



Inundation Frequency Determines the Post-Pioneer Successional Pathway in a Newly Created Salt Marsh

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Abstract The effect of inundation frequency on plant community composition, species turnover, total and growth form cover, species richness, and abundance of individual species was investigated in a newly created salt marsh (Belgium) with a gradient of inundation frequencies from 0.01% to 100%. Cover of all plant species was estimated in

119 permanent 2×2 m plots along seven randomly chosen transects perpendicular to the main inundation gradient in 2003, 2005, and 2007. Plant composition change clearly varied along the inundation frequency gradient. The cover of annual species increased at a higher rate at higher inundation frequencies, while cover of perennials increased at higher rate at lower inundation frequencies. Species richness and the abundance of most species increased over time, indicating general absence of competitive exclusion among species. Conversely, the abundance and frequency of *Atriplex* spp., *Chenopodium* spp., and *Salsola kali* strongly decreased over time, indicating their early successional character. Frequent inundations hampered plant species turnover because of the low number of species which can tolerate that environmental condition. The appearance of communities dominated by *Elymus athericus* or *Salicornia procumbens* strongly increased over time, leading to a stronger separation of plant communities and an appearance of typical salt-marsh zonation.

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Introduction

Succession on salt marshes includes both floristic change as a function of time and a spatial separation in relation to environmental factors (Odland and del Moral 2002). Some of the first hypotheses of the concept of succession, e.g., the replacement of plant species in an orderly sequence of colonization and development (Silvestri et al. 2005), were linked to zonation in salt-marsh habitats (Chapman 1976). These hypotheses are based on the assumption that, on emerging salt marshes, after an initial colonization phase,

the substrate would become more stable and sediments would be trapped by the vegetation. This would allow other species to invade the marsh, producing changes directed towards a mature and stable climax ecosystem (Odum 1971). Nevertheless, results from long-term monitoring revealed that the dynamics of salt-marsh vegetation did not always proceed according to these classical succession schemes (de Leeuw et al. 1993). Rapid succession of salt-marsh vegetation has been recorded, but in most studies, community boundaries remained relatively stable for years, while within those boundaries plant composition may subtly alter, held in a ‘dynamic equilibrium’ (Adam 1990). Some plant species can persist over long periods in an area, whereas other species disappear without recolonizing (Goetghebeur 1976).

Plant distribution in salt marshes is not random nor spatially uncorrelated (e.g., Beefink et al. 1977; Adam 1990; de Leeuw et al. 1993; Marani et al. 2003) but is, on the contrary, organized in characteristic patches whose observation has stimulated a long history of research into the phenomenon of zonation (Chapman 1976; Silvestri et al. 2005). A number of authors (Scholten and Rozema 1990; Packham and Willis 1997; Costa et al. 2003) have described plant zonation in salt-marsh habitats and have evaluated the environmental conditions affecting the distribution of plant species. Environmental factors, such as salinity, sediment subsurface drainage, sediment deposition and water logging, which are associated with tidal inundation and distance to creek systems, determine the distribution and biomass production of salt-marsh species and consequently salt-marsh vegetation patterns and plant species zonation (Rozema and van Diggelen 1991; Huckle et al. 2000; Ewanchuk and Bertness 2004; Silvestri et al. 2005). Nitrogen has also been shown to limit plant growth at different successional stages of salt-marsh development (Wijnen and Bakker 1999). Despite some geographic variations (Pennings et al. 2003), competitive interactions are also known to play a great role in plant distribution, in both European (e.g., Olf et al. 1988) and American (e.g., Pennings et al. 2005) salt marshes.

Although many studies have dealt with patterns in wetland vegetation and succession (e.g., van der Valk 1981, Noon 1996), few have measured rates of change (Odland and del Moral 2002). Vegetation change can be estimated in several ways, including changes in species cover (Prach et al. 1993; Oksanen and Tonteri 1995), species composition (Eilertsen et al. 1990; Odland and del Moral 2002), or species turnover or β -diversity (Rydin and Borgegard 1988). Vegetation changes are demonstrated most clearly at the composition or/and species level. Few studies of wetland vegetation are available in which vegetation changes were marked by a growth form progression, from annuals to perennials to clonal perennials

(Odland and del Moral 2002). In our study, we investigated the successional change in plant communities, growth form, and cover of common salt-marsh species in time and whether inundation frequency affected this temporal change. Working with a marsh creation project gave us the opportunity to document primary succession across an elevational gradient, and shed new insight into how primary succession in salt marshes works.

Salt marshes low in the tidal frame can experience complete litter removal and have greater likelihood of inorganic sedimentation due to the frequent tidal inundation. The relatively high allogenic influence leads to modification of the vegetation (Packham and Willis 1997; Huckle et al. 2000). Annual species have the ability to disperse widely since they produce many seeds (Bossuyt et al. 2005; Bossuyt and Honnay 2008). It can therefore be expected that the total cover and richness of annual plant species will increase over time in early primary succession. Conversely, perennial species generally produce fewer seeds or can reproduce clonally, as with *Elymus athericus*, an important species of higher salt marshes in temperate European regions (Erfanzadeh et al. 2010). It can be expected that the cover and richness of perennials will increase at higher elevation (or lower inundation frequency) due to the longer time between disturbances, which allows for the emergence of more stable conditions. We thus tested the first hypothesis that perennial species richness and cover increase with decreasing inundation frequency, while annual species richness and cover decrease during early primary succession, irrespective of inundation frequency. Although the rate of sediment deposition and erosion is higher at lower elevations because of more frequent inundation (Packham and Willis 1997), the dynamic conditions allow a very limited number of species to germinate and grow. It follows that species succession might occur at a lower speed in these zones and vegetation composition would be more stable. Consequently, species turnover and change in vegetation composition is likely to be more frequent at higher elevations, with less frequent inundation. We then tested the hypothesis that the composition of plant communities that experience high inundation frequencies is more stable than that of communities subject to lower inundation frequency. Finally, we described variation in plant communities and individual salt-marsh species over time during early succession.

Methods

Study Area

We worked at a restoration site in the IJzermording nature reserve on the IJzer estuary, Belgium. The restoration site

was created following the large scale demolition and removal of buildings and the underlying dredge material between 1999 and 2002. The land surface of the new marsh was smooth and the soil was mainly sandy, with low organic matter content. Approximately 3 to 4 m of material were removed prior to tidal inundation. The restoration site was profiled to provide a continuous gradient of inundation frequencies (= relative number of inundative high waters) from no inundation at the highest elevations up to 100% inundation frequency at high tide for lowest elevations. Vegetated sampled-plots had an inundation frequency gradient from 0.01 to 69.19% per year in 2003. Colonization started in a completely seed-free substrate, with no existing soil seed bank (Hoffmann and Stichelmans 2006).

Data Collection

Vegetation

Vegetation data were collected within the restoration site in permanent plots (Burrows 1990; Bakker et al. 1996; location of the plots in the Appendix A, Electronic Supplemental Materials; for a general map of the study site, see Erfanzadeh et al. 2010). Presence of vascular plant and bryophyte species was recorded and cover visually estimated, using a decimal scale (Londo 1978), in 119 permanent 2×2 m plots in 2003, 2005, and 2007. The plots were located along seven transects, randomly established perpendicular to the general inundation gradient (Appendix A, Electronic Supplemental Materials). The plots were located every 3 m along each transect in order to ensure sufficient replication across and along the elevational gradient.

Inundation Frequency

Tides in the IJzer estuary are diurnal and vary according to the season (see mean water levels in Appendix A, Electronic Supplemental Materials). As a result, some plots are frequently inundated and others only inundated on high spring tides. The elevation of each plot was measured using a total station (Leica TC1600) in 2003. Reference points from the National Geographical Institute (Belgium) in the vicinity were used as a bench mark for the measurements. The reference used was the Belgian Lambert '72 projection for x-y and 'Tweede Algemene Waterpassing' (TAW) for altitude. Tidal information is gathered permanently at the site by the administrative authorities of the Flemish Community. From these continuous data, we extracted all absolute high tide levels during the period 1991–2000. These gave a fairly reliable estimate of high tide levels for the vegetation study period, since mean tidal levels had not changed significantly over the last decade. From these data,

we calculated a general inundation curve (Fig. 1), from which we calculated the inundation frequency for each vegetation plot within the restoration site. The percentage inundation frequency for each plot was defined as:

$$\left(\frac{\text{the number of high tides that inundated the plot in one year}}{\text{total number of high tides in one year}} \right) \times 100.$$

Data Analysis

Plant community composition differentiation was visualized by detrended correspondence analysis (DCA, as recommended by McCune and Grace 2002), using CANOCO (Lepš and Šmilauer 2005). Since axes 1 and 2 explained a large proportion of the variation (eigen values: 0.92 and 0.59, respectively), only scores on the first two axes were used as a measure for plant community species composition.

Total species richness (number of species observed in 2×2 m plots), total cover, and the cover (and richness) of growth forms (annuals and perennials) were transformed to $\log_{10}(x+1)$ to normalize distributions. Repeated measurements ANOVA models with LSD tests were used to compare species richness, DCA scores, total cover, and the cover (and richness) of growth forms between years with respect to the inundation frequency. Species richness, DCA scores, total cover, and the cover (and richness) of growth forms were introduced to the model as within-subject variables while inundation frequency was introduced as covariate. The interaction between year and inundation frequency was also introduced to the model to improve normality.

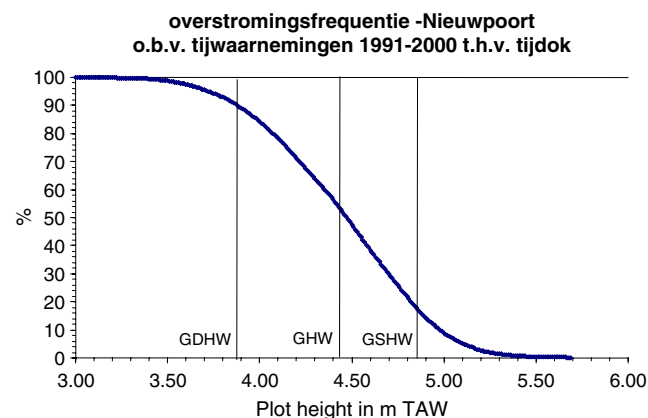


Fig. 1 Reconstructed inundation frequency curve, using tidal measurements (consecutive high tides) measured at the automatic measuring point on the northern pier along the former tidal harbor at the IJzermonding nature reserve, based on tidal observations in the period 1991–2000 (Fremout 2002). GDHW: mean neap tide high water; GHW: mean high water; GSHW: mean spring tide high water. All points at the left side of the curve are inundated at every high tide; all points at the right hand side of the curve are never inundated (during the 10 year observation period)

Because the interaction between year and inundation frequency was highly significant for most variables, we performed linear regressions separately on different year plots (2003, 2005, and 2007) for those variables that showed a significant effect of years, inundation frequency, and their interaction. Since linear regressions in some cases showed a low R^2 , we also tried to estimate the best fitting curve between inundation frequency and vegetation parameters (perennial cover, perennial richness, and annual cover) in 2003, 2005, and 2007. Linear, logarithmic, inverse, quadratic, cubic, power, compound, logistic, growth, and exponential regression were compared and the model with the highest R^2 was selected. Dependent and independent variables were transformed to positive values (by adding the value of 0.01) to enable the calculation of different models. Finally, the cover of the most common salt-marsh species (Packham and Willis 1997) was compared among years (2003 and 2005, 2005 and 2007, 2003 and 2007) using non-parametric Friedman and Wilcoxon tests. P values are given after Bonferonni correction for multiple comparisons.

Species turnover rates were calculated according to the method of Bakker et al. (2003): to calculate species turnover for a plot in a specific year, the number of species in that plot present in both year t and year $t-1$ was divided by the average total number of species in that plot and subtracted from 1. The species turnover rates between 2003 and 2005 and 2005 and 2007 were averaged. A linear regression model was used to test the relationship between species turnover and inundation frequency.

Data from 2003 to 2007 were clustered using TWINSpan (Hill 1979) in order to distinguish plant communities in different years (Dale 1995; Jongman et al. 1995; Roleček et al. 2009). There were 119 plots for each of the three years, and if no change occurred, each plot should be in the same class every year.

Results

A total of 138 species was observed in the permanent plots between 2003 and 2007 (see Appendix B, Electronic Supplemental Materials). The cover of annuals recorded in plots at higher elevations decreased over time (Fig. 2a). In 2003, *Atriplex* spp., *Chenopodium* spp., and *Salsola kali* were observed in 40, 37, and 39 plots, respectively, while in 2007 they were observed in only 15, 9, and 13 plots, respectively. Cover of perennials and annuals of the frequently inundated intermediate and lower elevations of the site (*Elymus athericus*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia europaea*, *Suaeda maritima*) increased over time (Fig. 2b). *Agrostis stolonifera*, *Elymus athericus*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia europaea*,

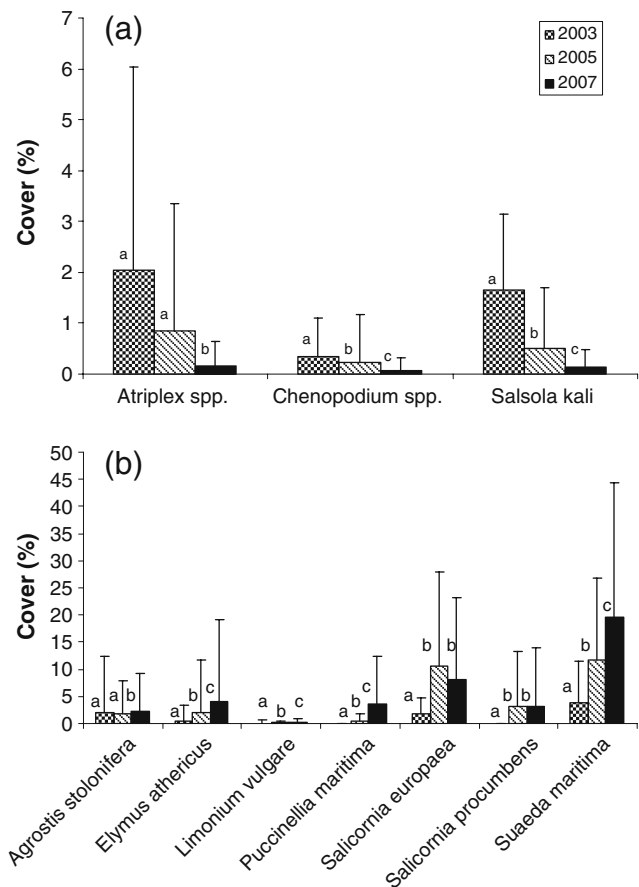


Fig. 2 Average of percentage cover (Mean + SD) of the most common salt-marsh species (Packham and Willis 1997) in different years; Different successive letters indicate significant differences (at $p < 0.05$) among years within every species individually (Friedman & Wilcoxon tests). Cover of some species were decreasing (a) while others were increasing (b) over time

S. procumbens, and *Suaeda maritima* all increased in occurrence between 2003 and 2007 (frequency in 2003 and 2007, respectively: 11→34, 14→51, 4→42, 2→60, 60→72, 0→32, and 59→85 of the 119 plots).

Total species richness increased over time (Fig. 3a). The number of annuals increased by 59% between 2003 and 2005, but remained constant between 2005 and 2007. The number of perennials increased by 86% between 2003 and 2005 and increased by another 63% between 2005 and 2007. There was a tendency for an increasing difference in the number of perennial species between years, with higher increase in the less frequently inundated plots (Table 1, Fig. 4).

The cover of both annuals and perennials increased rapidly between years (Fig. 3b), from an average of 5–10% in 2003 to a mean cover of more than 30% in 2007. Cover of annuals increased more rapidly over time at higher inundation frequencies, while this occurred for perennial species at lower inundation frequencies (Table 2, Fig. 5).

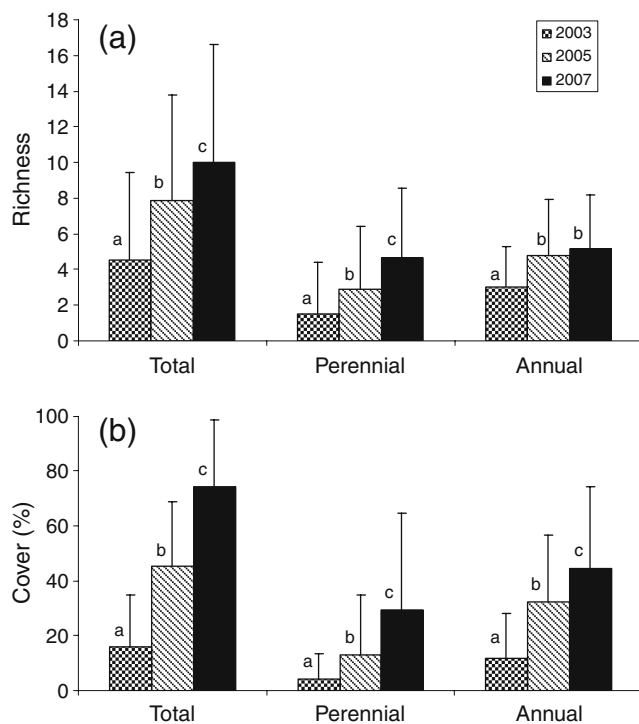


Fig. 3 The average (Mean + SD) of richness per 4 m² (a) and cover (b) in different years; Different successive letters indicate significant differences (at $p < 0.05$) between years and within every richness and cover class, respectively (from Repeated measurements ANOVA models)

Repeated measurement analysis revealed a significant effect of year, inundation frequency, and their interaction on plant community composition, measured as scores on DCA axes 1 and 2 (Table 1). The analysis of species turnover using a linear model regression showed that species turnover decreased with increasing inundation frequency (Fig. 6).

The TWINSPLAN classification revealed nine groups during the first years and six in later years. During 2003, the *Salicornia europaea*-*Suaeda maritima* vegetation occupied the highest number of plots while the *Suaeda*

maritima-*Parapholis strigosa* group dominated in 2007. The occupation of some vegetation types decreased over time (e.g., the *Atriplex* spp.-*Suaeda maritima* co-dominance type) while other groups increased over time (e.g., the *Salicornia procumbens* dominance type) (Table 2).

Discussion

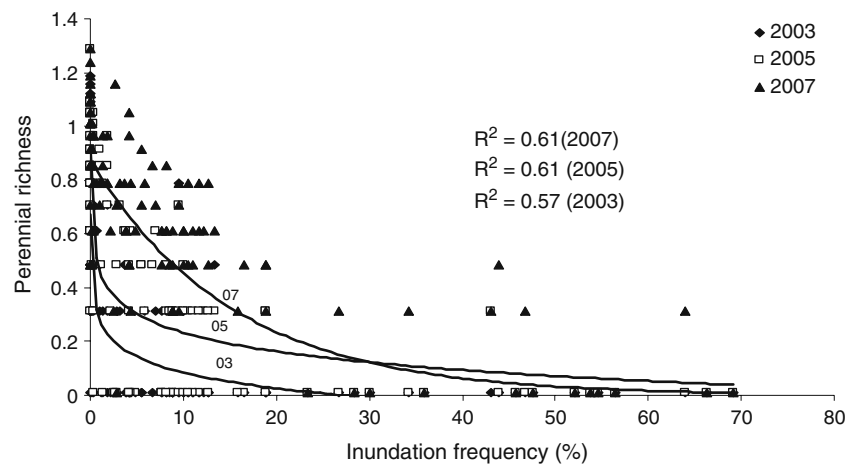
The spatial distribution of salt-marsh vegetation is organized in characteristic patches, or zones, related to the ability of individual species to tolerate environmental conditions associated with tidal inundation (Scholten and Rozema 1990; Silvestri et al. 2005). This study has shown that reassembly of plant species into these characteristic patches following restoration is rapid and primarily driven by the frequency of tidal inundation (regulated by elevation). The interaction between inundation frequency and a plant species' competitive ability, largely defined by an annual versus perennial growth form, appears to primarily determine salt-marsh zonal composition.

The number of annual species recorded within the restoration site initially increased, but remained constant in later stages. *Chenopodiaceae* species in particular were replaced by other annual or perennial colonizers. The rate of increase in annual cover was greatest at high inundation frequencies. The cover of perennials increased over time, with the speed of expansion rate higher with reduced inundation frequency. These results support our first hypothesis that perennial species cover and richness increase with decreasing inundation frequency while annual cover and richness decrease during early primary succession, irrespective of inundation frequency. The rapid expansion of *Puccinellia maritima* and *Elymus athericus* is characteristic of newly created salt marshes, and can lead to the exclusion of other, less competitive species (Eertman et al. 2002; Reading et al. 2008). Despite an increasing total species richness and cover over time, several plant species

Table 1 Result of the repeated measurements for species richness, cover and composition (DCA1 and DCA2 used as proxy) for plant species recorded in the IJzermondig restoration site between 2005 and 2007 ($n = 119$)

Effect	Year		Inundation frequency		Year × Inundation frequency	
	F-statistic	p-value	F-statistic	p-value	F-statistic	p-value
Total richness	111.5	<0.001	100.5	<0.001	2.1	0.131
Perennial richness	148.5	<0.001	81.6	<0.001	10.9	<0.001
Annual richness	27.7	<0.001	58.5	<0.001	0.2	0.84
Total cover	147.5	<0.001	15.3	<0.001	13.6	<0.001
Perennial cover	236.0	<0.001	67.3	<0.001	28.6	<0.001
Annual cover	24.6	<0.001	1.2	0.263	19.7	<0.001
DCA1	9.2	<0.001	88.9	<0.001	3.7	0.037
DCA2	98.8	<0.001	5.7	0.022	21.3	<0.001

Fig. 4 The best fit of regression between inundation frequency and perennial richness. In 2003: logarithmic, $p < 0.01$; in 2005: logarithmic, $p < 0.01$; in 2007: exponential, $p < 0.01$. Perennial species richness was transformed to $\log_{10}(x+1)$



were decreasing in average cover, probably indicating the existence of competitive interactions, likely to favor salt-tolerant species (Emery et al. 2001). Odland and del Moral (2002) showed that species richness in a wetland ecosystem peaked one year after exposure to tidal inundation, but then the number of species in the plots declined through competition, finally stabilizing. They demonstrated that a high species richness and density in the seed bank of exposed sediment resulted in a rapid appearance of high numbers of species in the above-ground vegetation in the first year, which initially limited competitive exclusion. Seed banks are important for rapid recovery of marsh vegetation after restoration and play an important role in early succession (Keddy and Reznicek 1986). In our study area, the establishment of plant species on exposed sediments was certainly due to seed dispersal by tidal water because the site was constructed on formerly developed land, excavated after demolition (Erfanzadeh et al. 2010). Tidal water movement was probably the main dispersal agent. The important role of tidal currents in seed dispersal of halophytes has previously been demonstrated (e.g., Huiskes et al. 1995; Tatyana 2000).

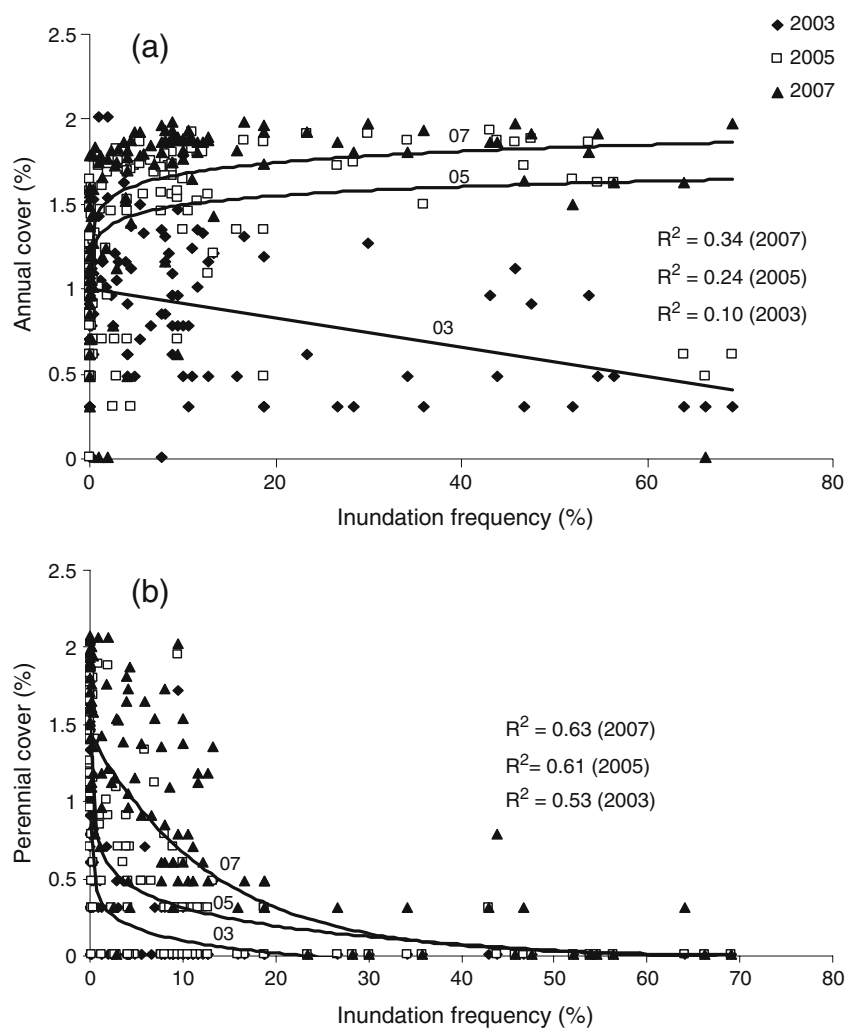
Our second hypothesis stated that the compositions of plant communities under high inundation frequencies are

more stable than those of communities under lower inundation frequencies because dynamic conditions allow a limited number of species to germinate and grow. This hypothesis was supported by our results because a significant linear relationship existed between inundation frequency and species turnover. It is worth noting that while the relationship was significant, there was still some species mobility at higher inundation frequencies. While *Suaeda maritima* expanded rapidly, the appearance of new species over time (e.g., *Salicornia procumbens*), and the change in the abundance of other species (e.g., *Salicornia europaea*), resulted in some temporal variation in plant composition. We expect this was a result of the species' differing abundance in the local species pool and from dispersal traits (Wolters et al. 2008; Erfanzadeh et al. 2010). At lower inundation frequencies, the expansion of some species (e.g., *Elymus athericus*), and turnover of others, resulted in a change in species composition. Frequent inundations hence restricted plant species turnover. This is likely to be a consequence of a high washing of soils and thus a lower nitrogen accumulation at these frequently inundated sites as compared to higher and less inundated sites (Olff et al. 1997). Difference in nitrogen accumulation may result in changes in plant growth (Rozema and

Table 2 The number of plots occupied by different communities in different years (from Twinspan analysis)

Plant community	2003	2005	2007
<i>Salicornia procumbens</i> dominant	0	12	14
<i>Salicornia europaea</i> - <i>Suaeda maritima</i> co-dominant	43	33	12
<i>Suaeda maritima</i> dominant	14	14	12
<i>Suaeda maritima</i> - <i>Parapholis strigosa</i> co-dominant	1	9	44
<i>Atriplex</i> spp.- <i>Suaeda maritima</i> co-dominant	14	10	0
<i>Elymus athericus</i> dominant	6	15	15
<i>Ammophila arenaria</i> - <i>Carex arenaria</i> co-dominant	14	16	22
<i>Salsola kali</i> - <i>Suaeda maritima</i> co-dominant	27	10	0

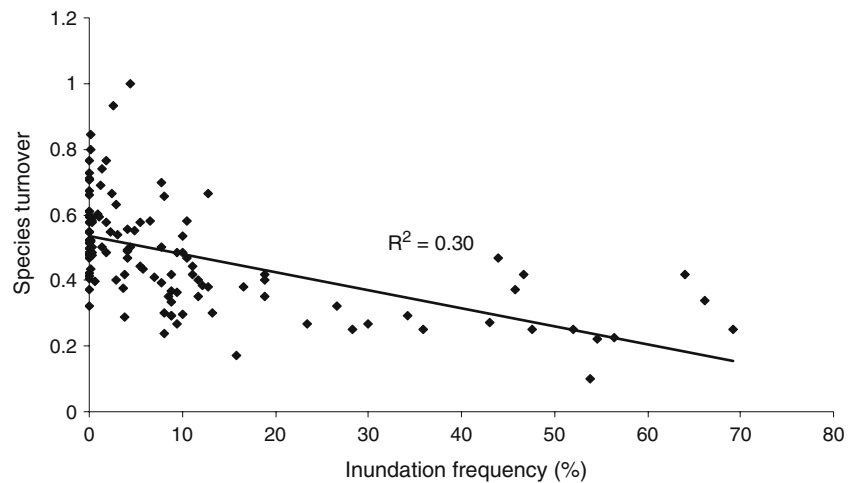
Fig. 5 The best fit of regression between inundation frequency and (a) annual cover (in 2003: linear, $p < 0.01$; in 2005: logarithmic, $p < 0.05$; in 2007: logarithmic, $p < 0.01$); (b) perennial cover (in 2003: logarithmic, $p < 0.01$; in 2005: logarithmic, $p < 0.01$; in 2007: exponential, $p < 0.01$). The annual and perennial cover was transformed to $\log_{10}(x+1)$



Blom 1977; Broome et al. 1995) and biomass production (Person and Ruess 2003), and is therefore likely to determine the rate of succession and turnover (Marrs et al. 1983). In addition, in the salt-marsh environment, an increase in elevation (and related opposite gradients in

salinity and flooding frequency) is associated with an increase in plant diversity associated with less salt tolerant, fresh-water species, finally resulting in greater potential species richness and a higher species turnover (e.g., Wijnen and Bakker 1999).

Fig. 6 The relationship between inundation frequency and species turnover (linear regression, slope = -0.05, $p < 0.01$)



The frequency of *Chenopodium* spp., *Atriplex* spp., and *Salsola kali* decreased by 76%, 51%, and 53%, respectively, between 2003 and 2007. As a result, these species disappeared from most plots by 2007, and it is expected that these species will no longer be present at the study site in the future through lack of competitive ability. In comparison with 2007, there were very few plots in which *Elymus athericus* and *Salicornia procumbens* dominated in 2003. Over time, vegetation patterns develop because species are adapted to a particular inundation frequency zone over the elevation gradient, and segregation of species, communities, and zonation in space occurs (Bockelmann et al. 2002; Costa et al. 2003).

Our study revealed rapid development of vegetation on exposed sediments after the creation of a new salt marsh. Succession was characterized by rapid spread of a limited number of salt tolerant annuals at higher inundation frequency levels and the rapid vegetative spread of some clonal salt-marsh species at lower inundation frequency levels. The distribution of plant species in the early stages of succession appears to be highly constrained by tolerance to tidal flooding at higher inundation frequencies, and probably by competition between perennials at low inundation frequencies.

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