Chapter 7 General conclusions

Permanent plots in this study gave detailed information about changes in species composition at a particular site during a relatively short period. The process of dispersal, establishment and colonization of most species was successful, and took place very quickly. Although viable seed availability was an important constraint for the appearance of some species in early colonization, most target species present in the local species pool, had colonized the new intertidal area in 2007, only five years after creation of (part of) the new salt-marsh; the similarity between restoration site and adjacent reference site drastically increased from 2003 to 2007, indicating that the restoration project was very successful in these early salt-marsh developmental years. However, after colonization, different species showed different patterns in space and time. Some of them decreased, most increased in abundance. Two main factors could be important in spatio-temporal succession and, decreasing and increasing of species abundance in time in the restoration site: inundation frequency (or elevation) and sheep grazing. Elevation was one of the most important indirect ecological factors affecting plant succession. Some species are well known to show expansion at higher elevation, e.g. *Elymus athericus* (Bakker 1989). It means that these species will expand if sedimentation remains dominant over erosion in future. The data on sedimentation (Provoost, unpublished) showed that in most parts of the area, sedimentation is still and rather constantly taking place in the newly created salt-marsh. On the other hand our data showed that *Puccinellia maritima* is expanding intensively. *Puccinellia maritima* has been identified as a key species in the process of trapping and stabilising sediment on European marshes (Andresen et al. 1990; Langlois et al. 2003). Therefore it can be expected that the percentage cover of high salt-marsh species will further increase by mere clonal growth of individuals and further enhanced by sedimentation, e.g. *Elymus athericus*. *Elymus athericus* is one of the main dominants at the older stages of a West European salt-marsh (Bakker 1989; van Wijnen & Bakker 1997). So far, there have been no indications that other species will replace *Elymus* *athericus* when salt-marshes become older (van Wijnen et al. 1997), although in the study area several individuals of *Phragmites australis* have established along the higher edges of old as well as newly created salt-marsh. However, the limited salt tolerance level of this species should prevent further colonization of this very competitive species. As a result, future vegetation development will probably depend on the sediment accretion. At high-elevated sandy or even silty sites a future dominance of *Elymus athericus* can be expected (cf. Bakker 1989; Bakker et al. 1997). Whether spreading of potential dominant species such as *Atriplex portulacoides* at lower elevation (cf. Jensen 1985) will occur in the lower salt-marsh is uncertain, since this species is very sensitive to grazing (Schröder et al. 2002) and did so far not spread in any part of the restoration site. In our study area, *Salicornia procumbens* appeared in 2005 for the first time and consecutively strongly increased later. It can be expected that it will become a dominant species in the pioneer zone, replacing the currently dominant species, *Salicornia europaea*.

The very low density grazing and the short term of sheep grazing did not indicate a clear impact on species succession, other studies indicate that grazing and trampling are important biotic factors in intensively grazed salt-marshes; possibly, grazer effects can only be significant at the longer run and with higher density grazing (Jensen 1985; Bakker 1989; Kiehl 1997). However, for more accurate conclusions about sheep grazing and its effect on plant succession, grazing should be further prolonged at the restoration site.

Studies of succession showed that communities, habitats and ecosystems were not static but constantly change in response to disturbance, environmental change, and their own internal dynamics (Molles 2005). The relationship between different parts of a habitat, community or ecosystem could be affected by the age of the successional stages (Molles 2005). Differences in determination of vegetation development by the same abiotic factors (soil and elevation), and between vegetation and seed bank in two different ages of salt-marsh (early primary and late primary) proved this hypothesis.

7.1 Constraints on species colonization

It has repeatedly been demonstrated that variation in the arrival time of species at a successional site can have a major effect on the pattern and outcome of succession (e.g. Drake 1991; Huston 1994), indicating the importance of studies on factors which affect arrival time of different species. The practice of creating salt-marshes on a new substrate provides an excellent opportunity to study plant colonization and subsequent development of vegetation. Insight into the process of salt-marsh development is extremely important in guiding the design, implementation and evaluation of salt-marsh restoration schemes and for determining the appropriate management strategies (Hoffmann et al. 2005). However, colonization and subsequent development are different for each salt-marsh restoration, since biotic and abiotic factors, influencing successional stages from beginning until climax, are site specific.

Three species are well known as pioneers: *Salicornia europaea*, *Suaeda maritima* and *Spartina townsendii*. In addition, some species are known as relatively low salt-marsh species i.e. *Puccinellia maritima*, *Halimione portulacoides*, *Aster tripolium*, *Spergularia* spp. *Triglochin maritimum*, *Limonium vulgare* and *Plantago maritima* (Beeftink 1965; 1966; 1977). For the restoration of salt-marsh vegetation after creation of intertidal circumstances, relatively rapid colonization may be expected from pioneer and low marsh species, provided they are present in a nearby source area (Wolters et al. 2005). We expected these pioneer and low marsh species to appear in the newly created salt-marsh as initial colonizers, since all were present in the local species pool. However, most species appeared during the first year, and even after five years some salt-marsh species that are present in the local species pool remained absent from the newly created intertidal area. Wolters et al. (2008) demonstrated that salinity was the most important factor determining the kind of initial colonizers, while according to Dausse et al. (2008) it would be seed dispersal and consecutive seed rain. We concluded that, besides these two factors, seed production is also an important constraint in colonization of salt-marsh habitats and the sequence of species establishment. Most perennial salt-marsh species are clonal species that spread mainly, some even solely by asexual propagules. This can be concluded from the fact that they appear neither in the seed bank (of neither old nor new salt-marsh) nor in the above-ground vegetation early in the primary succession. Seedling recruitment by salt-marsh perennials, that do produce generative propagules (e.g. *Aster tripolium, Artemisia maritima*, …), can be further constrained by low propagule supply due to insect predation (Louda 1983; Louda 1989) and disease (Bertness et al. 1987; Bertness & Shumway 1992). In this study we found that fungi could limit the production of perennials in salt-marsh habitat. Therefore, perennials appear later in comparison with species that produce a lot of viable seeds. Additionally, some perennial species might produce less viable seeds, because of their hybrid nature e.g. *Spartina townsendii*, a polyploid, hybrid species, that is known to produce only small quantities of viable seeds (Lambinon et al. 1998). For perennial species sexual processes play a minor role and their dynamics are maintained primarily by clonal growth (see also Shumway & Bertness 1992).

Although some species produced a lot of seeds, these seeds were probably not viable or they did not disperse well since they were not observed in both vegetation and seed bank in the newly created salt-marsh. A few empirical studies were conducted on seed dispersal in salt-marshes, indicating that the species composition of plant communities is potentially constrained by dispersal (Rand 2000; Wolters et al. 2005a). However, more studies are needed on dispersal ability of these species into newly created salt-marsh as dispersal constraints (species-specific traits, storage effects, landscape ecology and history) may influence community assembly *per se* (Belyea & Lancaster 1999).

In literature it is generally assumed that early succession in salt-marsh conditions is dominated by facilitation. This mechanism assumes that *only* certain “early-successional species” are able to colonize the site in the conditions that occur immediately after the perturbation, and that they consecutively change the environment in such a way that late successional species are able to establish in a later phase. They “facilitate” late successional species, and generally decrease themselves, because they have changed the environment to less optimal conditions. However, in the particular case of the newly created salt-marsh of the IJzermonding, we have no clear indications that this mechanisms is at hand here. It rather appears that colonization simply depends on available propagules, rather than on environmental suitability. For instance, it can be expected that *Elymus athericus* is perfectly able to establish and grow on most sites in the newly created marsh, but simply did not do so, because it has no or hardly any propagules present in the area. This implies that during early succession of the newly created salt-marsh, the tolerance mechanism is working. This mechanism assumes that species appearing later are probably those that simply arrived later. The sequence of species is determined solely by their life-history characteristics (annuals compared with perennials). In contrast to the early species, the propagules of the later ones are dispersed more slowly (MacArthur & Connell 1966; Farrell 1991). In our study area, some species (e.g. *Salicornia europaea* and *Suaeda maritima*) colonized earlier since they can produce many seeds. While some species particularly perennials (e.g. *Elymus athericus*) appeared later. These species are those that produce no or less seeds and the propagules are dispersed slowly, probably being mainly heavy vegetative parts (rhizomes) of the plant.

7.2 The effect of inundation frequency on vegetation succession

Directional non-replacement succession in harsh salt-marsh conditions occurs when a few species are able to invade, survive and succeed in slow expansion without eliminating or replacing each other. The restoration site still has free space available for further expansion.

Species replacement takes place due to modification of the habitat (facilitation) and there is no competition (see also Bernhardt & Koch 2003). Initially, allogenic succession occurs more than autogenic succession.

This study revealed a rapid development of vegetation on exposed sediments after the creation of a new salt-marsh habitat (restoration site). The succession was probably facilitated by rapid vegetative spread of some clonal salt-marsh species at lower inundation frequencies and rapid spread of some annuals in higher inundation frequency zones. We concluded that the distribution of plant species in the early stages of succession is highly constrained by inundation frequency.

In our study area, the vegetation remains dynamic after 6 years and it is considered to be in equilibrium with the new environmental gradient. However, annual changes as measured by permanent plots and mapping of vegetation zones will have to be further monitored.

7.3 Grazing and succession

Natural succession in the absence of livestock grazing of salt-marshes leads to declining suitability since species and community diversity decrease and forage quality and feeding value decline (Bos et al. 2005). Vegetation composition and diversity is strongly related to the management of salt-marshes, for example grazing by large herbivores (Bakker 1989). Since the cessation of livestock grazing in large areas leads to a strong progress of the vegetation into late successional stage, Esselink (2000) proposed that the areas must be kept under livestock grazing, so that the grazing by large herbivores can maintain the marsh vegetation at a younger successional stage. Grazing by hares has been shown to retard vegetation succession (van der Wal et al. 2000b) and herbivory by geese slowed down succession by retarding the establishment and spread of late successional species in the low salt-marsh. Our observations indicate that the current intensity of sheep grazing is not suited to maintain the IJzermonding salt-marsh in a young successional stage. Although until now no species have become extinct, some palatable and sensitive species to sheep grazing are prone to extinction in the future as they are drastically grazed by sheep. Some species such as *Atriplex* spp. and *Chenopodium* spp. were grazed so intense that all leafs and green stems were lost before the end of the growing season. Low stocking rate probably results in selection for the more palatable and nutritive plant species, resulting in an uneven pattern of grazed and ungrazed patches (Bakker 1985). *Elymus athericus* has the lowest forage quality, indicating it might never be grazed at the current grazer density (see also Milotic et al. 2008). However, the expansion of this species should be hampered, since it increased its cover and occurrence drastically. Although the increase of sheep grazing would decrease the patch selection, it may be dangerous for some of the above mentioned species. Introducing other grazers could be useful to save these species and to decrease the expansion of strong competitor species, like *Elymus athericus*.

7.4 Relationship between soil characteristic and vegetation in different stages

A major challenge in the restoration of salt-marshes is to identify which factors are important in salt-marsh development. For example, Keddy (2000) suggested salinity as most important factor, determining the species composition of salt-marsh communities, while Criel et al. (1999) concluded that salinity together with inundation frequency were the most important determinants in the brackish salt-marsh estuary of the river Scheldt. When considering salinity as an abiotic factor, species can be screened and then ranked in relation to a single trait: salinity tolerance. Consequently, if the salinity level of a local site is known, it is possible to predict which species from the species pool could potentially become established.

In our salt-marsh habitats, the degree to which abiotic factors determine vegetation composition is at least as high in early as in late successional stages. In early colonization the absence/occurrence of perennial as well as annual plants appears to be highly determined by abiotic environmental factors. This also holds for perennials, but not for annuals in old salt-marsh. The occurrence of these annuals in the old salt-marsh appears to be limited by competition from the established perennials. Gaps in that perennial vegetation cover are needed for annuals to germinate and grow. This explains why their occurrence is not so much determined by the abiotic (soil) environment, but rather by stochastically created gaps.

In contrast to other terrestrial habitats, assembly of species on new substrate in salt-marsh habitats is not stochastic. It is rather a deterministic process in which species with high seed production and salt tolerance start the colonization and facilitate the germination of later species by creating good sedimentation conditions. In addition, having an old salt-marsh adjacent to new substrate decreases the stochasticity in vegetation development. Stochastic factors act mostly in more isolated sites (del Moral 1999). If a site is sufficiently isolated, limited dispersal produces initially variable vegetation with a very weak correlation between environmental factors and species composition.

7.5 Seed bank and succession

The variation of seed bank density with age in salt-marsh habitats is different from that of other terrestrial habitats, in which a low density was found initially that rose with time (e.g. Flinska 1999; Bossuyt & Hermy 2004). In our study area the density of seeds appears to decrease with time. This is most probably caused by the difference in seed longevity and seed production between species of early and late successional stages. Most initial colonizers have more persistent seeds in comparison with plants of later stages. In general, seed bank accumulation in salt-marshes is low (Morzaria-Luna & Zedler 2007). Most restoration programs from seed bank did not succeed (Wolters et al. 2005); as well early as late successional species do not appear from the seed bank (Wolters & Bakker 2002). This implies that initial colonizers possibly have equally persistent seeds as species with low relative seed production, but their massive production of small seeds lead to a well represented in the soil of old salt-marshes. This is in opposition to the conclusions of Thompson et al (1997), who state that pioneer species generally have long persistent seeds.

About similarity of standing vegetation and seed bank, three possible relationships are proposed: the similarity between the vegetation and soil seed bank is, i) relatively high and does not consistently increase or decrease with age, ii) increases or decreases as the communities age and, iii) is relatively low and does not consistently increase or decrease with age (Chang et al. 2006). The relationship between the vegetation and soil seed bank for the salt-marsh communities of the IJzermonding most closely resembles the second proposed relationship, thus that standing vegetation does not reflect the below-ground seeds in late successional stages. Conversely, in early primary succession, vegetation is more reliable to predict below-ground seed bank. We have provided evidence that the seed bank during the whole succession is mostly composed of seeds of new colonizers. This explains the very low similarity between seed bank and above-ground vegetation in salt-marsh habitat in the late successional stage.

Plant species that were formerly recorded from the above-ground vegetation in the area, but that disappeared during the last decades (*Armeria maritima, Juncus maritimus, Halimione pedunculata, Carex extensa, Oenanthe peucedanifolia*: Pire 1862; Goetghebeur 1976) were not found back in the seed bank. Some of these species are among the most interesting and rare species of European saline habitats (Hoffmann et al. 2005). The recovery of these species from the local seed bank will be virtually impossible in the future.

7.6 **Management implications**

Conservation management usually concentrates on decreasing abundance and cover of dominant, highly competitive graminoids using several approaches like introducing large herbivores and mowing (Hoffmann et al. 2005). In the studied salt-marshes, *Elymus athericus* characterized as a late-successional salt-marsh species has become so dominant in the higher parts of the old salt-marsh that it can be considered as problematic. Our results showed that sheep grazing at the present low intensity had no significant negative effect on the expansion of this species. As sheep grazing appears to induce opposing selection on palatable species, any increasing intensity of sheep grazing should be made cautiously, since the larger number of animals might shift to the more palatable species like *Limonium vulgare, Triglochin maritimum* or *Plantago maritima*. However, introducing another herbivore, characterized as a bulk-feeder rather than as a selective feeder and that consequently is known to preferentially use this competitive species could be useful for hampering the expansion of this species and it may also facilitate sheep to graze more on *Elymus athericus* as well. Studies in feeding ecology of introduced ungulates (Konik and Shetland pony, donkey and Scottish highland cattle) in coastal dune grassland showed that all are grass-eaters consuming a high amount of competitive plant species (Hoffmann et al. 2005, Lamoot et al. 2005). Bakker (1985) stated that the cover of *Elymus athericus* on salt-marshes in the Netherlands decreased due to cattle grazing. Therefore, it can be recommended to introduce cattle into the area (single or mixed with sheep). It may also be a useful tool to hamper the expansion of competitive species of surrounding dune grasslands, such as *Phragmites australis*, *Calamagrostis epigejos* and *Arrhenatherum elatius*.

A management option that also would decrease the dominance of *Elymus athericus* and increase diversity is the construction of creeks to enhance tidal flooding of the interior parts, increasing water-logging rates and improving the colonization of early successional species. Additive effects of machinery practices to create the channels and dig out soil will also counteract the expansion of *Elymus athericus*. This possibility to create a pioneer low salt-marsh substrate should not be ignored.

Grazing in the entire year might promote the forage quality of several species. In addition, the rate of consumption of *Elymus athericus* might be increased as at the beginning of the growth season, the palatability of this species is higher (Vallentine 2001). Although early grazing in the growing season may be harmful for some sensitive species, it should be considered as a management option.

As the above mentioned valuable species that were present at the IJzermonding salt-marsh did not appear in the seed bank in the past, the re-appearance of these species in the area may take several years. The absence of nearby source populations makes that reintroduction by sowing or planting might be considered as a management option (cf. Wolters et al. 2008).

7.7 Lines of future research

1- Our results show that populations and plant communities are still dynamic in the relatively early stages of salt-marsh succession. Future monitoring is therefore necessary to learn about and to document long-term vegetation succession. This is also needed to evaluate nature restoration success in the long run.

2- Moving from a more or less descriptive pattern study towards a more mechanistic research level is the main line of thinking for future research. In that spirit, i) investigating the mechanism of seed dispersal, and more specifically loss and retention processes of the viability of seeds during dispersal would be meaningful, ii) study on possible long-distance dispersal, possible dispersal of seeds from regional species pools would be valuable. Focussing on the particular situation of the IJzer estuary, the effects of local and artificial levee-like structures between the newly created salt-marsh and the southern part (O2) of the old salt-marsh is of particular importance. Study on the mechanism of seed dispersal and the transportation of seed from this part of old salt-marsh to the newly created salt-marshes is necessary, and may elucidate why some species have not appeared in the restoration site, yet, although present in O2, iii) further study on post dispersal factors is recommended.

3- Although we could detect already some effects of sheep grazing on a few vegetation zones and on particular plant species, further monitoring is needed to analyze all effects of sheep grazing on vegetation, especially in communities dominated by palatable species, such as *Atriplex* spp. and *Chenopodium* spp..

4- Study on the impact of herbivores other than sheep and at fluctuating densities and combinations during different seasons would also be of great scientific interest. Finally, scale-related phenomena of grazing impact would be of great management interest and in the study of vegetation succession under grazing in general. Unfortunately the salt-marsh environment of the IJzer estuary is too small to study these spatial and temporal processes and interactions. The Verdonken Land Van Saeftinghe would be a good alternative to study these processes together. The Zwin area also has some potentials in this sense, certainly when the recently planned expansion of the salt-marsh area is combined with grazing management.