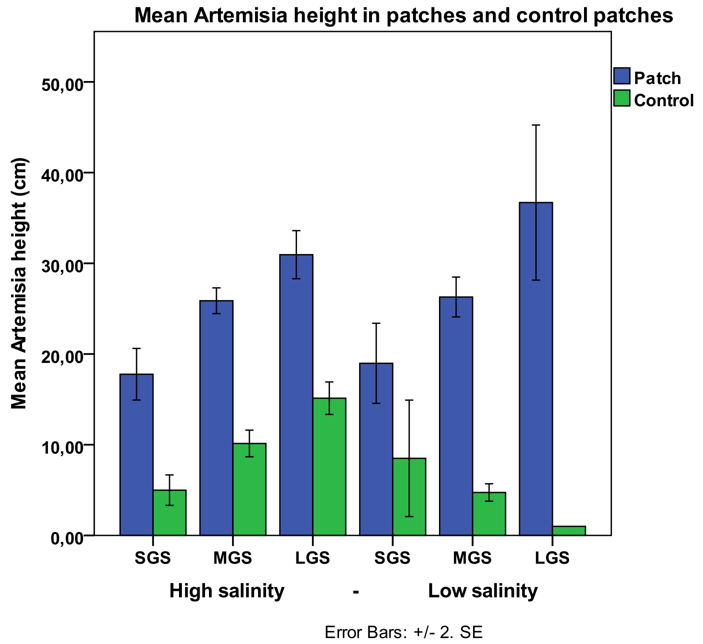

Figure 6. Mean *Artemisia* height in patches and control patches on the SGS, MGS and LGS at low and high salinity levels. The differences between blue and green bars are used as an indicator for facilitation.

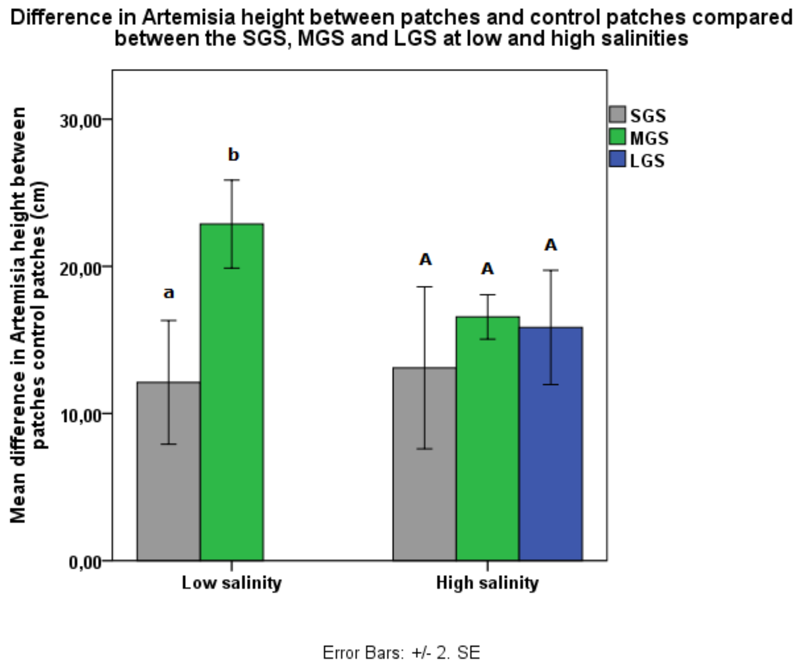

Figure 7. Mean *Artemisia* height difference between patches and control patches compared between the SGS, MGS and LGS at low and high salinity levels. Differences between the grazing regimes with low salinity are indicated with different letters and with high salinity with different capital letters.

An indicator for facilitating effects of *Juncus* on *Artemisia* is the difference in *Artemisia* height between patches and control patches (Figure 6). *Artemisia* height in patches and control patches increases with increasing biotic stress at high salinity levels, indicating no changes in facilitation under increasing biotic stress. *Artemisia* height increases in patches, but decreases in control patches with increasing biotic stress at low salinity levels, indicating an increase in facilitation with increasing biotic stress. This height difference was compared between the SGS, MGS and LGS for low and high salinity levels to test the effect of biotic stress on facilitation (Figure 7). No patches and control patches containing both *Artemisia* were present at the high marsh of the LGS. Therefore the facilitating effects of *Juncus* on *Artemisia* could not be measured there. Facilitation increased significant under increasing biotic stress at low salinity levels, but no significant differences were found between the SGS, MGS and LGS at high salinity levels. Thus facilitation increases under biotic stress in patches with low salinity but does not change under biotic stress in patches with high salinity.

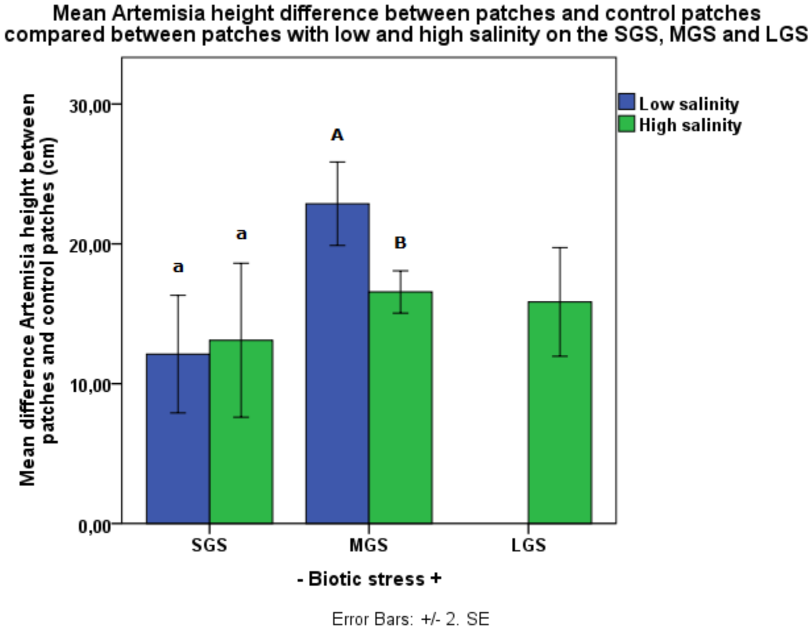

Figure 8. Mean *Artemisia* height difference between patches and control patches compared between patches with low and high salinity on the SGS, MGS and LGS. Differences between low and high salinity on the SGS are indicated with different letters and on the MGS with different capital letters.

The influence of abiotic stress on *Artemisia* height differences between in and outside patches was tested by comparing patches with low salinity to patches with high salinity on the SGS and MGS. Facilitation was similar in patches with varying salinity on the SGS. Facilitation was lower in patches with high salinity than in patches with low salinity on the MGS (Figure 8). No correlation was found between facilitation and salinity (ρ=-0,184, P=0,111).

3.2 Resource availability

3.2.1 Influence resource availability on plant height

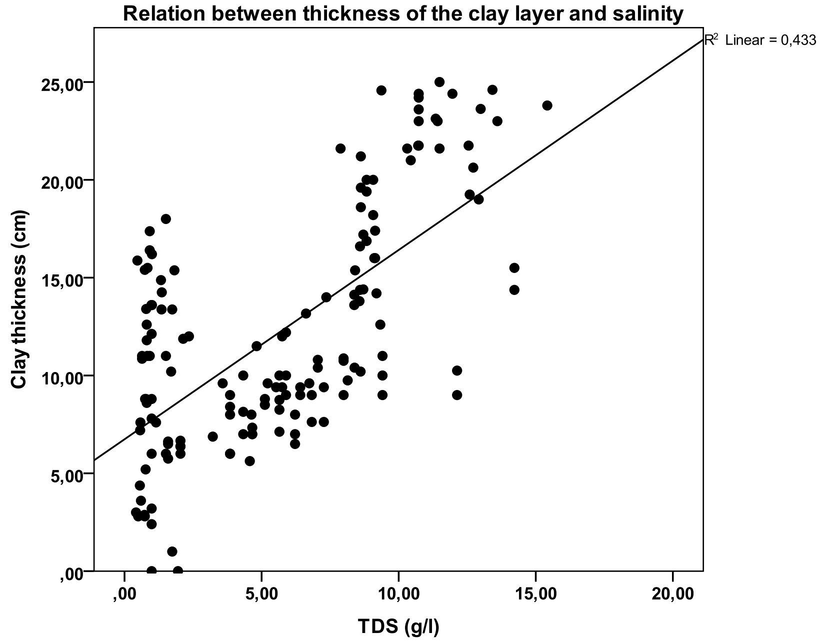

Figure 9. Relation between clay thickness and salinity. A correlation was found (ρ=0,608, P=0,000).

A correlation (ρ=0,608, P=0,000) between clay thickness and salinity was found. Clay thickness increases with increasing salinity (Figure 9).

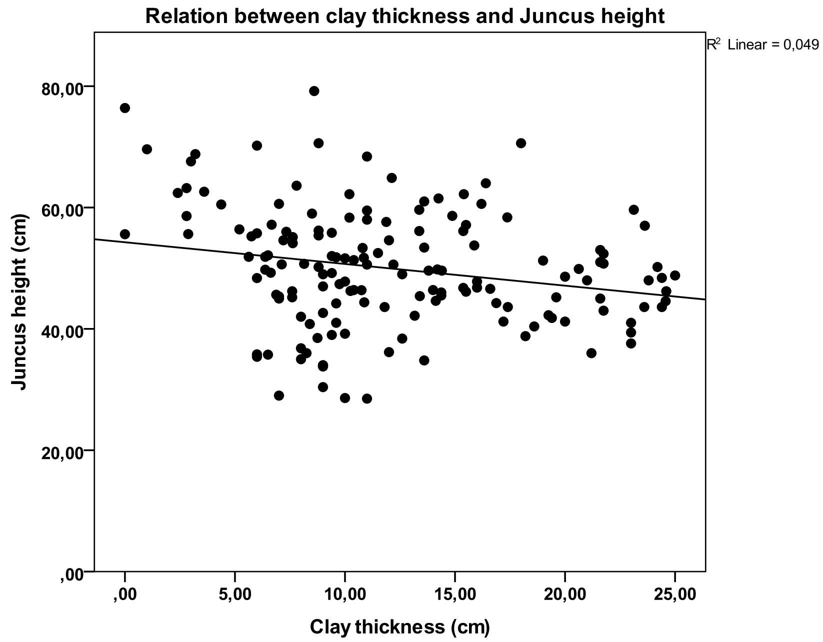

Figure 10. Relation between clay thickness and *Juncus* height. A negative correlation was found (ρ=-0,207, P=0,010).

Juncus height decreases with increasing resource availability (Figure 10). A negative correlation (ρ=-0,207, P=0,010) was found between clay thickness and *Juncus* height.

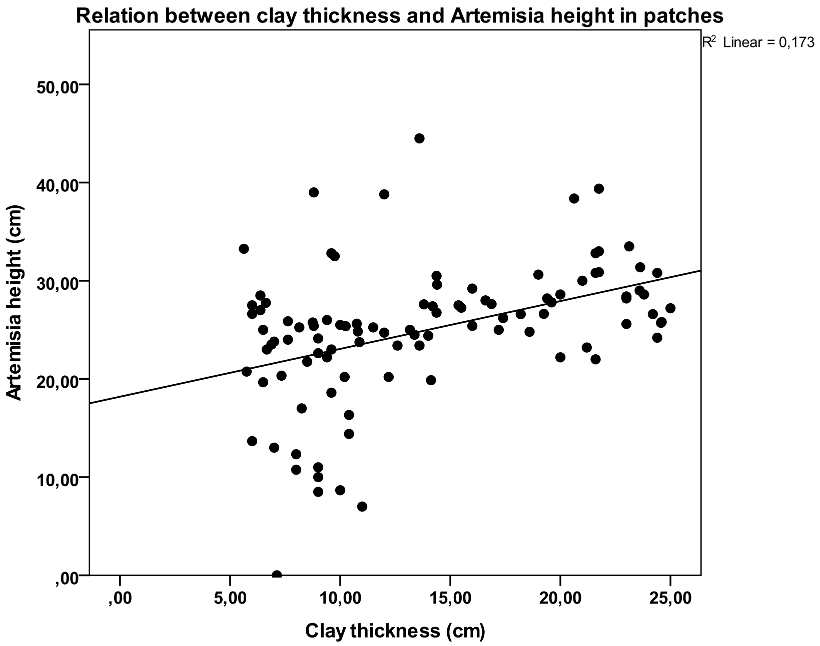

Figure 11. Relation between clay thickness and *Artemisia* height in patches. A correlation was found (ρ=0,456, P=0,000).

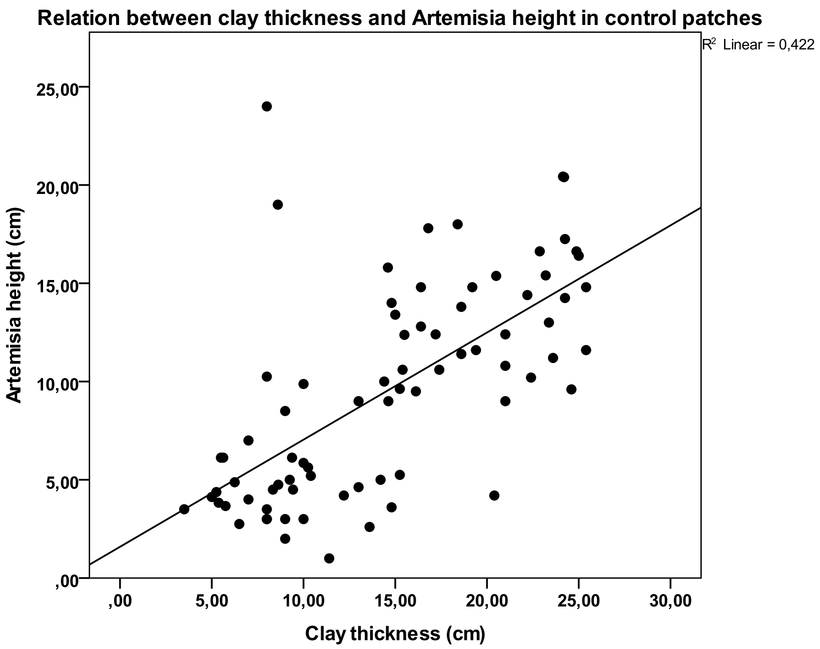

Figure 12. Relation between clay thickness and *Artemisia* height in control patches. A correlation was found (ρ=0,676, P=0,000).

Artemisia height increases with increasing clay thickness in patches (Figure 11) and in control patches (Figure 12). A correlation was found between clay thickness and *Artemisia* height in patches (ρ=0,456, P=0,000) an in control patches (ρ=0,676 P=0,000). Thus *Artemisia* height increases with increasing resource availability.

The flooding frequency in salt marshes influences salinity and clay thickness. Clay thickness increases with increasing salinity (Figure 10). *Juncus* height decreases and *Artemisia* height increases with increasing resource availability.

3.3 Patch size

3.3.1 Influence of biotic and abiotic stress on patch size

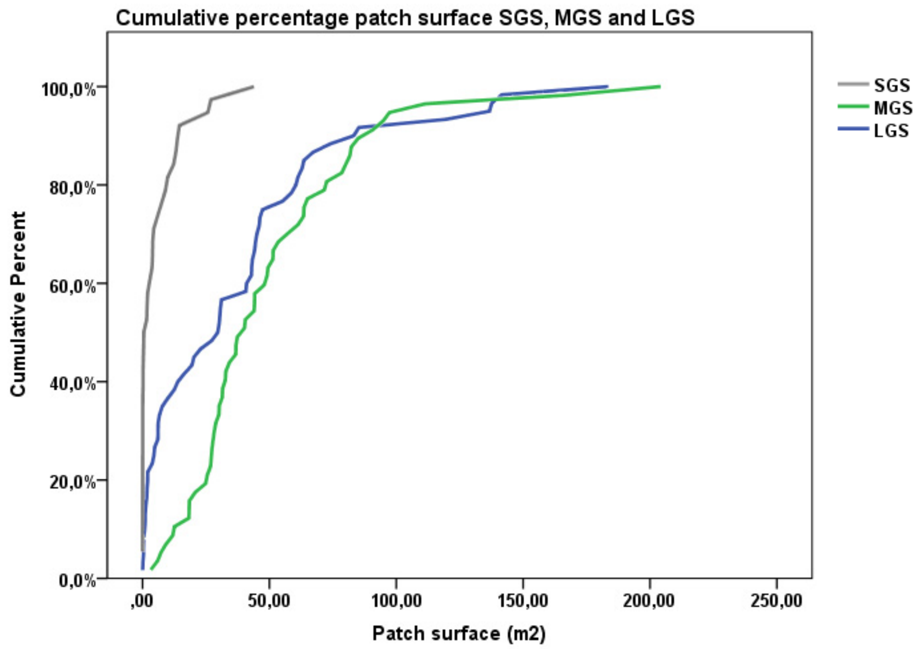

Figure 13. Cumulative percentage patch surface at the SGS, MGS and LGS.

Distributions of patch sizes on the SGS, MGS and LGS are depicted in Figure 13. Small patches are relatively more abundant on the SGS than on the MGS and LGS. No patches with sizes over 50m^2 are present on the SGS. The range of the patch sizes is smallest on the SGS and largest on the MGS. Small patches are relatively more abundant on the LGS than on the MGS. Patch sizes on the SGS were significantly smaller than patches at the MGS and LGS at low and high salinity levels. At low salinities patches on the MGS were significantly larger than patches on the LGS. No significant difference was found between patches at the MGS and LGS at high salinities.

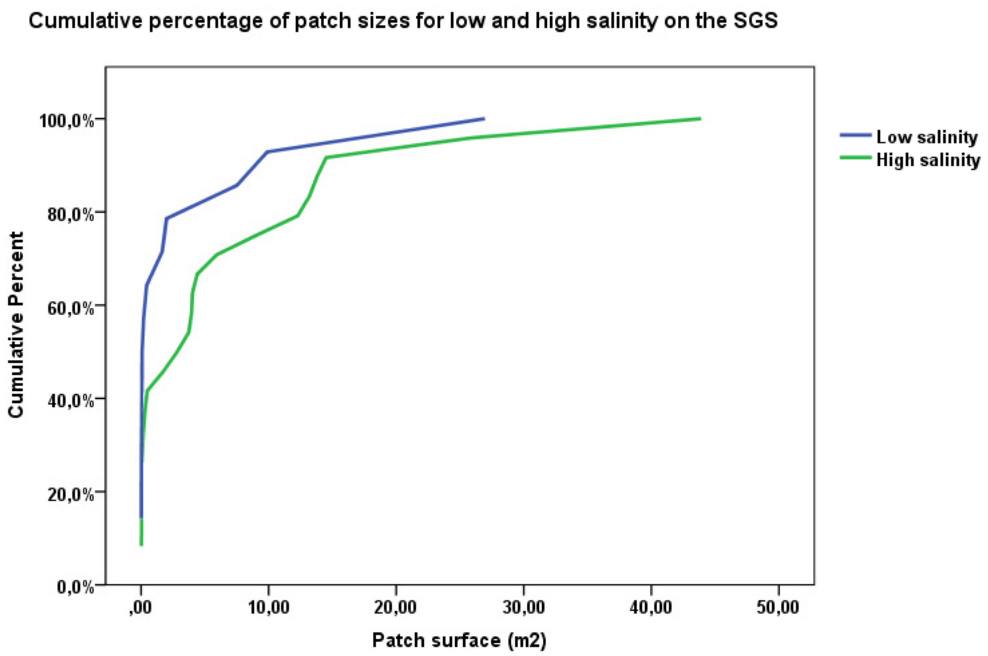

Figure 14. Cumulative percentage of patch sizes for low and high salinity on the SGS.

Cumulative percentage of patch sizes for low and high salinity on the MGS

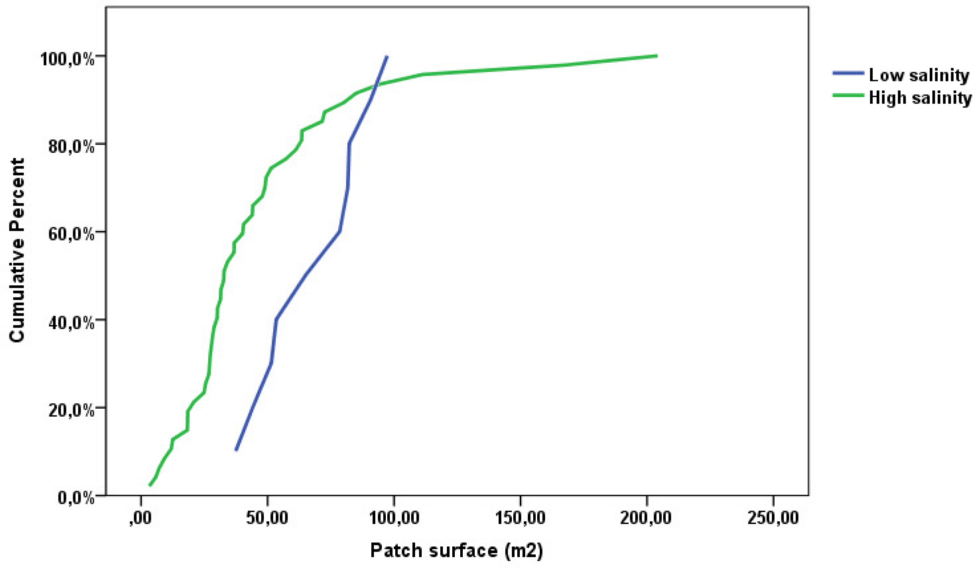

Figure 15. Cumulative percentage of patch sizes for low and high salinity on the MGS.

Cumulative percentage of patch sizes for low and high salinity on the LGS

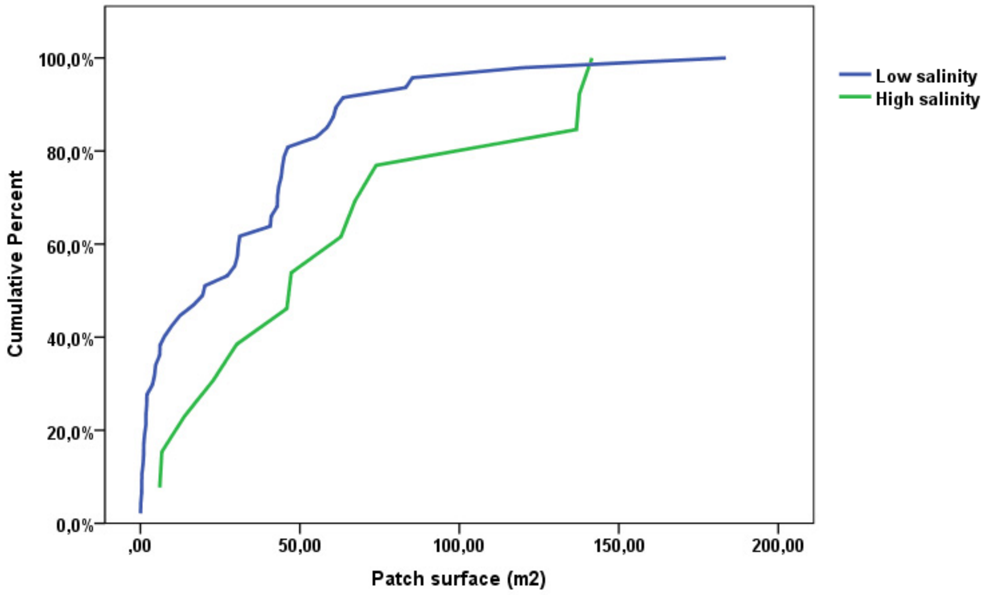

Figure 16. Cumulative percentage of patch sizes for low and high salinity on the LGS.

On the SGS small patches are relatively more abundant at low salinity levels than at high salinity levels. The range of patch sizes at low salinity levels is smaller than at high salinity levels (Figure 14). Relatively more small patches are present at high salinity levels than at low salinity levels on the MGS. The range of patch sizes at low salinity levels is smaller than at high salinity levels (Figure 15). On the LGS small patches are relatively more abundant at low salinity levels than at high salinity levels. The range of patch sizes at high salinity levels is smaller than at low salinity levels (Figure 16). No significant differences in patch sizes were found between low and high salinity at the SGS. Patches with low salinity were significantly larger than patches with high salinity at the MGS. Patches with high salinity were significantly larger than patches with low salinity at the LGS. Thus, most small patches can be found at low salinities on the SGS and LGS, but at high salinities on the MGS. The patch size range is larger at high salinities at the SGS and MGS, but larger at low salinities at the LGS. No correlation (ρ=0,123, P=0,128) was found between patch surface and salinity.

4. Discussion

This research was performed to determine the influence of abiotic and biotic stress on spatially patterned vegetation in a salt marsh community. It was found that *Juncus* cover in patches was not influenced by biotic stress but decreased under abiotic stress. Furthermore, facilitation increased under increasing biotic stress at low salinities but did not change at high salinities. This indicates that effects of a combination of biotic and abiotic stress on a plant community differ largely from effects of one type of stress posed on an ecosystem. Biotic stress had an obvious influence on the distributions of patch sizes; patch sizes were smallest in salt marshes with lowest biotic stress. Abiotic stress also influenced patch sizes, but no trend was observed. Thus spatially patterned vegetation in salt marshes changes under influence of biotic and abiotic stress. However, the observed differences between the salt marshes were not always as hypothesized.

Juncus cover was expected to decline under increasing biotic stress. The results show that *Juncus* cover did not change under increasing biotic stress. Wetzel and Howe (1999) found that shoots of *Juncus effucus* when fully senesced remained standing in the tussocks. This indicates that *Juncus* density does not decrease after senescence. Abiotic stress had a negative influence on *Juncus* cover, which corresponds with findings about other *Juncus* species. Naidoo and Kift (2006) found that the percentage *Juncus kraussii* decreased with increasing salinity and Pennings et al (2005) found that growth and performance of *Juncus roemerianus* was limited by salt stress. No effects of the combination of abiotic and biotic stress on *Juncus* cover were found since biotic stress did not influence *Juncus* cover.

Facilitation effects were measured by comparing *Artemisia* height differences in and outside patches under changes of biotic and abiotic stress. *Artemisia* suffered negative influences from cattle outside patches; *Artemisia* height inside patches is larger than outside patches. Jensen (1985) similarly found similar results. *Artemisia* height in patches increased under increasing biotic stress. However, *Artemisia* height outside patches increased at high salinities, but decreased at low salinities with increasing biotic stress. This difference between high and low salinity could be explained by grazing intensity. It was assumed that the grazing intensity in the salt marshes is similar in the whole research area. However, cattle prefer grazing at the high marsh over the low marsh because they avoid soft sediments (Kiehl et al, 1996; Andresen et al, 1990). Salinities are higher at the low marsh then at the high marsh (Bertness et al, 1992). A lower grazing intensity at places with high salinity could explain the increasing *Artemisia* height outside patches with increasing biotic stress. Facilitation increased at low salinities but did not change at high salinities with increasing biotic stress. Soil compaction due to cattle trampling outside *Juncus* patches might be an explanation for the increase of facilitation at low salinities. Soil compaction decreases nitrogen uptake and plant growth (Bezkorowajnyj et al, 1993). However, research at the influence of biotic stress on soil compaction could verify whether this is the cause of the increase in facilitation. The continuous level of facilitation at high salinity levels with increasing biotic stress could be the result of grazing preferences of cattle. An increase in grazing history will probably not influence species interactions when grazing intensity is rather low. Facilitating effects of *Juncus* do not change on the SGS and decrease on the MGS with increasing abiotic stress. The differences in facilitation between low and high salinities on the SGS and MGS seem be the result of a combination of soil compaction and varying grazing history. The combination of biotic and abiotic stress has different consequences for facilitating effects than the single stress types.

It was expected that plant height was positively related to resource availability. However, resource availability and salinity are connected. Salinity and resource availability both increase with decreasing elevation (Bertness and Ellison, 1987; Bertness et al, 1992; Olff et al, 1997; Van Wijnen and Bakker, 1997). *Artemisia* height increased with increasing resource availability. This corresponds to the findings of Van Wijnen and Bakker (1997) and Barkowski et al (2009) who found that *Artemisia* is a nitrophytic species which grows at nitrogen rich locations. *Juncus* height decreased with increasing resource availability and salinity. Greenwood and MacFarlane (2009) found that *Juncus* species direct energy from growth to survival ability as physical stress increases. Thus negative effects of salt stress outweigh the positive effects of nutrient availability. Furthermore, anoxic soil conditions due to water logging have a negative influence on plant growth and functioning (Hacker and Bertness, 1995; Yates et al, 2000). Water logging is related to the inundation frequency which is negatively correlated with elevation (Bockelmann et al, 2002). Experiments similar to those conducted by Hacker and Bertness (1995) can be performed to decouple the effects of salt stress, stress from anoxic conditions and nutrient availability on plant growth in salt marshes.

Patch sizes were expected to increase with increasing biotic stress. Results show that patches are smallest on the SGS, the salt marsh with the least biotic stress. These findings correspond with the findings of Wetzel and Howe (1999) who found that *Juncus effuses* is continuously expanding during the year and with the findings of Boughton et al (2011) who discovered that *Juncus effuses* expands under grazing pressure. Differences in distribution of patch sizes between low and high salinity were found, but they were too excessive to make out a trend. No correlation was found between salinity and patch sizes. In contrast, Kéfi et al (2007) found that the amount of large patches decreased under increasing stress. It should be noted that patches with a diameter higher than 15 metres were excluded from this research. No patches with a diameter larger than 15 metres were encountered on the SGS, but they were present on the MGS and LGS. This creates a distorted picture of the patch sizes on the MGS and LGS. Sizes of all patches should be included to get a complete picture of patch sizes. Finally it should be noted that salinity is a highly fluctuating factor. Salinity measurements were performed once and the amount of abiotic stress was based on these measurements. Repeated salinity measurements could improve the soundness of this research.

This study demonstrated that species growth, species interactions and patch sizes in salt marsh ecosystems are influenced by biotic stress, abiotic stress or a combination of biotic and abiotic stress. Further research at the influence of anoxic conditions on species growth, at the variations in grazing intensity on the salt marshes and at salinity fluctuations inside and around the *Juncus* patches would contribute to a better understanding of the influence of stress on salt marsh systems.

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