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Environmental determinism versus biotic stochasticity in the appearance of plant species in salt-marsh succession

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Background and aims – It is generally accepted that in terrestrial ecosystems the occurrence and abundance of plant species in late successional stages can be predicted accurately from prevailing soil conditions, whereas in early succession their presence is much more influenced by chance events (e.g. propagule availability). Late successional vegetation stages would therefore be deterministically structured, while early succession would be dominated by more stochastic features. To test this hypothesis in salt marsh conditions, we compared the effect of abiotic environmental factors on vegetation composition and probability of occurrence of individual species in two adjacent salt marshes, differing in age (i.e. successional stage).
Material and methods – In 2002, a new salt marsh was created on substrate devoid of plant diaspores in the nature reserve The IJzermonding (Nieuwpoort, Belgium). From 2002 onwards, primary colonization started on that sterile substrate by hydrochoric seed dispersal, induced by tidal water currents from an adjacent 5 ha relic of the old salt marsh. In 2005, three years after the start of the colonization process of the new salt marsh, vegetation and three abiotic environmental factors (soil texture, salinity and elevation) were recorded in a set of 155 relevés on the new and old salt marsh.
Key results – In contrast to the general observation in other terrestrial ecosystems, the vegetation composition of the early successional stage of the new salt marsh appeared 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 could be well predicted by the measured abiotic variables. For the old salt marsh this also held for the perennial species, but not for the annual species. The stochastic appearance of gaps in the perennial vegetation cover appeared to be important for the establishment of annuals in the older salt marsh.
Conclusion – In the case of salt marsh succession, the generally accepted hypothesis of early successional stochasticity dominance versus late successional environmental determinism must be rejected.

Key words – annuals, determinism, salt marsh, stochasticity, succession.

INTRODUCTION

One of the main aims of plant ecology is to try to understand the causes for patterns in plant distribution. Plants that persist at any particular site must be in balance with their environmental needs (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 frequency of inundation with salt water, and allowing other species to colonize the marsh which would eventually result in a mature and stable climax ecosystem (Odum 1971, Denaeyer et al. 1968 for salt marsh conditions). However, the dynamics 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, Erfanzadeh et al. 2010). Salt-marsh vegetation dynamics can therefore be considered to be quite complex and the spatial and temporal patterns of halophytic species 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 patterns 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 in early successional 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 (e.g. old fields (Myster & Picket 1990, Lepš et al. 2000), forest (Christensen & Peet 1984, McCune & Allen 1985, McClanaham 1986, Tsuyuzaki 1989) and sagebrush steppe (McLendon & Redente 1990)). Therefore, it can be hypothesized that the relationship between environmental factors and vegetation distribution is stronger in old than in early successional stages. Hence, the predictability of occurrence of a species related to soil factors is expected to be higher in old stages than in initial stages.

To test the validity of this hypothesis of environmental determinism of old successional stages versus stochasticity dominance in early successional stages in salt marsh conditions, we compared the relative importance 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. A unique opportunity to test the hypothesis in salt marsh conditions was created by a large-scale nature restoration project along the Belgian coast, which led to the creation of a new salt marsh adjacent to an old one (Hoffmann 2006a, Erfanzadeh 2009). Earlier research on critical success factors in the process of man-induced salt marsh restoration was reported by Wolters et al. (2005b, 2008) for the Blackwater Estuary in south-east England and for comparable initiatives all over north-west Europe in general by Wolters et al. (2005a). A comparison to test the "early stochasticity – late determinism hypothesis" has not been performed though in salt marsh conditions. Expected deterministic abiotic environmental factors considered in the present study were soil salinity (estimated indirectly through electric conductivity (EC) of soil water), sediment texture and elevation (the latter as a surrogate factor for inundation frequency; Hoffmann et al. 2006a).

If the above-mentioned "early stochasticity – late environmental determinism hypothesis" would be correct, we expect that there is a lower correlation between abiotic environmental factors and plant species distribution patterns in new salt marsh conditions than in old salt marsh conditions, since in the first colonization potential and stochastic factors are expected to be dominant over deterministic environmental differentiation. The reverse is expected in the latter, where time has allowed all locations to be potentially colonized by all halophyte diaspores present in the area. Following the early stochasticity – late determinism-hypothesis, we therefore expect species composition and plant occurrence to be more determined by abiotic factors (i.e. salinity, elevation and soil texture) in the old marsh than in the new one. A prerequisite to test the validity of the hypothesis is that no dispersal limitation from the adjacent old marsh to the newly created marsh exists (Wolters et al. 2005b). Knowing that both adjacent marsh areas have a long and immediate contact zone with a low barrier at an elevation level below mean spring tide height, it is expected that indeed no hydrochoric seed dispersal limitations exist between both areas (for a situation map, see Erfanzadeh 2009).

MATERIAL AND METHODS

Nomenclature of taxa follows Lambinon et al. (1998).

Study area and vegetation

The study was carried out in the estuarine part of the Flemish Nature Reserve the IJzermonding, situated along the Belgian coast. After a large-scale nature restoration project, in which approx. half a million m^3 of sand and slurry was removed from the original salt marsh – sand dune substrate between 1999 and 2003, primary succession on the newly created intertidal area (approx. 12 ha) started in 2002, when part of the newly created marsh was already suitable for colonization (Hoffmann et al. 2006a). In the newly created intertidal area a full inundation frequency ecotone was created (from 0 to 100% inundation of all high waters). The substrate texture was very heterogeneous, ranging from relatively coarse sandy texture (dominant) to local clayey texture. An initial seed bank analysis proved that the new salt marsh substrate was devoid of plant seeds (Stichelmans 2002, cit. in Hoffmann & Stichelmans 2006). During our survey, three years after plant colonization started, dominant plant species on the new marsh were *Salicornia europaea* (mean total cover in all relevés approx. 12%) and *Suaeda maritima* (11%). In general, annual plant species were largely dominant, perennial plant species were still rather infrequent and very low in cover (always < 1%).

Immediately adjacent to the developing salt marsh, an old salt marsh of approx. 5 ha, with full 0–100% inundation frequency range and variable soil texture (comparable to the soil texture variation in the new marsh), remained intact for at least two hundred years (the earliest cartographic evidence dates from 1779 on the De Ferraris maps). Dominant plant species were *Elymus athericus* (average cover 29,5%, mean characteristic cover 49,2%), *Limonium vulgare* (6,1% and 14,6%, respectively) and *Puccinellia maritima* (6,7% and 15,2%, respectively), accompanying but never dominating plant species were *Aster tripolium, Festuca rubra* and several other salt tolerant herbaceous annual and perennial plant species; in general, perennial plant species dominated over annual plant species; none of both salt marsh areas had been grazed in recent decades until the survey was carried out; nature management was restricted to local measures, such as debris removal (Hoffmann 2006b).

Vegetation analysis

Between mid August and late September 2005, vegetation was studied in a large set of relevés, each 2 × 2 m. In total, 95 relevés were sampled in the newly created salt marsh and sixty relevés in the old salt marsh. Plant species cover was estimated using the decimal scale of Londo (1976).

The elevation of relevés was measured using a 'total station' (Leica TC1600). The reference used is the Belgian Lambert 1972 projection for x-y and the 'Tweede Algemene Waterpassing' (TAW) for elevation. Permanent altitudinal and latitudinal fixed points from the NGI (National Geographical Institute) network, present in the immediate vicinity of the study area were used as reference points for height and latitudinal measurements. Plot elevation was compared with high tide levels during the ten year period, immediately preceding the nature restoration measures (Fremout 2002). The plots, both in old and new salt marsh, showed an inundation frequency range of 0–100% of all high tides.

Soil analysis

In each relevé three soil samples of the upper 5 cm layer were collected. The three soil samples were pooled per plot and transferred to the laboratory for chemical analyses. After shaking 5 gram of soil in 50 mm distilled water for two hours, the electric conductivity (EC) of the effluent was measured with a WTW Inolab EC metre level 1. Soil texture was determined with a Coulter LS Particle Size Analyser. Initially, mean, median, and percentages of particle diameter classes of more than 16 and 63 µm of each sample were determined. As the correlation among these particle percentages was very high and previous studies used the median particle size in their research (Jigorel 2000, Langlois et al. 2003), we also used the median particle size as soil texture characteristic.

Data analysis

To test whether a unimodal or a linear response curve should be expected, we first carried out a Detrended Correspondence Analysis (DCA) with Hill's scaling, for both datasets 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 could further be used. To test which environmental variables would be determining species composition most, we used a Canonical Correspondence Analysis (CCA), again for both salt marshes separately. It enables an evaluation of the relative influence of the environment variables on the composition of the community and provides a distribution-free Monte Carlo test of significance (ter Braak & Smilauer 1998). Analyses were done, using CANOCO for Windows, with 499 permutations. Conditional and marginal effects were estimated (following Lepš & Smilauer 2003), which enables attributing the explained variability to particular variables. Both edaphic factors and elevation level were introduced as explanatory variables.

The probability of occurrence (absence-presence) of the most common salt-marsh species (present in at least 40% of the relevés of one of both salt-marsh areas), i.e. *Salicornia europaea, Suaeda maritima, Spergularia* sp., *Limonium vulgare, Puccinellia maritima* and *Elymus athericus*, was estimated against the environmental variables, using forward stepwise binary logistic regressions (Hosmer & Lemeshow 2000). Spearman's coefficient was used to test the correlation between presumed independent environmental variables. As this correlation was highly significant (table 1), the environmental variables were introduced in a PCA and the scores of PCA1, PCA2 and PCA3 were used as indirect, independent variables.

Table 1 – Correlation among environmental variables in the new (first row) and old (second row) salt marsh.
Salinity has been measured indirectly by means of electric conductivity (EC; given the high NaCl content of the salt marsh environment, EC can be considered as an accurate surrogate for salinity).

Environmental variable	Elevation	Texture
Salinity – new marsh	-0.67**	-0.51**
Salinity – old marsh	-0.34**	-0.86**
Elevation – new marsh		0.52**
Elevation – old marsh		0.31*

RESULTS

Composition and environmental factors

Species-environment correlation on the first axis in CCA were high (0.92 for the new and 0.85 for the old salt marsh, respectively), indicating that the three environmental variables are potentially important determinants of species variation in both new and old salt marsh. The percentage of spe-

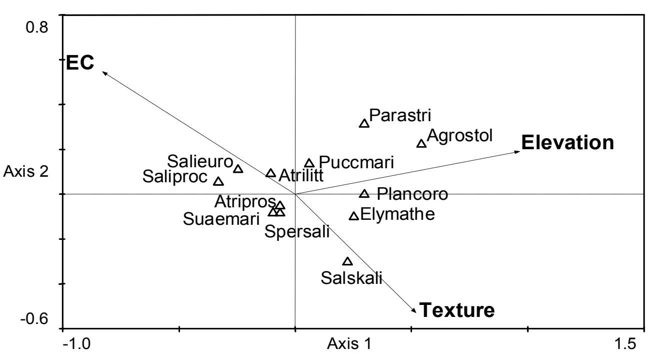

Figure 1 – CCA-ordination biplot based on the new salt marsh relevés (the arrows show the environmental variables; EC = electric conductivity, as a proxy of salinity; Texture = median of particle size). Only the more frequent and/or most abundant and typical salt-marsh species are shown. (Agrostol = *Agrostis stolonifera*, Atrilitt = *Atriplex littoralis*, Atripros = *Atriplex prostrata*, Elymathe = *Elymus athericus* (in some rare cases also *E. repens* occurred on the new marsh, it is included within Elymathe), Parastri = *Parapholis strigosa*, Plancoro = *Plantago coronopus*, Puccmari = *Puccinellia maritima*, Salieuro = *Salicornia europaea*, Saliproc = *Salicornia procumbens*, Salskali = *Salsola kali*, Spermari = *Spergularia marina*, Suaemari = *Suaeda maritima*).

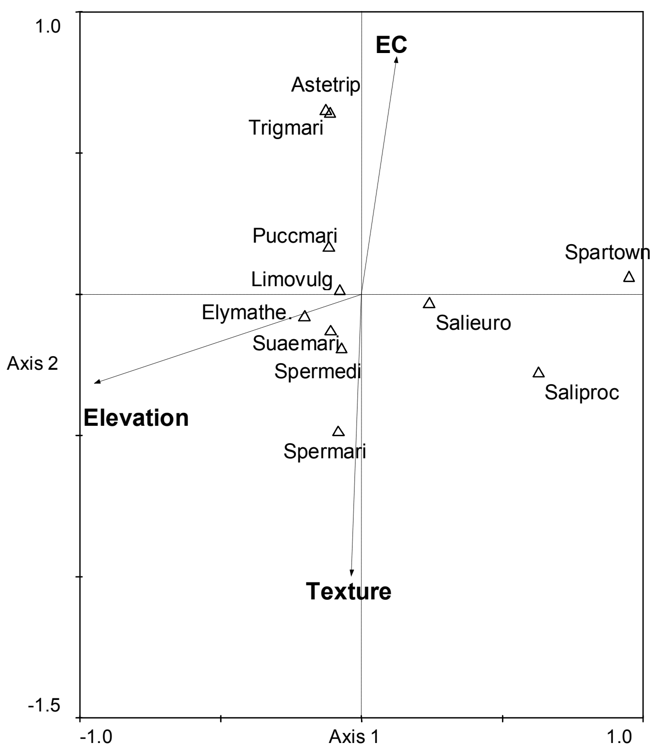

Figure 2 – CCA-ordination biplot based on the old salt marsh relevés (the arrows show the environmental variables; EC = electric conductivity, as a proxy of salinity; Texture = median of particle size). Only the more frequent and/or most abundant and typical salt-marsh species are shown. (Astetrip = *Aster tripolium*, Elymathe = *Elymus athericus*, Limovulg = *Limonium vulgare*, Puccmari = *Puccinellia maritima*, Salieuro = *Salicornia europaea*, Saliproc = *Salicornia procumbens*, Spartown = *Spartina townsendii*, Spermedi = *Spergularia media*, Spermari = *Spergularia marina*, Suaemari = *Suaeda maritima,* Trigmari = *Triglochin maritimum*).

cies variance explained by the three environmental variables together was 17.5% in the old salt marsh and 9.5% in the new one. Environmental variables had a significant effect on species composition in both old and new salt marshes (table 2; figs 1 & 2). Nonetheless, the effect of electric conductivity (EC, used as a proxy of salinity) was not significant in the old salt marsh, contrary to the new salt marsh (table 2).

Logistic regressions

From the correlation coefficient between PCA axes and the measured environmental variables (table 3), we can conclude that 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.

At the species level, environmental variables affected the probability of occurrence in both old and new salt marshes at different levels. In the new salt marsh, the occurrence of *Salicornia europaea*, *Elymus athericus* and *Suaeda maritima* were significantly affected by PCA1 (table 4). 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 any of the PCA axes.

In the old salt marsh, there was no significant correlation between the occurrences of any of the annual species and the PCA axes. There was a significant correlation between the occurrence of *Elymus athericus* and *Puccinellia maritima* and PCA3. The occurrence of *Limonium vulgare* was affected by PCA2 (table 4).

DISCUSSION

Environmental factors and species composition

Salinity and sediment texture were strongly correlated with elevation. Elevation largely determines the frequency and duration of tidal flooding (Packham & Willis 1997), not in the least so in the study areas, where no strong differentiation in levees and backlands appears (Hoffmann et al. 1996), and hence levee structures do not prevent inundation of backlands significantly. It was proven that in salt marshes with a regular inundation frequency, a range of abiotic factors varies in close 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).

At the vegetation level, it appears that in both our salt-marsh areas, 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 marsh and the significant effect of abiotic conditions on occurrences of most

Table 2 – Marginal and conditional effects obtained from the summary of forward selection in new and old salt marsh.

Salt marsh	Environmental variable	Marginal effects	Conditional effects		
		Lambda	Lambda	F	P
New	Elevation	0.7	0.7	9.12	**0.002**
	Salinity	0.56	0.19	2.58	**0.002**
	Texture	0.3	0.13	1.69	**0.022**
Old	Elevation	0.6	0.6	9.14	**0.002**
	Salinity	0.2	0.11	1.72	0.084
	Texture	0.23	0.27	4.38	**0.004**

Table 3 – Correlation coefficient between PCA-components and environmental factors in the old and new salt marsh.

Salt marsh	Environmental variables	PCA1	PCA2	PCA3
New	Salinity	1	0	0
	Elevation	0.02	-0.14	-0.98
	Texture	-0.45	0.9	0
Old	Salinity	1	0	0
	Elevation	0.09	0.12	-0.99
	Texture	-0.79	-0.62	0

species in old and new salt marsh. This is in contrast with previous studies in terrestrial habitats. Lepš et al. (2000), studying early succession after top soil removal in a semi-natural spruce forest in an area affected by acidic air pollution, stated that environmental determination of plant community composition increased with successional age. They 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, in their case seed availability. Similar succession observations were made after disturbances in other habitats such as forest (McClanahan 1986, Tsuyuzaki 1989), sagebrush steppe (McLendon & Redente 1990) and abandoned old fields (Myster & Pickett 1990, Osbornova et al. 1990, Lepš & Rejmánek 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 successional stages. Contrarily, in salt-marsh habitats with a daily inundation, propagules disperse very quickly (if the propagules are present). The importance of tidal water in seed dispersal of different salt marsh species between different elevations is well known (e.g. Huiskes et al. 1995, Wolters et al. 2005b, Chang et al. 2007). This dispersal by tidal currents 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 successional stages.

Determinism of plant occurrence in newly created salt marsh

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 individual 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 our study, *Salicornia europaea* had the highest positive correlation with electric conductivity. 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. The quick replacement of *Salicornia europaea* by *Elymus athericus* in the new salt marsh (as expected by Hoffmann et al. 2006a), because in the old salt marsh *Elymus athericus* occurs at the same elevation as *Salicornia europaea* in the new salt marsh, might therefore still take some time. Additionally, *Elymus athericus* has no easily dispersing diaspores available (Erfanzadeh et al. 2010). Also, Olff et al. (1997) conclude in their study of salt marsh

Table 4 – Variables in the equation calculated by logistic regression.
Only significant variables are shown per individual species.

Salt marsh	Species	Environmental variable	B	S.E.	Wald	df	P
New	*Salicornia europaea*	PCA1	2.09	0.34	38.38	1	**< 0.01**
		Constant	1.39	0.29	21.7	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	13.3	1	**< 0.01**
		Constant	-1.69	0.25	42.53	1	**< 0.01**
Old	*Limonium vulgare*	PCA2	-0.95	0.35	7.4	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**

vegetation succession, that *Elymus athericus* only became dominant in the late successional stages. Nonetheless, the newly created salt marsh in the IJzermonding nature reserve, is generally rather coarse in soil texture. Despite the positive relation between clay layer thickness and *Elymus* appearance and dominance found by Olff et al. (1997) and van Wijnen et al. (1997) in old, grazed salt marsh systems on a barrier island in the Wadden sea area, we expect the coarse sediment structure at the study site to have a positive effect on *Elymus athericus* dominance after colonization has taken place. This is indicated by the strong relation between *Elymus athericus* and PCA1, and between PCA1 of the new salt marsh and texture (see table 3 & 4). The species is particularly successful on coarser salt marsh textures (such as levees), since these allow relatively good soil aeration and temporary and quick top soil desalination. Except diaspore availability, soil texture and soil aeration, other factors, such as grazing (van Wijnen et al. 1997), nutrient availability and competition (Bockelmann & Neuhaus 1999) do interfere with *Elymus* success, making it particularly difficult to predict *Elymus* colonization and dominance in time reliably. When interpreting the salinity data, we at least expect that the salinity level will prevent early 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 substantially. The two species indeed show a pronounced difference in Ellenberg's salinity index (7 for *Elymus athericus* versus 10 for *Salicornia europaea*; Ellenberg et al. 1991).

Suaeda maritima was comparatively less affected by salinity than *Salicornia europaea*. Silvestri & Marani (2004) also stated that growth of *Suaeda maritima* was stimulated at lower salinity levels then *Salicornia europaea*; the latter reaching maximum biomass production and growth in more saline conditions than the first. In the case of *Suaeda maritima* dominated communities, 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. 1) and is the more competitive species of both.

Determinism of plant occurrence in old salt marsh

In the old salt marsh, the distribution of perennial species was related to environmental conditions but the distribution of annual species must be affected by other, more stochastic factors. It seems that biotic factors, particularly competition with perennial species, prevented the distribution of these annuals, according to their favoured environmental conditions. Annual species in old salt marshes 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 marshes is a consequence of various interacting factors of which abiotic factors are only a part. Biotic factors like competition between species, local diaspore availability 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 within the perennial vegetation seemed essential for the development of annual species (Tessier et al. 2000).

CONCLUSION

From our comparative study of two adjacent salt marsh areas with different age, we conclude that the generally accepted hypothesis that plant distribution patterns in early successional stages is primarily stochastic in nature while these patterns are much more deterministic in late successional stages, is false in a salt marsh environment. Vegetation analysis indicates 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 annual species, of which it is reasonable to assume that diaspores are equally present ad libitum in the old salt marsh. 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 perennial dominance.

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 facies, 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, as is the case in the nature reserve the IJzermonding (a flock of sheep was introduced in 2006), succession pathways might change significantly, with more probable dominance of grazing-tolerant grassland species, like *Puccinellia maritima* and other grass species (see e.g. Olff et al. 1997).

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REFERENCES

Armstrong W., Wright E.J., Lythe S., Gaynard T.J. (1985) Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. Journal of Ecology 73: 323–339.

Bockelmann A.C., Neuhaus R. (1999) Competitive exclusion of Elymus athericus from a high-stress habitat in a European salt marsh. Journal of Ecology 87: 503–513.

Bockelmann A.C., Bakker J.P., Neuhaus R., Lage J. (2002) The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. Aquatic Botany 73: 211–221.

Brereton A.J. (1971) The structure of the species populations in the initial stages of succession. Journal of Ecology 59: 321–338.

Brewer J.S., Levine J.M., Bertness M.D. (1998) Interactive effects of elevation and burial with wrack on plant community structure in some Rhode Island salt marshes. Journal of Ecology 86: 125–136.

Burrows C.J. (1990) Processes of vegetation change. London, Unwin Hyman Ltd.

Chapman V.J. (1976) Coastal Vegetation, 2nd ed. Oxford, Pergamon Press.

Chang E.R., Veeneklaas R.M., Bakker J.P. (2007) Seed dynamics linked to variability in movement of tidal water. Journal of Vegetation Science 18: 253–262.

Christensen N.L., Peet R. (1984) Convergence during secondary forest succession. Journal of Ecology 72: 25–36.

Clements F.E. (1916) Plant Succession: An Analysis of the Development of Vegetation. Washington, Carnegie Institution of Washington.

de Leeuw J., Van den Dool A., de Munck W. Nieuwenhuize J., Beeftink W.G. (1991) Factors influencing the soil salinity regime along an intertidal gradient. Estuarine Coastal and Shelf Science 32: 87– 97.

de Leeuw J., de Munck W., Olff H., Bakker J.P. (1993) Does zonation reflect the succession of salt marsh vegetation – a comparison of an estuarine and a coastal bar island marsh in the Netherlands. Acta Botanica Neerlandica 42: 435–445.

Denaeyer S., Lejoly J., Duvigneaud P. (1968) Note sur la spécificité biogéochimique des halophytes du Littoral Belge. Bulletin de la Société royale de Botanique de Belgique 101: 293–301.

Duvigneaud P. (1980) La synthèse écologique. Populations, communautés, écosystèmes, biosphère, noosphère. Paris, Doin éditeurs.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulissen D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18: 1–258.

Ellison A.M. (1987) Effects of competition, disturbance and herbivory on Salicornia europaea. Ecology 68: 576–586.

Erfanzadeh, R. (2009) Spatio-temporal aspects of early vegetation succession in a recently restored salt-marsh ecosystem: a case study of the IJzer estuary (Belgium). Ph.D. thesis, Ghent University, Ghent.

Erfanzadeh, R., Garbutt, A., Pétillon, J., Maelfait, J.-P., Hoffmann, M. (2010) Factors affecting the success of early salt-marsh colonizers: seed availability rather than site suitability and dispersal traits. Plant Ecology 206: 335–347.

Fremout A. (2002) Overzicht van de tijwaarnemingen langs de Belgische kust. Periode 1991–2000. Oostende, Min. Vlaamse Gemeenschap, Afd. Waterwegen Kust – Hydrografie.

Glenn-Lewin D.C., Peet R.K., Veblen T.T. (1992) Plant Succession: Theory and Prediction. London, Chapman & Hall.

Gray A.J., Bunce R.G.H. (1972) The ecology of Morecambe Bay. VI. Soils and vegetation of the salt marshes: a multivariate approach. Journal of Applied Ecology 9: 221–234.

Gray A.J., Scott R. (1977) The ecology of Morecambe Bay. VII. The distribution of Puccinellia maritima, Festuca rubra and Agrostis stolonifera in the salt marshes. Journal of Applied Ecology 14: 229–241.

Groenendijk A.M., Spieksma J.G.J., Vink-Lievaart M.A. (1987) Growth and interactions of salt marsh species under different flooding regimes. In: Huiskes A.H.L., Blom C.W.P.M., Rozema J. (eds), Vegetation Between Land and Sea: 236–258. Dordrecht, W. Junk Publishers.

Hoffmann M. (1993) Vegetatiekundig-ecologisch onderzoek van de buitendijkse gebieden langs de Zeeschelde met vegetatiekartering. Hasselt, Instituut voor Natuurbehoud.

Hoffmann M., ed. (2006a) Monitoring Natuurherstel IJzermonding 2001–2005. Brussel, Instituut voor Natuur- en Bosonderzoek.

Hoffmann M. (2006b) Beheerplan VNR De IJzermonding. Brugge, Agentschap voor Natuur en Bos, Cel Kustzonebeheer.

Hoffmann M., Hoys M., Monbaliu J., Sas M. (1996) Ecologisch streefbeeld en natuurherstelplan voor het integraal kustreservaat "De IJzermonding" te Nieuwpoort-Lombardsijde met civieltechnische realisatiemogelijkheden. Ghent, Ghent University.

Hoffmann M., Stichelmans E. (2006) Monitoring condities: de zaadbank. In: Hoffmann, M. (ed.) Monitoring Natuurherstel IJzermonding 2001–2005. Gent, Universiteit Gent: 107–113.

Hosmer D.W., Lemeshow S. (2000) Applied Logistic Regression, 2nd ed. Hoboken, USA, John Wiley & Sons, Inc.

Huckle J.M., Potter J.A., Marrs R.H. (2000) Influence of environmental factors on the growth and interactions between saltmarsh plants: effects of salinity, sediment and waterlogging. Journal of Ecology 88: 492–505.

Huiskes A.H.L., Koutstaal B.P., Herman P.M.J., Beeftink W.G., Markusse M.M., De Munck W. (1995) Seed dispersal of halophytes in tidal salt marshes. Journal of Ecology 83: 559–567.

Jigorel A. (2000) Sediment dynamics. Eurossan Final Report. Program 'Environment and Climate, GD XII/D1, sub program "Functioning of Ecosystem". Work program PL 970655, August 2000.

Lambinon J., De Langhe J.E., Delvosalle L., Duvigneaud J. (1998) Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden (Pteridofyten en Spermatofyten). 3rd ed. Meise, Nationale Plantentuin van België.

Langlois E., Bonis A., Bouzillé J.B. (2003) Sediment and plant dynamics in saltmarshes pioneer zone: Puccinellia maritima as a key species? Estuarine Coastal and Shelf Science 56: 239–249.

Lepš J., Rejmánek M. (1991) Convergence or divergence: what should we expect from vegetation succession? Oikos 62: 261–264.

Lepš J., Michálek J., Rauch O., Uhlík P. (2000) Early succession on plots with the upper soil horizon removed. Journal of Vegetation Science 11: 259–264.

Lepš J., Šmilauer P. (2003) Multivariate analysis of ecological data using CANOCO. Cambridge, Cambridge University Press.

Levine J.M., Brewer J.S., Bertness M.D. (1998) Nutrients, competition and plant zonation in a New England salt marsh. Journal of Ecology 86: 285–292.

Londo G. (1976) The decimal scale for relevés of permanent quadrates. Vegetatio 33: 61–64.

McClanahan T.R. (1986) The effect of seed source on primary succession in a forest ecosystem. Vegetatio 65: 175–178.

McCune B., Allen T.F.H. (1985) Will similar forests develop on similar sites? Canadian Journal of Botany 63: 367–376.

McLendon T., Redente E.F. (1990) Succession patterns following soil disturbance in a sagebrush steppe community. Oecologia 65: 293–300.

Myster R.W., Pickett S.T.A. (1990) Initial conditions, history and successional pathways in ten contrasting old fields. American Midland Naturalist 124: 231–238.

Odum E.P. (1969) The strategy of ecosystem development. Science 164: 262–270.

Odum E.P. (1971) Fundamentals of Ecology, 3rd ed. Philadelphia, Saunders.

Olff H., De Leeuw J., Bakker J.P., Platerink R.J., van Wijnen H.J., De Munck W. (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology 85: 799–814.

Osbornova J., Kovarova M., Lepš J., Prach K. (1990) Succession in Abandoned Fields. Studies in Central Bohemia, Czechoslovakia. Dordrecht, Kluwer Academic Publishers.

Othman S.B. (1980) The distribution of salt marsh plants and its relation to edaphic factors with particular reference to Puccinellia maritima and Spartina townsendii. Ph.D. thesis, Colchester, University of Essex.

Packham J.R., Willis A.J. (1997) Ecology of dunes, salt marsh and shingle. London, Chapman & Hall.

Ranwell D.S., Bird E.C.F., Hubbard J.C.E., Stebbings R.E. (1964) Spartina salt marshes in southern England. V. Tidal submergence and chlorinity in Poole Harbour. Journal of Ecology 52: 627–641.

Rozema J., Van Diggelen D.J. (1991) A comparative study of growth and photosynthesis of four halophytes in response to salinity. Acta Oecologica – International Journal of Ecology 12: 673–681.

Silvestri S., Marani M. (2004) Salt-marsh vegetation and morphology: Basic physiology, modelling and remote sensing observations. In: Fagherazzi S., Blum L., Marani M. (eds), Ecogeomorphology of tidal marshes. Coastal and Estuarine Studies Volume 59. American Geophysical Union, Washington DC.

Silvestri S., Defina A., Marani M. (2005) Tidal regime, salinity and salt marsh plant zonation. Estuarine Coastal and Shelf Science 62: 119–130.

Stichelmans E. (2002) Zaadbankanalyse in functie van natuurontwikkeling: de case-studie IJzermonding. M.Sc. Thesis, Ghent, Ghent University.

ter Braak C.J.F., Smilauer P. (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination, version 4. Ithaca, USA, Microcomputer Power.

Tessier M., Gloaguen J.C., Lefeuvre J.C. (2000) Factors affecting the population dynamics of Suaeda maritima at initial stages of development. Plant Ecology 147: 193–203.

Thompson J.D., McNeilly T., Gray A.J. (1991) Population variation in Spartina anglica C.E. Hubbard. 3. Response to substrate variation in a glasshouse experiment. New Phytologist 117: 141–152.

Tsuyuzaki S. (1989) Analysis of revegetation dynamics on the volcano Usu, northern Japan, deforested by 1977–1978 eruptions. American Journal of Botany 76: 1468–1477.

Ungar I.A. (1998) Are biotic factors significant in influencing the distribution of halophytes in saline habitats? Botanical Review 64: 176–199.

van Wijnen H.J., Bakker J.P., de Vries Y. (1997) Twenty years of salt marsh succession on a Dutch coastal barrier island. Journal of Coastal Conservation 3: 9–18.

van Wijnen H.J., Bakker J.P. (1999) Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. Journal of Ecology 87: 265–272.

Vince S.W., Snow A. (1984) Plant zonation in an Alaska salt marsh: II. An experimental study of the role of edaphic conditions. Journal of Ecology 72: 669–684.

Wolters M., Garbutt A., Bakker J.P. (2005a) Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. Biological Conservation 123: 249–268.

Wolters M., Garbutt A., Bakker J.P. (2005b) Plant colonization after managed realignment: the relative importance of diaspore dispersal. Journal of Applied Ecology 42: 770–777.

Wolters M., Garbutt A., Bekker R.M., Bakker J.P., Carey, P.D. (2008) Restoration of salt-marsh vegetation in relation to site suitability, species pool and dispersal traits. Journal of Applied Ecology 45: 904–912.

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