

Chapter 3 Inundation frequency determines the post-pioneer successional pathway in a newly created salt-marsh²

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² Not yet submitted to a scientific journal
Field data were collected by the first author

3.1 Abstract

The effect of inundation frequency on plant community composition, species turnover, total and growth form cover, species richness and abundance of individual common species was investigated. The study area was a newly created salt-marsh located along the Belgian coast with a more or less continuous gradient of inundation frequencies from 0.01% of all high waters for highest elevations to 100% for lowest elevations. Cover of all plant species was estimated in 119 permanent 2m × 2m plots along six randomly chosen transects perpendicular to the main inundation gradient with a 3m distance between the plots in 2003, 2005 and 2007. Detrended correspondence analysis (DCA) scores were used as a proxy for plant composition. Total cover, the cover of annuals and perennials, total species richness, species richness of annuals and perennials and species turnover was calculated for each plot. Repeated measurements and LSD were used to compare all variables in three different years for different inundation frequencies. In addition, TWINSpan was used to distinguish plant communities in different years.

The results showed that plant composition changed differently according to inundation frequency. The cover of annual species increased at a higher pace at higher inundation frequencies. The cover of perennials increased at higher pace at lower inundation frequencies. In total, species richness and the abundance of most species increased in time, indicating absence of a competitive exclusion among species. Nevertheless, the abundance and frequency of *Atriplex* spp., *Chenopodium* spp. and *Salsola kali* strongly decreased in time, indicating a declining natural succession. It seems that perennial species (e.g. *Elymus athericus*) are spreading by vegetative propagules from upward to downward. Frequent inundations hampered plant species turnover, because of the low number of species that can tolerate that environmental condition. The frequencies of communities dominated by *Elymus athericus* and *Salicornia procumbens* strongly increased in time, indicating that these species

are getting more and more spatially separated, leading to a stronger separation of plant communities and an appearance of a salt-marsh zonation.

Key words: Succession, Salt-marsh, Species turnover, Plant composition, Inundation frequency

3.2 Introduction

Tidal marshes are colonized by salt tolerant plant species adapted to complete their life cycle in saline environments. The spatial distribution of vegetation in salt-marshes is organized in rather well delineated patches (Beefink 1962; 1965; 1966; 1977; Adam 1990; de Leeuw 1992; Marani et al. 2003). The distribution is not random nor spatially uncorrelated but is, on the contrary, organized in characteristic patches whose observation has stimulated an increasing interest in the phenomenon of zonation (Silvestri & Marani 2004). A number of authors (Packham & 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. Scholten & Rozema (1990) demonstrated that the composition and distribution of plant communities along the elevational gradient (zonation) of a salt-marsh is related to the ability of individual species to tolerate environmental conditions associated with tidal inundation. Several abiotic factors vary in association with tidal inundation, including salinity (Rozema & van Diggelen 1991) and disturbance in the form of burial by debris (Brewer et al. 1998). Environmental factors, such as 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 (Huckle et al. 2000; Silvestri & Marani 2004). Olf et al. (1988) stated that there are several ways in which species are influenced by the inundation by seawater, i.e. increasing inundation frequencies reduce the cover of the vegetation by inducing anaerobiosis of the substrate, by deposition of sand and clay, or by the toxic effects of salt, changing competitive interactions between species.

Once vegetation is established, individual species cover and total composition change over time: succession takes place. A traditional view of succession is that assemblages slowly and progressively occupy a site until a homogeneous, sustainable community develops

(Odland & del Moral 2002). Similar to other habitats, succession on salt-marsh includes both floristic change as a function of time and a spatial separation in relation to environmental factors (Odland & del Moral 2002). Some of the first hypotheses of the concept of succession, i.e. 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). This hypothesis is based on the assumption that, on emerging salt-marshes, after an initial colonization phase, the substrate would be 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). Adam (1990) reported that rapid succession of salt-marsh vegetation has been recorded in some cases, but in most studies, community boundaries remained relatively stable for years. At the species level, some species persist over long periods in an area, whereas other species disappear without recolonizing (Goetghebeur 1976). Salt-marsh vegetation dynamics is thus seen to be complex, and a deeper understanding of halophyte spatial and temporal patterns is required in different environmental conditions. It is expected that environmental conditions affect the speed, rate and trajectory of vegetation succession.

It has been demonstrated that marshes high in the tidal frame, experience up to complete litter removal and greater likelihood of inorganic sedimentation due to the frequent tidal inundation. This relatively high allogenic influence leads to a change in vegetation (Packham & Willis 1997; Huckle et al. 2000). Although, the rate of sedimentation and erosion is higher at lower elevations because of higher inundation frequency (Packham & Willis 1997), dynamic conditions allow a very limited number of species to germinate and grow. It follows that species succession will occur with lower speed in these zones and vegetation would be

more stable. Consequently, species turnover and change in vegetation composition would be more frequent at higher elevation and hence at lower inundation frequency.

Although many studies deal with wetland patterns and succession (e.g. van der Valk 1981, Noon 1996), only few have measured vegetation change rates (Odland & del Moral 2002). Vegetation change rates can be estimated in several ways, including changes in species cover (Prach et al. 1993; Oksanen & Tonteri 1995), species composition (Eilertsen et al. 1990; Odland & del Moral 2002) or species turnover or β -diversity (Rydin & Borgegard 1988).

Vegetation changes are however demonstrated most clearly at the composition or/and species level. Few studies are available in which vegetation changes were marked by a growth form progression i.e. annuals, perennials and clonal perennials (Odland & del Moral 2002). In the present 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. Annual species can disperse everywhere since they produce many seeds (see chapter 2), therefore it can be expected that the total cover and richness of annuals increase in time in early primary succession. While perennials, of which *Elymus athericus* is the most important in the higher marshes, unable to produce seeds, spread by vegetative growth (see chapter 2). It can be expected that the cover and the richness of perennials increase in higher elevation (or lower inundation frequency). We tested the following hypotheses: 1- perennial cover and richness increase with decreasing inundation frequency while annual cover and richness decrease during early primary succession, irrespective of inundation frequency, 2- the composition of plant communities that experience high inundation frequencies are more stable than communities subjected to lower inundation frequency, and 3- species turnover in time is higher when inundation frequency is lower. In addition, we described variation in plant communities and individual salt-marsh species over time.

3.3 Material and methods

3.3.1 Study area

The study area (*ca.* 14 ha) is situated in the IJzermonding nature reserve on the IJzer estuary, Belgium. The restoration site was created following the large scale demolition and removal of buildings and the underlying slurry material between 1999 and 2002. The restoration site was profiled to provide a continuous gradient of inundation frequencies from 0.01% for highest elevations to 100% for lowest elevation of all high waters. The objective of the restoration project was to create or restore beach-dune-salt-marsh ecotones with salt-fresh, dynamic-stable, wet-dry and mud-sand ecotones. Colonization was started in a completely sterile substrate, i.e. no soil seed bank existed (tested in a pilot study, Stichelmans 2002 cit. in Hoffmann & Stichelmans 2006). Approximately 3 to 4 meters of slurry material were removed prior to tidal inundation. Site construction was carried out in such a way that a more or less continuous inundation frequency would be available. The vegetated–sampled plots had an inundation frequency gradient from 0.01% to 69.19% per year in 2003.

3.3.2 Data collection

3.3.2.1 Vegetation

Vegetation data were collected in the restoration site in permanent plots. Examining permanent plots on newly formed land surface is an obvious means of observing temporal changes in vegetation (Burrows 1990; Bakker et al. 1996). Cover of all vascular plant species (and bryophytes if present) was visually estimated, using a decimal scale (Londo 1976), in 119 permanent 2m × 2m plots in 2003, 2005 and 2007. The plots were located along six randomly chosen transects which were established perpendicular to the inundation gradient. The distance between the plots was three meters within transects.

3.3.2.2 *Inundation frequency*

The inundation frequency of a vegetation plot is defined here as the percentage of all tides during one year that are higher than the elevation of the vegetation plot. The elevation of each plot was measured using a 'total station' (Leica TC1600) in 2002. The reference used is the Belgian Lambert '72 projection for x-y and 'Tweede Algemene Waterpassing' (T.A.W.) for altitude. Reference points from the NGI (National Geographical Institute) that were present in the neighbourhood were used as a bench mark for the measurements. Tidal information is also 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 give a fairly reliable estimate of high tide levels for the vegetation study period, since tidal movements did not evolve significantly during the last decade. More recent tidal data were not available for that long period of time. From these data, we calculated a general inundation curve (Fig. 3.1), from which we calculated the inundation frequency for each vegetation plot within the restoration site. The percentage inundation frequency for each plot was defined:

(the number of high tides that inundate the plot in one year/ total high tide in one year) \times 100.

3.3.3 **Data analysis**

Plant community composition differentiation was visualized by detrended correspondence analysis (DCA), using CANOCO (Lepš & Šmilauer 2005). Since axes 1 and 2 explained a large proportion variation, only scores on the first two axes were used as a measure for plant community species composition.

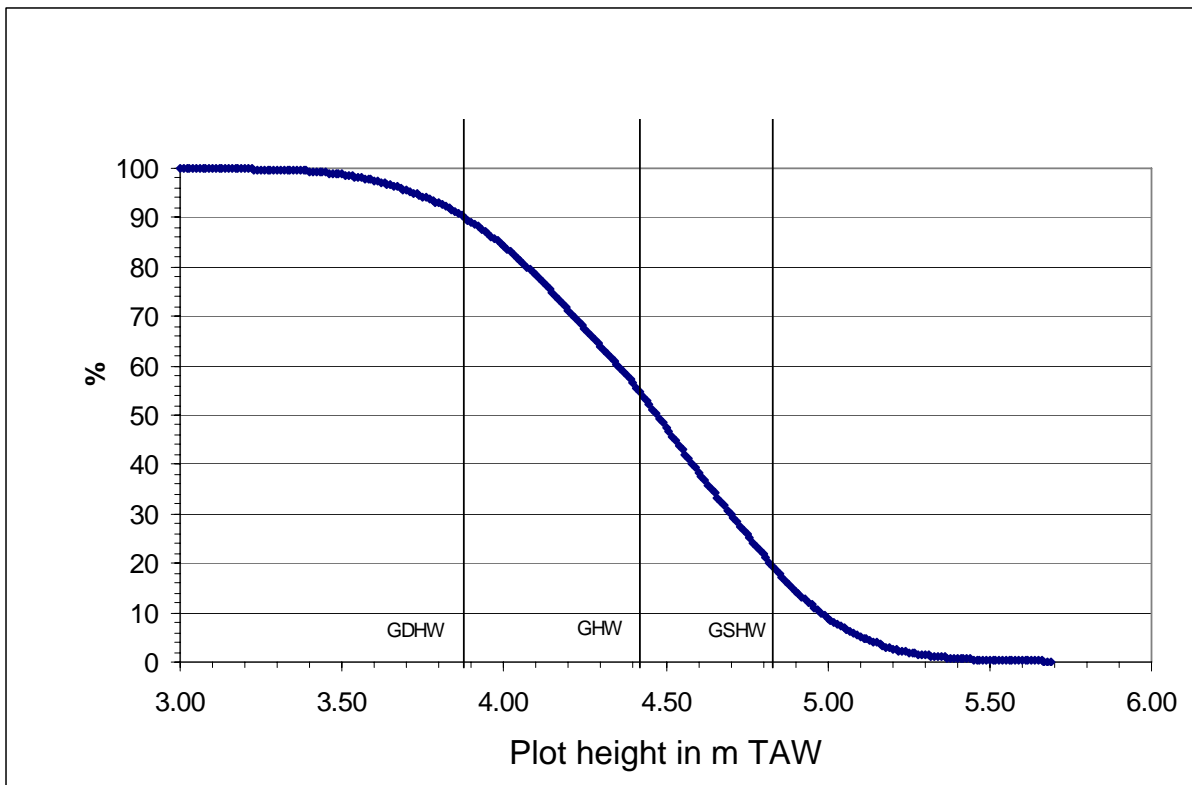


Fig. 3.1. Reconstructed inundation frequency curve, using tidal measurements (consecutive high tides) measured at the automatic measuring point on the northern pier along the former tidal harbour, based on tidal observations in the period 1991-2000 (Fremout 2002). GDHW: mean neap tide high water; GHW: 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 ten years observation period); redrawn from Hoffmann et al. 2006a.

Total species richness, total cover and the cover (and richness) of growth forms (annuals and perennials) were transformed to $\log_{10}(x+1)$ to meet the normal distribution. 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 (annuals and perennials) between years with respect to the inundation frequency. Species richness was the number of species observed in $2\text{m} \times 2\text{m}$ plots. 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.

Because the interaction between year and inundation frequency was highly significant for most variables, we did 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 (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. Dependent and independent variables were transformed to positive values (by adding the value of 0.01) to enable the calculation of different models. In addition, the cover of the most common salt-marsh species (Packham and Willis 1997) were compared between years (after Bonferonni correction for multiple comparisons) using Friedman and Wilcoxon test (a non-parametric test was used, since cover of individual species did not meet normal distribution criteria) two by two (2003 and 2005, 2005 and 2007, 2003 and 2007).

A species turnover rate was calculated according to the method of Bakker et al. (2003). To calculate species turnover for a plot in a specific year t , 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 2003-2005 and 2005-2007 were averaged. A linear regression model was used to test the relationship between the 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. There were 119 plots in each of the three years, and if no change occurred, each plot would be in the same class in each year.

3.4 Results

3.4.1 Variation in cover (and frequency) of individual species

The cover of the perennials and of the annuals of the frequently inundated zones (*Elymus athericus*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia europaea* and *Suaeda*

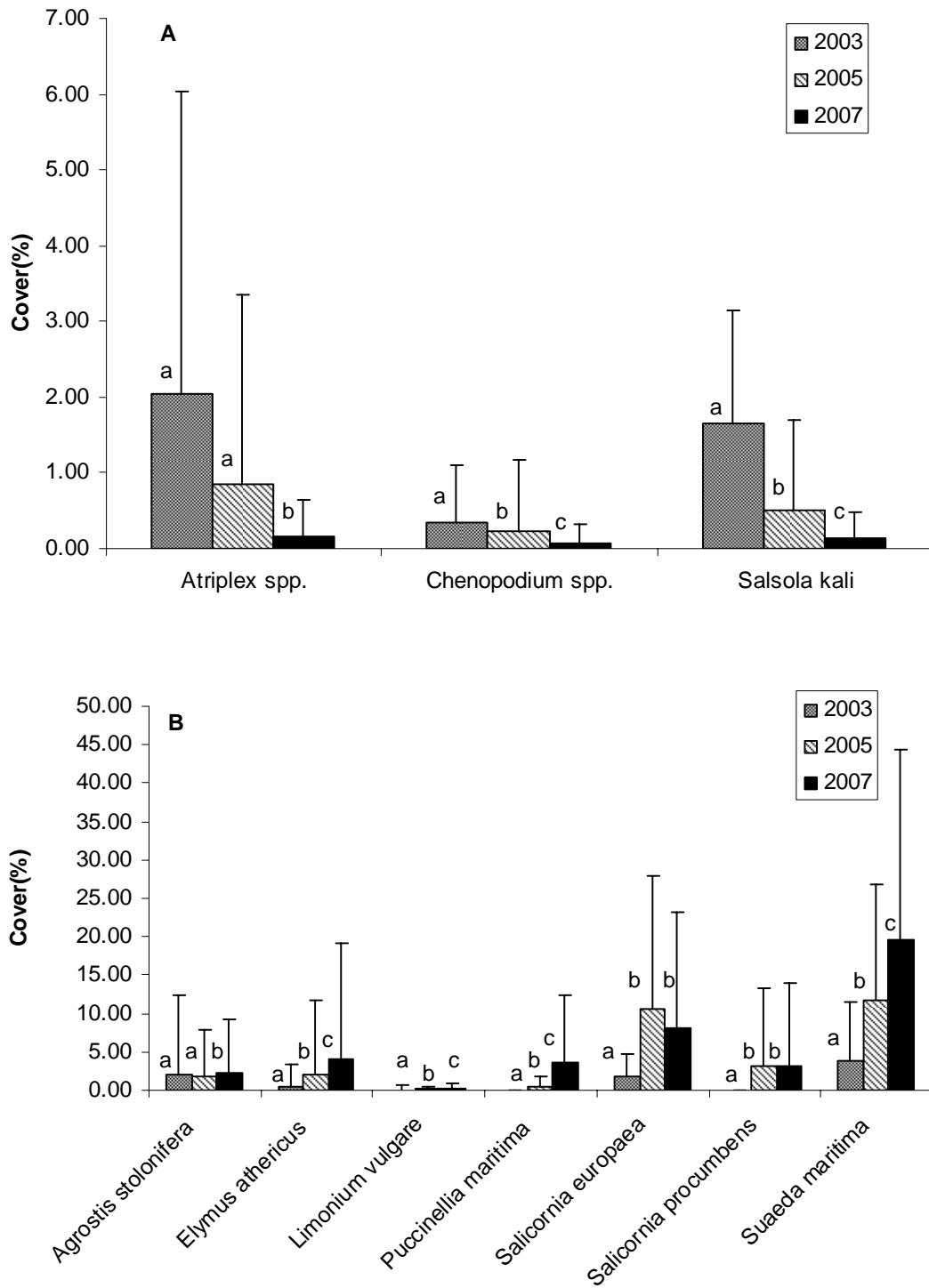


Fig. 3.2. Average of percentage cover (Mean + SD) of individual species in different years; Different successive letters indicate significant differences (at $p < 0.05$) among years within every species individually. Covers of some species were decreasing (A) and other species were increasing (B) in time.

maritima) increased over time (Fig. 3.2B). The cover of annuals of the higher zones (*Atriplex* spp., *Chenopodium* spp. and *Salsola kali*) decreased in time (Fig. 3.2A). *Atriplex* spp., *Chenopodium* spp. and *Salsola kali* were observed in 40, 37 and 39 plots, respectively, in 2003, while they were observed in 15, 9 and 13 plots in 2007, respectively. Without exception, *Agrostis stolonifera*, *Elymus athericus*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia europaea*, *Salicornia procumbens* and *Suaeda maritima* all increased in occurrence (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).

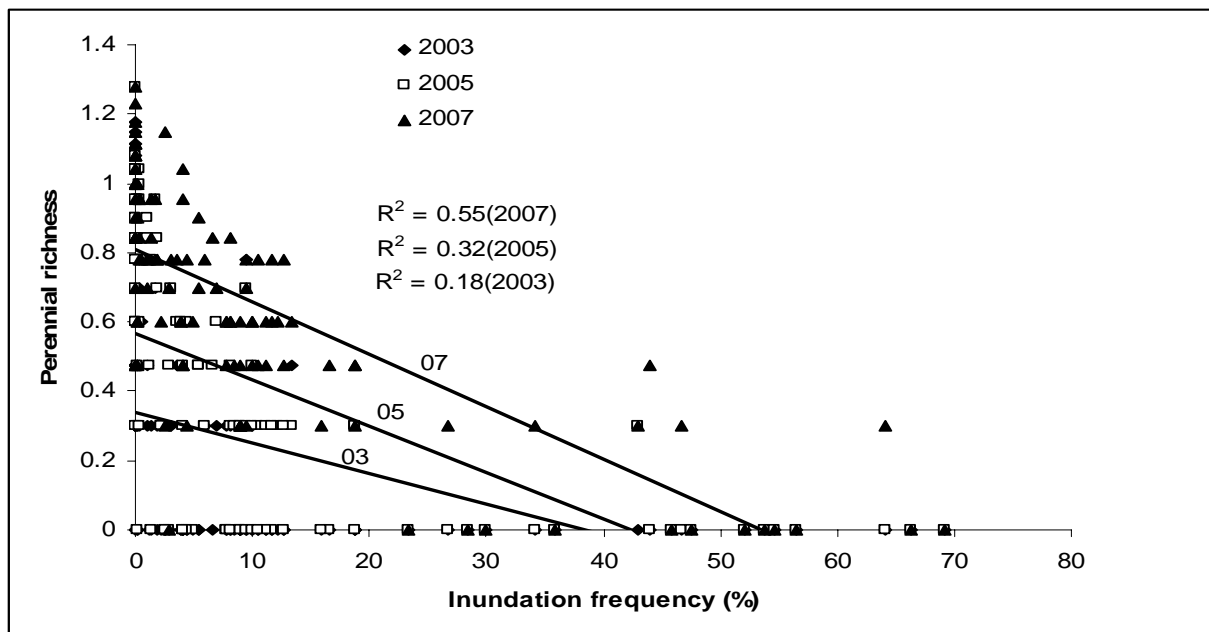


Fig. 3.3. Relationship between inundation frequency and perennial richness (slope-year 2003= -0.09, $R^2= 0.18$; $p<0.01$, slope-year 2005= -0.11, $R^2= 0.32$; $p<0.01$, slope-year 2007= -0.14, $R^2= 0.55$; $p<0.01$). Perennial species richness was the number of species per 4m² and transformed to $\log_{10}(x+1)$.

3.4.2 Change in richness, the cover of growth forms and composition (DCA1 and DCA2)

Total species richness increased with time (Fig. 3.4). 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

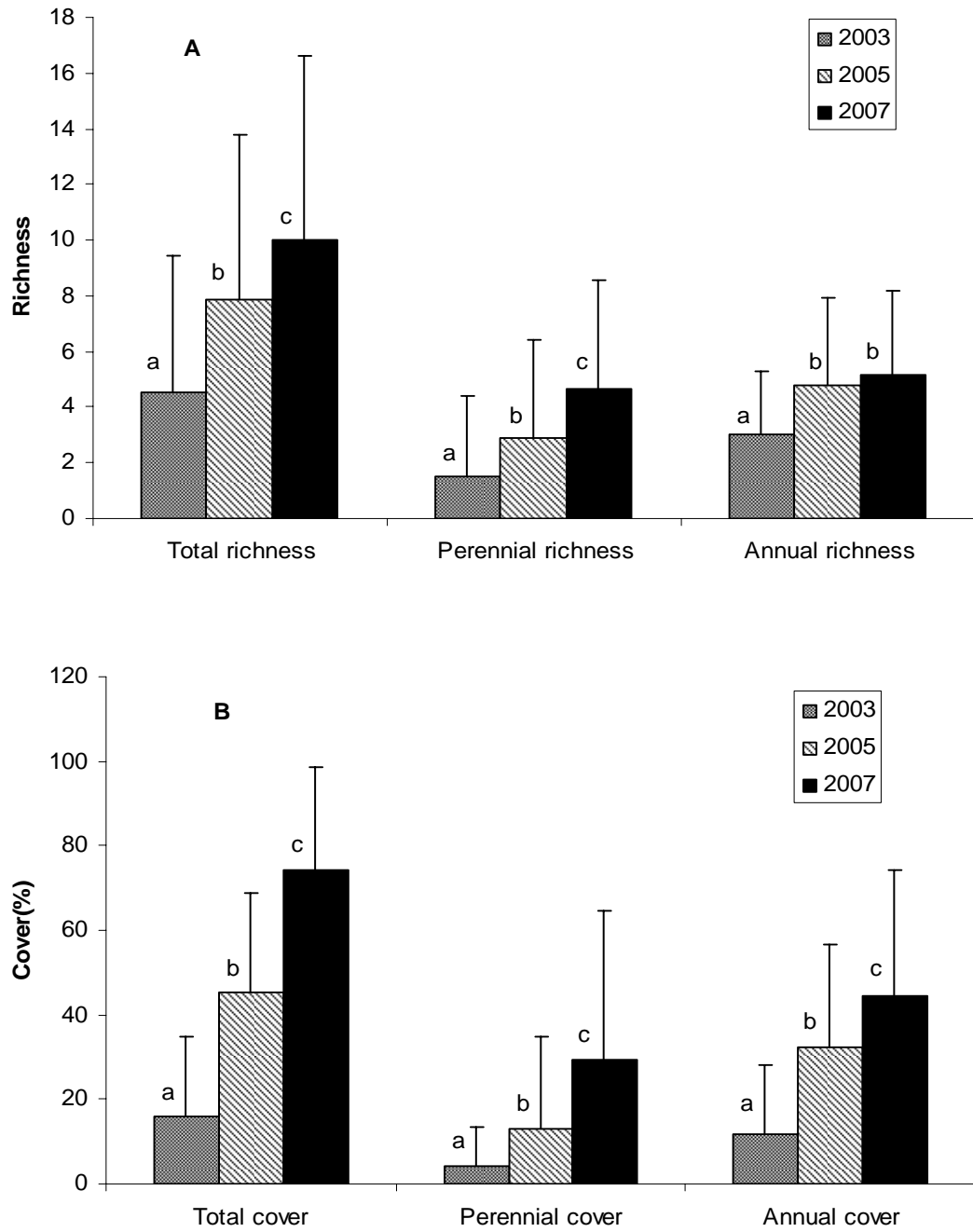


Fig. 3.4. The average (Mean + SD) of richness per 4m² (A) and cover (B) in different years; Different successive letters indicate significant differences (at $p < 0.05$) between years and within every richness and cover class, respectively.

perennial species between years, with higher increase in the less frequently inundated plots (Table 3.1 and Fig. 3.3).

Table 3.1. Result of the repeated measurements for richness, cover and composition for plant species recorded in the IJzermonding restoration site between 2005 and 2007 (n= 119).

Effect	Year		Inundation frequency		Year × Inundation frequency	
	F-statistic	<i>p</i> -value	F-statistic	<i>p</i> -value	F-statistic	<i>p</i> -value
Total richness	111.47	<0.001	100.47	<0.001	2.06	0.13
Perennial richness	148.53	<0.001	81.61	<0.001	10.87	<0.001
Annual richness	27.65	<0.001	58.49	<0.001	0.17	0.84
Total cover	147.46	<0.001	15.33	<0.001	13.55	<0.001
Perennial cover	235.97	<0.001	67.30	<0.001	28.62	<0.001
Annual cover	24.56	<0.001	1.24	0.26	19.68	<0.001
DCA1	9.16	<0.001	88.87	<0.001	3.76	0.03
DCA2	98.8	<0.001	5.74	0.02	21.28	<0.001

The cover by both annuals and perennials increased rapidly between years. The cover of annuals increased at a higher pace at higher inundation frequencies, while perennial species cover increased more rapidly at lower inundation frequencies (Table 3.2, Fig. 3.5). The repeated measurement analysis revealed a significant effect of year, inundation frequency and their interaction on plant community composition measured as scores on DCA axis 1 and 2 (Table 3.1).

3.4.3 Curve estimation

The curve estimation showed that in most cases between inundation frequency and vegetation, exponential or logarithmic regression showed a higher significance level of R^2 (Fig. 3.6 and 3.7)

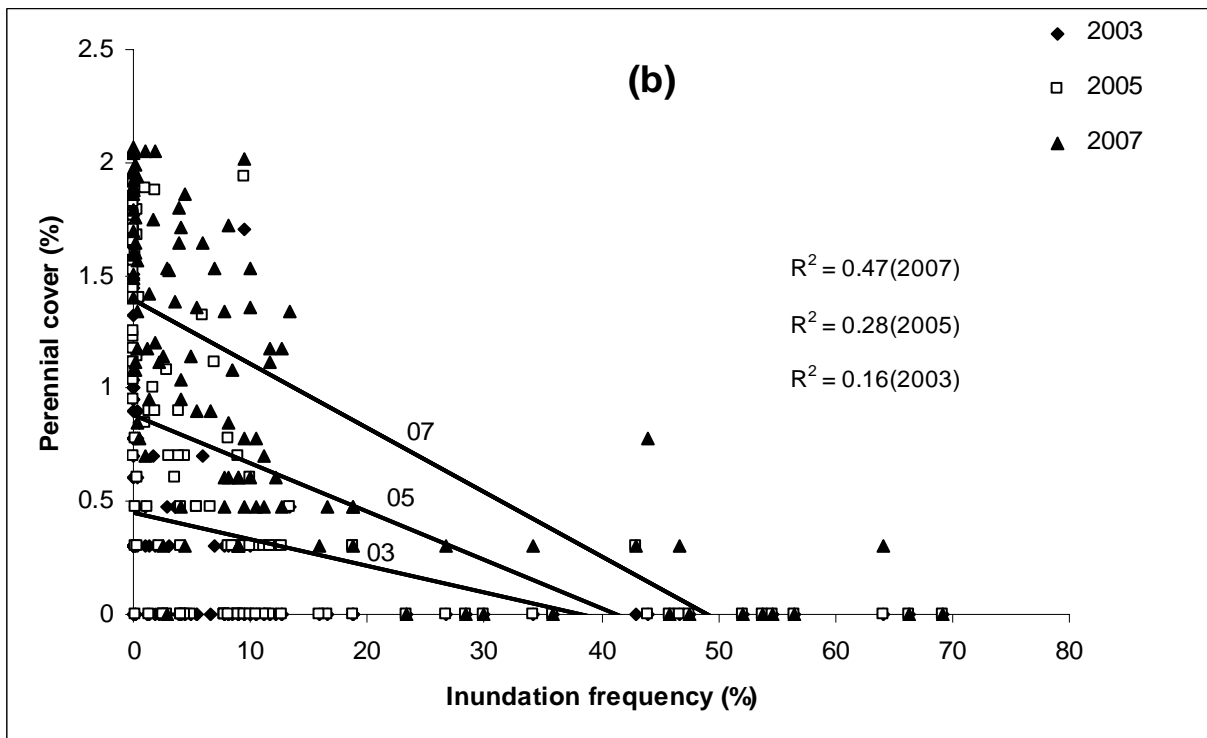
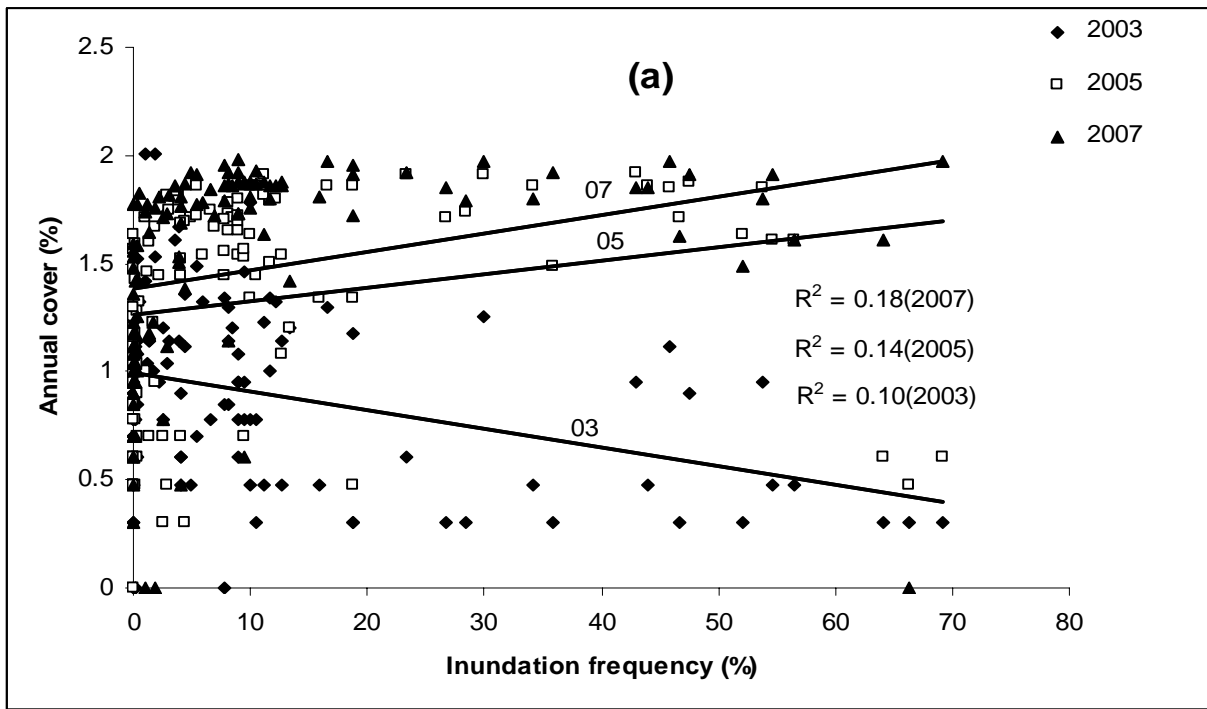


Fig. 3.5. Relationship between inundation frequency and (a) annual cover (slope-year 2003= -0.32, $R^2 = 0.10$; $p < 0.05$, slope-year 2005= 0.48, $R^2 = 0.14$; $p < 0.05$, slope-year 2007= 0.39, $R^2 = 0.18$; $p < 0.01$); (b) perennial cover (slope-year 2003= -0.40, $R^2 = 0.16$; $p < 0.01$, slope-year 2005= -0.53, $R^2 = 0.28$; $p < 0.01$, slope-year 2007= -0.69, $R^2 = 0.47$; $p < 0.01$). The annual and perennial cover was transformed to $\log_{10}(x+1)$.

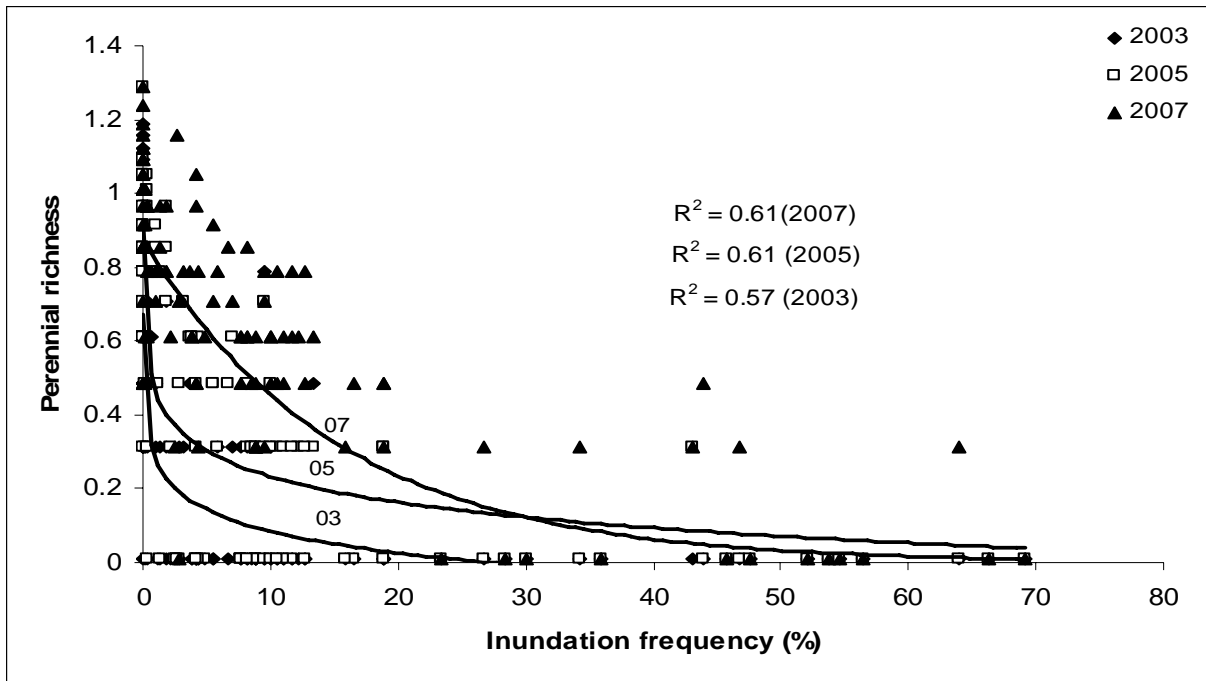


Fig. 3.6. The best fit of regression between inundation frequency and perennial richness. In 2003: logarithmic, $R^2 = 0.57$, $p < 0.01$, slope = -0.08; in 2005: logarithmic, $R^2 = 0.61$, $p < 0.01$, slope = -0.10; in 2007: exponential, $R^2 = 0.61$, $p < 0.01$, slope = -0.06. Perennial species richness was transformed to $\log_{10}(x+1)$.

3.4.4 Species turnover and inundation frequency

The analysis on species turnover using linear model regression showed that species turnover decreased with increasing inundation frequency (Fig. 3.8).

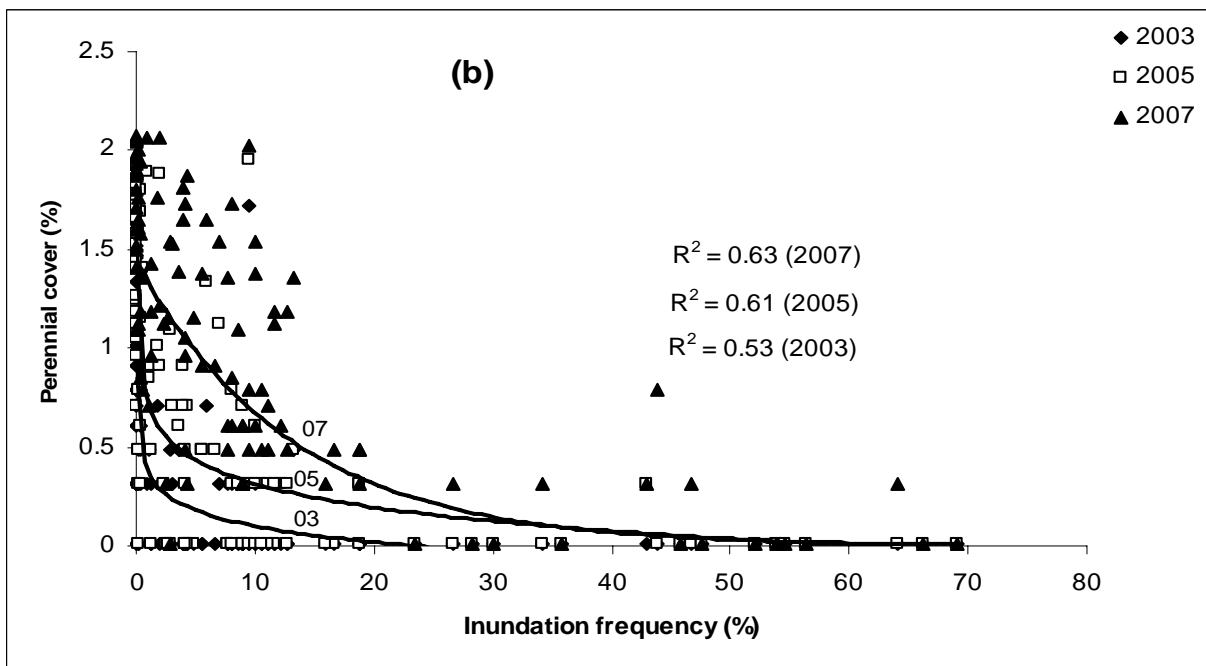
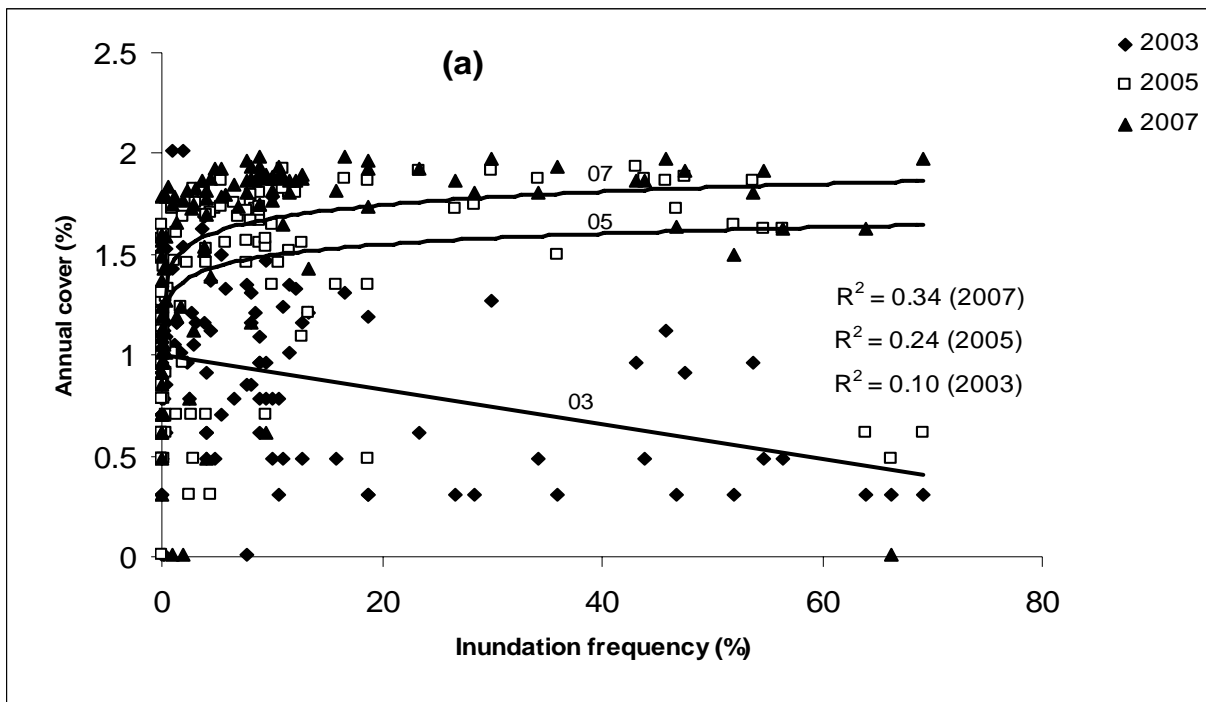


Fig. 3.7. The best fit of regression between inundation frequency and (a) annual cover (in 2003: linear, $R^2 = 0.10$, $p < 0.01$, slope = -0.32 ; in 2005: logarithmic, $R^2 = 0.24$; $p < 0.05$, slope = 0.10 ; in 2007: logarithmic, $R^2 = 0.34$, $p < 0.01$, slope = 0.10); (b) perennial cover (in 2003: logarithmic, $R^2 = 0.53$, $p < 0.01$, slope = -0.12 ; in 2005: logarithmic, $R^2 = 0.61$; $p < 0.01$, slope = -0.17 ; in 2007: exponential, $R^2 = 0.63$, $p < 0.01$, slope = -0.08). The annual and perennial cover was transformed to $\log_{10}(x+1)$.

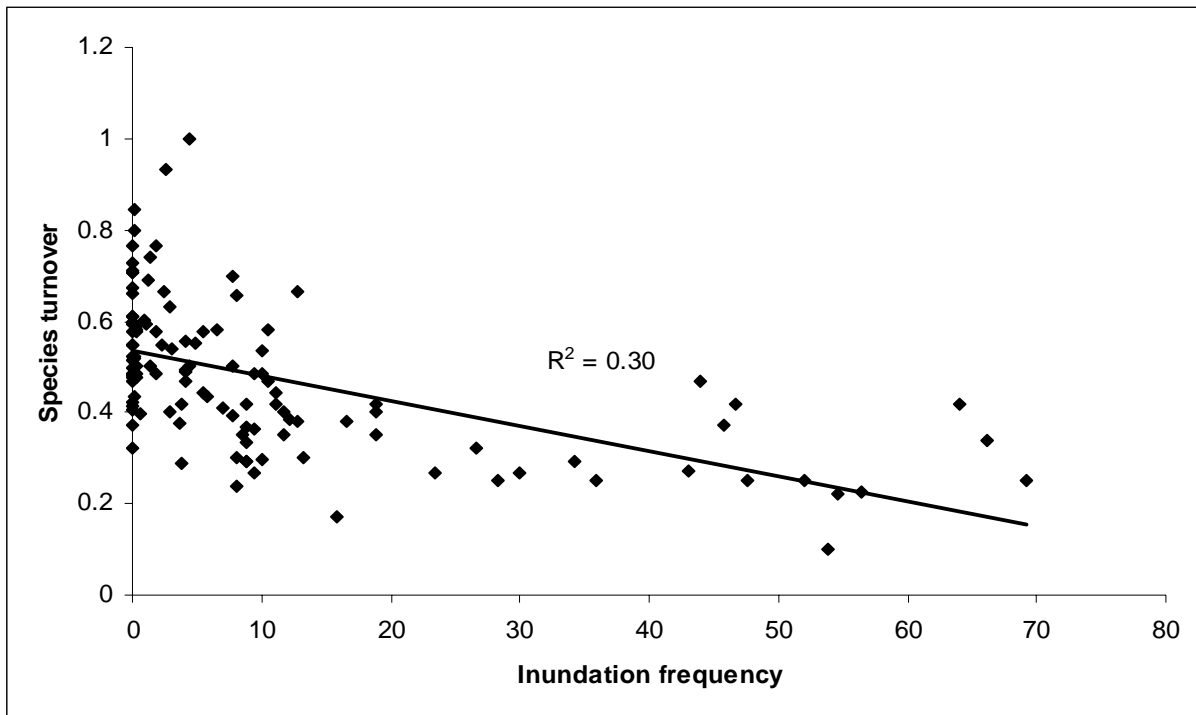


Fig. 3.8. The relationship between inundation frequency and species turnover (slope= -0.05, $p < 0.01$).

3.4.5 Change in plant communities

The TWINSPLAN classification revealed nine groups in 2003 and six in later years. In the first year *Salicornia europaea*- *Suaeda maritima* co-dominant vegetation occupied the highest number of plots while in 2007 this is the case for *Suaeda maritima*-*Parapholis strigosa* co-dominant. The frequency of some groups was decreasing with time e.g. *Atriplex* spp.-*Suaeda maritima* co-dominant while other increased with time e.g. *Suaeda maritima*- *Parapholis strigosa* co-dominant (table 3.2).

Table 3.2. The number of plots occupied by different communities in different years

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

3.5 Discussion

Annual species were the first species to colonize the salt-marsh and confirmed hereby their status as pioneer species. The number of annual species increased during the first years, but remained constant in the latest stage. While some pioneer species (*Salicornia europaea* and *Suaeda maritima*) increased, some other species decreased (*Atriplex* spp., *Chenopodium* spp. and *Salsola kali*) in cover. Some pioneer annuals (in particular members of *Chenopodiaceae* family) were replaced with other pioneer species or by new colonizing species. The rate of annual cover expansion increased with higher inundation frequency over time. The cover of perennials increased with time with the speed of expansion rate higher with reducing inundation frequency (hypothesis 1). *Puccinellia maritima* and *Elymus athericus* expanded more than other perennials, recorded within the site. *Puccinellia maritima* increased in frequency between 2003 and 2007. Drastically increasing of *Puccinellia maritima* has also been reported in natural succession in other salt-marshes (Eertman et al. 2002; Reading et al. 2008). However, increasing total species richness and total cover showed that competitive exclusion could not be demonstrated up to 2007. This is in contrast with the results of Odland and del Moral (2002), who showed that species richness in a wetland ecosystem peaked one year after the sediment exposition, then the number of species on the plots declined by competition, and finally stabilized. In our study area, this temporal pattern did not occur. In addition, in their study, vegetation establishment of different vascular species on exposed sediments was more rapid in comparison with our study, probably due to persistent seed banks and more favourable conditions in their study. Odland & del Moral (2002) demonstrated that existing 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 and starting the competitive exclusion quickly. Seed banks are important for rapid recovery of marsh vegetation after sediment exposition (Keddy &

Reznicek 1986). They therefore play an important role in early succession. In our study area, the establishment of plant species on exposed sediments was certainly due to seed dispersal by tidal water. The seed bank was likely to play no role in the establishment of pioneer plants, because most of the area was covered by buildings and the soil was dug out after the destruction of the building (see Hoffmann & Stichelmans (2006) for a pilot study of the mud flat seed bank). Tidal inundation is thought to be the main dispersal agent. The important role of tidal currents in seed dispersal of halophytes has already been proven (e.g. Huiskes et al. 1995; Tatyana 2000). The tide is an important vector for the dispersal of plant propagules in salt-marsh restoration.

The first dominant pioneer species were *Suaeda maritima*, *Salicornia europaea*, *Atriplex* spp., *Salsola kali* and *Chenopodium* spp. Observations of the surrounding area (adjacent existing salt-marsh) showed that all pioneer species occur at close distances from the study site and could be delivered to the restoration site by tidal water.

Plant composition within the restoration site changed over time (hypothesis 2). In areas of the site with a higher inundation frequency, the rapid expansion of some species (e.g. *Suaeda maritima*), the appearance of new species (e.g. *Salicornia procumbens*), and change in the abundance of other species (e.g. *Salicornia europaea*) resulted in a variation in plant composition. At lower inundation frequencies, the expansion of some species (e.g. *Elymus athericus*), and turnover of others, resulted in a change in species composition; as the results showed higher turnover and higher expansion of perennials at lower inundation frequencies. Nevertheless, species turnover was lower at higher inundation frequency (hypothesis 3). Frequent inundations hence hampered plant species turnover. This is likely to be a consequence of a higher rate of nitrogen accumulation at higher and less inundated sites (Olf et al. 1997), which may result in changes in biomass production and is therefore likely to determine the rate of succession and turnover (Marrs et al. 1983; Wijnen & Bakker 1999). In

addition, in the salt-marsh environment, an increase in elevation is associated with an increase in the species pool, or the number of potential species that can tolerate the abiotic conditions. In contrast, at low elevations where inundations occur frequently, few species can germinate and grow, so species turnover will be lower. Furthermore, at higher elevations and hence lower inundation frequency, the species pool is combined with less salt tolerant, glycophytic species, resulting in greater potential species richness and a higher species turnover.

The frequency of *Chenopodium* spp., *Atriplex* spp. and *Salsola kali* decreased by 76%, 51% and 53% between 2003 and 2007, respectively. As a result, these species disappeared from most plots in 2007, and it is to be expected that these species will locally go extinct in the future. Although, natural succession following the invasion and establishment of new species can change the floristic composition of wetland vegetation (e.g. van der Valk 1981), it is probable that sheep grazing caused a rapid decline after initial colonization of these highly palatable annual species (see more details in chapter 4).

In comparison with 2007, there were no or very few plots in which *Elymus athericus* and *Salicornia procumbens* dominated in 2003. This could be an indication of the progress of a more explicit zonation over time. Over time, vegetation patterns show species adapted to a particular inundation frequency zone over the elevation gradient: the segregation of species, communities and zonation in space occurs (Eilers 1979; Bockelmann et al. 2002; Costa et al. 2003).

Conclusion

Although the entire restoration site was created at one particular moment, an inundation frequency gradient was created artificially, leading to a zonation of different plant populations even in the first year after first colonization. It seems that vegetation succession is related with inundation frequency which is affected by sedimentation. At higher inundation frequencies, *Salicornia procumbens* and *Spartina townsendii* appeared later than *Salicornia europaea* and

Suaeda maritima. *Spartina* is well known as a key species in trapping of sediments. The colonization of *Spartina townsendii* at lower elevation can induce replacement of *Salicornia* populations by species typical of intermediate elevations (e.g. *Suaeda maritima*). The replacement of *Suaeda maritima* by high salt-marsh species (e.g. *Elymus athericus*) can happen quickly (see chapter 5). Since tidal inundation is a strong agent for seed dispersal and sedimentation (and/or erosion), it has a strong impact on species replacement and succession in time and space.