



Does vegetation in restored salt marshes equal naturally developed vegetation?

Jantsje M. Van Loon-Steensma, Han F. Van Dobben, Pieter A. Slim, Hendrik P.J. Huiskes & Gerard M. Dirkse

Keywords

Barrier islands; Erosion protection; Flood protection; Habitats Directive; Nature conservation; Salt-marsh restoration; Sedimentation; Wadden Sea

Abbreviation

NLR = Neerlands Reid (a Dutch salt-marsh area on Wadden barrier island Ameland).

Nomenclature

Plant nomenclature Van der Meijden (1996)

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Van Loon-Steensma, J.M. (corresponding author, jantsje.vanloon@wur.nl)¹,

Van Dobben, H.F. (han.vandobben@wur.nl)²,

Slim, P.A. (pieter.slim@wur.nl)²,

Huiskes, H.P.J. (rik.huiskes@wur.nl)²,

Dirkse, G.M.

(gerard.dirkse@natuurmuseum.nl)³

¹Earth System Science Group, Wageningen University & Research Centre, P.O. Box 47, 6700 AA, Wageningen, the Netherlands;

²Alterra, Wageningen University & Research Centre, P.O. Box 47, 6700 AA, Wageningen, the Netherlands;

³Natuurmuseum Nijmegen, Gerard Noodtstraat 121, 6511 ST, Nijmegen, the Netherlands

Introduction

Up to half of the salt marshes worldwide are degraded as a result of human modifications of the coastal zone (Barbier et al. 2011). Sea level rise due to climate change (IPCC 2014) is yet another threat to salt marshes (Nicholls et al. 2007). At the same time there is increasing interest in the flood defence service of salt marshes (e.g. Van Hemert et al. 2013; Van Loon-Steensma & Vellinga 2013). By lowering wave height and dissipating wave energy, a vegetated foreshore like a salt marsh forms a natural coastal defence (e.g. Brampton 1992; King & Lester 1995; Möller et al. 2001; Costanza et al.

Abstract

Question: Do low stone dams built to prevent erosion and to restore salt marshes through increased sedimentation affect plant species composition?

Location: Dutch Wadden Sea area (ca. 53°N 5°E).

Methods: Relevés ($N = 170$) were made of the vegetation of two restored salt marsh sites on the barrier islands Terschelling (Grië) and Ameland (Neerlands Reid). Existing relevés of salt-marsh vegetation ($N = 6198$) made along the entire Dutch Wadden Sea coast (both the mainland and the barrier islands) were used as a reference. The vegetation of the two restored sites (Grië NLR data) was compared with the reference by (1) simple species-by-species analysis based on frequencies in both data sets, and by (2) ordination, where relevés of the restored sites were projected into a multivariate space defined by the species' abundances in the reference relevés.

Results: Out of the 37 species that are common (i.e. have a frequency >5%) in either the Grië NLR data or the reference data, 31 have frequencies that differ by less than a factor of five, and 23 differ by less than a factor of two. Furthermore, the Grië NLR data occupy a space that is well in the centre of the ordination space defined by the reference data.

Conclusions: There are no conspicuous differences between salt-marsh vegetation behind low dams and the vegetation that has naturally developed on unprotected mudflats. We conclude that measures targeting salt marsh development in view of flood protection do not interfere with nature conservation.

2008; Gedan et al. 2011; Shepard et al. 2011). Furthermore, conservation and re-establishment of salt marsh in view of biodiversity and habitat protection, e.g. in the framework of the Ramsar Convention (Convention on Wetlands, United Nations 1987), the United States' Clean Water Act (Federal Water Pollution Control Act Amendments of 1972; United States Congress House, Committee on Public Works 1972), or the European Habitats Directive (Council of the European Communities 1992), forms an important issue. This results in a challenge to simultaneously strengthen both ecosystem services provided by salt marshes (Van Loon-Steensma & Vellinga 2013).

In the Netherlands, salt marshes are found adjacent to large stretches of dykes (earth structures designed to resist wave action and to prevent or minimize overtopping, also called levee or embankment) along the Wadden Sea coast and along the estuarine coasts of the South West Delta Area. Here we concentrate on the Dutch Wadden Sea, where the present salt marsh area is ca. 9000 ha (Dijkema et al. 2013), situated along the shores of both the mainland and the Wadden Sea barrier islands (Fig. 1). The area along the mainland coast is the result of man-made accretion works. Originally these accretion works were established for reclamation of agricultural land but since the 1970s the goals have changed towards nature conservation (Dijkema et al. 2001; De Jonge & De Jong 2002). In contrast, the salt marshes at the easternmost ends of the Wadden Sea islands are the result of natural processes (sedimentation, colonization by vegetation and subsequent succession), although their formation was greatly stimulated by the construction of sand dykes between 1880 and 1930. Nearly all Wadden Sea salt marshes are part of the European Natura 2000 network of protected habitats.

Wave damping is strongly dependent on the slope of the coastal profile, water depth, width of the salt marsh zone and vegetation (e.g. Anderson et al. 2011). Therefore, a flood protection strategy that includes wave damping by salt marshes must include measures to stabilize established salt marshes, and to stimulate sedimentation and vegetation development. The construction of a low stone dam (with a height around mean high water level) in front of the salt marsh edge may be such a measure. On the other hand, such measures may conflict with the value for protection of habitats of the existing or newly developed salt marsh. Such values are the result of the interplay between hydrological, morphological and ecological processes in the coastal zone (Allen 2000), leading to a habitat with a

characteristic plant and animal life (e.g. Adam 1990; Allen & Pye 1992; Schrama 2012).

According to Garbutt & Wolters (2008), restoration efforts such as the deliberate breaching of dykes to allow tidal inundation of former embanked salt marshes may never fully replace natural wetland functions. Mossman et al. (2012) conclude that marshes reactivated by managed realignment do not provide habitats and species comparable to natural marshes, and do not have equivalent biological characteristics. According to these authors, such salt marshes do not satisfy the requirements of the EU Habitats Directive. On the other hand, low stone dams in front of an eroding salt marsh allow hydrological, morphological and ecological processes that lead to natural salt marsh formation on mudflats. Therefore, sediment, vegetation and benthic invertebrates of such salt marshes may be equivalent to naturally developed salt marshes.

Here we explore the vegetation composition of stabilized and restored salt marshes by comparing vegetation relevés made in two restoration projects on Dutch Wadden Sea barrier islands (Ameland and Terschelling; see Fig. 1), with a reference set consisting of ca. 6000 relevés made in salt marshes all over the Dutch Wadden Sea area.

Methods

Vegetation description at the study sites

The two study sites are located on the Wadden Sea island Terschelling (Grië) and Ameland (Neerlands Reid, NLR; see also Van Loon-Steensma & Slim 2013; Fig. 1). Both are eroding salt marshes where attempts were made to prevent further erosion and loss of typical salt marsh vegetation by the construction of low (i.e. some 1 m above mean sea level) stone dams ca. 60 m (Grië) or ca. 10 m (NLR) seaward of the eroding salt marsh edge, in 1991 and 1998, respectively. The dam at Grië has five openings and the

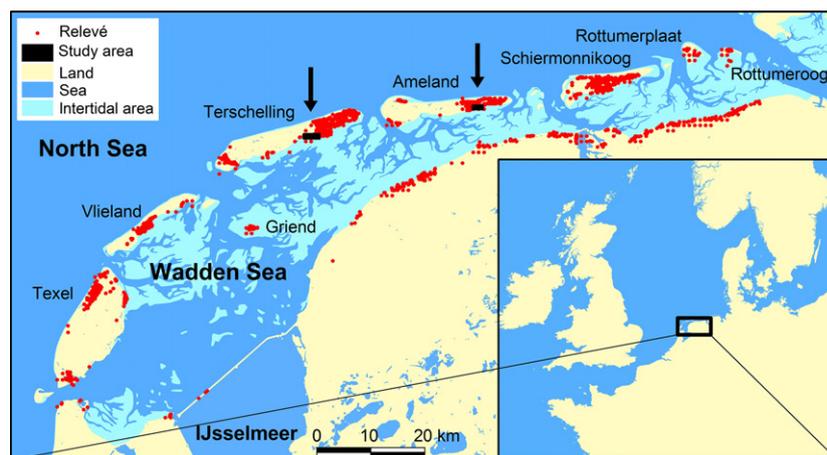


Fig. 1. Location of the study areas (black boxes indicated by arrows) and the relevés in the reference set.

east side is not connected with the coast, allowing seawater to enter and exit during high and low tide. To describe the vegetation of these sites we made vegetation relevés in 2011 and 2013. The relevés are circles with a radius of 1.13 m (surface area = 4 m²) where vegetation was recorded in terms of species quantities estimated as ground cover percentage. In total, 90 relevés were made in Grië and 80 in NLR; of these, 84 and 64, respectively, were made in the area between the stone dams and the original salt marsh edge. The other relevés were made just outside the area protected by the dams and were used as a local reference. The relevés are arranged in transects that run perpendicular to the coastline, from the unvegetated mudflats until the salt marsh. In total, 85 species (including bryophytes, algae and vascular plants) were found in our relevés.

In the relevés we determined the approximate location as X- and Y-coordinates using a handheld GPS (Trimble Juno SB Handheld and Trimble Nomad for GPS, with an accuracy of 2–5 m). We used the X- and Y-coordinates to estimate the elevation (Z-coordinate) using the digital elevation map of the Netherlands (*Actueel Hoogtebestand Nederland*, <http://www.ahn.nl>). In such a digital map the elevation of a given location is based on bilinear interpolation of the measured heights of the neighbouring four points of the grid, which may lead to levelling of local elevation differences in the data. In the statistical analysis we treat the data from Grië and NLR as a single data set that we refer to as 'Grië NLR'.

Reference data set

As a reference, we extracted vegetation relevés from the Dutch national Vegetation Database (Hennekens & Schaminée 2001; <http://www.givd.info/ID/EU-NL-001>). We used all relevés made after 1979 in the Dutch Wadden Sea area, and selected salt marsh relevés using syntaxonomic identifications with the program ASSOCIA (Van Tongeren et al. 2008). The syntaxonomic typology follows Schaminée et al. (1998). Our selection consisted of relevés identified as one of the associations (or their sub-associations) listed in Table 1, and resulted in a set of 6198 relevés. Some of the relevés had been manually identified by their authors, and if such identifications existed we used these instead of the automatic identifications. To our knowledge none of these relevés is made behind stone dams, although some are located in areas where sedimentation has been artificially increased by wooden groynes or artificial ditches.

We translated the associations to Habitat types according to the European habitat convention (European Commission DG Environment, Nature and Biodiversity 2007) using the translation table for the Netherlands given by

Table 1. Associations used in the reference set, and their translation to Habitat types. The associations given are an exhaustive list of vegetation types occurring in the Dutch Wadden Sea basin that can be qualified as 'salt marsh' (cf. Schaminée et al. 1998). Translation to Habitat types is according to Van Dobben et al. (2014): Appendix 2, except those marked with (*). Explanation of Habitat type codes: 1210, Annual vegetation of drift lines; 1310, *Salicornia* and other annuals colonizing mud and sand; 1320, *Spartina* swards (*Spartinion maritimae*); 1330, Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*). Habitat type 1310 was split into two subtypes based on the presence of either *Salicornia* spp. (subtype A) or other species e.g. *Sagina maritima*, *S. nodosa* or *Centaurium littorale* (subtype B). RG = community of impoverished vegetation (cf. Schaminée et al. 1995).

Association	Habitat
<i>Atriplicetum littoralis</i> (*)	1210
<i>Salicornietum dolichostachyae</i>	1310A
<i>Salicornietum brachystachyae</i>	1310A
<i>Suaedetum maritimae</i>	1310A
<i>Sagino maritimae-Cochlearietum danicae</i>	1310B
<i>Centaurio-Saginetum</i>	1310B
<i>Spartinetum maritimae</i> (*)	1320
<i>Spartinetum townsendii</i>	1320
<i>Puccinellietum maritimae</i>	1330
<i>Plantagini-Limonietum</i>	1330
<i>Halimionetum portulacoides</i>	1330
<i>Puccinellietum distantis</i>	1330
<i>Puccinellietum fasciculatae</i>	1330
<i>Puccinellietum capillaris</i>	1330
<i>Parapholido strigosae-Hordeetum marini</i>	1330
<i>Juncetum gerardi</i>	1330
<i>Armerio-Festucetum littoralis</i>	1330
<i>Junco-Caricetum extensae</i>	1330
<i>Blysmetum rufi</i>	1330
<i>Artemisietum maritimae</i>	1330
<i>Atriplici-Elytrigietum pungentis</i>	1330
<i>Oenanthe lachenalii-Juncetum maritimi</i>	1330
RG <i>Scirpus maritimus</i> -[<i>Asteretea tripolii</i>]	1330
RG <i>Agrostis stolonifera</i> - <i>Glaux maritima</i> -[<i>Asteretea tripolii</i>]	1330
RG <i>Triglochin maritima</i> -[<i>Asteretea tripolii</i>]	1330
RG <i>Aster tripolium</i> -[<i>Puccinellion maritimae</i>]	1330

e.g. Van Dobben et al. (2014) with two additions indicated in Table 1. As the Habitat types are more broadly defined than the syntaxonomic associations, this translation can be made in a straightforward way. The location of the relevés in the reference set is presented in Fig. 1, and their collection dates and distribution over the Habitat types in Appendices S1 and S2. Note that these relevés originate from many authors and may therefore have different sizes and abundance scales (but the vast majority has sizes between 1 and 25 m², and all consist of cover estimates per species). Before analysis the species were synonymized where necessary (see Jansen & Dengler 2010) and the various cover scales were transformed to percentages.

Data analysis

We used two methods to compare our relevés and the reference relevés. The first is a simple species-by-species analysis based on frequencies in both data sets; and the second is an ordination where our relevés were projected into a multivariate space defined by the species' abundances in the reference relevés. To this end we first performed a correspondence analysis (CA; Jongman et al. 1995) on the reference data set. Subsequently, we added our relevés as 'passive' samples, i.e. by computing their positions in the diagram using the species weights resulting from the reference relevés. A prerequisite for this procedure is that there is a large overlap in species composition between our relevés and the reference relevés, which is indeed the case. We limited the analysis of the reference data set to the 155 species with ten or more occurrences in order to reduce its heterogeneity (i.e. to species with a frequency of >0.16%; note that extremely rare species tend to blur the analysis in unimodal ordination techniques; Jongman et al. 1995). We considered (1) comparable frequencies per species in both data sets, and (2) placement of our relevés in the ordination diagram in or near the centre of the Habitat types as defined by the reference set, as indications of similarity in both data sets and hence, of the absence of a strong effect of the dams on the floristic composition of the salt marsh vegetation. To obtain an idea of the ecological interpretation of the ordination axes, we determined the correlation between the reference relevé's scores on the first three axes and mean indicator values per relevé. We used the indicator values for groundwater level, soil pH and nitrate and chloride concentration given in Wamelink et al. (2005, 2012).

Results

A complete list of species with their frequencies in both the Grië NLR data set and the reference set is given in Appendix S3. Out of a total of 175 species, 90 exclusively occur in the reference set, whereas 20 exclusively occur in the Grië NLR set. However, most of these 'exclusive' species in the reference set are rare in our data, i.e. they have frequencies <2%. There are a few exceptions: *Cochlearia danica*, *Sagina nodosa* and *Centaureium littorale* have frequencies of ca. 5% in the reference set and are absent from the Grië NLR set. On the other hand, *Vaucheria* sp. and *Ulva lactuca* have frequencies of >20% in the Grië NLR set and are absent from the reference set. However, this is most probably an artefact as these marine algae are not usually included in vegetation relevés.

Table 2 gives a comparison between the frequencies of the most common species in both data sets. Out of a total of 37 species that are common in either or both data sets,

31 have frequencies that differ by less than a factor of five, and 23 differ by less than a factor of two. Only two typical salt marsh species are rather common (ca. 5%) in the reference set and rare or absent in the Grië NLR set: *Cochlearia danica* and *Juncus maritimus*. It is concluded that the floristic difference between the two data sets is rather small and this is the justification behind 'passive' treatment of the Grië NLR data in the ordination.

A second comparison of the Reference and the Grië NLR data sets was carried out by making ordination diagrams. First, CA was applied to the reference set, resulting in the ordination diagrams given in Fig. 2; the correlation

Table 2. Comparison of frequencies per species in the two data sets (N reference set = 6198 and N Grië NLR set = 170) for species with a frequency of >5% in either data set. For species given in bold the frequencies differ by more than a factor five.

Species Name	Reference, %	Grië NLR, %	Ratio Grië NLR/Ref.
<i>Cochlearia danica</i>	5.1	0.0	0
<i>Phragmites australis</i>	7.7	0.6	0.08
<i>Juncus maritimus</i>	6.8	0.6	0.09
<i>Centaureium pulchellum</i>	6.2	1.2	0.19
<i>Atriplex prostrata</i>	37.9	13.5	0.36
<i>Carex extensa</i>	5.8	2.4	0.41
<i>Odontites vernus</i>	10.8	4.7	0.43
<i>Bolboschoenus maritimus</i>	8.6	4.1	0.48
<i>Atriplex littoralis</i>	5.6	2.9	0.53
<i>Limonium vulgare</i>	27.4	16.5	0.6
<i>Triglochin maritima</i>	22.5	14.7	0.65
<i>Aster tripolium</i>	54.7	41.2	0.75
<i>Juncus gerardi</i>	28.0	21.2	0.76
<i>Agrostis stolonifera</i>	36.3	27.7	0.76
<i>Seriphidium maritimum</i>	27.9	22.4	0.8
<i>Festuca rubra</i> agg.	44.3	38.2	0.86
<i>Glaux maritima</i>	39.8	35.3	0.89
<i>Plantago maritima</i>	36.6	32.9	0.9
<i>Suaeda maritima</i>	61.9	57.1	0.92
<i>Potentilla anserina</i>	13.4	12.4	0.92
<i>Atriplex portulacoides</i>	39.9	40.0	1
<i>Puccinellia maritima</i>	58.6	62.9	1.07
<i>Spergularia media</i> subsp. <i>angustata</i>	38.0	42.4	1.11
<i>Salicornia europaea</i>	58.6	65.9	1.12
<i>Spartina anglica</i>	35.3	40.6	1.15
<i>Armeria maritima</i>	9.3	12.4	1.33
<i>Elytrigia atherica</i>	24.1	33.5	1.39
<i>Cochlearia officinalis</i> subsp. <i>anglica</i>	8.1	11.8	1.46
<i>Spergularia marina</i>	8.5	12.4	1.46
<i>Plantago coronopus</i>	6.7	11.2	1.66
<i>Parapholis strigosa</i>	5.3	9.4	1.78
<i>Cirsium arvense</i>	2.9	6.5	2.27
<i>Trifolium repens</i>	6.3	15.9	2.53
<i>Lolium perenne</i>	2.4	7.1	2.98
<i>Cerastium fontanum</i>	2.0	6.5	3.23
<i>Vaucheria</i> sp.	0.0	41.8	
<i>Ulva lactuca</i>	0.0	21.8	

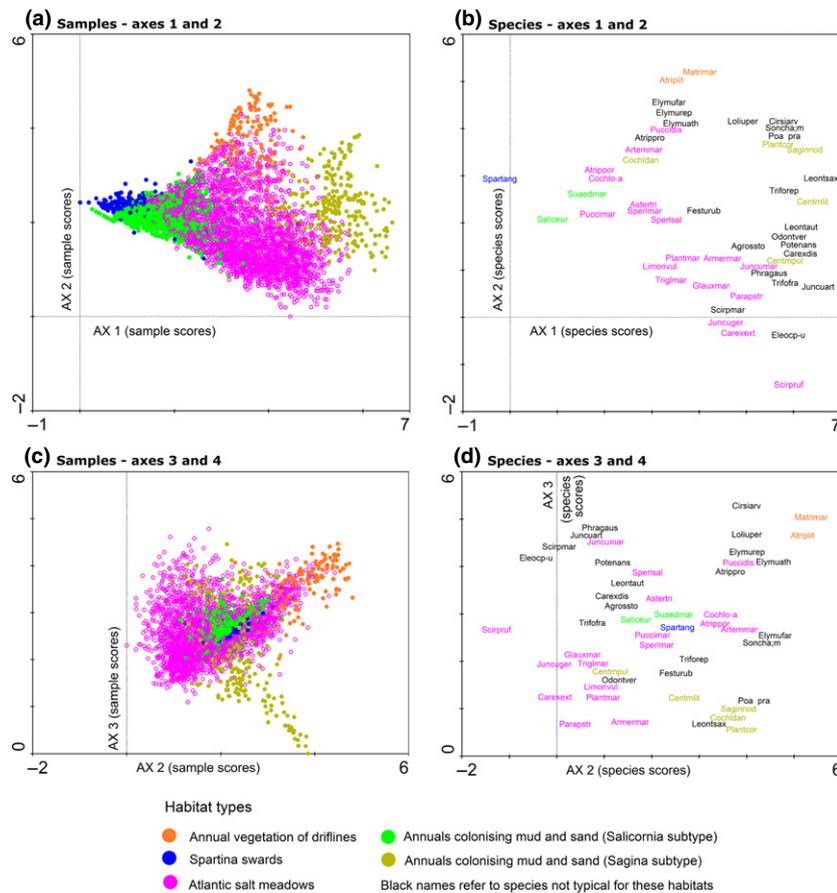


Fig. 2. Ordination of the reference set using CA. (a), samples, first and second axis; (b), species, first and second axis; (c), samples, second and third axis; (d), species, second and third axis. Colours in (a) and (c) indicate Habitat types; their full names are given in the caption of Table 1. The colours of the species names in (b) and (d) indicate their status as typical species of Habitat types (in the sense of the EU Habitats Directive), coded as in (a) and (c). Detrending by segments, no weighting of species or samples, species abundances are entered into the analysis as $\log(\text{cover percentage} + 1)$. Eigenvalues are 0.67, 0.36, 0.30 and 0.23, respectively, for the first four axes, sum of all eigenvalues: 11.07 i.e. these plots together explain 12% of the variance in the species data. Gradient length of the first axis is 6.6, which justifies CA instead of PCA. The plots have a distance interpretation i.e. if the sample and species plots are projected over each other in equal scaling, the expected abundance of a given species in a given sample increases as their distance decreases. Only species are displayed that have a minimum weight of 2% in CA, explanation of species codes: Agrossto, *Agrostis stolonifera*; Armermar, *Armeria maritima*; Artemmar, *Seriphidium maritimum*; Astertri, *Aster tripolium*; Atriplit, *Atriplex littoralis*; Atrippor, *Atriplex portulacoides*; Atrippro, *Atriplex prostrata*; Carexdis, *Carex distans*; Carexext, *Carex extensa*; Centmlit, *Centaureum littorale*; Centmpul, *Centaureum pulchellum*; Cirsiarv, *Cirsium arvense*; Cochldan, *Cochlearia danica*; Cochlo-a, *Cochlearia officinalis* subsp. *anglica*; Eleooc-u, *Eleocharis uniglumis*; Elymuath, *Elytrigia atherica*; Elymufar, *Elytrigia juncea* subsp. *boreoatlantica*; Elymurep, *Elytrigia repens*; Festurub, *Festuca rubra* agg.; Glauymar, *Glaux maritima*; Juncuar, *Juncus articulatus*; Juncuger, *Juncus gerardi*; Juncumar, *Juncus maritimus*; Leontaut, *Leontodon autumnalis*; Leontsax, *Leontodon saxatilis*; Limonvul, *Limonium vulgare*; Loliuper, *Lolium perenne*; Matrimar, *Tripleurospermum maritimum*; Odontver, *Odontites vernus*; Parapstr, *Parapholis strigosa*; Phragaus, *Phragmites australis*; Plantcor, *Plantago coronopus*; Plantmar, *Plantago maritima*; Poa pra, *Poa pratensis*; Potenans, *Potentilla anserina*; Puccidis, *Puccinellia distans*; Puccimar, *Puccinellia maritima*; Saginnod, *Sagina nodosa*; Saliceur, *Salicornia europaea*; Scirpmar, *Bolboschoenus maritimus*; Scirpruf, *Blysmus rufus*; Soncha;m, *Sonchus arvensis* var. *maritimus*; Spartang, *Spartina anglica*; Sperlmar, *Spergularia media* subsp. *angustata*; Sperlsal, *Spergularia marina*; Suaedmar, *Suaeda maritima*; Trifofra, *Trifolium fragiferum*; Triforep, *Trifolium repens*; Triglmar, *Triglochin maritima*.

between the sample scores and indicator values is given in Table 3. The Habitat types are rather well separated by CA, with the exception of the most common type 1330 (Atlantic salt meadows) that overlaps with all other types. However, this type is rather well separated from the other types along the fourth axis (not shown).

The first axis clearly represents the gradient from pioneer to late successional stages, exemplified by the pioneer

species *Spartina anglica* and *Salicornia europaea* on the left side of Fig. 2b, while species of wet or even dry grassland (e.g. *Leontodon* spp., *Trifolium repens*, *Centaureum littorale*) occur on the right side of Fig. 2b. This interpretation is confirmed by the correlation with the indicator values, where higher pH and chloride values occur at low values of the first axis, i.e. the influence of seawater increases from right to left on this axis.

Table 3. Correlation coefficients for the most important indicators. Pearson correlation coefficients between the sample scores on the first three axes and mean indicator (i.e. pH, groundwater level, NO₃, snf Cl) values per relevé (note that for the groundwater level indicator, a higher value denotes a drier situation).

	AX 1 (-)	AX 2 (-)	AX 3 (-)
pH	-0.94	0.23	-0.13
Groundwater Level	-0.15	0.80	0.00
NO ₃	-0.66	0.11	0.32
Cl	-0.81	-0.16	-0.34

The second axis is strongly and positively correlated with the groundwater level indicator, where the driest situations occur at high values of this axis, i.e. in the upper part of Fig. 2a and the right part of Fig. 2b. Here, type 1210 (Annual vegetation of drift lines) is found. This is understandable as drift lines are in places that are flooded only once or a few times per year, i.e. in the highest and consequently, driest parts of salt marshes. However, the species plots (Fig. 2b,d) show that there is probably another difference, namely the contrast between sandy soil at high values of the second axis, with e.g. *Elytrigia juncea* subsp. *boreoatlantica* and *Sonchus arvensis* var. *maritimus* and clayey soil at low values, with e.g. *Blysmus rufus* and *Juncus gerardi*.

The third axis is most strongly correlated with the nitrate and chloride indicators. This axis most probably mainly represents a trophic gradient, with eutrophic situations on the high side, represented by species like *Cirsium arvense* and *Lolium perenne*, and species like *Leontodon saxatilis* and *Sagina nodosa* on the low side. The trophic gradient apparently partly coincides with a chloride gradient where the most eutrophic situations are least influenced by seawater. This is probably because these eutrophic situations are mostly drift lines that are only incidentally flooded (cf. the position of type 1210 in Fig. 2c).

Surprisingly, the two subtypes of type 1310 (Annuals colonizing mud and sand) are completely separated in the diagrams, with low values on the first axis and high values on the third axis for subtype A (*Salicornia*) and vice versa for subtype B (*Sagina*). The combination in type 1310 of pioneer situations of mudflats (subtype A) with those of sandy banks (subtype B) – which are ecologically very different situations – may explain this separation in the diagram. In the diagrams, subtype A for a large part overlaps with type 1320 (*Spartina* swards) while subtype B partly occupies a space where no other types are found (cf. Fig. 2a,c). This is understandable as mudflats can be colonized by both *Salicornia europaea* (subtype 1310A) and *Spartina anglica* (type 1320). Figure 2c suggests that subtype 1310B mainly occurs in sandy, dry and oligotrophic situations (the ‘tail’ in the lower right of the diagram), although it is not strictly confined to such situations.

Apart from the overlap of types 1310A and 1320, there is also a large overlap between type 1330 (Atlantic salt meadows) and all other types. This is probably because 1330 is the most heterogeneous of all types, consisting of 14 associations and four communities of impoverished vegetation, while the other types are made up of between one and three associations (cf. Table 1). However, when inspecting the fourth axis (not shown) it becomes clear that type 1330 has a number of characteristic species, although ones with a broad ecology, e.g. *Festuca rubra*, *Seriphidium maritimum*, *Potentilla anserina* and *Elytrigia atherica*.

In Fig. 3 the Grië NLR data are projected into the ordination space defined by the reference data. The Grië NLR data mostly occupy a space that is well in the centre of the space defined by the reference data. Only a single sample point of the Grië NLR data falls outside the reference space, with an extreme value on the first axis. On the second and third axis the Grië NLR data never have extreme values compared to the reference data. Also, the local reference samples (i.e. those of Grië NLR that are not behind the dams) do not take positions that are clearly different from either the other Grië NLR data or the reference set. We used the elevations estimated in the Grië NLR data set as an indirect check of the interpretation of the ordination diagram of the reference set. If the first axis mainly reflects the influence of seawater (increasing from right to left), the elevation of the Grië NLR data projected on this axis should increase from left to right; which was the case as the elevation and the score on the first axis of the Grië NLR data have a correlation coefficient of 0.89. Also, the interpretation of the second axis as a wet–dry gradient is confirmed by this analysis, as the elevation and the second axis have a correlation coefficient of 0.31.

Discussion and conclusions

The vegetation behind the dams at Grië (Terschelling) and Neerlands Reid (Ameland) falls well into the centre of the variation of all Habitat types present in Dutch Wadden Sea salt marshes. Therefore, we conclude that salt marsh vegetation behind low dams is not different from salt marsh vegetation that has developed as a result of normal succession starting in unprotected mudflats. Apparently, the low stone dams at our study locations formed no impediment for natural salt marsh forming processes, in contrast, they created favourable abiotic conditions for sedimentation and subsequently the establishment of pioneer vegetation on the raised mudflats. Because the dam at Grië has openings and is at one side not connected to the shore, it allows (to some extent) the natural regime of tidal flooding and the related natural exchange of sediment. Furthermore, due to their low height (just above mean high water level),

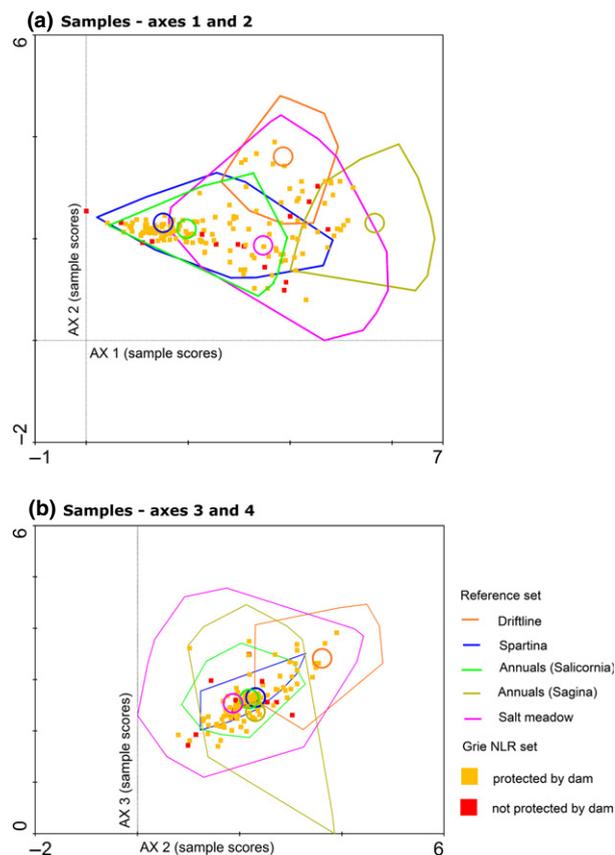


Fig. 3. Grië NLR data (squares) projected into the ordination diagram of Fig. 2: (a), first and second axis; (b), second and third axis. The colour coding is identical to Fig. 2, however the sample points of the reference set have been replaced by their convex hull (lines) and their centroid (circles). Note that the species weights are not influenced by the Grië NLR data and hence the corresponding species plots are identical to those in Fig. 2(b) and (d), respectively.

the dams on both locations are easily overflowed during rough wind conditions (when the sediment load of the seawater is relatively high). Inundation of the higher salt marsh during storms will therefore still result in an increase in elevation and on-going succession.

In comparing the two data sets it should be borne in mind that the Grië NLR data only represent young stages of the succession, which started ca. 20 (Grië) or ca. 15 (NLR) years ago. This may explain the absence or rarity of *Cochlearia danica*, *Sagina nodosa* and *Juncus maritimus* in the Grië NLR data, and in general, the absence of samples with high values on the first axis or with extreme values on the second and third axis. It is unclear if the dimensions of the low stone dams in relation to sea level rise allow further elevation of the adjacent salt marsh through sedimentation and subsequently on-going salt marsh succession. To gain more insight in the long-term effect and the optimal dimensions of coastal protection

measures in times of sea level rise, it is advisable to monitor the development of the salt marsh vegetation in restored salt marsh areas.

Fast colonization and salt marsh succession in restored salt marshes were also observed by Mossman et al. (2012), who compared plant communities of realignment sites (where the existing sea defences were deliberately or accidentally breached or replaced) with natural salt marshes in the UK. In contrast to our findings, they found differences in community composition. In the realignment sites, early successional species remained dominant, even on the high marsh. Even after many decades differences in vegetation between natural and realignment sites were still present (Garbutt & Wolters 2008). In contrast, the vegetation of our study sites is quite comparable with the reference set. Obviously, the low dams allowed natural salt marsh forming processes. One should also be aware that most salt marshes along the Wadden Sea mainland coast are the result of man-made reclamation works. Nevertheless, these salt marshes are included as Natura 2000 habitats.

Besides the fact that a stone dam is an unnatural element in the Wadden Sea, it fixes the transition from mudflats to salt marsh and prevents the natural retreat of the salt marsh edge in response to extreme events. Under natural conditions, sedimentation increases the elevation of salt marshes, and subsequently the slope increases between the adjacent mudflat and the marsh until it reaches the point of cliff formation (Allen 2000; Van de Koppel et al. 2005; Dijkema et al. 2008). Under favourable conditions, new salt marsh can develop in front of a cliff, resulting in a series of seaward descending terraces, each separated by a small cliff (Allen 1993). As such, cliff formation can be part of a cyclic process of salt marsh succession (Allen 1993; Dijkema et al. 2008). Our findings agree with those of Bilkovic & Mitchell (2013) who studied various effects of erosion prevention by creating a marsh in combination with a stabilizing structure, such as a low stone dam (as at our study sites). Such stabilized salt marshes are currently being implemented in many US coastal states, not only to control erosion but also to restore coastal habitats (see Currin et al. 2010). Bilkovic & Mitchell (2013) found that the vegetation of low and high marsh and restored marshes was similar to natural marshes. In our study we have not investigated other aspects than the vegetation at a single point in time. The comparison of e.g. sediment and fauna between natural and restored salt marshes, and the development of such aspects and vegetation over time have to be investigated in future research.

Because of the presence of dykes along the majority of the Dutch Wadden Sea coast, there is hardly any accommodation space for salt marshes to migrate landwards under sea level rise (Nicholls et al. 2013). It is therefore

likely that in a changing environment more measures are needed to conserve and stabilize the present salt marshes. To combine salt marsh restoration from a nature conservation viewpoint and salt marsh development from a coastal protection viewpoint is a challenging ambition. Our analysis shows that salt marsh vegetation behind low dams is comparable with the vegetation at other locations in the Wadden Sea. Therefore, we conclude that measures targeting salt marsh development as a means of shoreline protection do not frustrate nature conservation ambitions as formulated in the EU Habitats Directive.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Frequency distribution of collection dates of the relevés in the reference set.

Appendix S2. Frequency distribution of Habitat types of the relevés in the reference set.

Appendix S3. List of species found in the Grië NLR data set and the Wadden Sea reference set, with their frequencies.