Chapter 5   Environmentally determined spatial patterns of annual plants in early salt-marsh succession versus stochastic distribution in old salt-marsh conditions[4]

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5.1 Abstract

It is generally accepted that in terrestrial ecosystems the occurrence and abundance of plant species in late succession stages can be well predicted from prevailing soil conditions whereas in early succession their presence is much more influenced by chance events (e.g. propagule availability). In other words late successional vegetation stages would be deterministically structured, while early succession stages would be of a more stochastic nature.

To test this hypothesis, we compared the effect of abiotic environmental factors on vegetation composition and probability of occurrence of single species in two adjacent salt-marshes, differing in age (successional stage). A new salt-marsh of about 14ha was created in 2002 by removing a several meters thick layer of sand and slurry which was deposited on the major part of the salt-marsh along the IJzer estuary in the 1960s. From 2002 onwards, primary colonization started on that sterile substrate by hydrochoric seed dispersal, induced by tidal water currents from an adjacent 4ha old salt-marsh and the latter remained untouched as salt-marsh for more than two hundred years. Between mid August and the end of September 2005, three years after the start of the colonization in the new salt-marsh, vegetation and three abiotic environmental factors (soil texture, salinity and elevation) were described in a set of 155 plots (2m × 2m), distributed over the new and the old salt-marsh.

In contrast to the general rule for terrestrial ecosystems, the vegetation composition of the early succession stage of the new salt-marsh appears to be at least as much determined by the combined effect of the measured abiotic factors as that of the old salt-marsh. As revealed by logistic regression the presence/absence of perennial species as well as annual species of the young salt-marsh can be well predicted by the measured abiotic environment. For the old salt-marsh, this also holds for the perennials, but not for the annuals. The stochastic

appearance of gaps in the perennial vegetation cover appears to be important for the establishment of annuals in the older salt-marsh.

5.2   Introduction

One of the main aims of plant ecology is trying to understand the causes for patterns in plant distribution. Plants that persist in any particular site must be in equilibrium with their environment (Burrows 1990). In salt-marsh habitat, the spatial distribution of individual species is usually linked to the concept of succession, i.e. the replacement of plant species in an orderly sequence by colonization and population development (Clements 1916; Odum 1969; Chapman 1976; Glenn-Lewin et al. 1992). It is assumed that, on emerging salt-marshes, after an initial colonization phase, the substrate becomes more stable and sediments are trapped by the vegetation. This will lead to a change in topography, decreasing the inundation frequency with salt water, and allowing other species to colonize the marsh which would eventually result in a mature and stable climax ecosystem (Odum 1971). However, the dynamic of salt-marsh vegetation does not always seem to follow a deterministic succession scheme and many other (stochastic) factors influence it (de Leeuw et al. 1993). Salt-marsh vegetation dynamics can therefore be considered to be quite complex and the spatial and temporal patterns of halophytes and their interactions with multiple biotic and abiotic factors in their own environment remain largely unknown (Silvestri & Marani 2004). To elucidate the underlying reasons for species distribution in salt-marshes, most investigators have relied on correlations between plant distributions and soil properties (e.g. Gray & Bunce 1972). An important inference of this approach is that the set of physical conditions associated with each species represents the preferred or optimal habitat of that species (Vince & Snow 1984).

Chance events or historical factors, such as variation in the weather, disturbance intensity, colonization potential and seed availability are generally considered to be more important in determining spatial patterns and temporal changes at early succession stages, whereas the importance of site characteristics, such as soil factors, usually increases with succession age. This generalisation has been proven valid for several terrestrial habitats

(Christensen & Peet 1984; McClanaham 1986; Tsuyuzaki 1989; McLendon & Redente 1990; Myster & Picket 1990; Leps & Rejmannek 1991; Leps et al. 2000). Therefore, it can be expected that the relationship between environmental factors and vegetation distribution is stronger in older stages of succession than at the start of it. Hence, the predictability of occurrence of a species using soil factors is expected to be higher in old stages than in initial stages.

The aim of this study was to compare the relative influence of abiotic environmental factors on the vegetation composition and on the probability of occurrence of individual species between a young and an old salt-marsh. An unique opportunity to test this was brought by a large-scale nature restoration project along the Belgian coast, that led to the creation of a new salt-marsh adjacent to an old one. Abiotic environmental factors considered for the present study were soil salinity (estimated by electric conductivity), sediment texture and elevation (as a surrogate factor for inundation frequency: Hoffmann et al. 2006c).

The hypothesis we test here is that there would be less correlation between abiotic environmental factors and vegetation distribution in the new salt-marsh, since here colonization potential and stochastic factors are expected to be dominant over environmental differentiation (Leps et al. 2000), while this correlation is expected to be higher in the old salt mash, where time has allowed all locations to be potentially colonized by all halophyte diaspores present in the area.

5.3 Material and Methods

5.3.1 Study area and vegetation

The study was conducted in the estuary of the river IJzer, situated along the Belgian coast. After a large-scale nature restoration project, in which large amounts of sand and slurry were removed between 1999 and 2002, primary succession on the newly created intertidal

area started in 2002, when part of the newly created marsh was already suitable for colonization. The surface of the new salt-marsh is approximately 14ha (Hoffmann 2006b). During our survey, dominant plant species were *Salicornia europaea* (total cover about 12%) and *Suaeda maritima* (11%).

Adjacent to the developing salt-marsh, lays an old salt-marsh of *ca.* 4ha that remained intact for centuries (see Hoffmann et al. 1996, 2006a for an overview of consecutive topographic maps; the earliest cartographic evidence dates from 1779 on the De Ferraris maps). Dominant plant species were *Elymus athericus* (average cover about 35%), *Limonium vulgare* (7.5%). Between mid August and the end of September 2005, three years after the start of the succession in the new salt-marsh, vegetation composition was estimated in a large set of permanent plots, each 2m × 2m large in both new and old salt-marshes. Plant species cover was estimated using the decimal scale for permanent quadrates developed by Londo (1976). In total, 155 relevés were sampled: 95 in the newly created salt-marsh and 60 relevés in the old salt-marsh.

In each relevé, three soil samples of the upper 5cm layer were collected. The three soil samples were pooled per plot and transferred to the laboratory for chemical analyses.

The elevation of relevés was measured using a 'total station' (Leica TC1600). The reference used is the Belgian Lambert '72 projection for x-y and 'Tweede Algemene Waterpassing' (T.A.W.) for elevation. Reference points from the NGI (National Geographical Institute) that were present in the neighbourhood were used as a starting point for the measurements.

5.3.2 Soil analysis

After shaking 5gr of soil in 50mm distilled water for two hours, the electric conductivity (EC) was measured with a WTW Inolab EC meter level 1. Soil texture was determined with a Coulter LS Particle Size Analyzer. The instrument calculated mean, median, and the

percentages of particle diameter of more than 16 and 63μm of each sample. As the correlation among these particle percentages was very high and previous studies used the median particle size in their research (Langlois et al. 2003; Jigorel 2000), we also used the median particle size (D_{50}) as main soil texture characteristic.

5.3.3 Data analysis

First, a detrended correspondence analysis (DCA) with Hill's scaling was carried out to calculate the length of the axis for old and new salt-marsh separately. As the length of the gradient was more than 5 in both new and old salt-marshes (6.26 and 5.09, respectively), unimodal constrained methods were further used. Canonical correspondence analysis (CCA) was used for both kinds of salt-marshes separately. CCA enables an evaluation of the relative influence of the environment on the composition of the community and provides a distribution-free Monte Carlo test of significance (Pyšek & Lepš 1991). In all analyses, the number of permutations was 499 and centring by species and no standardization by samples was chosen as options. After the CCA analysis, the conditional and marginal effects were estimated (Lepš & Smilauer 2003), a procedure that enables attributing the explained variability to particular variables. Both edaphic factors and elevation were introduced as explanatory variables. These analyses were done using CANOCO for Windows (ter Braak & Smilauer 1998).

The probability of occurrence (absence-presence) of the more prominent species (Packham & Willis 1997) common in both old and new salt-marshes (*Salicornia europaea, Suaeda maritima, Spergularia* spp., *Limonium vulgare, Puccinellia maritima* and *Elymus athericus*) was correlated with the environmental variables using forward stepwise binary logistic regression (Hosmer & Lemeshow 2000). Spearman's coefficient was used to test the correlation among independent variables. As the correlation among independent variables was

high and highly significant (see Table 5.1), the environmental variables were introduced to

PCA and the scores of PCA1, PCA2 and PCA3 were used as independent variables.

Table 5.1. Correlation among environmental variables in the new (first row) and old (second row) salt-marshes.

| Environmental variables	EC (µs/cm)	Elevation (m)	Texture (µm)
EC (µs/cm)	—	-0.67**	-0.51**
		-0.34**	-0.86**
Elevation (m)	—	—	0.52**
			0.31*

5.4 Results

5.4.1 Composition and environmental factors

A high value of species-environment correlation on the first axis in CCA revealed that

the three variables are main determinants of species variation in our data set in both new and

old salt-marshes (Table 5.2; the same trend was observed by DCA).

Table 5.2. The results of CCA in the new and old salt-marshes.

Salt-marsh		Axes:	1	2	3	4
New	Eigenvalues		0.74	0.17	0.11	
	Species-environment correlation		0.93	0.60	0.45	
	Cumulative percentage variance of species data		9.50	11.60	13.60	
	Cumulative percentage variance of species – environment relation		72.50	88.80	100.00	
	Sum of all eigenvalues					7.79
	Sum of all canonical eigenvalues					1.10
Old	Eigenvalues		0.64	0.23	0.11	
	Species-environment correlation		0.85	0.66	0.46	
	Cumulative percentage variance of species data		17.50	19.80	22.20	
	Cumulative percentage variance of species – environment relation		65.60	89.30	100.00	
	Sum of all eigenvalues					4.40
	Sum of all canonical eigenvalues					0.98

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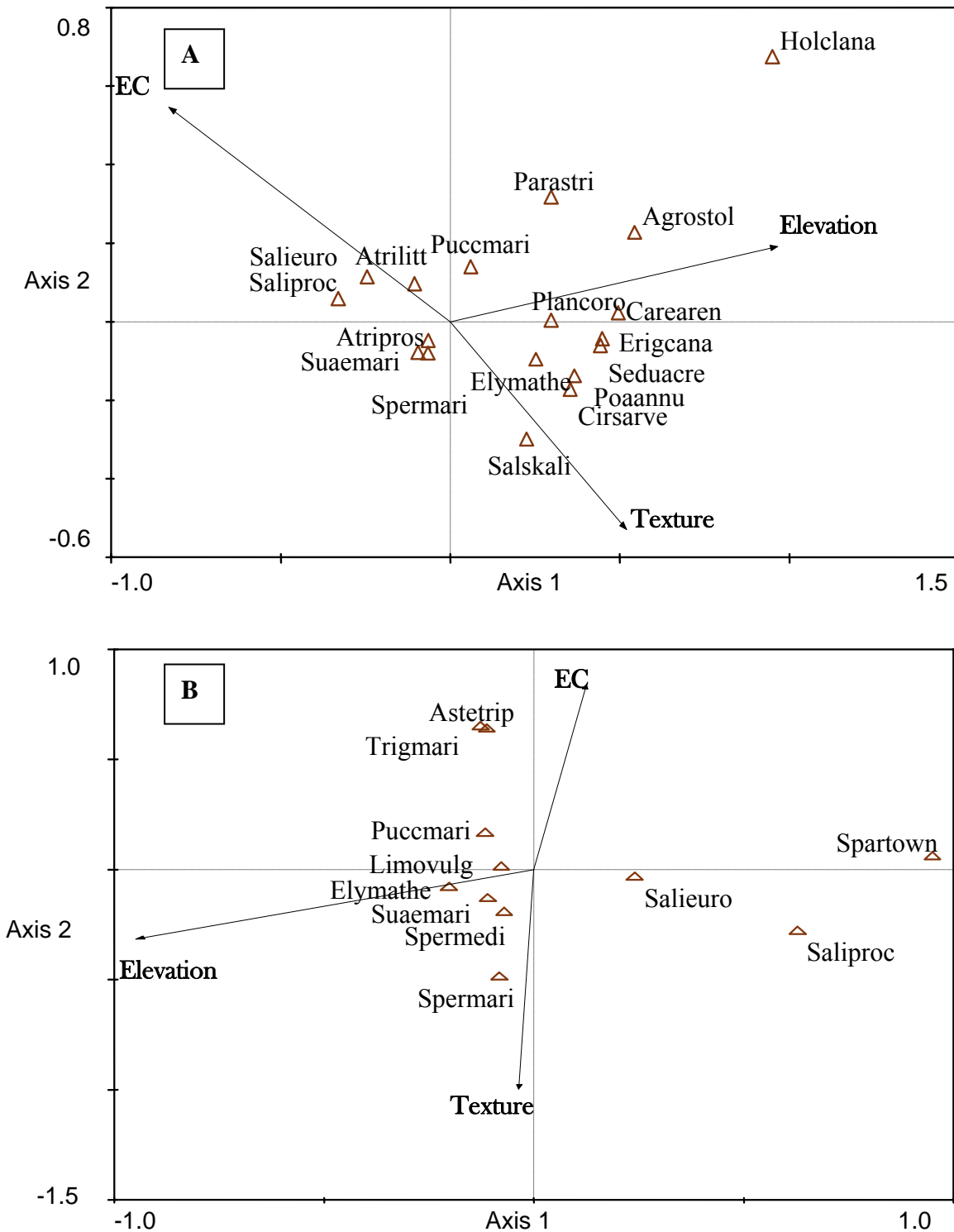
Fig. 5.1. CCA-Ordination biplot of analysis in the new salt-marsh (A) and old salt-marsh (B) (the arrows show the environmental variables). The highest weight species were shown according to the highest cover over all the samples. (Agrostol=*Agrostis stolonifera*, Astetrip=*Aster tripolium*, Atrilitt=*Atriplex littoralis*, Atripros=*Atriplex prosterata*, Carearen=*Carex arenaria*, Cirsarve=*Cirsium arvensis*, Elymathe=*Elymus athericus*, Erigcana=*Erigeron canadensis*, Holclana=*Holcus lanatus*, Limovulg=*Limonium vulgare,* Parastri=*Parapholis strigosa*, Plancoro=*Plantago coronopus*, Poaannu=*Poa annua*, Puccmari=*Puccinellia maritima*, Salieuro=*Salicornia europaea*, Saliproc=*Salicornia procumbens*, Salskali=*Salsola kali*, Spartown=*Spartina townsendii*, Spermari=*Spergularia marina*, Spermedi=*Spergularia media*, Suaemari=*Suaeda maritima,* Trigmari=*Triglochin maritimum*).

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Although the percentage of species variance explained by the environmental variables was higher in the old than in the new salt-marsh (17.5% compared to 9.5%), the environmental variables had a significant effect on composition distribution in both old and new salt-marshes (Table 5.3; Fig. 5.1). Nevertheless, the effect of EC was not significant in the old salt-marsh contrary to the new salt-marsh.

Table 5.3. Marginal and conditional effects obtained from the summary of forward selection in new and old salt-marsh.

Salt-marsh	Environmental variables	Marginal effects	Conditional effects		
		Lambda	Lambda	p-value	F
New	Elevation (m)	0.70	0.70	0.00	9.12
	EC (µs/cm)	0.56	0.19	0.00	2.58
	Texture (µm)	0.30	0.13	0.02	1.69
Old	Elevation (m)	0.60	0.60	0.00	9.14
	EC (µs/cm)	0.20	0.11	0.08	1.72
	Texture (µm)	0.23	0.27	0.00	4.38

5.4.2   Independent variables and PCA axes

For both young and old salt-marshes, PCA1 can be considered as an indicator of soil salinity and to a lesser extent texture, while PCA2 and PCA3 can be considered as indicators of texture and elevation, respectively (Table 5.4).

Table 5.4. Correlation between components and environmental factors in the old and new salt-marsh.

Salt-marsh	Environmental variables	PCA1	PCA2	PCA3
New	EC (µs/cm)	1.00	0.00	0.00
	Elevation (m)	0.02	-0.14	-0.98
	Texture (µm)	-0.45	0.90	0.00
Old	EC (µs/cm)	1.00	0.00	0.00
	Elevation (m)	0.09	0.12	-0.99
	Texture (µm)	-0.79	-0.62	0.00

5.4.3 The results of logistic regression

Environmental variables affected the probability of species occurrence in both old and new salt-marshes at different levels. In the new salt-marsh, the occurrences of *Salicornia europaea*, *Elyums athericus* and *Suaeda maritima* were significantly affected by PCA1 (Table 5.5). The occurrence of *Spergularia marina* was significantly affected by PCA2 and to a lesser extent by PCA1. The occurrence of *Limonium vulgare* was significantly affected by PCA3. There was no significant correlation between the occurrence of *Puccinellia maritima* and PCA axes.

In the old salt-marsh, there was no significant correlation between the occurrences of annual species and PCA axes. There was a significant correlation between the occurrences of *Elymus athericus* and between *Puccinellia maritima* and PCA3. The occurrence of *Limonium vulgare* was affected by PCA2 (Table 5.5).

Table 5.5. Variables in the equation calculated by logistic regression (only significant variables at the 0.05- significance level are shown).

Salt-marsh	Species	Environmental variables	B	SE	Wald	df	Sig.
New	*Salicornia europaea*	PCA1	2.09	0.34	38.38	1	**<0.01**
		Constant	1.39	0.29	21.70	1	**<0.01**
	Suaeda maritima	PCA1	1.11	0.25	19.83	1	**<0.01**
		Constant	1.27	0.23	30.16	1	**<0.01**
	Spergularia marina	PCA1	0.39	0.18	4.35	1	**<0.05**
		PCA2	0.79	0.23	11.38	1	**<0.01**
		Constant	-0.72	0.18	15.09	1	**<0.01**
	Limonium vulgare	PCA3	-1.12	0.38	8.66	1	**<0.01**
		Constant	-2.23	0.34	42.58	1	**<0.01**
	Elymus athericus	PCA1	-0.99	0.27	13.30	1	**<0.01**
		Constant	-1.69	0.25	42.53	1	**<0.01**
Old	*Limonium vulgare*	PCA2	-0.95	0.35	7.40	1	**<0.01**
	Elymus athericus	PCA3	-0.48	0.24	3.83	1	**<0.05**
	Puccinellia maritima	PCA3	-0.13	0.22	3.91	1	**<0.05**

5.5 Discussion

Not surprisingly, salinity and texture were strongly correlated with elevation. As inundation frequency is strongly correlated with elevation, elevation can be considered as a surrogate for inundation frequency (Hoffmann et al. 1996). Elevation largely determines the frequency and duration of tidal flooding (Packham & Willis 1997). It was proven that in salt-marshes with a regular inundation frequency, a range of abiotic factors vary in association with this tidal inundation, such as salinity (de Leeuw et al. 1991; Rozema & van Diggelen 1991), sediment texture (Othman 1980; Thomson et al. 1991), immersion duration (Ranwell et al. 1964), soil redox potential (Armstrong et al. 1985; Groenendijk et al. 1987), disturbance in the form of burial by debris (Brewer et al. 1998) and nutrient levels (Levine et al. 1998; van Wijnen & Bakker 1999).

It appears that in our salt-marsh patches, deterministic factors are important in both early and late successional stages. This is confirmed by a highly significant correlation between species composition and abiotic conditions in both new and old salt-marshes and the significant effect of abiotic conditions on occurrences of most species in old and new salt-marshes. This is in contrast with previous studies in terrestrial habitats. Leps (2000) stated that environmental determination of plant community composition increased with successional age. He alleged that the relationship between species and the most important environmental factor, soil texture, was non-significant in the early years but significant in later years and species composition in the early stages of succession was mainly influenced by stochastic factors, i.e. seed availability. Similar observations have been made by Osbornova et al. (1990), McClanahan (1986), Tsuyuzaki (1989), McLendon & Redente (1990), Myster & Picket (1990), and Leps (1991). They showed that the availability of propagules is usually more important in early stages of succession while site characteristics are more important in late succession stages. Nevertheless, in salt-marsh habitats with a daily inundation, the

propagules disperse themselves very quickly (if the propagules exist). The power of tidal water in seed dispersal of different species between different elevations is well known (e.g. Huiskes et al. 1995; Chang et al. 2007). This dispersal by tidal current can occur in both new and old salt-marshes. In salt-marsh habitats, the effect of stochastic factors (e.g. seed availability) in distribution and patterns of species is thus less pronounced than in terrestrial habitats in the early succession stages.

The composition and distribution of plant communities along the elevation gradient of a salt-marsh is related to the ability of individual species to tolerate environmental conditions. In the new salt-marsh, the distribution of almost all single species was affected by and distributed according to abiotic factors and salinity might be the most important of these factors. Indeed, Huckle et al. (2000) showed that salinity and water logging had highly significant effects on growth of some salt-marsh species. Silvestri et al. (2005) stated that at lower elevations, soil water salinity tends to increase due to progressively more frequent flooding of the marsh and associated enhanced salt inputs. Consequently, the dependence of soil salinity on elevation may thus partly explain the distribution of species along the elevation gradient. Brereton (1971) proved that salinity and water-logging affected both the distribution of species in a pioneer marsh dominated by *Salicornia europaea* and *Puccinellia maritima*.

In the new salt-marsh *Salicornia europaea* had the highest positive correlation with EC. This confirms findings of Ungar (1998), who stated that this species was the angiosperm that was able to grow at the most extreme end of the salinity gradient. Hoffmann et al. (2006c) stated that *Salicornia europaea* would be replaced by *Elymus athericus* in the new salt-marsh because in the old salt-marsh *Elymus athericus* occurs at the same elevation as *Salicornia europaea* in the new salt-marsh. We expect, however, that the salinity level will prevent the expansion of *Elymus athericus* into the most silty and most saline parts of the *Salicornia*

europaea zone as long as the elevation level does not increase. The two species show indeed a pronounced difference in Ellenberg's salinity index (7 for *Elymus athericus* versus 10 for *Salicornia europaea*).

Suaeda maritima was comparatively less affected by salinity than *Salicornia europaea*. Silvestri and Marani (2004) also stated that growth of *Suaeda maritima* was stimulated at lower salinity levels then *Salicornia europaea*; the latter reached maximum biomass production and growth in more saline conditions. In the case of *Suaeda maritima* dominated vegetations, it is more likely that in due time, these will be invaded more and more and in the end dominated by *Elymus athericus*. The latter indeed shows quite similar environmental conditions to those of *Suaeda maritima* (Fig. 5.1) and is the more competitive species of both.

In the old salt-marsh, perennial species were affected by environmental conditions but the distribution of annual species might be affected by other factors. It seems that biotic factors, particularly competition with perennial species, prevented to distribute these annuals species according to their favoured environmental conditions. Annual species in the old salt-marsh might germinate in the stochastically appearing vegetation gaps, unrelated to the abiotic factors, where competition with perennials did not prevent the colonization. Indeed, seed germination, cover and biomass of annuals were shown to increase after removal of perennials (Elisson 1987; Gray & Scott 1977) and in the absence of perennials (Packham & Willis 1977; Tessier et al. 2000). Bockelmann et al. (2002) stressed that plant distribution in old salt-marsh is a consequence of various interacting factors of which abiotic factors are only a part. Biotic factors like competition between species and local habitat adaptation within species are equally crucial for annual species. The fate of annual seedlings largely depends on the permeability of the perennial canopy for light. Thus, disturbance resulting in bare patches inside the perennial vegetation seemed essential for the development of annual species (Tessier et al. 2000).

5.6 Conclusion

Vegetation analyses indicate that diaspores of the annual colonizing species are present *ad libitum* in the newly created marsh area, but that abiotic factors determine whether they can germinate and establish a local population. Environmental rather than biotic determination of appearance also holds for perennials in old salt-marsh conditions, but not so for annuals. An interesting next step in understanding vegetation succession in salt-marsh conditions is the development of models that predict the occurrence of annuals in a context of perennials. As far as expectations on vegetation development in salt-marsh restoration sites is concerned, it seems that further succession beyond a pioneer stage of *Salicornia* and/or *Suaeda maritima* dominated vegetation will depend on all three environmental variables measured in this study. The most silty, saline and frequently inundated sites might continue to be dominated by *Salicornia* spp. for a relatively long time; the more sandy, less saline and more elevated sites, initially dominated by *Suaeda maritima*, might quickly evolve into *Elymus athericus* dominated vegetation. The speed of this succession sere entirely depends on the diaspore dispersal capacity of the late successional species and of the evolution of the textural quality of the accreting sediments. Whether the *Elymus*-stage in succession would further evolve into a *Phragmites australis* dominated stage, as is the case in more brackish salt-marsh environments such as the mid parts of the Scheldt-estuary (Hoffmann 1993) remains an open question; within the study area, it seems a possible successional climax in the least silty, least saline environments, since at the most elevated sites of the old salt-marshes, indeed *Phragmites* dominates or starts to dominate the vegetation. Once secondary disturbance, like grazing, is introduced, succession pathways might change significantly, with more probable dominance of grazing-tolerant grassland vegetation, dominated by *Puccinellia maritima* (see chapter 4).