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Dynamics of temporal wetlands under changing weather conditions

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Bikila Warkineh Dullo

Dynamics of temporal wetlands under changing weather conditions

Colophon

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Dynamics of temporal wetlands under changing weather conditions

PhD thesis

to obtain the degree of PhD at the
University of Groningen
on the authority of the
Rector Magnificus Prof. E. Sterken
and in accordance with
the decision by the College of Deans.

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by

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in Nekemte, Ethiopia

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Chapter 1

Introduction

Bikila Warkineh Dullo

Wet dune slacks

In a dynamic sand dune landscape new dune slacks are created under natural conditions by wind blowing in the sand dunes or by a development of dune ridges that cut off sandy beaches from the sea (Van Dieren 1934). In such dune slacks the groundwater reaches or approaches the surface of the sand (Tansley 1949). Colonization by vegetation begins on a nutrient-poor soil, limited by nitrogen or phosphorus (Lammerts & Grootjans 1997, Lammerts et al. 1998), but soil development is facilitated by colonization and succession, which leads to an accumulation of nutrients and to a lower soil pH, and the subsequent establishment of shrubs and trees (Lammerts 1997, Adema et al. 2005, van den Berg et al. 2005, van der Hagen et al. 2008). A schematic representation of relationships among succession, organic matter accumulation, changes in soil acidity and species richness is given in Figure 1. Young slacks are very nutrient poor and the vegetation cover is low but the diversity of species is relatively high with many life and growth forms such as: annuals, biennials, perennials, shrubs and small trees (Crawford and Wishart 1966, Grootjans et al. 2002). During succession, soil organic matter accumulates in the soil, soil acidity increases (lowering of pH) and species diversity decreases as taller and more productive species become dominant.

However, these interactions are affected by other exogenous environmental variables such as the hydrology of dune slacks, geomorphological features (isolation and size) and the nature of parent material. The nature of the substrate (Kooijman et al. 1998) and the hydrological regimes are important determinants of the vegetation (Grootjans et al. 2006). Several studies in dune slacks in the Netherlands have elucidated adaptation mechanisms of species to this dynamic landscape. Tolerance to anoxia is one important adaptation of early stage dune slack species, especially when the dune slacks are inundated. Plant species with aerenchyma, such as *Schoenus nigricans*, and several *Carex* spp., can thrive under waterlogged, anoxic condition as long as their top shoots are in contact with the atmosphere (Jones 1972). They can counteract the deprivation of oxygen by actively pumping oxygen into the soil, a mechanism called radial oxygen loss (ROL) (Armstrong 1967, Armstrong 1975). *Littorella uniflora* can even release oxygen when entirely submerged. However, late successional species with little or no ROL cannot establish under waterlogged and anoxic conditions.

Under such conditions, high concentrations of reduced sulfide, iron and manganese prevail in the rooting zone, to which late successional species such as *Calamagrostis epigejos* are not adapted (Lammerts 1998). Therefore, under extended waterlogged conditions during winter and spring, early successional species can survive the stress to which late successional species are not adapted (Adema et al. 2003, Adema et al. 2005). Low nutrient demand is another adaptation of early succession species such as *Littorella uniflora*, *Centaurium pulchellum* and *Radiola linoides* in dune slacks (Grootjans et al. 2008). Also when compared to the late successional species early successional sedge species such as *Schoenus nigricans* has lower demand for phosphorous and nitrogen. Unlike late successional species, their growth is not phosphorous limited. *S. nigricans,* which has tussocks up to 35 cm diameter, and is a dominant producer in an early stage of dune slack development, can retain 1g N per tussock for years, which is equivalent to 10-25kg N/ha (Grootjans et al. 1996). In this way it keeps nutrients locked in its biomass and makes them unavailable for the growth of high nutrient demanding late successional species (Grootjans et al. 2008).

Long-term changes

Wet dune slacks, both on the Wadden Sea Islands and along the coast of North-Holland, have suffered from water extraction during the 20th century (van Dijk and Grootjans 1993). In addition to water stress, increased availability of nutrients in the form of nitrogen deposition promoted organic matter accumulation and played an important role in altering both the species composition and the structure of wet dune slacks vegetation. Succession rates have accelerated and productive species, shrubs and small trees have increased, altering the landscape from open to overgrown.

A considerable number of endangered and red list species are found in young dune slacks such as: *Dactylorhiza incarnata, Eleocharis quinquefolia, Epipactis palustris, Equisetum variegatum, Gentianella amarella, Liparis loeselii, Parnassia palustris, and Schoenus nigricans* (Grootjans 1991). High biodiversity associated with non-forested dune slacks (Heslenfeld et al. 2008), the presence of many protected red-list species (Lammerts 1999) and the relatively short life span of natural dune slack habitat (Smith et al. 2007) led to the initiation of several restoration activities. Such activities include both restoration of hydrology through closing ditches or abandoning water abstraction facilities and the removal of nutrients by sod-cutting. The newly created bare soil is a suitable habitat for re-colonization of typical dune slack species from the local species pool and still existing soil seed banks (Bekker et al. 1999). These measures are often followed up by management (mowing or grazing) and by monitoring activities (Grootjans et al 2002) to ensure that the target community is achieved.

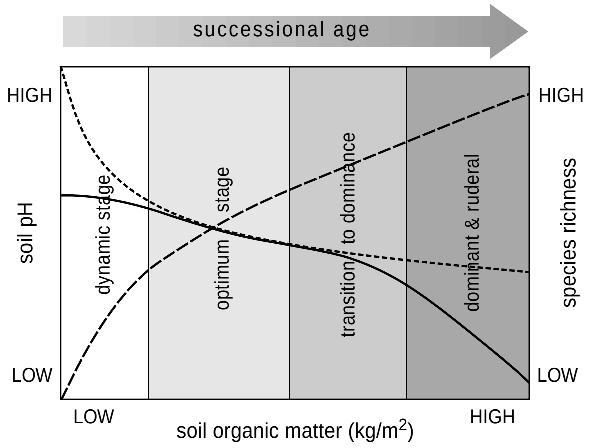


Figure 1. This diagram presents a schematic representation of the three-way relationship among soil organic matter (solid line), soil pH (dotted line) and species richness (dashed line) in dune slacks following sod cutting or when new slacks are formed by nature or human digging out sand dunes and create dune slacks. In each of this case, the initial soil pH will be higher, thus soil pH decrease from the left to the right whereas the soil organic matter increase from the left to the right. The species richness is low when soil organic matter is high and soil pH is low. Thus dune slack species perform best when the soil pH is higher and soil organic matter is lower, not the lowest.

Research interest

Climate predictions indicate an increased precipitation during the winter and less precipitation but more intense rainfall during short periods in summer, which might affect the flooding frequency of coastal wetlands (Christensen and Christensen 2003, Clarke and Rendell 2009, Clarke and Rendell 2011). In the Netherlands, global warming may lead to higher sea water levels along the coastal area, which will lead to increased flooding frequencies in interdunal wetlands (Allen and Ingram 2002). Lowering of the surface due to extraction of gas on the island of Ameland has a similar effect on a more local scale (Dobben and Slim 2012). It is likely that summer flooding will become more frequent and this may have a negative effect on the vegetation of dune slacks, which is adapted to prolong flooding in winter and spring, but to low water levels in the summer (Choi et al. 2008). Depending on the local hydrological and climatological situations, these wetlands can become quite productive within a decade by natural succession, or they can remain in a low productivity state for many decades (up to 80 years) (Adema 2002). The emphasis of this thesis is on the long-term dynamics of vegetation, soil development and effects of weather fluctuations on the hydrology of dune slacks. However, comparable wetlands are also found in mountain areas above the tree line, and this study will also pay attention to such wetlands.

Outline of the thesis

In this thesis, long-term monitoring data sets of both vegetation and environmental variables are used to understand the spatio-temporal dynamics of wet dune slacks (**chapter 2-5**) and in the last chapter of this thesis, a study on functional role of species adaptation in a mountain wetland is presented. A study on long-term colonization and establishment of plant species in dune slacks (Moksloot dune slack on the Island of Texel) after top soil removal is presented in **chapter 2**. We present the results of a monitoring project over 16 years and discuss the effects of landscape level variability, such as isolation and size of the slacks and the hydrological setting on the vegetation development. The difference between the cumulative number of species and the actual number of species established is explained in terms of differences in geomorphological features of the dune slacks. In this chapter dispersal strategies of species colonizing the dune slacks are also considered. Questions are: 1) how does the geomorphological position (isolated vs. non-isolated) and hydrological features (surface or groundwater) affect the pattern and rate of species colonization? 2) How successful is the restoration of the target community (basiphilous dune slack species) under different geomorphological and hydrological conditions?

Chapter 3 deals with the effect of weather conditions on water levels of a dune slack (Koegelwieck on the Island of Terschelling) and the response of vegetation to changes in the fluctuations pattern of the water table. The relationship between groundwater level fluctuations and species compositional change is studied with a combination of long-term hydrological modeling, vegetation monitoring and changes in soil organic matter and acidity. We used four chronosequence sites to answer the following questions: (i) how is species composition influenced by dry years and wet years? (ii) Can large weather fluctuation trigger shifts in successional patterns? (iii) What are the implications for restoration?

Chapter 4 deals with the stability of dune slack plant communities. Literature has shown that the adaptation of certain dune slack species to anoxic conditions may in exceptional cases lead to alternative stable states in pioneer stages of dune slacks. Some species have the capacity to oxidize their rooting zone, which keeps the nutrient availability at a low level. In this chapter, we studied the same chronosequence in the Koegelwieck (see chapter 3) to analyze the stability of different successional stages: pioneer stage, mid-successional stage and mature stage). Questions are: (i) do alternative stable states in dune slacks really occur or are successional stages always in transition. (ii) which successional stages are most stable and why?

Chapter 5 deals with the long-term vegetation development (ranging from 16-77 years) in dune slacks on the Dutch Wadden Sea islands. We used data of an on-going monitoring program associated with several restoration projects. We used several soil chronosequences to study soil and vegetation development. Field measurements consisted of pH, soil organic matter, above ground standing crop and water levels.

Water level regimes (inundation duration and mean minimum water level), were simulated using a hydrological model. Questions are: (i) which factors regulate accumulation rates of soil organic matter (SOM) in wet dune slacks. (ii) how long can pioneer species, such as *Littorella uniflora*, retard the accumulation of organic matter in dune slacks?

Chapter 6 deals with a (cushion) plant species (*Eriocaulon schimperi)*, growing in mountain wetlands of the Bale Mountains in Ethiopia. The species shows adaptations comparable to those of the dune slack species *Littorella uniflora* to release oxygen in the root zone. But *Eriocaulon schimperi* grows in peatlands, and appears to prevent methane emissions in a similar way as was reported from Tierra del Fuego peatlands in South America. Here the cushion plant *Astelia pumila* is slowly invading peatlands by changing key ecosystem functions due to its ability to oxygenate soil layers through radial oxygen loss. Soil and vegetation analyses of these two cushion plants will be compared. Questions are: (i) does the cushion plant *Eriocaulon* schimperi prevent methane emissions? (ii) If so, what are the functional traits that make *E. schimperi* an efficient methane emission suppressor in mountain wetlands?

Chapter 7 provides the overall conclusions

Chapter 2

Long-term success of restoration in dune slacks: vegetation response after large-scale sod cutting

Bikila W. Dullo, Han van Dobben, Eddy Van der Maarel & Albert P. Grootjans

Submitted to Applied vegetation Science

Abstract

Rationale: Due to habitat losses and absence of new dune slack formation, several basiphilous dune slack species have become critically endangered along the NW-European coastal zone. Conservation of these species requires restoration of the hydrology and removal of the decalcified top soil. **Questions**: What are the long-term results of vegetation development after large-scale top soil removal in dune slack wetlands? How does the topographical position (isolated vs. non-isolated) and hydrological features (surface or groundwater) affect the pattern and rate of species colonization? What are the main dispersal factors for species in isolated and non-isolated dune slacks? And how does this affect restoration success? **Location**: Restored dune slacks on the Dutch Wadden Sea island of Texel (53°01'18"N, 4°43'E), the Netherlands. **Methods**: We analyzed vegetation changes over a period of 18 years, in six large permanent plots of 10m × 10m, using multivariate analysis. Changes in soil conditions such as soil organic matter and soil pH were analyzed using univariate statistics. **Results**: In slacks influenced by surface water from other parts of the dune area, the rate of organic matter accumulation was three times higher than in a dune slack influenced by local groundwater discharge, while the soil pH there was lower. In most slacks the species richness of the monitoring plots increased rapidly over the first six years, and then stabilized after that. Large slacks developed higher species richness than small slacks and those close to a local species pool had higher species richness than isolated ones. Generally, the number of newly appearing species was high during the early phase of colonization. There is not much difference in terms of the pattern of species colonization in isolated versus non-isolated slacks. **Conclusions**: The differences in species richness among slacks appear to be related to the flooding regime, isolation of the slacks, availability of a local species pool and the prevalence of dispersal mechanisms. Seepage slacks appear the most suitable for the long term development of basiphilous dune slack vegetation.

Keywords: *Actual species richness; Cumulative species richness; Dispersal vectors; Hydrology; Restoration; Soil organic matter; Succession.*
Nomenclature Van der Meijden (1996).

Introduction

In many European landscapes, including coastal dunes and salt marshes, habitat loss and the absence of new habitat development are amongst the main causes of declining biodiversity. Dunes and dune slack habitats (depressions within the dune landscape) have particularly suffered from human activities such as groundwater extraction, drainage, afforestation, mass recreation and atmospheric nitrogen deposition. These activities have altered the environmental conditions of existing dune slacks and as a result typical dune slack species have declined (Van der Laan 1979, Grootjans et al. 1991, van Dijk and Grootjans 1993, Grootjans et al. 1996, Grootjans et al. 1998, Lammerts and Grootjans 1998, Lammerts et al. 2001, Munoz-Reinoso 2001, Grootjans et al. 2006). Young stages of dune slacks, in particular, show a large variability in vegetation composition, life- and growth forms (Crawford and Wishart 1966b, a) and usually have a considerable number of endangered (Red-list) species. Such young stages have become endangered in the past four decades in most parts of NW Europe in the past four decades (Grootjans et al. 1991). Therefore, restoration of existing dune slack habitats is required to prevent the permanent loss of these species.

Topsoil removal or sod cutting, combined with hydrological restoration, are widely practiced in Dutch coastal dunes to this end (Ernst et al. 1996, Sival and Grootjans 1996). This type of restoration results in a quasi-virginal habitat where colonization and extinction processes can start anew, resembling those of primary succession particularly when the seed bank has been removed. During primary succession, species from local and regional pools colonize the newly created surface (Gorham et al. 1979, Walker and Del Moral 2003). The present study is based on the results of a 16-year vegetation monitoring project following a large-scale sod cutting project on the Dutch Wadden Sea Island of Texel. This project started in 1993 and was aimed at restoring typical dune slack vegetation after the closure of a groundwater abstraction facility on the island. The area consists of about 250 hectares of dunes and dune slacks. The dune slacks differ in landscape setting. Some are originally blow out slacks, which are relatively small, isolated and fed by nutrient poor groundwater. Other slacks are larger and regularly flooded by surface water from surrounding areas, which may add many floating seeds, but also dissolved minerals to the newly sod cut slacks.

Due to its size the project offers a unique possibility to study some landscape ecological aspects of restoration, isolation versus non-isolation, groundwater-fed versus surface water-fed. We expect to find differences in terms of species colonization, establishments and species dispersal mechanisms among these dune lacks due to their differences in geomorphological and hydrological differences. We expect that hydrochory in non-isolated dune slack is important, due to regular flooding with surface water. Few recent studies have used the concepts derived from the theory of island biogeography for a study of species turn-over on a small scale in dune slacks

(Bossuyt and Hermy 2004). Similarly, we used area and geomorphological positioning of the dune slacks since they could determine species colonization. In line with the theory of biogeography, size could determine species richness in dune slacks whereas isolation could affect species colonization. On the other hand, flooding with surface water could promote species colonization. By looking at cumulative species richness, which is the number of all species that colonize a given site whether it is extinct from the plot or not, we can see if there is a difference in species colonization between isolated and non-isolated dune slacks but also between surface water flooded and non-flooded dune slacks. The actual species richness of a given site tells about the surviving species at that given time, species that were able to withstand the prevailing environmental conditions. The difference between the two indicates the number of species that went extinct from the site probable due to harsh environment or harsh completion.

The conceptual framework for the restoration and assessment of this and similar projects is presented in Figure 1. The concept relies on an assumption that if old species assemblages and the organic topsoil are removed through sod cutting, and hydrology is successfully restored, new and desirable species assemblages will colonize the dune slacks. Thus, the study of the pattern of species colonization and establishment and the dynamics of the species assemblage over time can be used to assess the success of restoration. After how many years will the vegetation composition be adapted to the new environmental conditions? We expect that the rate of colonization was higher than the rate of local extinction during the early stage of vegetation development and approached equilibrium during the later stages of vegetation development as this was predicted by the theory of island biogeography (MacArthur and Wilson 1967). We expect that succession will be slower in groundwater fed slacks than in surface water influenced slack because studies demonstrate that the calcareous groundwater stimulate nutrient mineralization and thus keeping buildup of soil organic matter at low level and maintaining high soil pH (Adema et al. 2002, Lammerts et al 1995). These two conditions elongate the life span of early successional stages in dune slacks thus slowing vegetation successions.

The following questions are addressed: 1) how does the geomorphological position (isolated vs. non-isolated) and hydrological features (surface or groundwater) affect species colonization? 2) How successful is the restoration in terms of endangered (basiphilous dune slack species) under different geomorphological and hydrological conditions? 3) What are the main means of dispersal for species in isolated and non-isolated dune slacks? And 4) what are the implications for management?

Methods

The study area, known as 'Moksloot valley', consists of approximately 250 ha. of dunes and dune slacks and is located in the south-western part of the Dutch Wadden Sea island of Texel (53°01'18"N, 4°43'E; Figure 1b). This area has a large number of both primary and secondary dune slacks. Primary dune slacks develop behind newly formed dune ridges on a sandy beach. Secondary dune slacks are formed by wind blowing until the groundwater level is reached. The Moksloot area originated c. 1770 when a long dune ridge was formed which enclosed a former beach plain. Around 1850 the largest slacks had an abundance of basiphilous pioneer and salt marsh communities (Grootjans et al. 2001 and references therein).

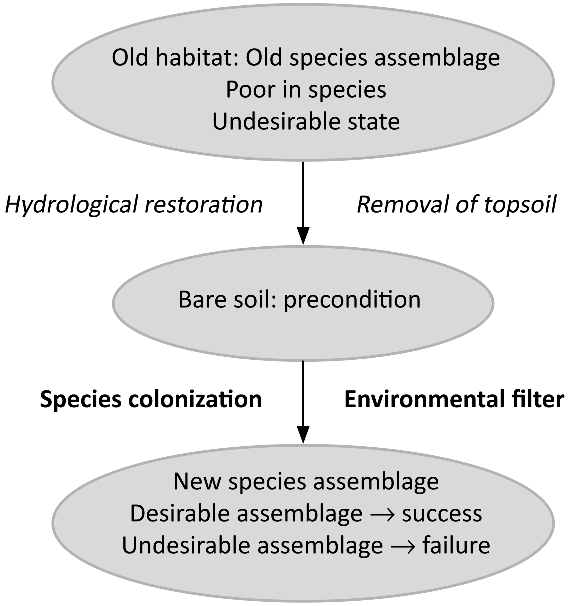


Figure 1. A simplified theoretical model of restoration research of old dune slacks along the Dutch coast. Italics indicate intervention and bold indicates processes.

Later on the slacks have become much drier due to drainage and extraction of groundwater for the public water supply since 1956, but also due to a retreat of the fore dunes along the west coast of the island. In 1991, a vegetation survey was carried out in order to assess the restoration prospects of the area. At that time eutrophic reed beds with *Phragmites australis*, *Cladium mariscus* and *Carex disticha* dominated the lower part of the slacks, while the higher parts of the slacks were primarily dominated by tall grasses such as *Calamagrostis epigejos* and shrubs such as *Salix repens* (Grootjans et al. 2001).

In 1993, groundwater extraction on the island was terminated. This created an opportunity for restoration of the damaged dune slacks. In July and August 1993 the organic layer, together with the vegetation, was removed by top soil removal over an area of approximately 35 ha. Depending on the thickness of the organic layer, removal depth varied from 10 to 40 cm. In 1995, a small herd of highland cattle and Exmoor ponies were introduced to prevent a rapid re-growth of vegetation. One small sand-blown valley (B in Figure 2) was fenced to prevent grazing and trampling by cattle and ponies. In 1994, six monitoring plots of 10m × 10m were established in five dune slacks of different size and hydrological setting. The slacks were considered groundwater fed when precipitation of iron oxide was observed along the valley margin. When the electrical conductivity was higher than 70mS.m^{-1}, the slacks were considered to be influenced by surface water, which is not only calcareous, but also slightly brackish (Grootjans et al. 2001). Slacks were further differentiated according to their proximity or distance to existing neighboring slacks, which could serve as a source of seeds. Isolated slacks are separated from their neighboring slacks by sand dunes, while non-isolated dune slacks are situated in a single dune valley with exfiltration in one end and infiltration in the other end. Slacks also differed in the number of resting birds and grazing animals which have impacts on the vegetation. A detailed description of the study area can be found in Grootjans et al. (2001) and in Table 1.

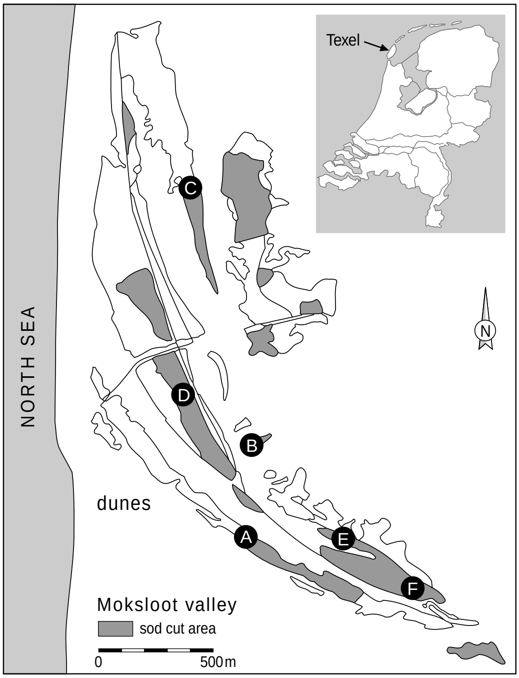


Figure 2. Locations of permanent plots that were monitored (A-F) in the Moksloot area on the Wadden Sea Island of Texel. Sod-cut areas are shaded (Grootjans et al. 2001). Upper right small box: position of Texel in The Netherlands.

Vegetation monitoring

Figure 2 shows the location of the six monitoring plots. We show and discuss results of three isolated slacks (A-C) and three non-isolated (D-F) slacks. Vegetation monitoring was done in July and August each year from 1993 onwards. The percentage cover of each species on each plot was estimated according to a decimal scale (London 1975). Furthermore, species were recorded in the sand dune and dune slack complex around the sod cut slacks, which we consider as the local species pool in our analysis. The number of species found in the surrounding area was 232.

Soil monitoring

In addition to the vegetation monitoring, soil samples were taken five times over the course of the monitoring period and the organic matter content and soil pH were measured in the laboratory. Soil organic matter (SOM) was measured as weight loss after ignition for 4hrs at 550°C. The soil pH was measured in fresh soil samples (0-5cm) by mixing a volume of fresh soil sample (one to five) with aqua dest.

Species data analysis

First, the actual species number per plot per year was determined based on the annual records of plant species on permanent plots (10m × 10m). Also, the cumulative species richness of each plot was calculated by taking the species number in year 1 as a basis and adding the newly arrived species in subsequent years (van der Maarel and Sykes 1993). For instance cumulative species richness in year two includes the actual species richness in year one and the newly arrived species in year two. This way all the newly arrived species in n year is added onto all the species that already arrived in year n-1.

Table 1. Some characteristics of six dune slacks that were monitored in Moksloot. Symbols: – = absent, + = present and ++ = present in large numbers.

	A	B	C	D	E	F
Size of the slack (in ha)	2.57	0.62	3.78	5.2	7.31	0.62
Distance to nearby seed source (in m)	167	133	233	133	50	83
Influenced by basic surface water (EC > 600µS/cm)	–	–	+	+	+	+
Nearby seed sources	++	–	–	++	+	+
Fe precipitation along the margin of the valley	–	+	+	–	–	–
Resting birds	+	–	–	+	+	+
Grazing	+	–	+	++	++	++

Dispersal vectors were used to explain differences in colonization rates. Possible dispersal mechanisms per species were inferred from Cappers (1994), Van Dorp (1996), Boedeltje et al. (2003) and Pollux (2007). We distinguished three major dispersal mechanisms; anemochory (dispersal by wind), hydrochory (water dispersal) and zoochory (dispersal by animals). Species that employ more than one dispersal mechanisms are categorized in a separate category (mixed strategy). Which dispersal mechanism is more important in isolated dune slacks and which is more important in non-isolated dune slacks? Between isolated and non-isolated dune slacks, are there differences in terms of dispersal mechanisms? Paired mean difference analysis between identical dispersal types in isolated and non-isolated dune slacks were performed using SPSS 20.

The direction of development of permanent plots, which indicate successional pathways of vegetation in each dune slack, was studies by using CANOCO 4.5 (Ter Braak Šmilauer 2012). The analysis was based on percentage cover-abundance. The relationship between species and environmental factors were analyzed using redundancy analysis (RDA). Age of the vegetation, organic matter and soil pH measurements were used to describe the variability of species composition on the permanent plots.

Environmental data analysis

Organic matter accumulation and changes in soil pH were measured repeatedly in 1994, 1996, 1999, 2002 and 2009. Whether these factors showed increasing or decreasing trends are shown graphically. For each permanent plot we performed statistical test to see if the trends over time are significant or not. For each of the plots we compared soil pH of 1994 to those of 1996, 1999, 2002, and 2009. Similarly we compared pH of 1996 to those of 1999, 2002 and 2009. Also pH of 1999 was compared to that of 2002 and 2009 and finally pH of year 2002 to 2009. For organic matter we did the same. These tests were performed on the significance of changes between the means using one way ANOVA.

Results

Soil monitoring

Over the first 9 years, between year 1994 (the start of monitoring) and including year 2002, for both isolated and non-isolated dune slacks the soil pH showed an increasing trend with the highest values recorded in 2002 (Figure 1 and Appendix 1). On plot A, which is located in heathland, soil pH increased significantly between 1994 and 2002 and then it declined significantly between 2002 and 2009. On plot B, statistical tests indicate that only year 2002 is significantly different from the rest. Plot C, which is situated in seepage dune slack has pH levels higher than 6.5 (Figure 3). Similar to plot A and B, soil pH significantly increased between 1994 and 2002 while between 2002 and 2009 it declined significantly on plot C (Table 2). On plot D, similar to the other plots the pH significantly declined. On plot E, the soil pH was always higher than the rest of the plots in non-isolated dune slacks and in terms of difference between the years, pH levels of 1994 and 1996 were significantly different from both 2002 and 2009. Plot F has pH values fluctuating around 5 and between 2002 and 2009, the pH declined significantly (Figure 3, Appendix 1). In general, the soil pHs in calcareous surface water influenced dune slacks are higher in non-isolated dune slacks except slack F, which is located in an infiltration zone. In isolated dune slacks, heathland slack (A) has lower pH while seepage slacks have the highest pH.

In all slacks, including those with seepage and surface water, SOM was low over the first five years, but thereafter SOM in surface water fed slacks increased rapidly (Figure 4). After about 15 years, SOM in surface water fed dune slack (D-F) became about three times higher than in seepage slacks (C). On plot A, the increase in organic matter was not significant between 1994 and 2002 but between 2002 and 2009 it increased significantly from the rest of the years (Figure 4, Appendix 2). Plot B also shows a similar trend with plot A except that the organic matter on this plot was lower than that plot A in 2009. Plot C, which is located in a seepage dune slack, the increase in organic matter was less than 2 kg/m$^{2.}$ In plot D, the organic matter content decreased significantly between 1994 and 1999 but after 1999, it increased significantly from less than 2 kg/m^2 to more than 12 kg/m^2. Plot E and F reveal the difference between an exfiltration zone and infiltration zone in one dune slack respectively. Plot E accumulated less organic matter than plot F with a significant increase in organic matter between 2002 and 2009. Plot F also showed a significant increase in organic matter accumulation in 2009, which is significantly different from the rest of the years.

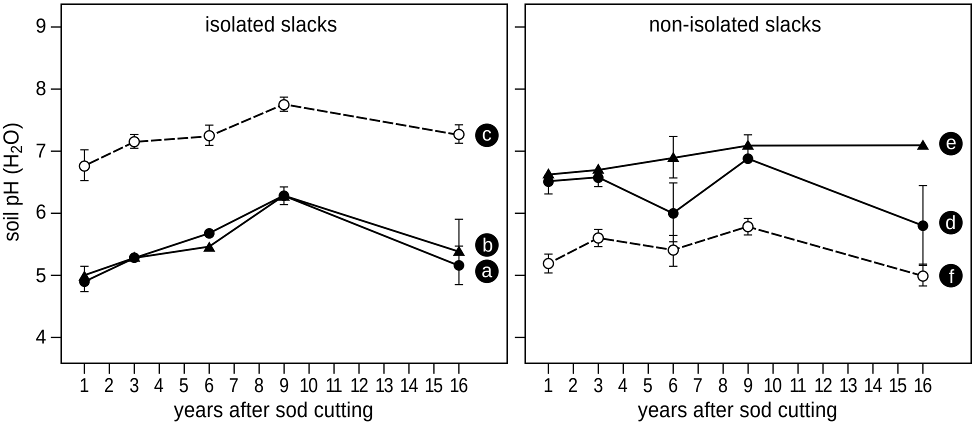


Figure 3. Changes in soil pH in three isolated dune slacks (A-C) and three non-isolated dune slacks (D-F) following top soil removal.

Vegetation monitoring

Actual species richness

The actual species richness for each site is determined in an equal plot sizes of 10m^2. In the isolated groundwater fed slack (C) the highest actual species richness recorded in the permanent plot, (55 species) was reached already within one year (Figure 5).

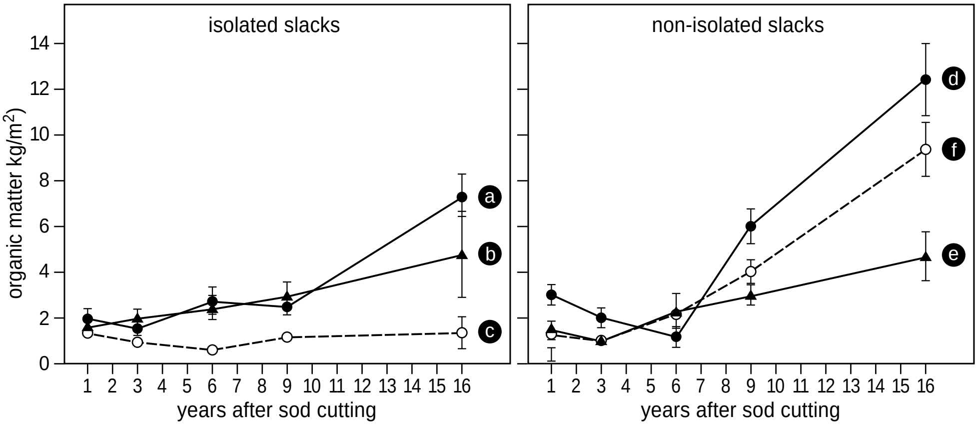


Figure 4. Changes in soil organic matter (SOM) in three isolated dune slacks (A-C) and three non-isolated dune slacks (D-F) following top soil removal.

The two other isolated slacks (A and B) started with a low species richness and showed an increasing trend over the first five years. The peak species richness in these two plots is below 60 species, which further declined to less than 35 species after 18 years of monitoring.

The surface water fed dune slacks (D-F) showed an increase in species number over the first six years, except site E (located in an infiltration area) which has a high initial species number but only a small increase after the first five years. The large non-isolated dune slack D has the highest species richness compared to the other non-isolated dune slacks and small isolated dune slacks. The species richness in this site remained high, more than 75 species, while in site E it decreased from about 70 species six year after sod cutting to around 50 species in later years. The infiltration site F showed a weak decrease after 5 years, but maintained about 55 species over the monitoring period.

Cumulative species richness and species dynamics

Cumulative species richness (Figure 5) ranges from 93 species on plots in small slacks (A) to 125 species on plots in large slacks (D). However, this difference between small slacks and large slacks in terms of the total number of species that have arrived on the plot is not very large. Overall, plots influenced by surface water tend to approach a saturation level in two to four years following sod cutting. For the plots not influenced by surface water during the growing season (A & B), the cumulative species richness approached a saturation level after six years. Seepage slack (C) lost the most species while the largest slack D lost the least species.

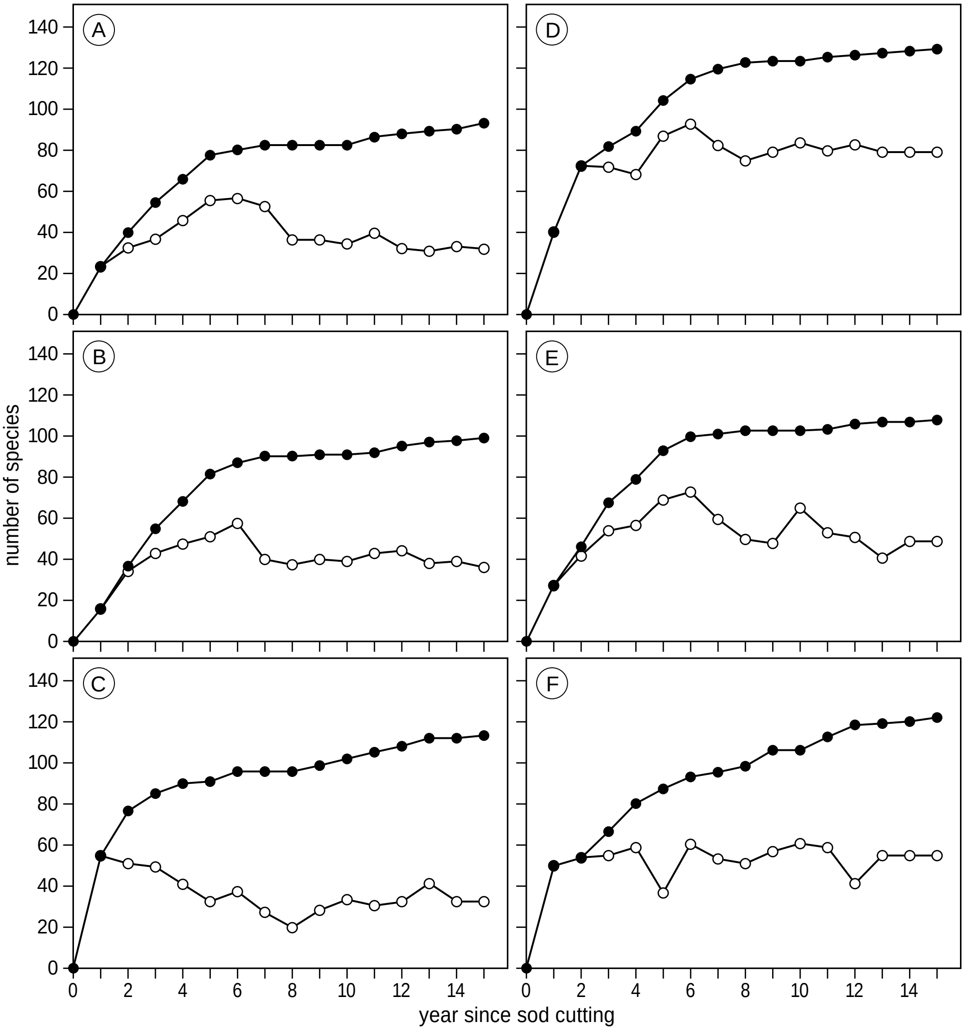


Figure 5. Patterns of cumulative and actual species richness in six permanent plots, three isolated (A-C) and three non-isolated (D-F). The lower curve in each graph indicates the actual species richness, i.e. the actual number of species recorded on the permanent plots in the corresponding year after the sod cutting. The upper curve shows the cumulative number of species in the plots at that particular year.

The species dynamics (Immigration – Extinction) during the monitoring period (1994-2008) is shown below (Figure 6). The dynamics varies from plot to plot but during the early stages of vegetation development, immigration is generally higher than local extinction but for plot C, the rate of extinction was higher during the early stage of colonization. After the initial high immigration, species tend to fluctuate over the year, with more fluctuation in non-isolated plots and less on the isolated plots. For the isolated plots (A-C), the species dynamics reached a more or less stable stage for all the plots within seven years after sod cutting. However, the fluctuation continues in the non-isolated plots (D-F).

Vegetation development

Figures 7 and 8 show the results of a Redundancy analysis (RDA), and the first axis explain about 16% of the species variation and the first two axes combined explained 26%. The direction of succession of the permanent plots and the assemblage of species along their line of development are indicated in the graphs of axis 1 and axis 2. Plots in sites where the soil pH is lower (A, B and F) developed in a similar direction. On these sites, heath species and acidophilous species such as *Erica tetralix,* and *Empetrum nigrum* are the dominant species. Similarly sites with high pH (C, D and E) developed in a similar direction. Not the isolation of the dune slack but the age of the vegetation and soil organic matter determine the direction of the succession.

Species dispersal

Table 2 shows that the non-isolated dune slacks have a higher number of species that reached the monitoring plots than the isolated ones. The predominant dispersal mechanisms appear to be anemochory, hydrochory and zoochory. Most of the dune slack species, however, appear to disperse in several ways (mixed dispersal strategy). The percentage of species dispersed through both anemochory and hydrochory are higher in non-isolated dune slacks (Table 2). Dispersal by animals, zoochory does not show much difference between isolated and non-isolated dune slacks.

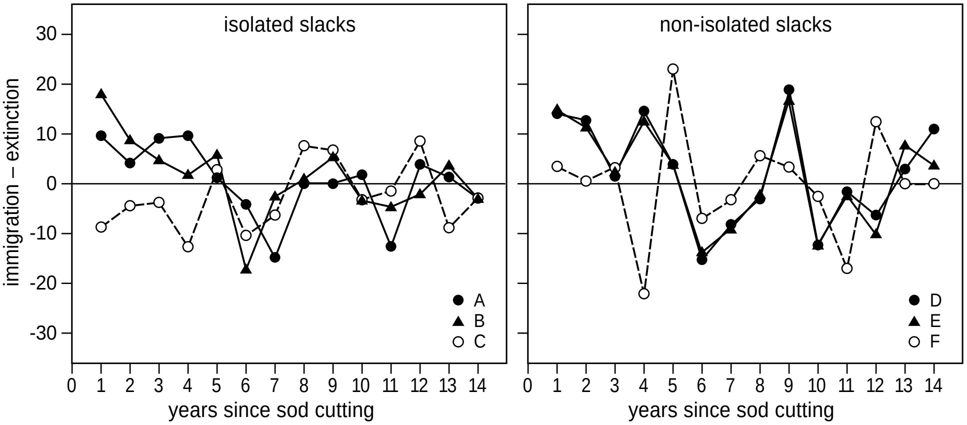


Figure 6. Dynamics of species establishment (I-E; I = Immigration and E = Extinction) over the years calculated for three isolated (A-C) and three non-isolated (D-F) dune slacks. The top graph represents those slacks which are not isolated from the local species pool and the bottom represents those slacks that are isolated from the local species pool. Legends in both graphs refer to individual permanent plots.

Discussion

We expected to find differences in soil development under different hydrological and geomorphologic conditions because some previous studies showed low organic matter accumulation in seepage dune slacks (Berendse et al. 1998, Lammerts and Grootjans 1998, Adema et al. 2005, Bakker et al. 2005, Bodegom et al. 2005, Bakker et al. 2006, Bakker et al. 2007). We found that organic matter builds up rapidly in surface water fed slacks, while the build-up of organic matter is low in groundwater fed dune slacks. This is consistent with other studies in dune slacks that showed that soil acidity and organic matter accumulation rates are associated with the hydrological setting of the slacks (Grootjans et al. 1991, Lammerts and Grootjans 1998, Adema and Grootjans 2003). The very high soil organic matter accumulation rate in the surface water fed slack (D) is an indication of high nutrient input from surface water and the presence of many resting birds and cattle. In the isolated slacks A and B the initial soil pH was acidic, indicating that the pH was not yet buffered by calcareous groundwater in 1994. After ten years the pH had increased considerably, but after 16 years it dropped again to ca. 5. Apparently the groundwater discharge was not sufficient to counteract the acidifying processes associated with increased organic matter in the top soil (Walker & Del Moral 2003; Jones et al. 2008). In the non-isolated slacks D and F a similar drop in pH can be observed after 16 years.

Species colonization dynamics

Grootjans et al. (2001) reported that more than 96% of the soil seed bank had disappeared after sod cutting in this dune slack. Hence, this development resembles a primary succession (Gorham et al. 1979). The distance between the diaspore source of most species and the target plots varies from 50 to 233 meters (Table 1). After a disturbance, such as sod cutting, the effective dispersal distance could vary depending on the scale and magnitude of the disturbance that has led to the creation of the new surface (Glenn-Lewin and van der Maarel 1992, Turner et al. 1998).

In slack C, where strong seepage occurs (Grootjans et al. 2001), newly arrived wet basiphilous dune slack species are the dominant group while, in contrast, eutrophic species are dominant in surface water influenced slacks. Differences in grazing intensity could also play a role, because this slack is smaller, and has less open water. The grazing intensity and presence of water birds, therefore was less. The suitable environment for the target group, wet basiphilous dune slack species, appeared to be present only in the groundwater-fed slacks. Here, basiphilous species have a long lifespan (Lammerts 1997, Lammerts and Grootjans 1998, Lammerts et al. 2001). This is probably because exfiltration of base rich groundwater keeps the nutrient availability low (Lammerts and Grootjans 1998). This indicates that regardless of the stochastic nature of species arrival in the plots, environmental conditions determine which species establishes and survives.

The variation in environmental and colonization conditions causes the pattern of species accumulation to vary as well. First, the initial species number varies from plot to plot. The initial number of species is remarkably high in almost all plots (compared to sod cut experiments on the mainland; Verhagen et al. 2001). This is probably because all dispersal mechanisms were quite effective on the island of Texel, even though some studies suggest the failure of dispersal as a cause for the loss of species in Northwest Europe (Ozinga et al. 2005, Ozinga et al. 2009). However, the dispersal vector presented here results from a post facto analysis based on data obtained from the literature (see methods). The data are not detailed enough, for instance no distinctions were made among various dispersal vectors by animals (internal via manure, external via feather, and hair). Therefore, it does not necessarily mean that the species did arrive at the plot by the stated vector, even if this is implied.

Nevertheless some interesting results appear. In the isolated slacks, hydrochory appears to be less important than zoochory and anemochory, which could be due lack of exchange via surface water flooding. On the other hand, hydrochory in non-isolated dune slacks is significantly different from that in isolated slacks, which is in line with our expectation because surface water influence is predominant in non-isolated dune slacks.

The size of the slacks also appears to have an effect on cumulative species richness, i.e. large slacks (D) have more cumulative species than the smaller ones. Overall, the cumulative species richness on the individual plots decreased gradually and the slope of the curve became flattened. However, species colonization becomes saturated after six years in isolated slacks while species continue to colonize at higher rate on non-isolated and surface water fed slacks (D, E & F). It appears that two factors, isolation and occurrence of surface water play an important role in determining colonization whereas discharge of groundwater plays a filtering role in species establishment in dune slacks. Groundwater fed slack C lost most species and became dominated by wet basiphilous dune slack species. In addition, our results agree with the theory of island biogeography (MacArthur and Wilson 1967). As the theory predicts, the rate of colonization was higher than the rate of local extinction during the early stage of vegetation development for all slacks except slack C, and it approached equilibrium during the later stages of vegetation development. However, in plots highly influenced by surface water, grazing and resting birds, the species diversity is high but the difference between local immigration and extinction remains chaotic and does not seem to stabilize. Organic matter and soil pH have a significant effect on the development of dune slack vegetation.

Table 2. The table gives the number of species dispersed into the dune slacks through different dispersal mechanisms. The percentage of species dispersed by a given dispersal mechanism is provided in parenthesis next to the number of species dispersed via that mechanism. * and ** indicates that the dispersal mechanism is significantly different in isolated slacks compared to non-isolated slacks.

	Isolated slacks			**Non-Isolated slacks**		
Dune slacks	**A**	**B**	**C**	**D**	**E**	**F**
Dispersal types						
Anemochory	20 **(18)**	20 **(18)**	19 **(17)**	26 **(24)**	30 **(28)**	23 **(21)**
Hydrochory**	10 **(9)**	15 **(14)**	19 **(17)**	33 **(30)**	19 **(17)**	30 **(28)**
Zoochory	21 **(19)**	21 **(19)**	24 **(22)**	27 **(25)**	21 **(19)**	25 **(23)**
Mixed*	23 **(21)**	27 **(25)**	33 **(30)**	40 **(37)**	33 **(30)**	34 **(31)**
No info.	17 **(16)**	16 **(15)**	14 **(13)**	16 **(15)**	14 **(13)**	18 **(17)**
Total number of species**	91	99	109	142	117	130

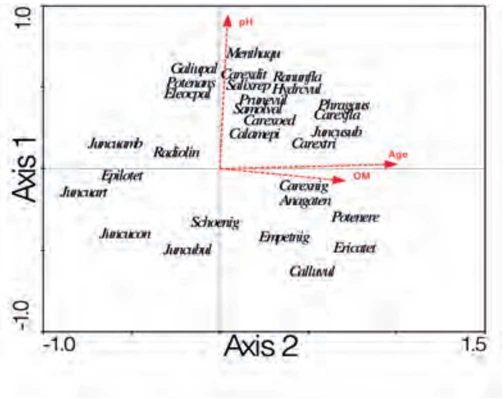


Figure 7. RDA analysis of permanent plots in Moksloot dune slacks. The species were selected based on their weighted range from 5% to 100%. *Anagallis tenella*= Anagaten, Calamagrostis epigejos, *Carex disticha*= Carexdit, Carex flacca = Carexfla, *Carex nigra = Carexnig, Carex oederi ssp. Oederi = Carexoed, Carex trinervis = Carextri, Calluna vulgaris, Eleocharis palustris = Eleocpal, Empetrum nigrum = Empetnig,, Erica tetralix = Ericatet, Galium palustre = Galiupal, Hydrocotyle vulgaris = Hydrovul, Juncus articulatus = Juncuart, Juncus bufonius = Juncubuf, Juncus conglomeratus = Juncucon, Juncus subnodulosus = Juncusub, Mentha aquatica = Menthaqu, Phragmites australis = Phragaus, Potentilla anserina = Potenans, Potentilla erecta = Potenere, Prunella vulgaris = Prunevul, Radiola linoides = Radiolin, Ranunculus flammula = Ranunfla, Salix repens = Salixrep, Samolus valerandi = Samolval, Schoenus nigricans = Schoenig.*

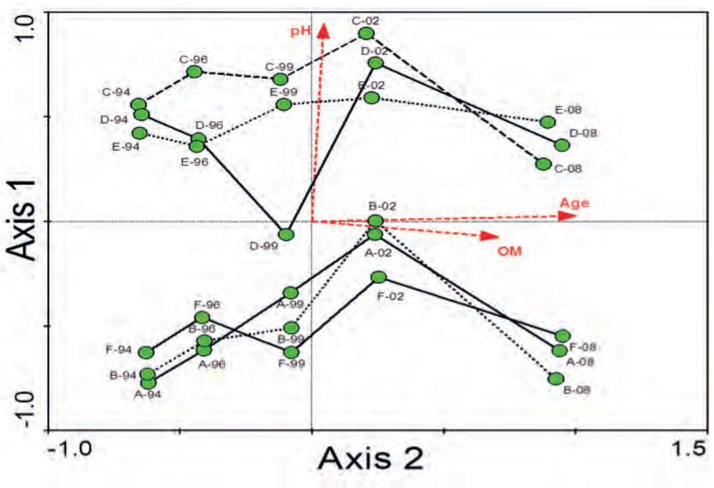


Figure 8. RDA analysis (same data as presented in Figure 7) of permanent plots in Moksloot dune slacks. Poly lines indicate the directions of movements of the permanent plots over the years from 94 (1994) to 08 (2008).

Uncertainties in restoration

The species accumulation suggests a high rate of species mobility and colonization in the early phase of vegetation development and a subsequent loss of species due to environmental filtering. In addition, the stochastic nature of species mobility and establishment implies that restoration projects aiming at promoting certain species might not work even when suitable habitat conditions have been created. When the hydrology of dune slacks has been restored, seepage slacks favor the establishment of basiphilous vegetation and allows its persistence. Surface water will trigger a rapid succession of dune slack vegetation in which eutrophic species will reach dominance. Therefore, restoration of wet basiphilous dune slack species is probably not feasible when there is a high input of surface water from the surrounding landscape. Therefore, frequent removal of organic matter should be incorporated in the future restoration of basiphilous dune slack species in order to keep the nutrient load at a low level. This is because more intense rainfall is expected along the coast of NW Europe, which might lead to more frequent surface water flooding (Walther et al. 2002, Christensen and Christensen 2003) and thus a higher nutrient load. This may also indicate that restoration of a historic ecosystem might not be possible any longer and therefore calls for a "futuristic restoration", which could mean a promotion of natural dune slack formation through wind activities (Choi 2004, Young et al. 2005, Harris et al. 2006, Choi 2007, Choi et al. 2008), and which should incorporate realistic and dynamic goals of restoration projects.

Acknowledgments
Between 1994 and 2000, funding for the Moksloot monitoring project was provided by the Dutch Government within the framework of the Dutch Survival Plan of Nature (OBN). The continuation of monitoring was made possible by money provided by the Dutch Gas and oil Company (NAM). We would acknowledge all persons involved in this project from vegetation mapping to soil sampling, particularly Henk Everts and Nico de Vries who managed the data base and were involved in all monitoring activities.

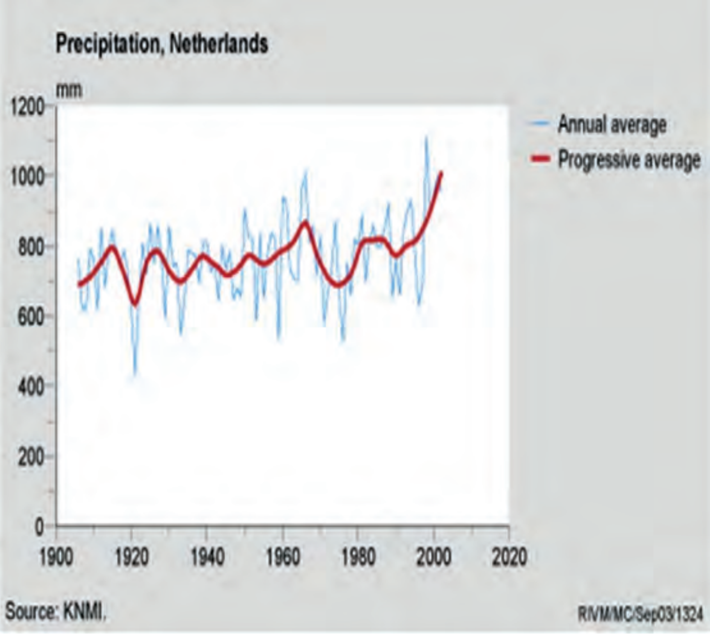
Appendix

Table 2. Results of comparisons of changes mean of soil pH using one-way ANOVA to show the significance of difference in means over time on each permanent plot.

Comparison of means of soil pH of permanent plots over time							
Years compared		A	B	C	D	E	F
1994	1996	*	ns	***	ns	ns	*
	1999	***	ns	***	ns	ns	ns
	2002	***	***	***	ns	*	**
	2009	ns	ns	***	*	*	ns
1996	1999	ns	ns	ns	ns	ns	ns
	2002	***	***	***	ns	*	ns
	2009	ns	ns	ns	**	*	***
1999	2002	**	**	*	ns	ns	ns
	2009	*	ns	ns	ns	ns	*
2002	2005	***	**	***	***	ns	***
*The mean difference is significant at $p = 0.05$ level, **at > 0.001, & ***at < 0.000							

Table 3. Results of comparisons of changes mean of soil organic matter using one-way ANOVA to show the significance of difference in means over time on each permanent plot.

Comparison of means of organic matters of permanent plots over time							
Years compared		A	B	C	D	E	F
1994	1996	ns	ns	ns	*	ns	ns
	1999	ns	ns	**	***	ns	ns
	2002	ns	ns	ns	***	***	ns
	2009	**	***	ns	***	***	***
1996	1999	ns	ns	ns	ns	**	ns
	2002	ns	ns	ns	***	***	ns
	2009	**	***	ns	***	***	***
1999	2002	ns	ns	*	***	*	ns
	2009	*	***	**	***	***	***
2002	2005	*	**	ns	***	***	**
*The mean difference is significant at $p = 0.05$ level, **at > 0.001, & ***at < 0.000							



Source: KNMI.

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Chapter 3

Temporal dynamics of wet dune slacks: effects of weather on species dynamics

Bikila W Dullo, Camiel J.S. Aggenbach, Han van Dobben & Albert P. Grootjans

Abstract

Successful restoration of coastal wetlands is a complex process that requires a comprehensive approach based on a thorough knowledge of dune systems. This paper investigates the effect of weather fluctuations, i.e. an increase or a decrease of precipitation on the restoration success of basiphilous dune slack vegetation. We hypothesized that the observed meteorological changes has caused an accelerated succession toward more productive but species-poor stages that have become much more common all along the Dutch coast. We investigated the relationship between measured environmental variables such as pH, organic matter, different management regimes, groundwater levels and precipitation regimes by using multivariate analyses. Our result shows a rapid acidification process associated with intense spring or summer rainfall, high rates of organic matter accumulation within a few years and rapid establishment of competitive tall grass species and shrubs. Therefore, an increase in precipitation could lead to a feedback mechanism by raising water levels, decreasing soil pH and facilitating organic matter accumulation and thus facilitating the establishment of competitive species. We conclude that restoration projects should take the unpredictability of weather conditions into account and should aim at restoration approaches that mimic natural dune forming processes.

Keywords: *climate, groundwater level, hydrology, restoration, vegetation succession.*

Introduction

The aim of this paper is to elucidate the effect of an aspect of weather fluctuation, i.e. precipitation, on the development and succession of wet dune slack plant species. Dune slacks are low lying wetlands within sand dunes complexes, which mainly occur in coastal areas, but they can be present far from the coast as well (Clarke and Rendell 2009, Clarke and Rendell 2011, Provoost et al. 2011). In terms of geomorphology, dune slacks are categorized as primary or secondary, based on how they were created; primary if a beach plain is enclosed by dune ridges, and secondary slacks when they were formed due to wind blowing, creating depression within the sand dunes (Ranwell 1959). According to Ranwell, dune slacks can be classified into three categories based on the relationship between vegetation composition and the level and seasonal fluctuations of the water table (Ranwell 1959, 1960a, 1960b). These are: (i) slacks where the water table never falls 1 m below surface, (ii) slacks where the water table falls in the range of 1 m and 2 m below surface and only deep-rooted plant species reach the water and (iii) slacks where the water table does not have an influence on the vegetation because it is too deep.

In the Netherlands, dune slacks constitute about 6.5% of the Natura 2000 habitats and in the coastal area they are among the most studied habitat types (Houston 2008). This study will focus on dune slacks on one of the Dutch Barrier Islands (Terschelling). Dune slacks in the Wadden district in the Netherlands often serve as last refugia for endangered and rare plant species and community types such as *Junco baltici-Schoenetum nigricantis*. These species often thrive in calcareous habitats where either the soil lime content is high or where calcium rich groundwater from the deep soil reaches the surface (Lammerts & Grootjans 1998).

The flow chart below (Figure 2) depicts the dynamic interaction among environmental factors and vegetation of dune slacks. The availability of nutrients (mostly derived from organic matter), water level and flooding dynamics, and soil pH all influence the species composition and the productivity of the vegetation, as shown in many studies (Van der Laan 1979, Grootjans et al. 1991, Olff et al. 1993, Sival and Grootjans 1996, Lammerts 1997, Lammerts et al. 2001, Sýkora et al. 2004, Adema et al. 2005). However, climatological models predict increased precipitation in the coastal areas, in particular in the Wadden sea areas (Noest et al 1995, Clarke and Rendell 2009, Clarke and Rendell 2011). During summer, rain showers will be more intense, leading to increased temporary flooding in dune slacks (KNMI 2003).

The present paper focuses on possible effects of climate change and coastal expansion vegetation on the vegetation development in restored dune slacks on the Wadden Sea island of Terschelling. The effects of restoration measures (top soil removal) have been monitored for over 20 years since 1990, including changes in species composition (every year) and changes in water level (from 1990 to 1996), and changes in soil organic matter (SOM), and pH (1991, 1996, 1999, 2003 and 2008). We used a hydrological simulation model to standardize and predict water level regimes (1985-2010), using measured precipitation, evaporation, site elevation relative to sea level and water level data as explanatory variables. We address the following questions: (i) What are the important factors that determine water levels regimes in Koegelwieck dune slacks and how is the species composition of the vegetation influenced by these factors? (ii) Can large weather fluctuation trigger shifts in successional patterns? (iii) What are the implications for restoration?

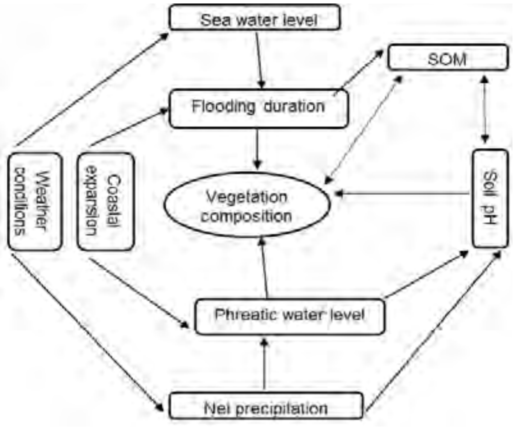


Figure 1. Possible interactions among environmental parameters, weather conditions and vegetation within the dune and dune slack landscape.

Methods

Study site description

The study site is located on the Wadden Sea Island of Terschelling, the Netherlands, in an area called "Koegelwieck" (53°24'N, 5°20'E). The Koegelwieck is a secondary dune slack of about 50 ha. It was formed between 1825 and 1865 (Van Dieren 1934) when large dunes were blown away and a large flat plain remained. Between 1915 and 1980 much coastal erosion occurred and the foredunes retreated about 150 meters, which resulted in a drop in groundwater level in the Koegelwieck (Grootjans et al. 1996). Since then coastal expansion occurred. Vegetation development in the Koegelwieck started between 1910 and 1920. Further habitat descriptions can be found in (Lammerts 1999 and Sýkora et al. 2004).

Species-rich basiphilous plant communities disappeared in 1950 from the Koegelwieck and a series of sod-stripping experiments were initiated in 1956, to see if the typical dune slack vegetation (*Junco baltici-Schoenetum nigricantis* community type) could be regenerated. Because this experiment was quite successful, sod-stripping was repeated in 1959, 1986, 1990, and 1995 (Lammerts 1999). These sod-cut plots were situated next to each other, providing a chronosequence of sites with known vegetation ages.

Vegetation, soil organic matter and pH data

Regular monitoring activities in the area started in 1990 (Lammerts 1999,, Grootjans et al. 1998, Grootjans et al. 2002, Sýkora et al. 2004, Adema et al. 2005). Soil samples (0-15 cm, depending on the depth of the organic layer) were collected in 1991, 1993, 1996, 1999, 2003 and 2008. The samples were dried and the percentage organic matter was measured by loss ignition (LOI). Similarly, the soil pH was measured in the laboratory right after dissolution of fresh soil samples in water and salt. Each year since 1991, exactly the same plots were surveyed and all plant species were recorded using the decimal cover-abundance scale of Londo scale (Londo 1975).

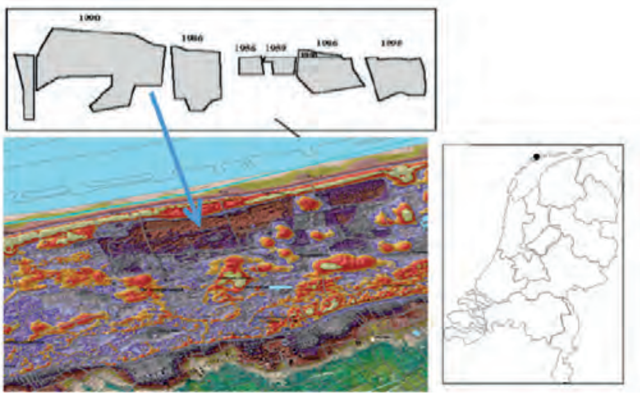


Figure 2. Sketch map of study site showing the different sod-stripping experiments (1954, 1986, 1990, and 1950) on the island of Terschelling.

Climatological data and groundwater level data

The Royal Dutch Meteorological Institute (KNMI) provided us with daily evapotranspiration data collected at De Kooy weather station near Den Helder. We obtained precipitation data from the public domain database of KNMI. Groundwater level data came from 14 piezometers established in 1990, within and in the surrounding of the dune slack, which were monitored every two weeks for six years. The effect of coastal (beach) expansion was incorporated as an explanatory variable in the hydrological modeling. Coastal growth was measured as the change of surface of sand above 0 m NAP (the Dutch Ordinance level) in the cross section of the beach.

Data analysis

Groundwater levels were simulated over longer period by using a computer program MENYANTHES (Von Asmuth et al. 2004). The simulation was based on the following parameters: measured groundwater levels, precipitation and evapotranspiration and site specific factors such as water tube length, surface elevation, coastal expansion, and geographical position of the water tubes. The correspondence between simulated series and measured series was assessed based on the amount of variability explained by the parameters used in the simulation. Furthermore, deviations from mean weather conditions along the coast of the Netherlands, were derived from local weather stations (see also: Grootjans et al. 1991).

From the groundwater level series, MENYANTHES calculates several parameters such as: mean lowest groundwater level (MLGL), mean groundwater level (MGL), mean spring groundwater level (MSGL), and mean highest groundwater level (MHGL). These groundwater level parameters were calculated over the whole period. The average groundwater level during the growing season (mean spring groundwater level (MSGL)) is related to vegetation composition in our data analysis. This is because it has been shown that spring and early summer weather conditions show a significant relationship with changes in vegetation in dune slacks (Van der Laan 1979, De Leeuw et al. 1990).

The changes in species composition in all chronosequential sites, the relation between environmental variables and the vegetation compositional changes were analyzed using CANOCO 4.5 software (ter Braak and Šmilauer 2002). The analysis was conducted in an exploratory approach, by starting with the whole data set. The underlying gradient in the vegetation data and the pattern of spatio-temporal changes (succession) on each permanent plot was studied using Detrended Correspondence Analysis (DCA). Permanent plots from all four chronosequence sites, in total 29, were used in the analysis. Prior to the analysis, the Londo scale was square root transformed in order to minimize the effect of dominant species on the analysis. Detrended Correspondence Analysis (DCA) was then applied. Axes were detrended by segment and rare species down-weighted. Based on the length of gradients and eigenvalues, some axes were selected and interpreted in ecological characteristics of the species. Then the changes in vegetation were related to some measured environmental variables using Redundancy Analysis (RDA) (CANOCO 4.5; Ter Braak and Smilauer 2002).

The effects of mean spring groundwater level (MSGL), soil pH, soil organic matter and plot specific parameters such as plot height, age of the vegetation were assessed using RDA. The age of the vegetation was determined, starting from the time when vegetation development has started on bare soil after sod-striping in each site. In RDA analysis, scaling was focused on inter-sample distance and bi-plot scaling was applied. Based on their significance, each variable was included in the model by forward selection following Monte-Carlo permutation (999 permutations) with a significance level of 0.05 tests on each variable.

In addition, the percentage cover of growth forms over the monitoring periods were presented graphically so that observations can be made about which growth forms increased or decreased in wet as well as dry periods.

Results

Groundwater levels

Precipitation and evaporation are two variables that govern the hydrology of Koegelwieck dune slacks. Combined, they explained more than 80% of the variances for each water level series presented in this paper Table 1), indicating that meteorology governs the hydrology of Koegelwieck dune slacks. Groundwater levels have increased in all chronosequence sites of the Koegelwieck. This rise of groundwater level shows a pattern of fluctuations (Appendix 1). Between 1987 and 1992, the general trend among all sites was a decreasing water level; the water levels reached the surface only during winter times. This pattern changed between 1992 and 1995, when a clear rise of groundwater level can be seen from the hydrographs (Appendix 1 and Figure 3). The period between 1995 and 1998 consisted of relatively dry years across all sites in the Koegelwieck. The water level has increased again between 2000 and 2003 before the pattern shifted to a decreasing trend from 2004 onwards.

Table 1. Site information and percentage of explained variance of water level series in Figure 1 by precipitation and evaporation. Water level measurements were given in reference to surface level, which is a measured using Dutch Ordinance Scape (NAP).

Site name	x-coord.	y-coord.	Soil surface (m)	Drainage Base (m)	MLGL	MGL	MSGL	MHGL	Exp Var (%)
Site 1956	151130	602730	1.94	1.44	1.47	1.82	1.97	2.11	89.8
Site 1986b	150970	602720	1.85	1.35	1.42	1.76	1.88	2.07	82.7
Site 1986a	151300	602720	1.97	1.26	1.48	1.8	1.94	2.09	89
Site 1990	150880	602730	1.79	1.53	1.5	1.83	1.98	2.11	90.2
Site 1995	151130	602670	1.96	1.13	1.45	1.78	1.9	2.08	88.1

However, these general trends of fluctuation of water level hide a detailed variation among the monitoring sites. For instance, the percentage of inundation days in a year, which is the number of days when the water level remain above ground in a certain year, shows a clear variability; Figure 3 shows three distinctly ‘dry’ periods in five measuring sites, in which little flooding in the slack occurred. These periods are: 1989-1991, 1996-1997 and 2006-2008.

Response of dune slack vegetation to changes in environmental variables

In an exploratory analysis of all permanent plots from across all the four chronosequence sites of the Koegelwieck dune slack, most of the plots shifted toward the upper middle part of the DCA ordination space where species that indicate wet-moist conditions are dominant (Appendix 2). Site 1990, which is the lowest and wettest site in the Koegelwieck, is still dominated by *Littorella uniflora*.

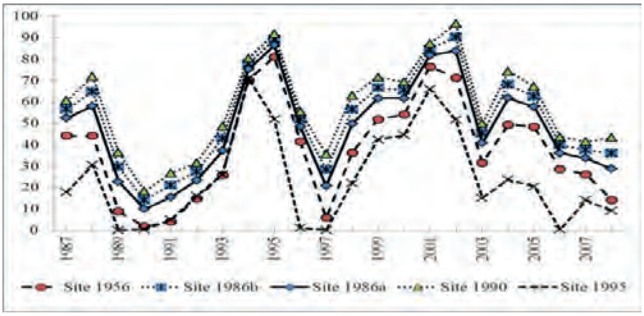


Figure 3. Percentage of number of inundation days in a year in all chronosequence sites in Koegelwieck.

Changes in plots of the site sod-cut in 1956

During the monitoring period (1991-2008), the change in species composition is very small in the older late-successional stage of 1956. In the Detrended Correspondence Analysis (DCA) of this site alone (Figure not shown), the length of the gradient of the first two axes was only 1.78 and 1.06 respectively, indicating no or very little changes in species composition and turn over.

The result of species and environmental relation analysis using RDA indicate that mean spring groundwater level (MSGL) and time (given as age of the vegetation since sod cutting) are to the two most important factors that explain vegetation variance of this site, however, soil organic matter and soil pH are also important (Figure 4). The effect of MSGL is reflected by the fact that during the period of rising water levels (between 1991 and 1996), species that indicate moist to wet conditions such *Phragmites australis* and *Hydrocotyle vulgaris* have become more abundant.

Changes in plots of the site sod-cut in 1986

In the site that was sod-cut in 1986 (Figures 5 and 6), the two sub-sites showed a divergent trend but they eventually converged and moved toward the older sites of 1956. Both sub-sites reflect a shift to more acidophilic and eutrophic species, but this shift starts earlier in sub-set 1986a. In both these two sub-sites, the effects of time is most important, while the effect of mean spring water level is more important in sub site 1986a, whereas soil pH and organic matter are more important in sub-site 1986b.

Changes in plots of the site sod cut in 1990

One permanent plot site 1990, which stands in a drier position shifted toward the older sites of 1956. All other permanent plots of site 1990 moved from a species rich stage with *Schoenus nigricans* and orchids toward more wet condition with few species and dominated by *Littorella uniflora* (Figure 7). Compared to other sites, this site has low organic matter content and higher pH values. In addition the water levels indicate that this site is the wettest site of all chronosequence sites. The results of the RDA analysis also reveal that MSGL is the most important factor on this site. The second important factor is time, while soil organic matter and soil pH are less important.

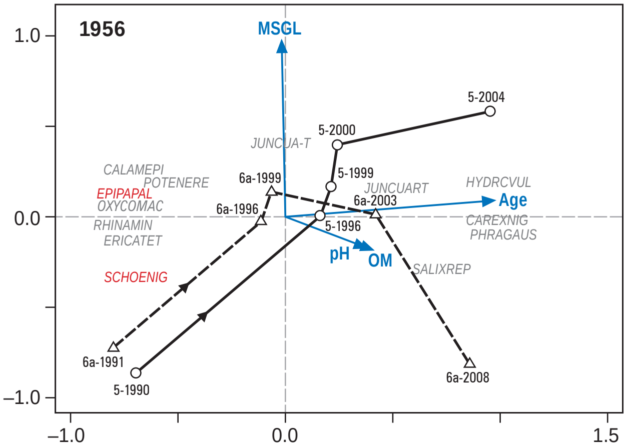


Figure 4. Redundancy Analysis (RDA) of the permanent plots of site 1956, plot number 4 and 6 were analyzed over time from 1990/91 to 2008. Blue arrows indicate environmental variables, their length indicating their relative importance in the direction they indicate. Species in red are target species. Connected dots indicate changes in permanent plots over time. Species coded: *CALAMEPI = Calamagrostis epigejos, CAREXNIG =Carex nigra, ERICATET = Erica tetralix, EPIPACPAL = Epipactis palustre, JUNCUA-T = Juncus alpinoarticulatus s. atricapillus, JUNCUART = Juncus articulates, JUNCUTEN = Juncus tenella, SALIXREP = Salix repens, PHRAGAUS = Phragmites australis, HYDRCVUL = Hydrocotyle vulgaris, SCHOENIG = Schoenus nigricans, RHINAMIN = Rhinanthus minor, OXYCOMAC = Oxycoccus macrocarpos, POTENERE = Potentitilla erecta.*

Changes in plots of the site sod-cut in 1995

In the youngest site, sod-cut in 1995, the level of organic matter is low and so is the pH. This site is positioned in between the wettest site of 1990 and the drier and older sites of 1956. The species composition of this site is still species rich, however high productivity species are dominant. This site showed a sudden shift in species composition and became dominated by late successional species. The RDA analysis revealed that time is the most important for this site, while the effect of MSGL is not very large (Fig 8), which is in line with the result of hydrological analysis.

In general, interaction variables between organic matter and age of vegetation as well as organic matter and pH are also significant. The directions of arrows indicate where the value for the variable has a larger value and a stronger effect. The effect of mean spring water level is higher for the site 1990, which is also the wettest site among all the chronosequence sites. The pH of this site is higher. The result also shows a positive correlation of organic matter with the age of the vegetation and the inverse relation between pH level and organic matter content because the pH is higher in the opposite direction to the organic matter.

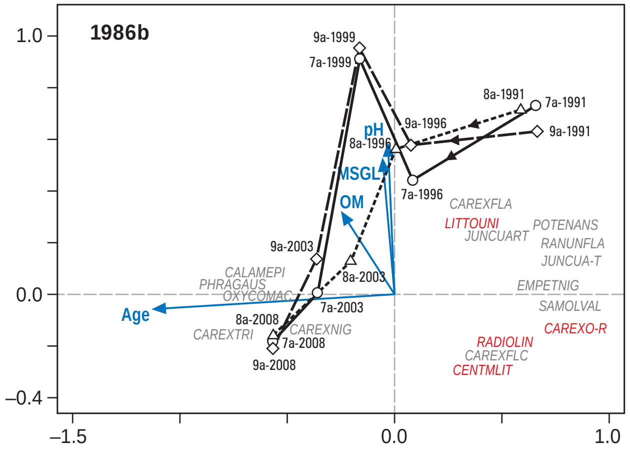


Figure 5. Redundancy Analysis (RDA) of the permanent plots of site 1986b, plot 7a, 8a and 9a were analyzed from 1991 to 2008. Blue arrows indicate environmental variables, their length indicating their relative importance in the direction they indicate. Species in red are Target species. Connected dots indicate changes in permanent plots over time. Species coded: *CAREXO-R = Carex oederi s. oederi, LITTOUNI = Littorella uniflora, CALAMEPI = Calamagrostis epigejos, CAREXNIG =Carex nigra, PHRAGAUS = Phragmites australis, CAREXFLA = Carex flacca, CAREXTRI = Carex trinervis, OXYCOMAC = Oxycoccus macrocarpos, PHRAGAUS = Phragmites australis, JUNCUART = Juncus articulatus, JUNCUA-T = Juncus alpinoarticulatus s. atricapillus, POTENANS = Potentilla anserina, RANUNFLA = Ranunculus flammula, EMPETNIG = Empetum nigra, SAMOLVAL = Samolus valerandi, CAREXOED = Carex oederi, RADIOLIN = Radiola linoides, Centalium, CAREXFLA = Carex flava, CENTMLIO = Centaurium littorale.*

Growth forms

Figure 9 presents the results of average growth forms from the four chronosequence sites. In older site, such as 1956, scrubs are the dominant growth form. However, during the very wet period between 2000 and 2004 the cover of annual forbs increased, while the cover of scrubs decreased.

For the sites of 1986, perennial graminoids and perennial forbs appear to have been the dominant groups between 1990 and 1999 and the cover of annual forbs increased between 2000 and 2004, while the cover of scrubs seems to decrease during this period. After 2004, the cover of scrubs increased. In the site of 1990 perennial forbs and perennial graminoids were the two dominant growth forms between 1991 and 2000 but during the wet periods of 2000 to 2003, annual forbs increased in cover. However, the data show a collapse of the vegetation in 2004, when only annual forbs were recorded. Afterwards, the result indicates that annual forbs remained the dominant growth form in this site. In the site of 1995, perennial forbs and perennial

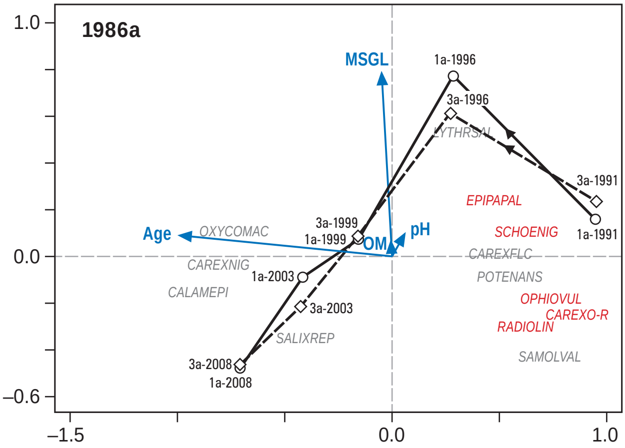


Figure 6. Redundancy Analysis (RDA) of the permanent plots of site 1986a, plot 1a and 3a were analyzed from 1991 to 2008. Blue arrows indicate environmental variables, their length indicating their relative importance in the direction they indicate. Species in red are target species. Connected dots indicate changes in permanent plots over time. Species coded: *CAREXNIG =Carex nigra, CAREXO-R = Carex oederi s. oederi, SAMOLVAL = Samolus valerandi, RADIOLIN = Radiola linoides, OPHIOVUL = Ophioglossum vulgaris, POTENANS = Potentilla anserina, CAREXFLA = Carex flacca, SCHOENIG = Schoenus nigricans, EPIPACPAL = Epipactis palustris, LYTHRSAL = Lythrum salicaria, SALIXREP = Salix repens, CALAMEPI = Calamagrostis epigejos.* Connected dotes indicate changes in permanent plots over time.

graminoids were the dominant growth forms during the earlier stages (1995-2000) and after 2000 the cover of annual forbs increased, but also the cover of shrubs increased after 2004.

Discussion and Conclusions

Groundwater levels and weather

The result of groundwater level analysis indicates a strong correlation between fluctuations in weather conditions and water level in the dune slack. The variability in water level is mainly explained by precipitation and evapotranspiration, which means the amount of precipitation plays a significant role after water lose via evapotranspiration is discounted, thus surplus precipitation being a driving factor. Similar responses were recorded elsewhere in dune slacks (Ranwell 1972, Van der Laan 1979, Studer-Ehrensberger et al. 1993, Moreno-Casasola and Vázquez 1999, Munoz-Reinoso 2001).

The effect of coastal expansion does not appear to be a significant factor in Koegelwieck dune slack. Factors such as site elevation are also important in Koegelwieck, since despite the similar hydrology of this slack, there is variability among different

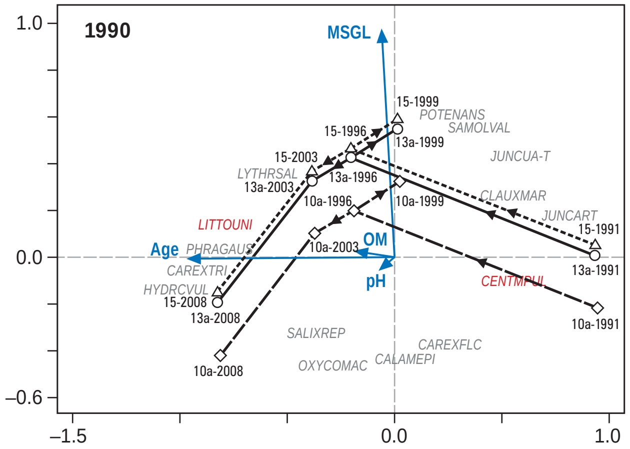


Figure 7. Redundancy Analysis (RDA) of the permanent plots of site 1990, Plot 10a, 13a and 15 were analyzed between 1991 and 2008. Blue arrows indicate environmental variables, their length indicating their relative importance in the direction they indicate. Species in red are target species. Species coded: *CENTMLIO = Centaurium littorale, CAREXO-R = Carex oederi s. oederi, SAMOLVAL = Samolus valerandi, POTENANS = Potentilla anserina, CAREXFLA = Carex flacca, CAREXTRI = Carex trinervis, LYTHRSAL = Lythrum salicaria, SALIXREP = Salix repens, CALAMEPI = Calamagrostis epigejos. HYDRCVUL = Hydrocotyle vulgaris, LITTOUNI = Littorella uniflora, PHRAGAUS = Phragmites australis, OXYCOMAC = Oxycoccus macrocarpos, LYTHRSAL = Lythrum salicaria, GLAUXMAR = Glaux maritima.* Connected dots indicate changes in permanent plots over time.

chronosequence sites and also among different permanent plots in the same chronosequence sites. A related phenomenon, for instance land subsidence due to gas abstraction, could also enhance the effect of surplus precipitation, since the drop in soil surface could lead to prolonged inundation. A recent publication on the effect of soil subsidence and climate change on dune vegetation on Wadden sea island of Ameland, the Netherlands, indicated that weather fluctuation, soil subsidence and eutrophication are drivers of temporal changes in vegetation, even though the change identified was small (Van Dobben and Slim 2012). However, our results show a large temporal changes in vegetation, which coincide with the pattern of changes in water level regime.

Vegetation response to weather conditions and other environmental factors

In dune slacks, hydrology is a very important factor that determines the types of vegetation and life span of successional stages (Grootjans et al. 1996, Lammerts and Grootjans 1998, Grootjans et al. 2002). Especially in dune slacks that are cut off from sea water flooding, such as the Koegelwieck presented in this paper, the hydrology of the slacks are governed by net precipitation. The result of our hydrological analysis and modeling confirm this phenomenon. However, a direct assessment of the effect of weather condition on vegetation is difficult because establishing causality with changes in vegetation composition is an arduous task. However, studies show that mean groundwater level during the growing season (mean spring water level = MSGL) can have a marked effect on the vegetation (Van der Laan 1979, Lammerts and Grootjans 1998, Lammerts et al. 2001).

The results of the RDA analyses (Figures 4-8) show that the mean spring groundwater level (MSGL), is indeed a significant variable that affect the vegetation. The effect of MSGL is more pronounced in the chronosequence site of 1990; however it affected all the chronosequences sites especially between 1996 and 1999. This effect between 1996 and 1999 could be due to time lag effect of high precipitations received in this area from 1994 to 1996. The effects of organic matter accumulation and soil pH are not strong on this site, which is due to very little accumulation of organic matter and a near neutral pH condition at this site. Time, which indicates succession, is still an important factor because species turn-over over several years can be a significant factor. On this site, the cover of vegetation low, especially the cover of scrubs indicating that due to the high water level on this site these species are incapable of establishment. In the oldest site of 1956, MSGL is also a significant factor, and it seems that the rising of water level caused an increase or reappearance of species favoring moist to wet

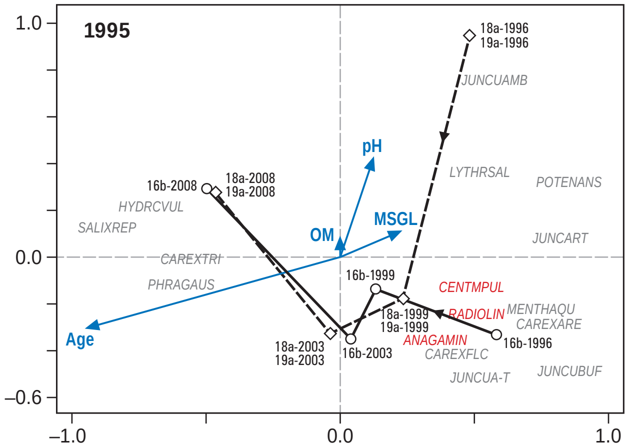


Figure 8. Redundancy Analysis (RDA) of the permanent plots of site 1995, plots 16b, 18a and 19a were analyzed between 1995 and 2008. Blue arrows indicate environmental variables, their length indicating their relative importance in the direction they indicate. Species in red are target species. Species coded: *CAREXOED = Carex oederi, CAREXFLA = Carex flacca, CAREXTRI = Carex trinervis, LYTHRSAL = Lythrum salicaria, SALIXREP = Salix repens, HYDRCVUL = Hydrocotyle vulgaris, CAREXARE = Carex arenaria, JUNCUA-T = Juncus alpinoarticulatus s. atricapillus, JUNCUBUF = Juncus bufonius, MENTHAQU = Mentha aquatica, ANAGLMIN = Anagallis minima, CENTMLIT = Centaurium littorale, JUNCUART = Juncus articulatus, POTENANS = Potentilla anserina, JUNCUAMB = Juncus ambiguus, PHRAGAUS = Phragmites australis.* Connected dotes indicate changes in permanent plots over time.

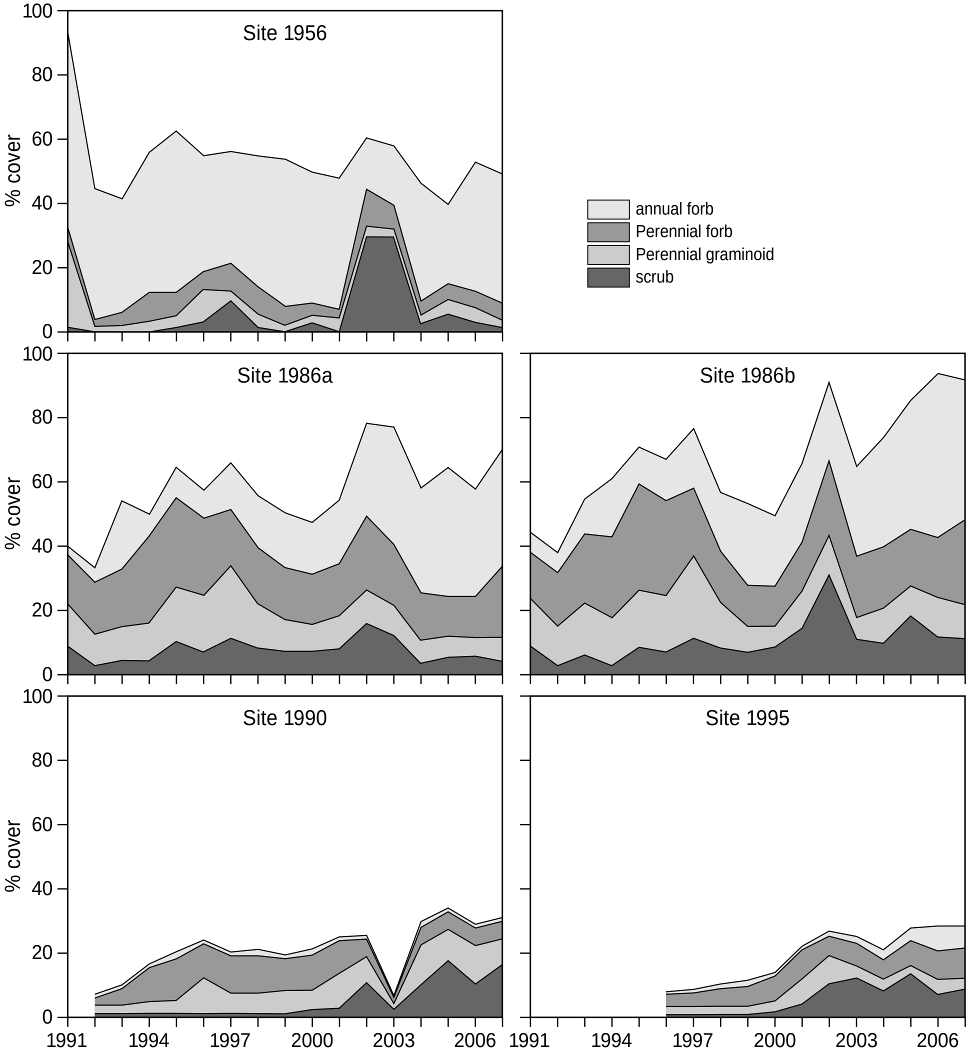


Figure 9. Percentages cover of four growth forms (Perennial graminoids, Perennial forbs, Annual forbs and scrubs) on a permanent plot in the older (1956) chronosequence site of the Koegelwieck dune valley.

conditions. The effects of time, organic matter and pH are all significant on this site. On this old chronosequence site, the amount of organic matter is the highest and pH is the lowest indicating ageing of the vegetation. Similarly the effect of MSGL on the site of 1986 is significant but effects of organic matter and pH are minimal on the sub site of 1986a. The site sod-cut in 1995 shows a rapid change (within 13 years) in species composition between the pioneer and late-successional stages. This rapid shift in vegetation could be due to the dry spell of 1996/97, which was just two years after the site had been sod was.

Studies showed that plant communities respond to change in patterns of precipitation (Pitt and Heady 1978, Van der Maarel 1981, Morecroft et al. 2004). One response of plant communities to experimentally induced precipitation pattern was that annual forbs increase in cover in wet periods and perennial species increase in cover during dry periods (Van der Maarel 1981, Morecroft et al. 2004). The changes in percentage cover of growth form in Koegelwieck dune slacks also show patterns of change that are in line with such experimental studies. A close observation of water level patterns and observations of changes in growth form in Koegelwieck (Figure 3 and Figure 9) shows that during a dry period the cover of perennial forbs and perennial graminoids and cover of scrubs increase, while annual forbs decreased. On the other hand, sustained wet period causes a decline in cover of perennial forbs and graminoids and shrubs but the cover of annual forbs increase.

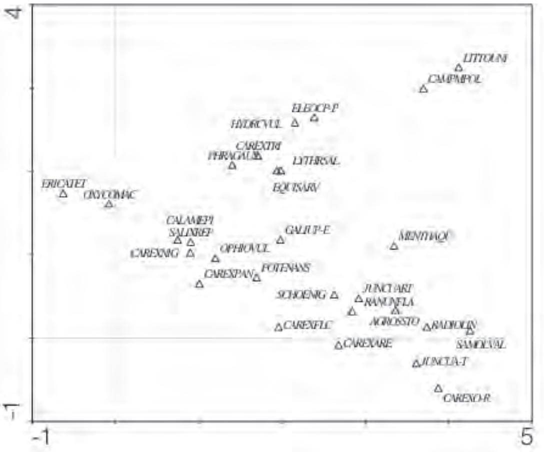
In this paper, results of long-term water level observation and simulations of past long-term water level indicate an increasing trend in water levels in Koegelwieck dune slacks. The simulation was done basically to fill the gaps in the data set due to absence of recorded water levels for the whole monitoring period. Between 1990 and 1996, we measured water levels in the field within and around the Koegelwieck area. Our simulated water levels from the period 1997-2008 are also quite reliable because the fit between measured and modelled water levels was 98%.

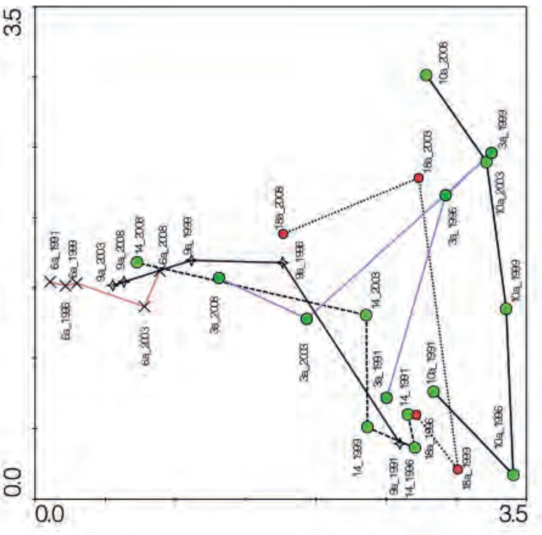
In general, global climate conditions are changing with an unprecedented speed. Studies show a decadal increase of precipitation by 0.5-1.0% in mid- and high latitude areas of the Northern Hemisphere while the reverse is true in sub-tropics and tropics and in Northern hemisphere climate warming has resulted in a decreased diurnal temperature due to an increase in minimum temperature at about twice the rate of an increase of the maximum temperature (Walther et al. 2002). The Dutch coast has an Atlantic climate where precipitation dominates over evaporation (Grootjans et al. 2002), which coupled with the current increase of precipitation could mean more precipitation water getting into dune systems. This increase in precipitation could lead to a feedback mechanism by raising the water level, reducing soil pH and facilitating organic matter accumulation and thus facilitating the establishment of competitive species. We conclude that restoration projects should take into account the unpredictability of weather conditions and should aim to more dynamic approaches.

Acknowledgments
Long-term monitoring of the Koegelwieck dune slacks was done by many persons especially Evert Jan Lammert who conducted part of his PhD studies in these dune slacks in late 1990's. Ab Grootjans through ERA foundation provided funding for continuation of monitoring from early 2000 to 2008. The continuation of monitoring was made possible by money provided by the Dutch Gas and oil Company (NAM) beginning from 2008. We would acknowledge all persons involved in this project from vegetation mapping to soil sampling, particularly Henk Everts and Nico de Vries who managed the data base and were involved in all monitoring activities.

Appendix

The figures below show Detrended Correspondence Analysis (DCA) of all permanent plots from four chronosequence sites of Koegelwieck dune slacks. The top figure is for species and the bottom one for sampling points (permanent plots). In the bottom figure, polyline indicate the direction of change in a given permanent plot (years indicated with the plot name). The plots name are as follows: 6a for site 1956, 9a for site 1986b, 3a for site 1986a, 10a and 14 for site 1990 and 18a for site of 1995.





Chapter 4

Alternative stable states in dune slacks revisited: stability of pioneer stages

Bikila Warkineh Dullo, Rohani Shahrudin, Han van Dobben, Eddy van der Maarel & Albert P. Grootjans

Abstract

The theory of alternative stable states (ASS) predicts that contrasting ecosystem states can co-exist under the same environmental conditions. In dune slacks, several feedback mechanisms can lead to the development of ASS. For instance, species capable of radial oxygen loss can modify their micro-environment to their own advantage for a considerable period of time leading to positive feedbacks. In the present study, we analysed the possible occurrence of alternative stable states in dune sacks using long-term data sets of vegetation, soil, water levels and weather conditions. To identify the stability of system states, we combined multivariate analysis techniques, hydrological modelling and regression models. Our results showed absence of long-term stability of pioneer stages; all successional stages converged towards a homogeneous community within 10-12 years, although a large difference in the rate of change was observed depending on hydrological conditions and vegetation types. It is concluded that plant communities in dune slacks can rapidly change in response to relatively small perturbations in hydrological and meteorological conditions. A dry period occurring between wet periods can drastically shift a wet basiphilous community into a more productive stage, after which the initial community cannot be recovered without human intervention.

Keywords: *adaptive management, hydrology, soil organic matter, restoration, succession*

Introduction

The theory of alternative stable states (ASS) predicts that ecological systems may potentially co-exist in contrasting states under the same environmental conditions (Beisner et al. 2003, Suding et al. 2004). While the debate continues on whether ASS are actually stable or transient (Fukami and Nakajima 2011), many field observations suggest the prevalence of ASS in natural as well as human influenced ecosystems. A mechanism that potentially could sustain ASS is the phosphorus cycle in temperate lakes. Low *versus* high phosphorus input, which is associated with clear water *versus* turbid water states, could cause a regime shift under certain conditions (Scheffer et al.

1997, Carpenter 2003, Folke et al. 2004). The occurrence of ASS in tropical lakes has also been suggested by observations, experiments and models, where a stage with free-floating water plants and a stage dominated by submerged plants occur as alternative states (Scheffer and Carpenter 2003). Similarly, ASS have been suggested to occur in wetlands, estuaries and coastal seas (Kautsky et al. 1986, Elmgren 2001, Gunderson 2001, Van der Heide et al. 2013); in savannahs (Kelly and Walker 1976, Anderies et al. 2002); coral reefs (Nystrom et al. 2000, Jackson 2001, Jackson and Johnson 2001, Nystrom and Folke 2001); and other ecosystems (Folke et al. 2003, Folke et al. 2004). However, only a few experimentally induced ASS have been reported (Van de Koppel et al. 2002, Petraitis and Dudgeon 2004, Schroeder et al. 2008).

Bossuyt et al. (2005), working in Belgian and French dune slacks, suggested that intraspecific processes can lead to non-random vegetation composition. Even though the authors did not specifically mention alternative stable states in their study, they indicated that species may modify their environment and create a positive feed-back mechanism, thus forming an aggregated community. Adema et al. (2002), working in dune slacks on the Dutch Wadden Sea islands, showed a clear case of the existence of ASS in dune slacks, where a pioneer stage co-existed with later successional stages over a period of more than 80 years. They suggested three possible feed-back mechanisms that could lead to ASS (Adema et al. 2002; see Figure 1). The first mechanism is associated with enhanced nitrogen loss, caused by radial oxygen loss (ROL). Wetland species with ROL capabilities, such as *Littorella uniflora* are able to release large quantities of oxygen into a predominantly anoxic environment *via* their root system, thus stimulating nitrification in the root zone. In a system with groundwater flow, the nitrate produced can be transformed into N_2 by micro-organisms when the water leaves the root zone. This causes loss of nitrogen (N_2) gas and to the atmosphere (N-loss through coupled nitrification-denitrification; Reddy et al. 1989, Engelaar et al. 1991, Bodegom et al. 2005). The second mechanism discussed is sulfide toxicity caused by microbial mats sealing off the surface layer of the slack and facilitating the development of high sulfide concentrations. In this case, sulfide prevents the establishment of productive species because in dune slacks, most of these species cannot cope with high levels of sulfide; thus pioneer species, which are often adapted to this environment, are favored (Van Gemerden 1993, Lamers et al. 1998). The third possible mechanism involves productive species growing in nutrient-rich conditions (Olff et al. 1993, Lammerts et al. 1997, Walker and Moral 2003). Such species store a large amount of nutrients in the soil organic matter (SOM) or in their biomass, which can be retrieved again during the next growing season. This mechanism favors late successional species, such as *Salix* and *Betula* species (Ernst et al. 1996). This development towards dune woodland can be considered an alternative stable state (Beisner et al. 2003).

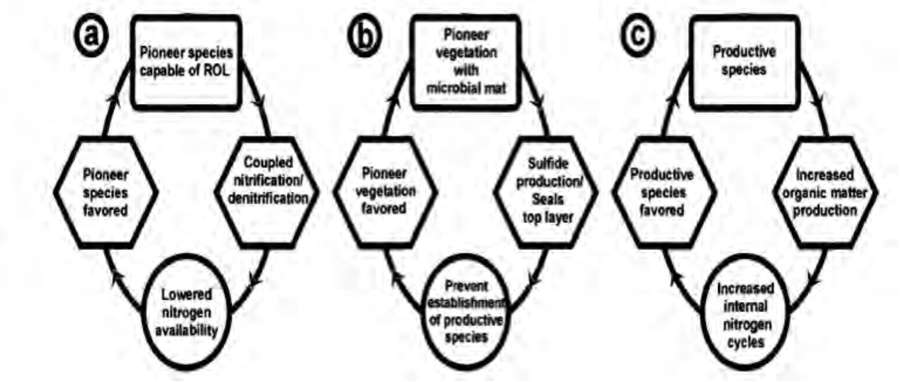


Figure 1. Three possible feedback mechanisms are recognized in calcareous wet dune slacks: **(a)** Enhanced nitrogen loss; **(b)** Sulphide toxicity; and **(c)** Nutrient accumulation in an internal cycle. The diagram was adopted from Adema et al. (2002).

In this study, we focus on evidence for alternative stable states (ASS) in dune slacks. We attempt to unravel the long-term trends and shifts in plant communities by analyzing a long-term data set collected from permanent quadrats. Our objective was to detect spatio-temporal changes in the vegetation and soil parameters that point to community shifts toward one system state (transience) instead of several or at least two other system states (stability). In this paper, long-term monitoring data (from 1991 to 2008) in combination with a chronosequence of successional stages (up to *ca.* 90 years) were used to investigate whether alternative stable states in dune slacks are stable or in transition. Vegetation changes were analyzed using a similarity index in species composition as a measuring tool for ASS.

We assume that if a local plant community has a permanently low similarity with neighboring community types under comparable abiotic conditions that community may be in an ASS. An increasing similarity over time with other communities under comparable abiotic conditions can be considered as evidence for the absence of ASS. Accumulation rates of organic matter in dune slacks were used as another indicator for the occurrence of ASS; low accumulation rates over a rather long period of time (*c.* 30 years) point to restricted succession and the presence of enhanced nitrogen loss as depicted in Figure 1a (Adema et al. 2002, 2005).

From an applied perspective, the occurrence of stable states in pioneer stages of dune slacks is relevant for nature conservation. If natural (hydrological or meteorological) conditions can prolong the lifespan of these pioneer species, it would save money that is now used in regular management (mowing and sod cutting, Grootjans et al. 1998, Bakker et al. 2006, Bakker et al. 2007, Chapter 2).

Methods

Study area

The study site is located on the Wadden Sea Island of Terschelling, the Netherlands, in a large dune slack known as Koegelwieck (53°24'N, 5°20'E). A detailed description of the study site is provided in chapter 3 of this thesis. The Koegelwieck is a secondary dune slack of about 50 ha, which was formed between 1825 and 1865 (Van Dieren 1934) as a result of intensive sand blowing. In this dune slack, five sites have been monitored with known ages, vegetation, soil and hydrological parameters. The vegetation records from each of these sites form a chronosequence (see Shahrudin et al. 2014, chapter 3). Top soil removal was carried out in the Koegelwieck dune slack several times experimentally in order to see if target species could re-establish populations after they had been lost due to rapid succession. The vegetation of the oldest site is almost 90 years old; vegetation development started after sod-cutting in 1920. At the next oldest site, vegetation dates from 1956, when this site was sod-cut. More recent sod-cuttings were carried out in 1986, 1990 and 1995, respectively, in order to restart vegetation succession (Figure 2).

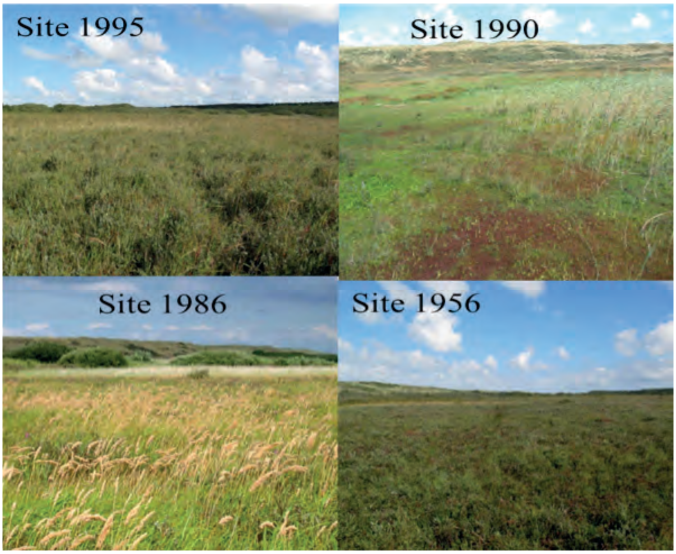


Figure 2. Four chronosequence sites investigated since 1956, 1986, 1990 and 1995. Photographs of sites 1986 and 1990 were taken in 2004; those of sites 1956 and 1995 were taken in 2009 (all photographs taken by A. P. Grootjans).

Vegetation, soil organic matter and pH data

Detailed descriptions of the sampled sites and continued monitoring activities in our study area since 1990 have been well documented elsewhere (Lammerts et al. 1997, Grootjans et al. 2002, Sýkora et al. 2004). Soil samples were collected in 1991, 1993, 1996, 1999, 2003 and 2008. They were dried and the percentage of organic matter was determined by loss through ignition. Similarly, the soil pH (KCl) was measured in the laboratory using 17.5 g of fresh soil dissolved in demineralized water and mixed thoroughly for two hours. The peak standing crop of each chronosequence site was measured in September 2009 by cutting the total above-ground vegetation (20 × 20 cm; 7 replicates) in sampling plots located next to the permanent plots. All vegetation samples were dried in an oven for 12 hours and the dry weight was measured. Statistical analyses were carried out using IBM SPPS statistics 20 (repeated measure analysis).

Each year from 1991 to 2008, 26 plots were surveyed and all plant species were recorded using the cover-abundance scale of Londo (1975). Changes in species composition in the four chronosequence sites were analyzed using CANOCO 4.5 software (Ter Braak and Šmilauer 2002). The underlying latent gradients in the vegetation data and the temporal changes in each permanent plot during subsequent years were analyzed using Detrended Correspondence Analysis (DCA). For DCA, the cover abundance scale values (measured as percentages) were square-root transformed in order to reduce the effect of dominant species on the analysis. The method used to detrend axes was detrending by segments, and rare species ($n < 3$) were down-weighted. Based on the length of gradients and eigenvalues of axes, we were able to interpret some axes as latent variables, based on ecological characteristics of the species. In the DCA diagram, average positions of sampling points of each site for the corresponding years were calculated and used to visualize changes in vegetation. The effects of soil pH and soil organic matter were derived from related work in Chapter 3 of this thesis. Here, they are presented graphically to demonstrate the changes that took place over the years.

The similarities within each site (changes in plant species composition over time at the same location) and among different sites over the years (changes over time at different places) were calculated with the Diserud–Ødegaard similarity index (Diserud and Ødegaard 2007). This index is a modification of the similarity index of Sørensen (1948) and is very suitable for comparing species composition data set of different sites; it can calculate similarities within and among two or more communities. To give an example of comparing three relevés, A, B and C, the index of similarity is given by the following equation:

$$\frac{ab + ac + bc - abc}{a + b + c} \qquad \textit{Equation 1}$$

where '*a*', '*b*' and '*c*' are the numbers of species found in the relevés A, B, & C, respectively; and '*ab*' is the number of species common to A and B; '*ac*' is the number of species common to A and C; '*bc*' is the number of species common to B and C; and '*abc*' be the number of species common to all 3 relevés.

When calculated using the above formula (Equation 1), this index will be exactly 2/3 if all three relevés share exactly the same species and 0 when all three relevés have no species in common. Diserud and Ødegaard (2007) suggested that the index value can best be multiplied by 3/2 in order to obtain a range from 0 and 1 and, according to the authors, this equation can be expanded to compare more than three relevés at the same time.

In this paper, we used the Diserud and Ødegaard similarity index to make two types of comparisons. We first made comparisons in species composition within the same permanent plot over time. To detect changes over time on a given chronosequence site, we calculated the similarity index between vegetation survey data taken at the start of monitoring (1956, 1986, 1995 and 1990, respectively, for the four chronosequence series) and at four different sampling times. This would enable us to see if the permanent plot remained stable or showed changes in species composition over the years. We then compared changes between two chronosequence sites: 1956 with 1986, 1956 with 1990, 1956 with 1995, and 1986 with 1990. For this purpose, we calculated similarity indices between two permanent plots from each chronosequence sites. Since the two compared plots from the chronosequence sites are permanent plots, we repeated similar calculations for the period the vegetation had been recorded. These comparisons of different chronosequence sites with one another will help us discover whether the species composition of these sites converged or diverged over time.

After the indices of similarity were computed, these indices were plotted against the time interval over which they were calculated. In order to test whether there was a shift in community composition as a result of changes in species composition, we tested if a significant change over time existed in species composition. Our null hypothesis was: there is no change in species composition and thus no shift in community types, which means similarity indices should not indicate any significant differences. Thus, the test of significance was based on the assumption that the similarity index should not change significantly over the time interval for which indices were calculated if the communities had not changed. To test this, we used a t-test in SPSS 20.

Results

Vegetation dynamics

The relative positions of 29 species are presented in a DCA ordination diagram (Figure 3). The first DCA axis explains 25% of the species variance; axes 1 and 2 combined explain 34.7%, while all axes together (1–4) explain 42.2% of the variation. The gradient length of the first axis is 3.48 and for the remaining axes the length is < 2.0. Eigenvalues are 0.55, 0.21, 0.12 and 0.05 for axes 1–4, respectively. The positions of the species in the ordination space are related to variation in wetness and time, which are the latent variables underlying the first and the second axes, respectively (Table 1).

The relative positions of all sites of the chronosequence sequences and monitoring years are given by the DCA diagram (Figure 4). Two shifts can be noticed. To the left, small changes in vegetation composition can be observed in the old sod-cut experiment (1956) over time; plots 'moved' in the direction of the top of the diagram. The 1986 site, found in the middle, shifted left to more acid conditions as early as 1996 and, within 17 years, resembled the 1956 site. To the right, the very wet site that had been sod-cut in 1990 also showed relatively little change until 2004. Between 2004 and 2008, a relatively large change occurred toward more eutrophic conditions at the top of the diagram (see Fig 3; large changes can be observed in the 1986 and the 1956 sites). The youngest site from 1995 changed toward a more productive stage between 2001 and 2008, also moving up the diagram, with rapid increases of *Salix* and *Phragmites*.

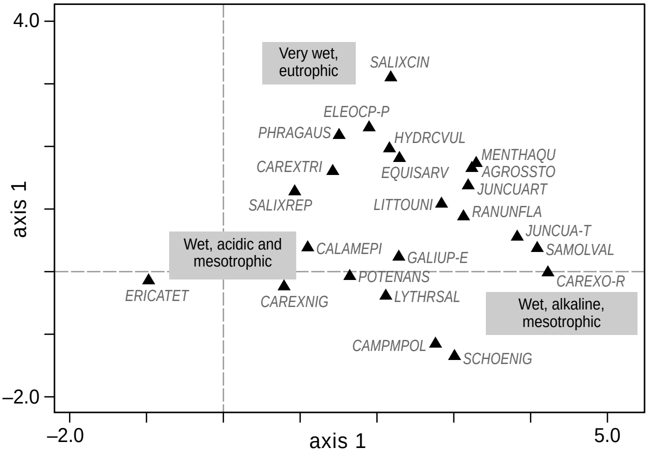


Figure 3. Distribution of plant species in ordination space (DCA). *AGROSSTO = Agrostis stolonifera, CAREXNIG =Carex nigra, CAREXO-R = Carex oederi s. oederi, CAMARPOL = Camarops polysperma, CAMPSINT = Campylopus introflexus, CAREXTRI = Carex trinervis, CALAMEPI = Calamagrostis epigejos, ELEOCP-U = Eleocharis uniglumis, EQUISARV = Equisetum arvense, ERICATET = Erica tetralix, GALIUP-E = Galium palustre, HYDRCVUL = Hydrocotyle vulgaris, JUNCUA-T = Juncus alpinoarticulatus s. atricapillus, JUNCUART = Juncus articulates, LITTOUNI = Littorella uniflora, LYTHRSAL = Lythrum salicaria, MENTHAQU = Mentha aquatica, OXYCOMAC = Oxycoccus macrocarpos, PHRAGAUS = Phragmites australis, POTENANS = Potentilla anserina, RANUNFLA = Ranunculus flammula, SALIXCIN = Salix cinerea, SALIXREP = Salix repens, SAMOLVAL = Samolus valerandi, SCHOENIG = Schoenus nigricans.* Only 29 species with a cover of at least > 1% are shown. These species range from acidophilous heathland species (left bottom corner) to wet pioneer species (right bottom corner), and scrub species including *Salix* of old dune slacks (top).

Table 1. Summary of results of the Detrended Correspondence Analysis for ordination graph shown in Figures 3 and 4.

Axis	1	2	3	4	Total inertia
Eigenvalues	0.55	0.21	0.12	0.05	2.21
Lengths of gradient	3.48	1.66	1.83	1.46	
Cumulative percentage variance of species data	25	34.7	40	42.2	
Sum of all eigenvalues					2.21

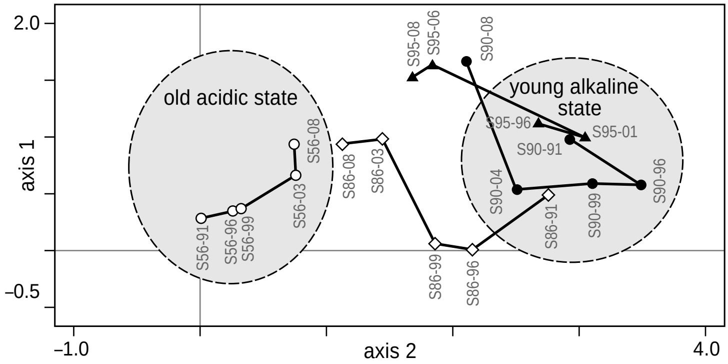


Figure 4. Site distribution graph (DCA) corresponding to the species distribution graph given in Figure 3 above. The large circles indicate the boundaries of two states (an older acidic state and a younger alkaline state), which can be considered as alternative stable states.

Temporal changes (from 1991 to 2008) in the similarity index within chronosequence sites are given in Figure 5a. The result is an indication of how a given chronosequence site changed over time in terms of species compostion. The statistical significance of the changes in slopes of the lines are indicated in the graphs. The only chronosequence site that showed a significant change in species composition was site 1986, with a similarity index dropping from above 70% in the beginning to about 45% at a later stage. Two chronosequence sites, 1956 and 1990, showed a slight decrease in species similarity as shown by the slope of the graph (a negative slope indicates a decrease and a positive slope indicates an increase in similarity of species composition), but for both sites, the similarity index varied from just above 50% to about 48%, indicating that this sites maintained at least 50% of all its species over time. The youngest site from 1995 had a high similarity index (about 60%) over time.

The similarity index (Figure 5b) among the chronosequence sites shows a general increasing trend over the sampling period. Comparison between the chronosequence sites of 1986 and 1990 revealed a 60% similarity already when their respective vegetation stands were only five years old. Despite this high early stage similarity, however, their index of similarity only slightly increased to about 65% over a longer

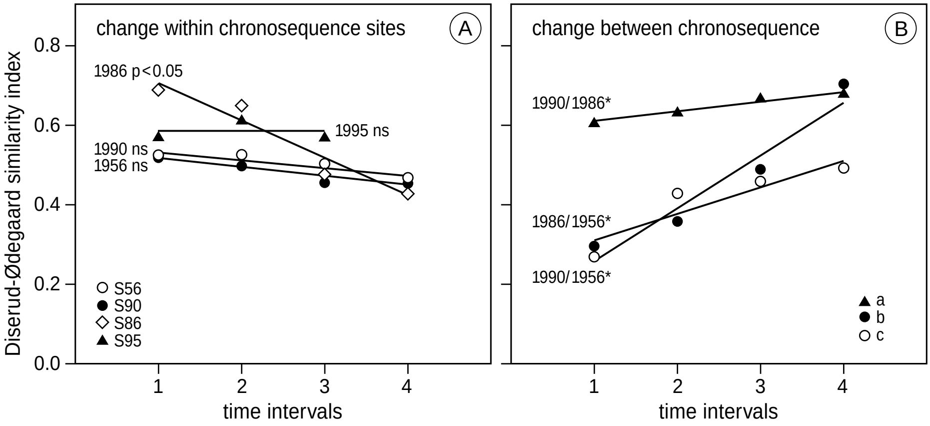


Figure 5. a. Changes in species composition over time (compared to the start of the monitoring) of four chronosequence sites (1956, 1986, 1990 and 1995) using the Diserud–Ødegaard index. Only changes within the site sod-cut in 1986 were significant. **b.** Changes in species composition between chronosequence sites (1956 compared to 1986, 1956 compared to 1990, 1956 compared to 1995, and 1986 compared to 1990) over time. The site that was sod-cut in 1986 came to closely resemble the 1956 site at the end of the monitoring period. The 1990 site (pioneer) did not develop toward either the 1986 site (target community) or the 1956 site.

period of time. A similar comparison between site 1956 and site 1986 shows a rise in similarity from about 25% in the beginning to about 65% when the vegetation stand at site 1986 was only 17 years old and that of site 1956 was 47 years old. A similar comparison between site 1956 and site 1990 shows less pronounced similarities between the two sites: less than 30% in the beginning and about 40% at a later stage. The younger site of 1995 attained a much higher similarity with site 1956 in only ten years. Their similarity index increased from about 35% at age six of the vegetation to above 80% at age ten.

Changes in environmental factors

Organic matter (OM) accumulation, soil pH and peak standing productivity in five sites in the Koegelwieck are shown in Figure 6. The sites vary in OM accumulation. In the oldest site, sod-cut in 1920, it was *ca.* 7 kg/m^2 in 1991, increased to *ca.* 9.7 kg/m^2 between 1991 and 1999, and decreased slightly after that. The samples (n = 8) showed a high variation, however. The second oldest site, sod-cut in 1956, showed a linear increase between 1991 and 2008 from 6.5 kg/m^2 to ca. 10 kg/m^2. For site 1986, for which we sampled two sub-sites, soil samples taken in 1991, *i.e.* 5 years since top soil removal, showed an OM accumulation of ca. 3.5 kg/m^2, after which the OM values of the sub sites started to deviate from each other. The younger sites, 1990 and 1995, accumulated very little OM compared to the older sites over 18 years and 13 years, respectively.

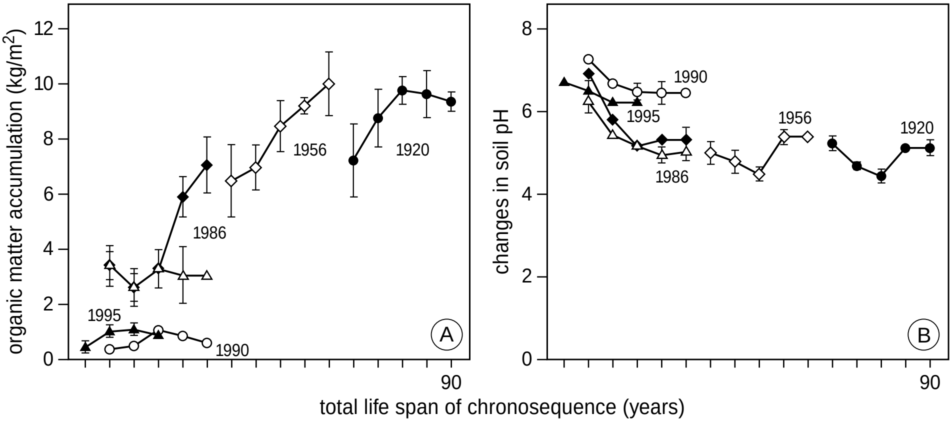


Figure 6. Changes in organic matter content (A) and pH (B) of the top soil over time in 5 chronosequence sites at Koegelwieck. The data points from left to right represent data collected over time from 1991 to 2008. For site 1995, the first sample was taken in 1996. The diagram shows younger sites to the left and older sites to the right. The age displayed on the x-axis refers to known age of vegetation in the dune slack, tracing back to 1920.

The corresponding soil pH data in Figure 6B show a general trend of lower pH at older sites and higher pH at younger sites. At the older sites, 1920 and 1956, soil pH data measured in 1991 were below 6. The pH values in the 1986 sub-sites were similar, although organic matter contents were different (Figure 6a). Five years after top soil removal, the pH at this site was still above 6 but it dropped to around 5 over the 18 years that followed. In the younger sites (1990 and 1995), the pH also decreased but remained above 6.

The above-ground biomass measured in September 2009 (Figure 7) did not show much variation between the chronosequence sites. Only the 1990 site (at pioneer stage) still had a low peak standing crop, which was significantly lower than that found at other chronosequence sites.

Discussion

A convincing example of the occurrence of alternative stable states (AAS) during succession in dune slacks on the Dutch Wadden Sea island of Texel was provided by Adema et al. (2002). They found that pioneer stages (*Littorella uniflora*) could co-exist with later successional stages (*Salix repens, Phragmites australis*) and proposed several mechanistic explanations regarding how ASS could develop and maintain themselves under natural conditions.

The main question in our study on the long-term development of dune-slack vegetation on the Wadden island of Terschelling was whether alternative stable states (ASS) could also develop after restoration measures, notably sod-cutting and hydrological manipulations, to increase groundwater discharge to a degenerated dune slack, Koegelwieck.

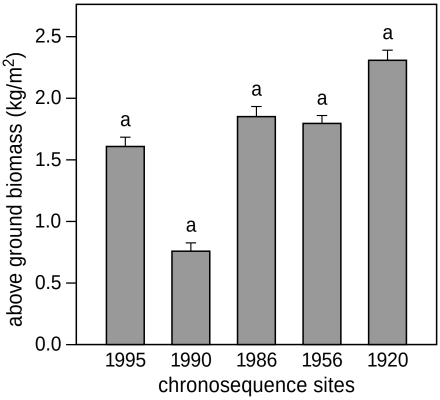


Figure 7. Peak standing crop at the chronosequence sites in the Koegelwieck dune slacks. Significant differences indicated by different letters; only the chronosequence site initiated in 1990 was significantly ($p<0.005$) different from the rest of the sites.

Stability in species composition

In the present study, we found that the stability of a vegetation type that had developed after restoration measures depended on the hydrological and climatological conditions that prevailed immediately after restoration (chapter 3 of this thesis). Our analyses showed that early pioneer stages (sites 1986 and 1990) may first diverge into very different vegetation types. Site 1986, with many rare and protected plant species, was quite unstable and quickly shifted into a late successional stage after only 5 years of succession. The ordination diagrams show that the oldest site (1956) and the young site dominated by *Littorella uniflora* (1990) were relatively stable (Figure 5). In contrast, site 1986 shifted rapidly from a community type rich in basiphilous species towards a community with more productive and acidophilous species, such as *Calamagrostis epigejos, Oxycoccus macrocarpa* and *Phragmites australis*. The similarity within this site, as compared with the starting situation, decreased during succession, because the early colonizers had disappeared from this site. This may have happened because certain colonizers became dominant and outcompeted other early colonizers or because most early successional species had been replaced by later successional species. The second explanation is more likely because the similarity index of site 1986 with the older site from 1956 increased during succession. Site 1990 became more dominated by wet species, such as *Littorella uniflora* and *Mentha aquatica*. This site seemed more stable than site 1986 when considering the within-site similarity values. Site 1990 had a low similarity with the old site from 1956, probably because of the absence of the late-successional species common in site 1956. The vegetation at the younger site from 1995 was similar that at site 1956 during an earlier stage. A sudden shift in vegetation composition probably occurred at this site, maybe due to the occurrence of the dry years following sod-cutting.

Stability of environmental factors

The strong relationship between age of a young successional stage and amount of soil organic matter (SOM) during the first 50 years of succession has already been mentioned by Olff et al. (1993) and Sival (1997). However, this relationship is not always linear, especially during the build-up phase. For example, Jones et al. (2008) showed that for dunes systems in Wales (UK),, the SOM increase followed a sigmoidal pattern over time. In dune slacks, discharge of calcareous groundwater and the presence of calcareous substrates appear to be responsible for the initially slow increase of organic matter during the pioneer phase (Sival and Grootjans 1996, Kooijman et al. 1998, Kooijman and Besse 2002, Kooijman 2008)**.**

SOM accumulation in the Koegelwieck also showed a clear sigmoidal curve. In fact, only one site (site 1986) showed a rapid increase during the monitoring period. However, another sampling site only a few meters away did not show this rapid increase during the monitoring period that was analyzed. This difference could be attributed to the specific characteristics of their locations within the dune slacks. There was about a 20 cm site height difference between these two sub-sites, which would result in a difference of water level between them. Indeed, the sub-site with the lower elevation accumulated less organic matter. From evidence here and also that collected from site 1990, which was the lowest site in the dune slacks, we may state that higher water levels lead to lower organic matter accumulation. This phenomenon has been extensively discussed elsewhere (Bakker 2005, this thesis, chapter 2 and 5).

Stable or transient?

We were able to test assumptions about the occurrence of alternative stable states because the Koegelwieck dune slack provided a unique opportunity to study spatial and temporal aspects of ecosystem development. The combination of regular vegetation monitoring in (permanent) plots with precisely known ages and regular sampling of soil parameters within this chronosequence has provided us with this opportunity. Our research has shown that restoration measures do not necessarily lead to the development of an ecosystem that can be considered stable over a considerable period of time as was shown for a natural dune slack on Texel (Adema et al. 2002). In Koegelwieck, seemingly similar restoration measures led to different vegetation types, with different stability characteristics, depending on the hydrological characteristics of the time during which the measures were carried out (wet/dry periods).

Most pioneer stages were not resilient and could not return to the same state after relatively small disturbances. For instance, site 1995 in our study shifted toward a more productive stage as a consequence of relatively dry conditions shortly after the site was sod-cut (1996). However, this shift in vegetation has not yet been reflected in the measured soil parameters, although it had already been apparent in the above-ground biomass after 13 years. In contrast, the older site sod-cut in 1990 remained at a rather stable pioneer stage, with almost no accumulation of organic matter and low above-ground biomass for more than 14 years. However, after a period of relatively wet years (2000-2008; Chapter 3), the pioneer stage with *Littorella uniflora* was slowly replaced by a more productive stage dominated by *Phragmites australis*.

We found that changes in vegetation preceded changes in soil factors, such as soil OM and soil pH, and that relatively small changes in species composition could trigger big changes when accompanied by unpredictable changes in hydrological or meteorological conditions (see also chapter 3). The competitive advantage that early successional species may have during the first years following restoration (Bakker et al. 2006, 2007) may not always last very long. Even small changes in vegetation composition could lead to drastic shifts in vegetation when exogenous environmental factors are suddenly changed (Grootjans et al. 2001). For instance, one dry year in the summer could shift wet basiphilous vegetation into moist vegetation dominated by species such as *Oxycoccus macrocarpa* (Chapter 3 of this thesis). However, if ASS at an early stage can be sustained, it would benefit nature conservation, because pioneer stages that could maintain themselves in a stable state without additional management measures would be a cost-efficient way to conserve threatened plant species for an extended period of time.

Acknowledgement

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Chapter 5

Accumulation rates of soil organic matter in wet dune slacks on the Dutch Wadden Sea islands

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Abstract

Background and aims: A long-term monitoring program (ranging from 16-77 years) on the Dutch Wadden Sea Islands provided well-documented examples of vegetation succession in wet dune slacks. We used this opportunity to study soil organic matter (SOM) accumulation in relation to vegetation succession. The aim of this paper is to identify the factors which regulate accumulation rates of SOM in wet dune slacks. *Methods:* We used several soil chronosequences using data from the monitoring program together with data from a long-term research activity and more recent measurements. We used several soil chronosequences using data from the monitoring program together with data from a long-term research (up to 150 years) and more recent measurements. Field measurements included pH, soil organic matter, above ground standing crop and water levels. Water level regimes (inundation duration and mean minimum water level), were simulated using a hydrological model. Capable of simulating inundation duration and water-level fluctuations, this model used field measurements collected over more than 5 years, as well as precipitation and evapotranspiration data collected over a period of 25 years. *Results:* Sampling two synchronic chronosequences showed that SOM accumulations increased linearly during the first 50-60 years and then levelled off. Sampling various diachronic chronosequences over time showed a wide variation in accumulation rates. Slacks with low productive species, such as *Littorella uniflora*, showed low accumulation rates (0.02-0.08 kg/m^2/year), and persisted even over a period of more than 90 years. In contrast, slacks dominated by high productive species, such as *Phragmites australis*, showed ten times higher accumulation rates (0.17- 0.26 kg/m^2/year) over a similar time period and comparable annual inundation periods (176-240 days). A multiple linear regression showed that variation in SOM accumulation rates was best explained by above-ground biomass of the vegetation. *Conclusions:* We conclude that the rate of SOM accumulation in wet dune slacks is primarily controlled by plant productivity. Both above-ground biomass and SOM accumulation can remain very low over a long period of time when dune slacks are flooded during most of the year and plants with adaptive traits are able to maintain vegetation succession at a pioneer stage.

Keywords: *above-ground biomass, hydrology, nitrogen deposition, ROL, soil chronosequence, succession*

Introduction

Soil organic matter (SOM) is an important component in almost all terrestrial ecosystems, affecting the biological, chemical and physical properties of soils that influence plant growth. Changes in SOM accumulation alter many soil properties during primary succession (Walker and del Morel 2003). For example, a sharp decline in soil pH usually leads to a rapid increase in SOM and an increase in soil moisture (Jenny 1980, Van Breemen and Buurman 2002). These strong effects on soil properties indicate that SOM has profound influences on vegetation succession.

The accumulation rate of SOM is determined by litter production and litter decomposition rates, which are controlled by climatic factors, such as precipitation and temperature, and more local factors such as soil moisture, pH and type of vegetation (Alvarez and Lavado 1998, Dai and Huang 2006, Kirschbaum 1995, Parè et al. 2006). In general, climatic factors such as precipitation and temperature are recognized as the most influential factors (Jenny 1980, Alvarez and Lavado 1998). High temperatures usually stimulate decomposition rates, although excessively high temperatures may inhibit growth of soil organisms, and may consequently reduce decomposition rates (Dai and Huang 2006). Additionally, high precipitation that leads to high soil moisture promotes biomass production of the vegetation, which provides more litter input to the ecosystems thus leading to high accumulation of organic matter (Mukhortova 2008). Increased atmospheric nitrogen deposition that is observed in many European countries (20-25 kg N $ha^{-1}yr^{-1}$ in the Dutch Wadden Sea islands; Sival and Strijkstra-Kalk (1999) compared to 3–8 kg N $ha^{-1}yr^{-1}$ in the Baltic states; Remke et al. 2009), also can increase accumulation rates in wetlands (Adema et al. 2002).

With respect to soil moisture, complete water saturation leads to anaerobic conditions in the soil, which inhibit the activity of decomposers (Day 1982). Thus, prolonged inundation may lead to lower rates of litter decomposition. In peatlands, for instance, the continual process of litter accumulation and slow decomposition activity under saturated conditions leads to a high build-up of organic matter. In wet dune slacks, however, such high rates of organic matter accumulation do not always occur. Adema et al. (2002) found remarkable differences in SOM accumulation between two sites located in the same 80-year-old dune slack, both of which were inundated for most of the year. The authors suggested that these differences in SOM accumulation represented alternative stable states, listing three possible positive feedback mechanisms to explain these differences: (1) sulphide toxicity from microbial mats; (2) occurrence of pioneer species with radial-oxygen-loss (ROL) capability; and (3) differences in the productivity of species. Dune slack species with ROL capability such as *Littorella uniflora* and *Schoenus nigricans* could facilitate rapid decomposition (Ernst et al. 1996, Adema et al. 2002). On the other hand, species with recalcitrant components in their tissues are known to slow down mineralization rates as has been shown in *Schoenus nigricans* (Ernst et al. 1996), species of *Sphagnum* (moss) (Van Breemen 1995, Verhoeven and Toth 1995, Scheffer et al. 2001) and those found in the Leguminosae (Palm and Sanchez 1991). Finally, it has been demonstrated that highly productive species usually have higher litter inputs into soil, which eventually leads to higher SOM accumulation rates, compared to species with low productivity (Smith et al. 2008).

Studying SOM accumulation rates ideally requires long-term observation but such studies are difficult to accomplish. A viable, alternative technique is to use soil chronosequences: soils of different age, situated close together (Huggett 1998). The chronosequence approach has been used by many authors to interpret soil changes along time scales in many habitat types such as volcanoes (Peña-Ramírez et al 2009), moraines (Sollins et al. 1983), floodplains (Wigginton 2000) and dunes (Salisbury1925, Wilson 1960, Olff et al. 1993, Jones et al. 2008). Most studies use a *synchronic* approach, where sampling is done at the same time but in different adjacent plots. However, this method must be used with extra precaution as it is vulnerable to the confounding effects of high spatial variability (Walker et al. 2010). Using a *diachronic* chronosequence, in which sampling is done repeatedly within the same plot, avoids these potentially confounding effects of high spatial heterogeneity. This method was used, for example, by Abreu et al. (2009) to evaluate the restoration dynamics in the alpine belt of the northern Andes.

In order to study SOM accumulation during primary succession, we used wet dune slack systems on the Dutch Wadden Sea islands because they are relatively young and their history is well known, which allows reconstruction of soil chronosequences (Berendse et al. 1998, Lammerts et al. 1999). In Dutch coastal areas, restoration projects have been carried out for more than 30 years. These projects were aimed at restoring pioneer stages with many rare and endangered plant species. Restoration measures usually included turf stripping and several of these projects have been carefully monitored (Grootjans et al. 2002). Such monitoring programs enable us to assess the exact starting date of vegetation succession after restoration measures, such as turf stripping as well as the natural rejuvenation of dune slacks after sand blow outs. In this study, we present results from chronosequences covering time periods of up to 150 years and data on soil development collected from the monitoring of restoration projects.

Jones et al. (2008) found that differences in SOM accumulation in dune habitats in Wales were primarily associated with climatic factors and the amount of N deposition, and less so with local habitat conditions. However, they did not present information on the hydrological regimes of these wet dune slacks. In our study, we will investigate whether SOM accumulation rates are regulated over time by local factors, such as differences in hydrological regimes, pH, and productivity (measured as above-ground biomass) of the vegetation.

As was discussed above, prolonged flooding in wetlands can lead to high accumulation rates in wetlands, due to restricted mineralization, but also to very limited accumulation rates when low productive pioneer species keep the productivity of the vegetation low. We hypothesize that the relationship between flooding duration and accumulation rates in slacks is influenced by the productivity of the vegetation. We, therefore address the following questions:

1) Do slacks with similar flooding regimes show the same accumulation rates?
2) Do other factors, such as soil pH and plant productivity, also affect SOM accumulation rates?

Materials and methods

Site description

This study was conducted in wet dune slacks on four Dutch Wadden Sea islands. Sample sites were selected on the islands of Texel (53° 4' 58.7994"N 4° 49' 58.8"E), Vlieland (53°16'28"N 4°58'47"E), Terschelling (53°24'0"N 5°19'0"E) and Schiermonnikoog (53°29'29"N 6°13'43"E) (Figure 1).

Soil chronosequences

Both types of soil chronosequences addressed earlier were used in this study. We sampled two synchronic chronosequences (Schiermonnikoog and Terschelling) to study SOM accumulation trends in wet dune slacks over longer time scales. The soil chronosequence on Schiermonnikoog consisted of seven sites covering different stages of vegetation succession (16, 18, 20, 52, 60 and 150 years old). The chronosequence on Terschelling included six sites within a secondary dune slack of *ca.* 50 ha. The ages of these sites were 15, 20, 24, 54 and 99 years. In order to study variation in SOM accumulation rates within soils of the same successional stage, we used several diachronic chronosequences. For this purpose, we sampled four 50-60 year-old sites on Schiermonnikoog: Kapenglop-1, Kapenglop-4, Vuurtorenvallei-1 and Strandvlakte-2. Kapenglop-1 and Kapenglop-4 are located in the same slack and have not been managed since *ca.* 1964. The Kapenglop sites were sampled 4 times with intervals ranging from 5-10 years. In 2010, Kapenglop-1 was still in a pioneer stage, while Kapenglop-4 was in a late successional stage with scrubs and trees up to 5 meters high. Vuurtorenvallei-1 is a 52 year-old blow-out dune slack that has been mown yearly since 2000. This site has been sampled 5 times with intervals of c. 5 years. The vegetation consists of typical dune slack species, as *Epipactis palustris* and *Schoenus nigricans*, with occasional shrubs like *Salix repens* and *Hippophae rhamnoides*.

The Strandvlakte-2 is a 50 year-old beach plain that is periodically flooded by sea water and is dominated by *Schoenus nigricans*. It has been sampled 3 times with intervals of 15-30 years.

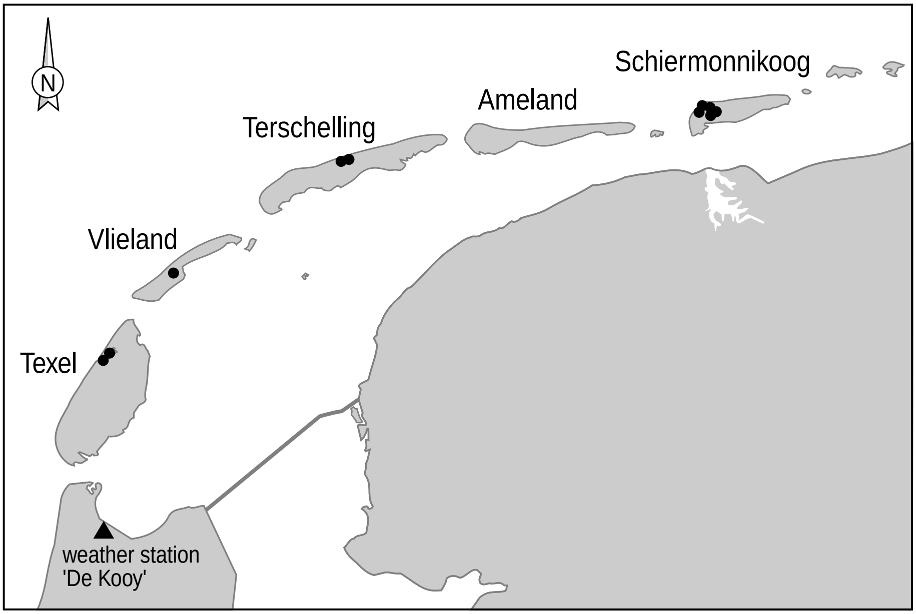

Figure 1. Study sites on the Dutch Wadden Sea Islands

In addition to these chronosequence sites, we also included data on SOM accumulation from older dune slacks. These ~90 year-old slacks, Buiten Muy-1 (Texel) and Kroon's polder-1 (Vlieland), has been unmanaged from the moment they were first vegetated. The dune slack Buiten Muy-1 originated from a beach plain that was separated from the sea by dune ridge formation between 1920 and 1925 (Adema et al. 2002). The site of Kroon's polder-1 was artificially closed off from the sea in 1924. De Vries (1961) mentions that the dune slack of Kroon's polder-1 had almost no vegetation in 1941. We included this site because the development of the ecosystem was very peculiar. The site had been dominated by a dense vegetation of *Phragmites australis* during most of the last century. We observed that after about 60 years the above ground biomass of *Phragmites australis* in part of the dune slack declined dramatically due to the increase of a semi-parasitic species *Pedicularis palustris* (De Bakker et al. 2004) Since 2002 several endangered species that are typical for early stages of dune slacks started to increase in numbers as well. This shows that early successional species, such as *Dactylorhiza incarnata, Epipactis palustris* and *Liparis loeselii* can co-exist with late successional species, such as *Phragmites australis*, even on a soil with a thick layer of organic material.

Kroon's polder-1 and Buiten Muy-1 do not represent a real chronosequence because they have not been monitored frequently enough to reconstruct vegetation development. We also added two other sites i.e. Primary valley-3 (Schiermonnikoog; sampled 5 times with intervals of 3-5 years) and Koegelwieck-1 (Terschelling; sampled 5 times with intervals of 3-5 years) that had similar vegetation composition to Buiten Muy-1. Although both these sites were much younger than Buiten Muy-1 (only 20 years old), they had been monitored frequently enough to reconstruct chronosequences.

Estimating soil age

The soil age of sites was determined using various methods. Primarily, we used data from the restoration projects on the Dutch Wadden Sea islands (Grootjans et al. 2002). The age estimation from these projects is very reliable because we know the exact time of turf stripping. The ages for sites without management activities were determined by referring to literature. These descriptions are usually also very precise, since the new formation of dune slacks or enclosure of dune ridges, forming new slacks is well documented on the Dutch Wadden Sea islands. Additionally, aerial photographs and topographical maps were used to assess the starting date of vegetation development at each location.

Sample collection and analysis

Soil samples were taken within one meter of permanent vegetation plots in homogenous vegetation units. At each sampling site, five soil samples were taken from the 0-5 cm layer, and also from deeper layers if the organic layer was thicker than 5 cm, using metal rings with an inner volume of 100 cm^3. The organic matter thickness was measured in the field as the depth of dark-colored organic sand. The soil samples were then homogenized after removing litter, living mosses and roots in the lab. The organic matter was determined by loss of mass after ignition at 550° C for at least 15 hours. Soil pH(KCl) was determined by adding 2.5 mL of 1M KCl to 15 g of fresh soil.

Above-ground biomass

Above-ground biomass (peak standing crop) was measured from August to September 2012. All above-ground vegetation was clipped in 5 replicate plots of 0.25 m^2. The samples were oven-dried at 105°C for at least 12 hours. After the drying process, the samples were directly weighed. Forest stand information was obtained from Van der Koppel (unpublished data).

Simulation of water levels

Groundwater level data came from fourteen piezometers with filters at 100-120 cm below the surface. The tubes were placed within 2-20 meters from the soil sampling sites. Groundwater levels were measured every two weeks during 6-10 years. The water level data were collected by the Dutch State Forestry Service (SBB) and

Natuurmonumenten (The Society for the Preservation of nature monuments in the Netherlands). Variations in water levels were simulated using the computer program, MENYANTHES (Von Asmuth et al. 2010). For these simulations the aforementioned long term water measurements were used. Precipitation data were obtained from weather stations on the respective islands. Groundwater levels were simulated for a period of 25 years (1985-2010). Evaporation data were obtained from the meteorological station, De Kooy. For the present study we used the following (calculated) variables: Mean Higest Level (MHL), Mean Lowest Level (MLL), Mean Fluctuation of levels (MFL) and Inundation Duration (ID). MFL = MLL + MHL.

Data analyses

Differences in SOM contents were tested using the Student-Newman-Keuls test when the sites had three or more sampling years, whereas the Mann-Whitney test was used for the sites with only two years of sampling. We tested for homogeneity of variances using the Levene test and excluded sites with heterogenous variance from further statistical analysis. The relationships between SOM content, successional age, pH and above-ground biomass of the vegetation were assessed using multiple linear regression. All statistical tests were carried out using R for Windows 2.11 (R development core team 2010).

Results

Synchronic chronosequences: similar long-term trends in SOM accumulation

The first chronosequence, established from a series of SOM accumulation (kg/m^2) on Schiermonnikoog (Figure 2a), showed an increase of 0.26 kg. m^{-2}.yr^{-1} during the first 60 years of succession, after which SOM accumulation slowed down.

The maximal accumulation of 17.5 kg/m^2 occurred at 150 years and this stage was dominated with trees (*Betula pubescens*). Between 60 to 150 years, the SOM accumulation rate had reached a stable state and no further significant increase was observed.

The second long-term chronosequence from Terschelling (Figure 2b) shows a total SOM accumulation *ca*. 2.0 kg/m^2 in the first 20 years. Between 20 to 50 years, there is a steep increase in SOM accumulation, after which SOM levels off. The maximum content of organic matter reached was ca. 10.0 kg/m^2, which is almost half of the maximum amount of SOM at Schiermonnikoog. The dominating species in this late successional stage were *Salix repens* and *Oxycoccus macrocarpas.* SOM accumulation on the Terschelling chronosequence showed a similar decelerating trend to that measured on Schiermonnikoog, both levelling off after 50-60 years, but the final values of SOM were much lower.

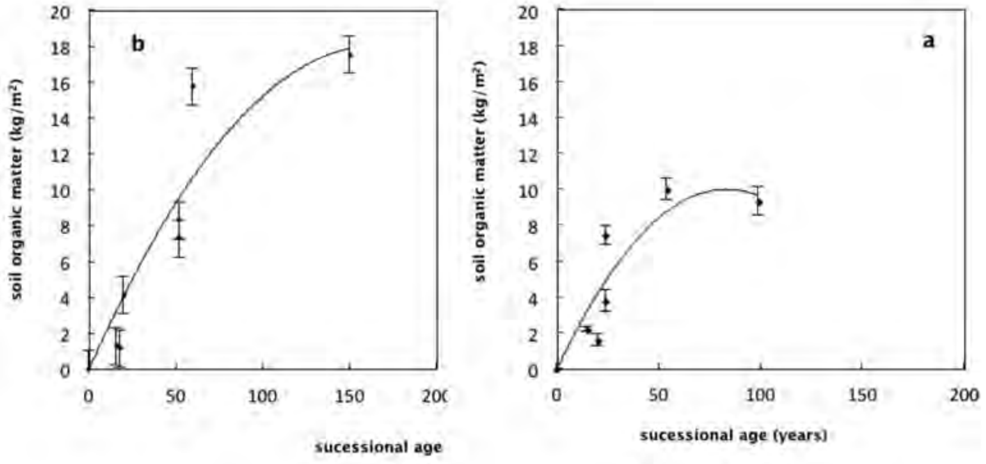

Figure 2. Trends of SOM accumulation from synchronic chronosequence on (a) Schiermonnikoog and (b) Terschelling.

Diachronic chronosequences: different rates of SOM accumulation between sites
Four diachronic chronosequences aged 50-60 years were sampled in dune slacks on the island of Schiermonnikoog (Figure 3).

Rates of SOM accumulation were remarkably different between dune slacks. The Kapenglop 4, which showed a steep trend during the last 20 years and had the highest SOM content (15.8 kg/m^2) in 2010.

Late-successional plant species, such as *Salix cinerea* and *Betula pubescens*, dominated the vegetation of this sampling site. In contrast, Kapenglop 1, which was situated 50 meters away in the same slack, showed a very low organic matter build-up of only 3.5 kg/m^2 after 50 years. The vegetation was still in a pioneer stage (*Samolo-Littoreletum*), dominated by *Littorella uniflora*. Vuurtorenvallei 1 and Strandvlakte 2 both had developed the targeted dune-slack vegetation, with many rare species of the *Junco baltici-Schoenetum nigricantis* community. These sites showed a slow accumulation rate over the first 30 years (*ca*. 0.1 kg. m-^{2}.yr^{-1}. However, for Vuurtorenvallei 1, the SOM-accumulation rates appeared to increase gradually until a final amount of 8.0 kg/m^2 after 50 years.

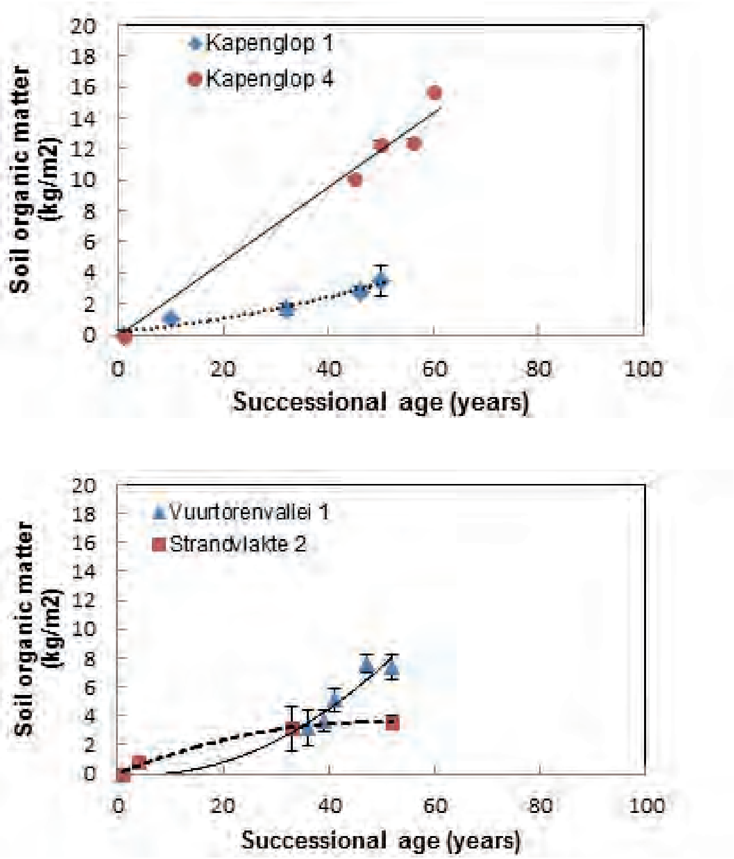

Figure 3. SOM accumulation trend from diachronic chronosequences of various dune slacks on Schiermonnikoog, all aged between 50-60 years. The graph above shows the SOM accumulations in two sites within the same slack (Kapenglop), while graph below shows the accumulations in slack that has been mown (Vuurtorenvallei 1) and without management (Strandvlakte 2).

Despite an irregular mowing regime during the last 10 years, the slack was at a mid-successional stage, yet retained many orchid species. On the other hand, Strandvlakte 2 that never been mown, had accumulated a lower SOM with the final accumulation of 3.6 kg/m^2 after 50 years.

Dominant species and SOM accumulation

In Figure 4, we present SOM accumulations in slacks dominated by pioneer species *Littorella uniflora*, but with different successional age (Primary Valley 3 and Koegelwieck 1 – 20 years old; Buiten Muy 1 – 89 years old). Although Primary Valley 3 and Koegelwieck 1 were much younger than Buiten Muy 1, they accumulated similar amounts of SOM (only 1.6 kg/m^2 and 1.2 kg/m^2 of SOM respectively) after 20 years of succession.

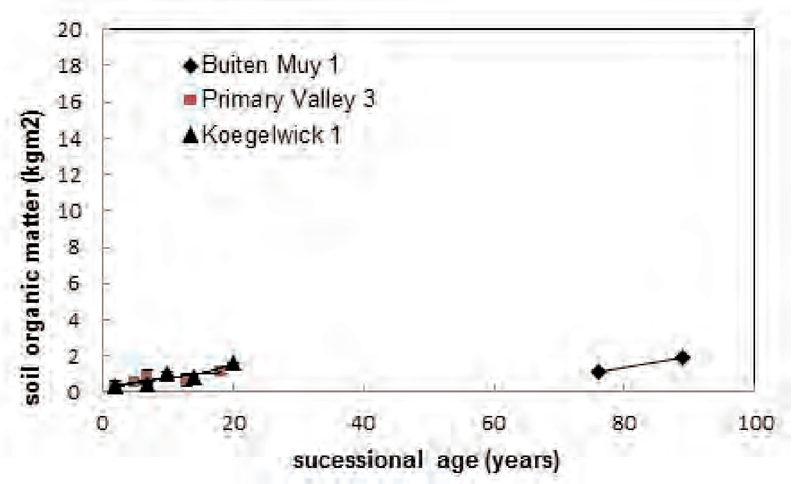

Figure 4. SOM accumulation in slacks dominated by *Littorella uniflora* (Buiten Muy 1, Primary Valley 3, Koegelwieck 1).

The accumulation remained low in Buiten Muy 1 (1.9 kg/m2) even when the slack reached almost 90 years. In order to see the effect of different dominating species on the SOM accumulation, we compared the four oldest dune slacks that range between 89 to 105 years old (Figure 5). From the graph we can see that the accumulation rates varied widely between sites with different dominating species. The site with *Littorella uniflora* resulted in an extremely low SOM accumulation, while site with woody species, such as *Betula sp.* showed the highest accumulation.

Local factors (pH, water level regime, and above-ground biomass) in relation to SOM accumulation

In general, pH tended to decline over time for both the synchronic chronosequences (Figure 6). The soil pH of the pioneer stages (between 15-20 years) was 6.3 and decreased gradually in the late successional stages to a value of 4.2 (150 years on Schiermonnikoog) and 5.1 (90 years on Terschelling) respectively. Table 1 shows the summary of each variable for the diachronic chronosequences, also including the non-chronosequence sites of Kroon's polder 1 and Buiten Muy 1.

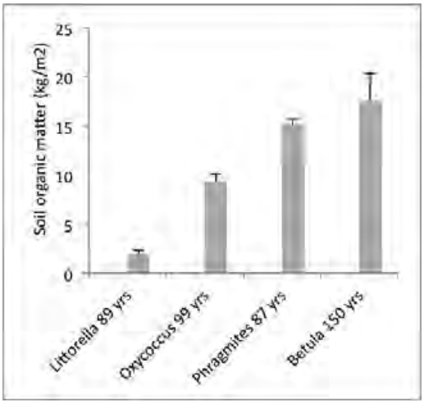

Figure 5. Maximum SOM accumulation among the oldest (unmanaged) sites. The sites have been labelled with their dominant species and age: Buiten Muy 1 on Texel (89 years) Koegelwieck on Terschelling (99 years), Kroon's polder 1 on Vlieland (87 years) and Kobbeduin on Schiermonnikoog (150 years).

In all sites SOM increases with age, except for Buiten Muy 1. As described earlier, this site has hardly accumulated any organic matter for almost a century. In contrast the Kroon's polder-1 site shows a very high SOM while the pH is relatively high. A high SOM accumulation was strongly associated with low water levels in summer (MLG). However, sites with long inundation periods (more than 200 days) showed either very low (Buiten Muy 1) or very high SOM accumulation (Kroon's polder 1), depending on the dominant species at the sites (*Littorella* and *Phragmites*, respectively).

In order to assess which environmental factors best explained the SOM accumulation in the dune slacks presented in Table 1, we carried out a multiple linear regression analysis. The results show that only above-ground biomass of the vegetation was significant; Age and mean fluctuation of the water level were not significantly correlated with an increase in SOM.

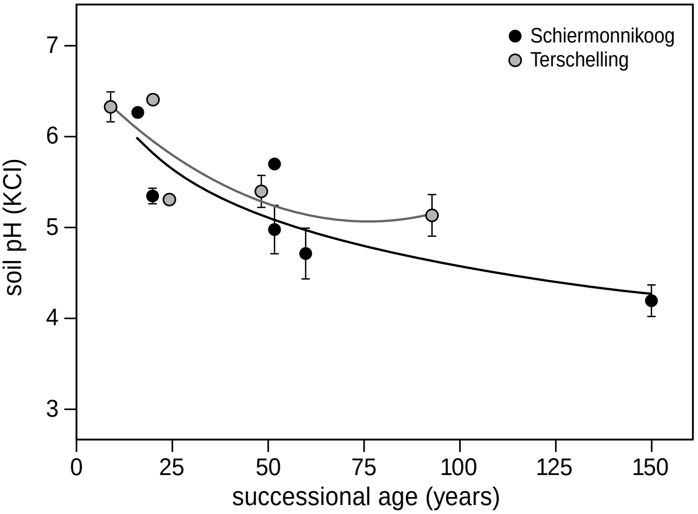

Figure 6. Soil pH (KCl) of Terschelling and Schiermonnikoog chronosequences.

Table 1. Summary of variables for diachronic chronosequence sites: Age – successional age (years); pH(KCl) – soil pH, ID – inundation days i.e. the amount of days per year when the site was inundated; MLG – mean lowest groundwater level below soil surface (m); Biomass- Aboveground biomass, SOM – soil organic matter; and SOM accumulation; MF – Mean Fluctuation i.e. mean lowest groundwater level + mean highest water level (m). The non-chronosequence sites of Kroon's polder 1 and Buiten Muy 1 are also included.

Study site	**Age**	**pH (KCl)**	**dation Dur**	**MLG**	**Biomass**	**SOM**	**MF**
	yrs		**days**	**m**	**kg/m²**	**kg/m²**	**m**
Primary valley 3	18	6.7	244	0.2	0.42	1.18	0.43
Koegelwieck 1	20	6.4	227	0.28	0.75	1.59	0.48
Kapenglop 1	50	5.8	176	0.48	1.24	3.5	0.62
Strandvlakte 2	52	5.7	192	0.24	0.91	4.65	0.35
Vuurtoren valley 1	52	5	52	0.6	0.64	7.31	0.63
Kapenglop 4	60	4.7	69	0.64	3	15.77	0.66
Kroon's polder 1	87	5.9	186	0.4	20.5	15.5	0.54
Buiten Muy 1	89	6.3	236	0.24	0.2	1.92	0.5

Table 2. Result of multiple linear regression analysis with soil organic matter as dependent variable. Three variables were selected after correlation test; Age, above ground biomass and mean fluctuation. Significant variables are shown in bold.

	β	coefficient	*t*-value	p
Age	0.062	0.272	1.44	0.222
Biomass	**5.076**	**0.801**	**3.74**	**0.02**
Mean fluctuation	1.798	0.033	0.153	0.886

Discussion

The vegetation of dune slacks in coastal areas of north-west Europe normally changes from pioneer stages with sparse vegetation to mature stages dominated by *Betula* forest within 150 years (Olff et al. 1993, Sival 1996). Using a traditional chronosequence approach, in which ecosystems of different age but with a (supposed) similar development history are compared, we found that soil organic matter (SOM) increased more or less linearly during the first 50-60 years and then levelled off to a maximum between 10 and 18 kg/m^2. We also studied ecosystem development in dune slacks using a diachronic chronosequence approach, in which we monitored soil and vegetation development in permanent plots over a period of 20-46 years. We found a large variation in accumulation rates, which varied between 0.02 and 0.26 kg/m^2/year. In general, we found that slacks with a long inundation period accumulated less organic matter than drier slacks, which appears to support our original hypothesis that high water levels, combined with a high pH would lead to slow accumulation of SOM (see also Adema et al. 2002). Some very wet slacks with a very strong discharge of calcareous groundwater showed either very low or very high accumulation rates over a period of *ca*. 90 years. A multiple linear regression showed that variation in SOM accumulation rates were best explained by above-ground biomass of the vegetation. However, this result cannot be generalized. With a greater number of sites the relationships between SOM and hydrological variables would also become significant. But our results show that the accumulation of organic matter does not follow simple rules, but depending on the hydrology and the productivity of the vegetation can result in very different outcomes.

Slacks that were dominated by highly productive species, such as *Betula spp.* and *Phragmites australis,* accumulated a large amount of organic matter over time. This is in line with the results of Smith et al. (2008), who studied SOM accumulation of dune slacks in Massachusetts, USA. These authors suggested that growth of woody plants was the main driver in SOM accumulation in their wetlands. Additionally, wetlands dominated by *Phragmites australis* are among the most productive ecosystems (Westlake 1963, Bakker et al. 1997, Windham and Lathrop 1999). Differences in above-ground biomass of the vegetation may also explain the difference in SOM accumulation in our two synchronic chronosequences; with higher SOM found on Schiermonnikoog than on Terschelling. Previous studies indicated that the aboveground biomass on Schiermonnikoog (Olff et al. 1993) was much higher (3 kg/m^2) than on Terschelling (~1 kg/m^2) (Berendse et al. 1998).

Consequently, factors that increase plant productivity such as nitrogen deposition will also influence SOM accumulation rates as was previously suggested by Jones et al. (2008), when studying wet and dry dune ecosystems in Wales (UK). Since pioneer stages of dune slacks are N-limited (Lammerts and Grootjans 1997), they are very susceptible to atmospheric nitrogen deposition (Lammerts et al. 1998). In the past decades, atmospheric nitrogen deposition has increased significantly in Dutch coastal area (Stuyfzand 1993) and is now becoming a major threat to nutrient-poor habitats (Bobbink et al. 2010, Sparrius 2011). Apart from man-made influences, invasion of certain plant species, such the N-fixing shrub *Hippophae rhamnoides,* may accelerate OM accumulation rates.

Above-ground biomass of the vegetation had a stronger effect than age on SOM accumulation in our study. We found that four older dune slacks of roughly the same age (*ca*. 90-150 years old) had very different SOM accumulation values (Figure 5). The very low accumulation rates in the three dune slacks dominated by *Littorella uniflora* (Figure 4) are quite uncommon and, to our knowledge, have never be found in dune slacks. All sites are very wet; they are flooded for more than 200 days per year. Long inundation periods apparently allow the small pioneer plant species, *Littorella uniflora*, to dominate the vegetation. This species has the ability to decompose its own litter efficiently (Armstrong 1982), hence reducing SOM accumulation. Additionally, this species has ROL capability, and is thus able to reduce nitrogen and phosphate available for competing species (Adema et al. 2002). When inundation periods would decrease, by artificial or natural causes – changes in coastline have immediate consequences for local hydrological conditions (Stuyfzand 1993) – the dune slack may become drier and would enable the invasion of shrubs, like *Salix repens* or tall marsh species, like *Phragmites australis*. The higher litter input of these species to the soil would soon accelerate SOM accumulation and accelerate succession (Walker & Del Moral 2003). Most of our dune slacks, however, showed similar SOM accumulation trends to those reported by Jones et al. (2008) for dune slacks of the Newborough Warren in Wales. However, some dune slacks on the Dutch Wadden Sea islands showed much higher SOM accumulation rates than the slacks in Wales (Figure 7).

Jones et al. (2008) suggested that turf stripping activities or management measures in the Dutch dunes might explain the observed differences. However, several sites in our study have never been sod-cut or mown but the accumulation rates were still higher than values found in Wales. The differences could be due to differences in management; dune slack in Wales were all mown or grazed. Several of our slacks were not managed for at least 50 years. The higher accumulation rates in the Dutch dune slack may also reflect differences in annual nitrogen deposition, which are lower in Wales (c.10-15 kg N $ha^{-1}yr^{-1}$ in Wales; Jones et al. 2013, compared to 20-25 kg N $ha^{-1}yr^{-1}$ in the Dutch Wadden Sea islands; Sival and Strijkstra-Kalk 1999). Furthermore differences in hydrological systems and associated differences in water level regimes could be responsible for the observed differences in SOM accumulations rates.

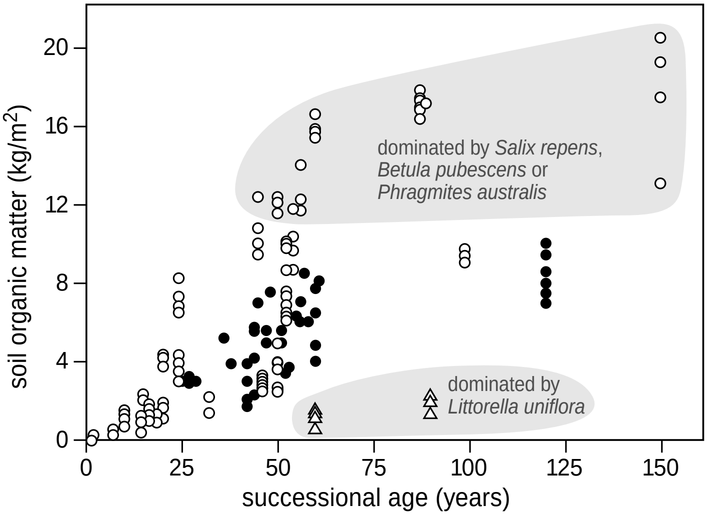

Figure 7. SOM accumulation data from dune slacks in the Netherlands (open symbols) and also the dunes in Wales (black filled circles). Older dune slack with high values of organic matter accumulation are dominated by shrubs or trees (*Salix repens* or *Betula pubescence*), while older dune slack with low accumulation values are dominated by *Littorella uniflora.*

Dune systems in the Dutch Wadden islands are generally much larger than the Newborough dunes, thus generating also more stable water table levels in the dunes slacks, creating wetter conditions. Furthermore, the sandy soils in several dune systems in western England and Wales are more alkaline due to high initial carbonate content compared to most of the coastal dunes included in the present study. Both these factors could lead to higher mineralization rates of organic matter, and lower SOM accumulation rates, in Wales.

An unexpected result was that above-ground biomass drastically declined in a site with very high water levels and prolonged inundation (and very high associated SOM accumulation rates) after 87 years, enabling (re-)establishment of plant species that are typical for early successional stages (*Dactylorhiza incarnata, Epipactis palustris* and *Liparis loeselii)*. This was observed only in one dune slack (Kroon's polder 1), which is influenced by a very regular discharge of calcareous groundwater and where the above ground biomass of *Phragmites australis* was drastically reduced by the spread of the semi-parasitic species *Pedicularis palustris* (see description of chronosequence sites) A possible explanation for the occurrence of a peat layer of c. 20 cm might be the very anaerobic conditions in the topsoil combined with low decomposition rates in *Phragmites* stands due to its highly lignified tissues (Farmer and Morrison 1964, Windham and Lathrop 1999; Meyerson et al. 2000). This results in low nutrient availability. Such conditions favor the spread of *Pedicularis palustris*, a hemi-parasitic species capable of reducing the growth of *Phragmites australis* (Ter Borg 1979, Decleer et al. 2013). From the perspective of nature conservation, the re-establishment of pioneer species in a late-successional stage is quite interesting, since it shows that dune slacks have much in common with natural mires (living peatlands), such as fens that are characterized by high peat accumulation under nutrient-poor conditions. Many rare species, for instance *L. loeselii, S. nigricans* and *P. palustris*, also can be found in nutrient-poor fens, indicating that Kroon's polder 1 is probably developing into a fen.

In conclusion, our results indicate that there is a significant relation between above-ground biomass of the vegetation and the accumulation of organic matter in dune slack ecosystems. This factor however, is closely related to the water level as already discussed above. Even small changes in the hydrology of the system can affect water levels, resulting in drier and more acidic conditions. This leads to the disappearance of basiphilous species and eventually to the encroachment of shrubs. Therefore, it is important to study hydrology of systems at a landscape level in order to understand the successional process in dune slacks and to develop better management strategies. Furthermore, our results support the findings of Adema et al. (2005), who suggested the occurrence of alternative stable states in wet dune slacks. We also found both very high and very low SOM accumulation rates under similar environmental conditions. Whether sudden shifts between such states really occur can only be confirmed when long-term monitoring activities are in place after carrying out restoration projects.

Chapter 6

Radial oxygen loss by the cushion plant *Eriocaulon schimperi* prevents methane emissions from an East-African mountain mire

Bikila W. Dullo, Christian Fritz, Leon, P.M. Lamers, Abate F. Senbeta, Jan, G.M. Roelofs, & Albert P. Grootjans

Abstract

Groundwater-fed mires (i.e. fens) are known sources of methane (CH_4) emission to the atmosphere, but these effects are known to be mediated by vegetation. In a mire system located on a mountain in Bale Mountains National Park (Ethiopia), we assessed the effects of dominance by either a cushion plant (Eriocaulon schimperi) or a sedge species (Carex monostachya) on rhizosphere biogeochemistry. At the Carex-dominated site, CH_4 concentrations in the soil pore water increased from 70 μmol L^{-1} at a depth of 10 cm to 130 μmol L^{-1} at a depth of 100 cm. In strong contrast, CH_4 concentrations at Eriocaulon-dominated sites were extremely low (< 1 μmol L^{-1}) in the rhizosphere, and the effect extended to a depth of 60 cm. Simultaneously, soil redox potentials and CO_2 concentrations were higher at Eriocaulon-dominated sites, indicating low potential for CH_4 production and high potential for CH_4 oxidation. Concentrations of nutrients and elements in the pore water and soil samples were low, but they were similar for both vegetation types. Similarly to the hummock-forming plant Astelia pumila found in Patagonian bogs, E. schimperi displayed a root-investment strategy to cope with the harsh, oligotrophic, wet environment. This strategy is characterized by high root/shoot ratios, high root density, high root porosity, and high redox values and CO_2 concentrations in the pore water of the rhizosphere. It seems that both E. schimperi and A. pumila create an aerobic rhizosphere by radial oxygen loss from their deep roots. This stimulates CH_4 oxidation, preventing CH_4 accumulation in deeper layers, and is expected to strongly reduce CH_4 fluxes to the atmosphere.

Keywords: *Bale Mountain National Park, bog, carbon dioxide, Ethiopia, fen, peat, rhizosphere*

Introduction

It has now widely been established that the emission of CH_4 from wetlands is strongly mediated by vegetation type (Ding et al. 2004, 2005, Bergström et al. 2007, Laanbroek 2010; Olde Venterink et al., 2014). A study conducted in ombrogenous and minerogenous peat-forming systems (i.e. mires) in southern Finland (Bergström et al. 2007) showed that about 78% of the total CH_4 efflux was emitted by emergent plant species that dominate the littoral zone, such as *Phragmites australis* and *Equisetum fluviatile*. The same study also showed that a littoral zone dominated by species with floating leaves, such as *Nuphar lutea, Potamogeton natans* and *Sparganium* spp., only emitted about 2% of the CH_4 emitted by a littoral zone dominated by emergent macrophytes, even though the area they covered was about 44% larger. Similarly, it has been shown in an alpine wetland on the Qinghai-Tibetan Plateau, China, that submerged vegetation dominated by *Potamogeton pectinatus* emitted only about 0.5, 0.9 and 9.2% of the CH_4 emitted by the emergent macrophytes species *Hippuris vulgaris, Carex allivescers* and *Scirpus distigmatis*, respectively (Hirota et al. 2004, Duan et al. 2005).

The clear differences in CH_4 emissions from different wetland types dominated by different vegetation types result from the cumulative outcomes of biogeochemistry, including microbial activities, species adaptations and climatic conditions (Bergman et al. 1998, Cao et al. 1998, Aerts et al. 1999, Bergman et al. 2000, Basiliko and Yavitt 2001, Bergström et al. 2007, Askaer et al. 2011, Bhullar et al. 2013). Some authors have suggested that the dominant plant species can be used as a proxy to predict CH_4 fluxes from different wetland types (Ding et al. 2005, Dias et al. 2010, and Couwenberg et al. 2011). The production of CH_4 is determined by the concentration of easily degradable organic matter in the soil (Valentine et al. 1994, Bergman et al. 1998, Bergman et al. 2000). Wetlands dominated by highly productive vascular species produce large amounts of readily decomposable litter, which stimulate CH_4 production by methanogenic bacteria, under anoxic conditions, by increasing the availability of acetate and/or H2 (Whiting and Chanton 1993, Joabsson et al. 1999, Joabsson and Christensen 2001, Whiting and Chanton 2001). Thus, CH_4 emission may be facilitated by the funneling effect of vascular plants.

Cushion plants, such as *Eriocaulon schimperi, Astelia pumila*, and *Donatia* species, form dense vegetation cover in many parts of the world. However, studies on wetlands dominated by cushion plants are limited and are often only descriptive studies, which lack data on soil biogeochemistry (Mark and Bliss 1970, Gibson and Kirkpatrick 1985, John 1988, Gibson 1990, Williams 1991). The vast majority of these studies were carried out in New Zeeland and Tasmania, where cushion plants occupy extensive areas. However, cushion plants are not restricted to the southern hemisphere, but also occur to some extent in the northern hemisphere. Phillips (1996) mentioned the occurrence of a number of *Eriocaulon* species that form cushion carpets in the highlands of Ethiopia, Kenya, Tanzania and also Mozambique. However, accurate descriptions about whether or not these species occur in mires are lacking. One species of *Eriocaulon* apparently also occurs in alpine wetlands of the Drakensberg Mountains in South Africa and Lesotho (personal communication Dr. E. Sieben of Free State University).

Despite the extensive occurrence of cushion bogs in Argentina and Chili (Kleinebecker et al. 2007, 2008), studies on the role of cushion plants in CH_4 emissions from such bogs are limited (Fritz et al. 2011). A recent study conducted over a period of three years in Tierra del Fuego, Patagonia, Argentina (Fritz et al. 2011), illustrated for the first time the important role that cushion plants play in CH_4 emissions from bogs. The cushion plant Astelia pumila can dominate wind-exposed bogs in the eastern part of Tierra del Fuego. By oxygenating peat soil with its deep roots, which leads to a high redox potential in the rhizosphere, it prevented CH_4 accumulation to a depth of 2 meters. The authors concluded that Astelia-dominated bogs thus keep CH_4 emissions close to zero, in contrast to adjacent Sphagnum magellanicum-dominated bogs that emit small amounts of CH_4. The study unequivocally established correlation of low CH_4 levels in bogs to the high root density of cushion plants. This effect is in strong contrast to the positive effect of helophytes on CH_4 emissions, as described above.

In this paper, we will discuss the role of the cushion plant species E. schimperi on rhizosphere biogeochemistry, including CH_4 levels, in wetland soils of the Bale Mountains in Ethiopia. These wetlands are located at a height of 3000-4000 meter above mean sea level and have not been studied before. Rhizosphere biogeochemistry of Eriocaulon-dominated vegetation is compared with that of adjacent vegetation dominated by Carex monostachya. We investigated whether the mountain species E. schimperi plays a similar role as A. pumila does in the lowlands of Patagonia, Argentina. Specifically, the following questions will be addressed: (i) does the cushion plant E. schimperi prevent CH_4 emissions, and (ii) if so, what are the functional traits that make E. schimperi an efficient suppressor of CH_4 emission in mountain mires?

Materials and Methods

Study Site

Background information

The study was conducted in Bale Mountains National Park (BMNP) (6°29’ – 7°10’ N and 39°28’ – 39°57’ E), which is located ca. 400km south-east of Addis Ababa in Ethiopia’s moorland Eco-region. Field surveys, field measurements and data collections were conducted between April 4th and 8th, 2013. The climate of this eco-region is complex, and data is mostly lacking. The annual rainfall is highest in the south-western part, reaching a maximum of 2,500 mm/year, with the dry season lasting only about two months. Mean maximum temperature on the mountain peaks is between 6° and 12°C, while mean minimum temperature is between 3° and 10°C. Frost is very common all year round, especially during the winter months of November to March (Rundel 1994). An extreme diurnal temperature range of about 40°C (-15°C to + 26°C) has been recorded on the Sanetti Plateau of Bale Mountains National Park, which is where the present study was conducted (Hedberg 1997).

The formations of the Bale Mountains are older than that of the Great Rift Valley, which dissects through Ethiopia and extends to Mozambique. The mountains were formed due to lava eruptions between 38 and 7 million years before present (Mohr 1963), with the lava covering all underlying rock formations. The volcanic rocks include trachytes, rhyolites, basalts, and associated agglomerates and tuffs. The main Bale highlands consist of a vast lava plateau with at least six volcanic cones, each more than 4,200 meters high, which have been considerably flattened by repeated glaciations (Mohr 1963).

Bale Mountains National Park (BMNP) is the largest continuous area above 3000 m AMSL in Africa with a total area of about 2220 km^2 (Yalden 1983, Yalden and Largen 1992). The park encompasses unique flora and fauna and is divided into five different habitat types: the Northern Grasslands (Gaysay Valley), Northern Woodlands (Park Headquarters), Afro-alpine Meadows (Sanetti Plateau), Erica Moorlands, and the Harenna Forest. This range of habitats combined with its climate, expanse and isolation from other Ethiopian highlands west of the Great Rift Valley has resulted in high endemism in and around the Mountains (Hillman 1988). Consequently, there are more than 1300 flowering plants in BMNP, of which 163 are endemic to Ethiopia, amounting to about 12% of Ethiopia's endemic flora. From the 163 endemic plant species, 23 species are endemic to BMNP, which is equivalent to 14% of Ethiopia's endemic plants. BMNP is well known for its fauna, for it is home to 20 mammal endemic to Ethiopia, of which five are only found in the park. Ethiopian wolf (*Canis simensis*), mountain Nyala (*Tragelaphus buxtoni*), giant mole rat (*Tachyoryctes macrocephalus*) and Bale monkey (*Chlorocebus djamdjamensis*) are considered flag-ship species for the conservation of the park; however, the park is home to 26% of the endemic fauna including mammals, bovines, hares, rodents, amphibians and reptiles. In BMNP alone there are 282 resident bird species, and 9 of 16 endemic Ethiopian bird species live here. In addition, about 170 migratory bird species are recorded in this park (Hillman 1993). The Bale Mountains are important for providing water to more than 12 million people in Ethiopia, Somalia and Kenya. The mountain is a source for more than 40 small rivers, which contribute to five major rivers, including the Web, Wabe Shebele, Welmel, Dumal and Genale rivers (Hillman 1986, 1988, 1990). Locally the mountain is a source for countless springs year round and used by local communities as the sole source of water for their herds.

Research location

The present study area is located on the Sanetti Plateau at an altitude between 3100 m to 4377 m with alpine vegetation and almost no trees. The Sanetti Plateau has a high density of rodents (2500kg km^{-2}), a high diversity of birds and is also home to the endemic Ethiopian wolf. The Sanetti plateau was shaped by a series of glaciations, which eventually formed flat plateaus with small lakes and streams and locally even small peatlands. The peatlands that we studied were all fed by groundwater and surface water, so they are technically fens by definition (Maltby et al. 2008). *E. schimperi* forms small cushion carpets, mostly at the edge of the peatlands, but also on slightly drained peat areas. The wetland we studied also included the tussock-forming species *C. monostachya,* which dominates the wettest parts of the wetland. There are numerous small streams and springs, originating from surrounding hills, which feed the fen.

We established three transects in one large stretch of fen wetland (Figure 1). The height difference between the upper and lower side of the fen was about 60 m. The fen is bordered by a small stream that locally caused erosion, thereby draining part of the fen. One transect was set up on the upper side of the fen and two on the lower side. Transects were chosen to be able to make a comparison between two vegetation types that were dominated by different species: the cushion plant species *E. schimperi* and the tussock forming sedge species *C. monostachya*. The two species form two distinct vegetation types with a sharp boundary between them. The peat depth above the bedrock, measured by inserting a metal rod, on sites with *E. schimperi* was between 10 and 200 cm. Unlike *Carex*-dominated sites, *Eriocaulon*-dominated sites are not grazed, but rodents may sometimes destroy the cushions by eating the roots, in particular when the water table has dropped (personal observations). In total, there were six sampling locations: three for each vegetation type.

Field measurements and sample collection

We collected pore water from both *Eriocaulon*- and *Carex*-dominated sites by connecting vacuumed 60 ml syringes to ceramic soil moisture samplers (10 cm Rhizon SMS; Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands). The samplers (pore size: 0.1 µm) were installed at 10 cm, 25 cm, 50 cm and 100 cm below the soil surface. From separate samples we measured redox potential and pH in the field, using a portable redox-pH multimeter. Pore water was collected anaerobically and kept under anaerobic conditions until analysis. In total 24 pore-water samples were collected (6 sampling sites, 4 depths); samples were stored below 20^0C and brought to the laboratory for further analysis.

In addition, soil samples and samples of *E. schimperi* plants were collected. Soil samples were collected from the top 10 cm to a depth of 60 cm and, at each depth, four replicates samples were taken. Twelve replicate cores (10 cm^2 surface, 30 cm depth) with *E. schimperi* were collected and transported in sealed plastic bags to the laboratory. Due to a combination of high altitude and harsh weather, it was not possible to collect soil cores deeper than 60 cm.

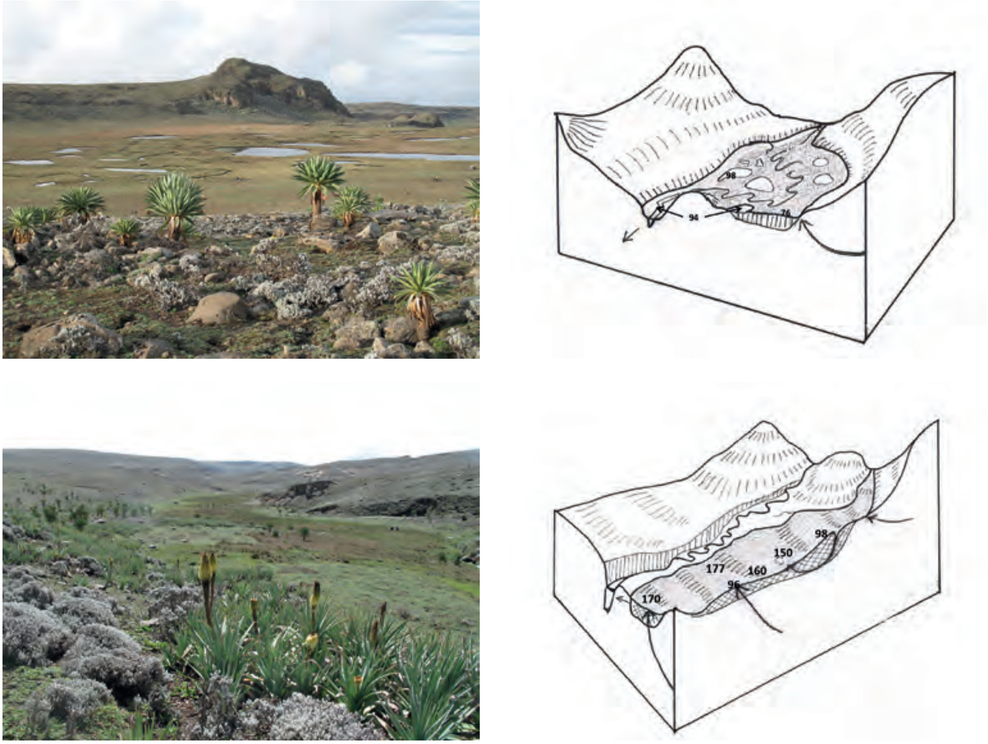

Figure 1. Pictures of the study sites (left), and schematic drawing (right) showing the area studied on Bale Mountain National park in Ethiopia. The numbers on the schematic drawing refer to electrical conductivity values as measured in the field. The relatively low electrical conductivity values indicate that the wetland is fed by groundwater that has only been slightly enriched with minerals. Pictures and drawings by A.P. Grootjans.

Laboratory Analyses

Methane

CH_4 concentrations in the samples were measured by analyzing head space samples on a Hewlett-Packard 5890 gas chromatograph (Avondale, California, USA) equipped with a flame-ionization detector and a Porapak Q column (80 ⁄ 100 mesh), operated at 120^{0}C with nitrogen as carrier gas, in the laboratory at Radboud University, Nijmegen, the Netherlands (accuracy 0.2 ppm). Bicarbonate and carbon dioxide concentrations were estimated from pH measurements during sampling and total inorganic carbon (TIC) measured in the laboratory using an infrared gas analyzer (ABB Advance Optima).

Root density and root porosity

Root density (expressed in g l^{-1} of fresh soil) of *E. schimperi* was determined from six core samples (10 × 10 × 30 cm) collected randomly. Roots were washed thoroughly and dried at 70^{o}C for 48 hours. The porosity of the roots was determined using the microbalance method (Visser and B...gemann 2003) by cutting root samples of 12 cm into 1 cm pieces incrementally from the root base to the apex.

Nutrient and elemental analyses

Nutrient concentrations in plant tissue were analyzed using digestates of dried samples. Plant material was dried for 48 hours at 70°C and ground into liquid nitrogen. Homogenized portions of 200 mg each were digested with 4 ml HNO_3 (65%) and 1 ml H_2O_2 (30%), using an Ethos D microwave lab-station (Milestone srl, Sorisole, Italy). Digestates were diluted and concentrations of P, Al, Ca, Fe, Mg, Mn, Na, S, Si, and Zn were determined by ICP spectrometry (IRIS Intrepid II, Thermo Electron Corporation, Franklin, MA). K was measured on a FLM3 Flame Photometer (Radiometer, Copenhagen, Denmark). Concentrations of nitrate, ammonium and phosphate in pore water were measured colorimetrically (Auto Analyser III systems, Bran &Luebbe, Germany). Similarly, ICP and AA analysis were used to measure concentrations of nutrients and elements in the soil after extraction of 35 g of fresh soil with 100 ml of either 0.2 M NaCl or H_2O. Plant-available phosphorus was determined by lactate extraction (Egner et al. 1960). Concentrations of nitrogen and carbon in *E. schimperi* tissues and peat were measured with a CNS analyzer (Model NA 1500; Carlo Erba Instruments, Milan, Italy).

Statistical analyses

The nutrient and elemental concentrations in pore-water samples and soil extracts between *Eriocaulon*- and *Carex*-dominated sites were compared using the software program IBM SPSS Statistics 20. We used One-Way ANOVA and post hoc multiple comparisons of means using the Tukey test. Concentrations of nutrients and elements were set as dependent variables and the depth from where either pore-water samples or soil samples were collected was set as an independent variable. Comparisons were made both to compare mean concentrations of nutrients or elements at the same depth for both species, and among different depths for one particular species.

Results

CH_4 in pore water

The pore water found at the two investigated vegetation types, dominated respectively by *E. schimperi* and *C. monostachya*, showed large differences in CH_4 concentrations at different depths. While CH_4 levels for the *Eriocaulon*-dominated sites were extremely low (<1 μmol/L) at both 10 cm and 25 cm below the surface, *Carex*-dominated sites showed concentrations at these same depths of 40 and 90 μmol l^{-1}, which are 90 and

160 times higher. Down to a depth of 100 cm, CH_4 levels remained lower in the cushion vegetation sites than in the sedge sites (Figure 2). For both vegetation types, CH_4 levels increased with depth.

Functional traits of *Eriocaulon schimperi*

E. schimperi had a compact rooting zone with very high root density in the first 30 cm below the soil surface (Figure 2). Root density decreased below 30 cm and roots extend to a depth of about 60 cm. Note that as root density for *C. monostachya* was not measured, it is not possible to relate root density and CH_4 concentrations for this species. The increase in CH_4 concentration at *Eriocaulon*-dominated sites coincided with the decrease in root density. For the first 10 cm, root density of *E. schimperi* exceeded 10 g L^{-1} of fresh soil and then decreased to 2 g L^{-1} at 30 cm in depth, which is still high for such a depth. Possibly the rooting zone of this species extended beyond 50 cm below the surface, albeit with a low density of roots. In addition, *E. schimperi* invested heavily in root biomass, as the average above-ground to below-ground ratio was only 0.10 (SEM = 0.04, n=6,); this means that the plant allocates 90% of its biomass belowground. Excluding the rhizomes, it had an average root to shoot ratio of 8.2 (SEM = 1.7, n = 6). In addition, roots showed high porosity with an average value of 64% (SEM = 4.2, n=12) calculated from eight 12 cm-long root samples collected from different individual plants of *E. schimperi*. Generally the root porosity of this species tended to decrease toward the root tip.

With respect to nutrients, *E. schimperi* had an N: P ratio of 26 g g^{-1}, as measured in its green leaves indicating phosphorus limitation. The C: N ratios of shoots were lower than those of roots, indicating reallocation of N from roots to the shoots and C in the opposite direction (Appendix 1).

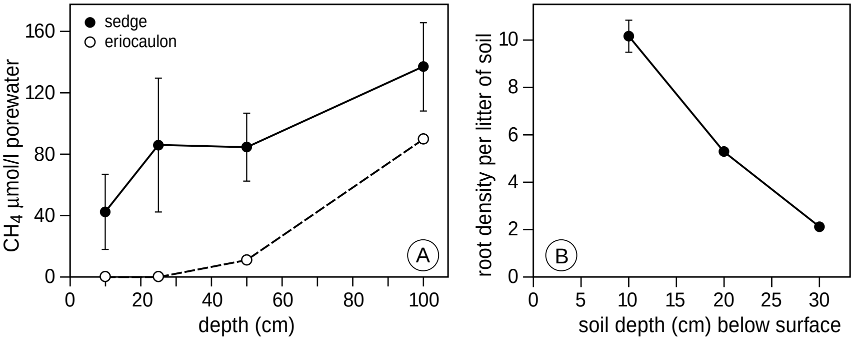

Figure 2. Methane levels in pore water samples in *Eriocaulon schimperi* and *Carex monostachya* sites (left panel) and root density of *E. schimperi* presented in g per l of fresh soil (right panel). Methane concentrations are low in the rooting zone of *E. schimperi.*

Redox potential and CO_2

Redox potential (E_h) values at the *Eriocaulon*-dominated sites differed distinctly from those at *Carex*-dominated sites (Figure 3). At 10, 25 and 50 cm in depth, E_h at cushion sites remained above 350 mV, indicating the presence of freely available oxygen. At sedge sites, in contrast, the E_h was always below 300 mV, indicating low availability of oxygen. At 100 cm in depth, E_h values were identical for both species. Similarly, CO_2 concentrations from the two sites differed markedly. *Eriocaulon* dominated sites had higher levels of CO_2 in the pore water than *Carex*-dominated sites (Figure 3). The values of pH ranged from 5.4-7.5 and were slightly higher for *Eriocaulon*-dominated sites (Figure 4).

Table 1. Mean porewater nutrient concentrations for *Eriocaulon* and *Carex* sites, with their standard deviations in parentheses. There were no significant changes with depth for each species, nor differences between species.

	Eriocaulon site				**Sedge site**		
Pore depth (cm)	**NH4**	**NO3**	**PO4**		**NH4**	**NO3**	**PO4**
	µmol/l	**µmol/l**	**µmol/l**		**µmol/l**	**µmol/l**	**µmol/l**
10	1.1 (0.4)	0.3 (0.4)	1.6 (2.6)		2.8 (0.8)	0.3 (0.3)	0.6 (0.6)
25	3.2 (2.6)	0.6 (0.8)	0.1 (0.1)		2.0 (0.8)	0.1 (0.2)	0.1 (0.1)
50	3.2 (0.3)	0.0 (0.0)	0.4 (0.6)		3.0 (2.7)	0.0 (0.0)	0.2 (0.2)
100	3.9 (2.7)	1.2 (2.0)	2.0 (3.3)		6.6 (2.3)	0.0 (0.0)	0.3 (0.1)

Nutrient availability in pore water and soil

Nutrient analyses of pore water reveal low availabilities of nitrate, phosphate and ammonium in the *Eriocaulon*- and *Carex*-dominated sites. Compared to nitrate, ammonium concentrations were slightly higher at both sites, but they were still low (Table 1). Statistical tests indicated no significant changes for the three nutrients along the depth gradient for either vegetation type. Similarly, there were no significant differences between the two species, when depth classes were compared. Both nitrate and phosphate were depleted from the rooting zone (0-50 cm) of *Eriocaulon*-dominated sites, but ammonium was still present in low concentrations in the pore water.

There were also no notable differences between the two vegetation types in the availability of the three major nutrients (NaCl-extractable nitrate and ammonium, and lactate-extractable phosphorus) in the soil (Figures 5 and 6). At both sites nitrate was depleted from the soil, and ammonium was only present in low concentrations (< 3 µmol g^{-1} DW). Similarly, plant-available phosphorus was less than 5 µmol g^{-1} DW of soil. A notable difference between the cushion vegetation and sedge vegetation was the significant depletion of Fe, Mn and P at the *Eriocaulon*-dominated sites compared to *Carex*-dominated sites (Table 2). The lower concentration at the cushion plant sites seemed to be the consequence of higher radial oxygen loss by *E. schimperi*.

A notable difference between sedge vegetation and cushion vegetation (Table 2) is the significant depletion of Fe, Mn and P at the *Eriocaulon* sites compared to *Carex* vegetation. The lower concentration on cushion sites seems to be the consequence of higher radial oxygen loss by *E. schimperi.*

Elemental concentrations of *Eriocaulon schimperi*

Eriocaulon schimperi has a N:P ratio of 26 g g^{-1}, as measured in its green leaves, which indicates phosphorus limitation. The C:N ratios of shoots are lower than those of roots, indicating reallocation of N from roots to the shoots and C in the opposite direction (Appendix 1).

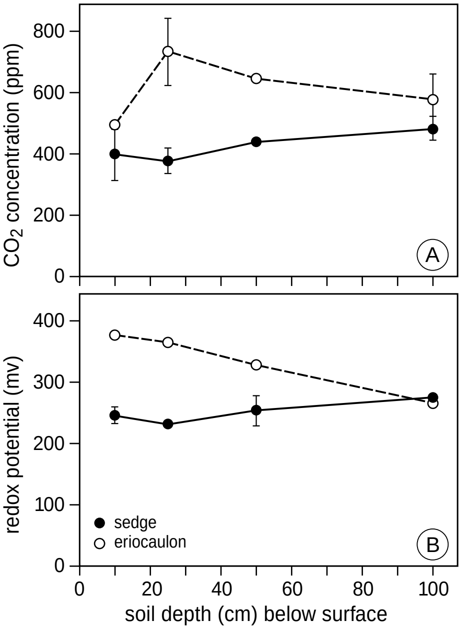

Figure 3. Redox potentials at cushion plant *Eriocaulon* sites and *Carex* sites (B) and concentrations of CO_2 in pore waters from both sites (A). In agreement with the root density profile shown in Fig. 2, the redox potential of the *Eriocaulon* site is higher than that of the *Carex* site, indicating higher radial oxygen loss from roots.

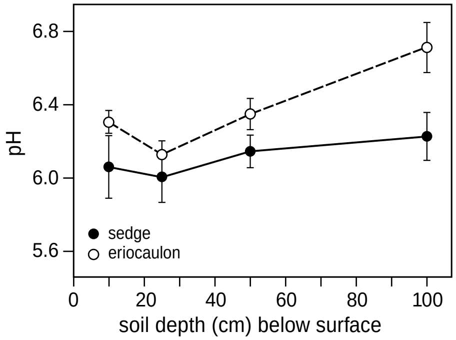

Figure 4. The pH of pore water on both vegetation types indicates that the wetland is circumneutral. *Eriocaulon* sites tend to have slightly higher pH values.

Table 2. NaCl-extractable element concentrations in soil profiles from *Eriocaulon* and *Carex* sites (standard deviations in parenthesis).

Concentration of elements in soil profile in µmol/g DW of soil (salt extractable)											
Veg. type	Depth (cm)	Al	Ca	Fe	K	Mg	Mn	P	S	Si	Zn
Eriocaulon	10	0.10 (0.07)	27.27 (4.26)	0.02 (0.01)	6.26 (2.27)	8.82 (1.65)	1.11 (0.86)	0.00 (0.00)	0.94 (0.20)	1.23 (0.24)	0.01 (0.00)
	30	0.09 (0.08)	30.98 (9.84)	0.01 (0.00)	4.26 (3.62)	10.56 (3.40)	0.06 (0.10)	0.01 (0.00)	0.98 (0.35)	1.05 (0.44)	0.01 (0.01)
	45	0.40 (0.36)	23.89 (8.70)	0.01 (0.00)	1.97 (0.99)	6.61 (2.66)	0.18 (0.09)	0.00 (0.00)	0.50 (0.16)	1.10 (0.55)	0.00 (0.00)
Sedge	10	0.09 (0.07)	26.93 (3.19)	0.22 (0.28)	7.29 (3.40)	7.91 (1.17)	0.70 (0.35)	0.00 (0.00)	3.28 (1.78)	1.46 (0.39)	0.01 (0.01)
	20	0.21 (0.19)	18.85 (4.72)	0.10 (0.08)	2.43 (0.83)	5.29 (1.47)	0.75 (0.28)	0.00 (0.00)	3.57 (3.19)	1.08 (0.16)	0.03 (0.01)
	40	0.88 (0.30)	79.24 (20.45)	0.03 (0.00)	4.11 (2.48)	27.84 (7.33)	1.07 (0.11)	0.01 (0.00)	3.81 (0.96)	2.27 (0.46)	0.08 (0.03)
	60	0.12 (0.12)	12.89 (12.89)	0.00 (0.00)	1.34 (1.34)	4.99 (4.99)	0.18 (0.18)	0.00 (0.00)	0.43 (0.43)	0.42 (0.42)	0.01 (0.01)

Table 3. Root characteristics of *Eriocaulon schimperi* and *Astelia pumila*. Data derived from the present study and from Fritz et al. (2011).

	Eriocaulon schimperi	***Astelia pumila***
Root biomass density	8.16 (SD = 4.16, n = 6)	2.15 (SD = 0.33, n = 3)
Total root biomass/square meter	1704 (SD = 632, n = 6)	3590 (SD = 550, n = 3)
Average root porosity (%)	64	60-70

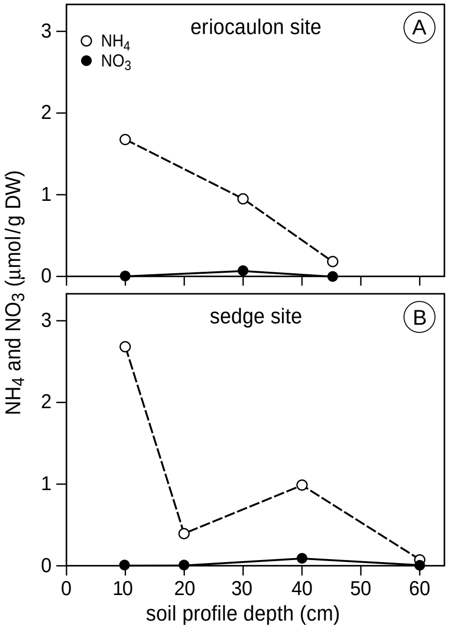

Figure 5. Concentrations of NaCl-extractable ammonium and nitrate in the soil profiles of the *Eriocaulon* (A) and sedge (B) sites.

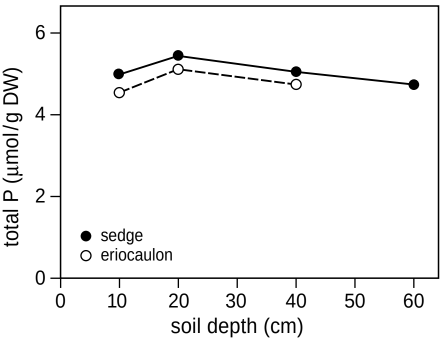

Figure 6. Concentrations of lactate extractable phosphorus in soil profiles of the *Eriocaulon* and the sedge sites.

Discussion

Cushion plants in minerotrophic fens in Bale Mountains

Our results on the pH of the pore water and the mineral concentrations of both the pore water and the soil clearly showed that the wetland studied on BMNP is a minerotropic fen. The dominance of cushion plants found in these fens is contrary to earlier reports that cushion plants seem to be limited to raised bogs and blanket bogs (Gibson and Kirkpatrick 1985, Kleinebecker et al. 2008, Fritz et al. 2011, Fritz et al. 2012). These bogs are usually nutrient deprived and contain minerogenic elements, which are potentially phytotoxins, such as Fe, Al, and S at very low concentration at rainwater-fed, pristine sites. The existence and dominance of cushion plants in such harsh environments makes sense from an evolutionary point of view, since they employ a strong root investment strategy, which provides a competitive advantage in bogs where above-ground competition is low due to low nutrient levels. The roots release oxygen via radial oxygen loss (ROL), also reducing the potential risks of intoxication, thus allowing young roots to explore a large soil volume when foraging for nutrients. Our results showed that both *E. schimperi* and *C. monostachya* on the Bale Mountains can come to dominate sites in minerotrophic peats where the level of nutrient availability is meso- to eutrophic. These relatively high levels of nutrients compared to the bogs mentioned above can probably be explained by the fact that the Bale Mountain fens are groundwater-fed, intermixed with rain water lenses, and parts of the vegetation are probably also temporarily flooded by streams.

Does Eriocaulon suppress CH_4 emission to the atmosphere?

Our research has shown that the cushion plant *E. schimperi* most likely keeps CH_4 levels in the peat low in a similar way as has been reported for another cushion plant, *Astelia pumila* (Fritz et al. 2011). As a result of high root density and high root porosity, *E. schimperi* is able to release sufficient oxygen into the soil to oxidize potential phytoxins such as sulphide and reduced metals in its rhizosphere. The redox potential of the rhizosphere and to some distance below this zone is above 350 mv, meaning that oxygen is still available around the roots of this plant, and its supply is higher than its consumption. When root density decreased (below 50 cm), there was an accompanied rise in CH_4 levels (Figure 2). At the *Carex*-dominated sites, redox potential values were lower. Concentrations of redox-sensitive metals such as Fe and Mn in the rhizosphere of *E. schimperi* were also very low compared to the *Carex*-dominated sites, which give further evidence for root oxidation. The high oxygenation of the rooting zone by radial oxygen loss of *E. schimperi* led to almost zero CH_4 concentrations in the pore water and thus, should lead to zero CH_4 emissions to the atmosphere.

Important functional traits of *E. schimperi* that suppress CH_4 emission

Similarly, the work of Fritz et al. (2011) on *A. pumila* from ombrogenic bogs in Patagonia, Southern Argentina, indicated similar adaptations as found here for *E. schimperi* in minerotrophic fens in the Bale Mountains. Despite living in very different habitats, they still employed related survival strategies. Both species had high root biomass compared to their above-ground biomass (4), and show root porosities above 60% (Fritz et al. 2011). The combination of high redox potential, high root density, high root porosity and high CO_2 concentrations in sites dominated by *E. schimperi* indicates low CH_4 production rates and potentially high CH_4 oxidation rates. In addition, they suggest high root respiration rates and high peat mineralization rates, enabling the species to mobilize nutrients. When we further compare the characteristics of *E. schimperi* with those of *A. pumila,* more remarkable resemblances appear. Both species form very dense cushions (Figure 7 a & b) and possess leaves that can survive for several years (Phillips 1996). The cushions, formed by tightly clustered *E. schimperi plants,* are so strong that it is even possible to walk on them without damaging them or affecting the peat below.

Figure 7a. *Eriocaulon schimperi*. (Picture: A.P. Grootjans)

Figure 7b. *Astelia pumila*. (Picture: C. Fritz)

Both *E. schimperi* and *A. pumila* invest 90% of their biomass underground, which not only leads to high radial oxygen loss (ROL), but also enhances peat accumulation from dead roots. In addition, dead leaves remain attached to the shoots for a longer period of time, allowing for internal nutrient reallocation (Appendix 1). Table 4 shows a comparison between major element concentrations in the green leaves of *E. schimperi* and *Astelia pumila* as presented by Fritz (2012). Despite the large ecological difference between the *A. pumila*-dominated cushion bogs in Patagonia and *E. schimperi*-dominated fens in the Bale Mountains, the two cushion plants that dominate these mires show remarkable similarity in nutrient concentrations in their tissue. *E. schimperi* has more nitrogen and potassium in its leaves but lower sulfur and manganese. Note that the major element concentrations in *Sphagnum magellanicum* from Patagonia are much lower than in the two cushion plant species.

Table 4. Comparative data for the concentrations of elements in the leaves of *Eriocaulon schimperi* from Bale Mountains in Ethiopia and *Astelia pumila* and *Sphagnum magellanicum* from Patagonia, Argentina (data from Fritz 2012 and Fritz et al. 2011).

Element (µmol/gDW)	***Eriocaulon schimperi***	***Astelia pumila***
N	1856 (156)	1014 (104)
P	36 (10)	26 (3)
K	1191 (235)	326 (36)
S	84 (15)	118 (28)
Mg	49 (12)	55 (11)
Mn	2 (1)	15 (5)
Fe	3.2 (1.7)	

Threats to minerotropic fens on Bale Mountains National Park

The main threat to the vegetation in the study area is the increase of cattle and sheep grazing on this plateau (Hillman 1988, Stephens et al. 2001). We observed that *C. monostachya* was heavily grazed everywhere but *E. schimperi* seemed to be unpalatable since we observed no grazed spots. As the density of grazers increase in the mountains, more biomass from the sedges will be removed and their tussocks destroyed. *C. monostachya* plays a crucial role in regulating water flow, especially when heavy rainfall leads to flooding. Removal of the tussocks will stimulate erosion. Evidence of erosion is already visible in the field, with erosion gullies exposing deeper soil layers. In addition, higher grazer densities could lead to eutrophication by their dung, which is expected to result in shifts in vegetation composition. Further research is therefore urgently needed in the wetlands of the Bale Mountains to understand the potential effects of grazing on emergent wetland vegetation. This includes addressing questions on how grazing affects further erosion, and how it affects CH_4 emissions from *Carex*-dominated stands. It has been shown that grazing may well increase CH_4 emission rates from helophytes (Bodelier et al, 2006). In addition, a more fundamental question concerns the nature of the competition between *E. schimperi* and *C. monostachya*, which is not yet well understood.

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Appendix 1. Concentration of elements in the tissues of *E. schimperi* from green leaves to root at 30 cm below the soil layer and the peat soil.

Concentration of element in different tissues of *Eriocaulon* and in the peat in µmol/gDW (n=6 for each sample in the table)													
Depth (cm)	Tissue part	Al	Ca	Fe	K	Mg	Mn	Na	P	S	Si	Zn	N
0-10	Green leaves	4.3 (2.9)	69.4 (43.1)	3.2 (1.7)	1190.5 (235.5)	48.9 (11.6)	1.6 (0.7)	93 (44.7)	35.9 (10.4)	84.1 (15.2)	9.4 (3.1)	0.6 (0.1)	1856.3 (156.1)
	White leaves	30 (35.6)	98.8 (12.0)	20.3 (30.0)	1058.8 (743.9)	25.5 (7.0)	1.7 (1.9)	97.6 (67.2)	32.1 (19.4)	63.8 (15.7)	10 (1.9)	0.3 (0.1)	1242.6 (227.3)
	Dead leaves	13.5 (6.8)	70.6 (23.7)	8.4 (4.0)	497.4 (223.2)	41.1 (7.8)	3 (1.0)	75.1 (39.1)	10.6 (5.9)	51.1 (11.9)	12.8 (1.7)	0.3 (0.1)	827.2 (141.7)
	Rhizomes	17.8 (8.9)	116.2 (12.7)	11.4 (9.3)	242.1(79.2)	22.3 (4.2)	2.1 (1.1)	49.5 (21.0)	14.1 (8.6)	45.3 (5.4)	9.6 (1.7)	0.2 (0.0)	678.5 (77.7)
	Roots	25.3 (16.9)	119.2 (13.0)	16.5 (6.5)	31.5 (13.2)	25.6 (1.1)	2.9 (0.4)	30.5 (14.2)	8.4 (2.2)	37.7 (2.0)	11.9 (3.0)	0.3 (0.1)	623.6 (35.8)
	Peat	32 (4.2)	149.6 (48.5)	18.1 (4.1)	66.6 (56.8)	32 (4.0)	4.3 (1.2)	24.9 (16.2)	8.2 (2.0)	41.3 (5.8)	12.9 (4.9)	0.4 (0.2)	704.9 (84.7)
10-20	Roots	54.4 (45.4)	171.5 (34.1)	58.4 (16.9)	26.6 (7.3)	33.4 (6.6)	2.4 (1.2)	41.7 (29.1)	13 (3.3)	43 (6.9)	10.5 (1.4)	0.2 (0.1)	730 (109.7)
	Peat	76.3 (71.9)	128.5 (24.6)	75.3 (24.5)	27 (11.1)	40.8 (11.9)	2.7 (2.5)	14.4 (5.9)	15.2 (5.6)	51.2 (12.0)	11.1 (2.3)	0.2 (0.1)	837.5 (183.0)
20-30	Roots	77.5 (63.5)	169.5 (31.2)	138.7 (14.1)	24.5 (10.4)	33.3 (20.0)	1 (0.9)	30.2 (13.9)	12.9 (6.6)	42.1 (3.6)	8.1 (0.9)	0.2 (0.1)	723.8 (148.7)
	Peat	81.1 (77.2)	116.8 (34.4)	187 (81.8)	12.3 (4.0)	29.7 (13.8)	1 (1.4)	10 (6.7)	13.2 (7.3)	49 (9.1)	9.7 (2.9)	0.2 (0.1)	815.4 (223.8)

Chapter 7

Discussion and Synthesis

Bikila Warkineh Dullo

The topics discussed in this thesis are: the dynamics of wet dune slacks in terms of geomorphological factors; plant species dynamics; and the effects of weather on hydrology and species composition of dune slacks (**Chapters 2-5**). The general research question of the thesis addresses whether vegetation succession in dune slacks is predictable and mainly governed by long-term environmental changes in soil and hydrological conditions, or whether unpredictable fluctuations in weather or climate conditions have a decisive role in the course of the succession.

In addition, Chapter 6 of this thesis deals with the functional role of wetland plant species in their habitat. The wetlands described in this thesis are affected by spatio-temporal dynamics, spatial and seasonal events such as weather conditions, landscape settings and geomorphologic factors. Here, a synthesis of the findings in this thesis and a brief discussion of the concepts that were implicitly used in this thesis are presented.

Factors affecting species dynamics and soil processes at the landscape level

Factors operating at the landscape level, such as isolation, and factors that create habitat mosaics may strongly influence vegetation succession (Walker & del Moral 2003, Provoost et al 2011) as well as the outcome of restoration measures (Grootjans et al. 2002). In Chapter 2 we studied factors operating at the landscape level that could influence the results of restoration projects in dune slacks. The questions addressed were: 1) how the geomorphological position of dunes slacks (isolated vs. non-isolated) and hydrological features (surface or groundwater input) affect the pattern and rate of species colonization; and 2) how the success of target community restoration, including basiphilous dune-slack species, is influenced by different geomorphological and hydrological conditions.

We found that relatively isolated dune slacks that were not influenced by surface water from other wetland areas could best sustain oligotrophic wet dune-slack species (for more than 16 years) when discharge of calcareous groundwater occurred. Slacks that were not isolated and regularly flooded by surface water from other areas showed higher species richness in the beginning, but most pioneer species and species of nutrient-poor habitats, including many typical dune slack species, disappeared after about 10 years. Isolated dune slacks accumulated less organic matter than non-isolated dune slacks, which is important in sustaining conditions suitable for oligotrophic wet dune-slack species. Surface water that came from nearby areas with higher loads of nutrients favored species of eutrophic environments, such as *Calamagrostis epigejos* and *Phragmites australis*. In **Chapter 2**, non-isolated dune slacks in the Moksloot area on the Island of Texel were able to accumulate up to three times more organic matter than isolated dune slacks only fed by groundwater despite only small differences in soil acidity. This indicates that processes such as nutrient enrichment of surface water can affect soil development and, consequently, species composition and succession (Wassen et al. 1991). Therefore, the prevalence of surface-water runoff within a landscape does not promote persistence of desired species of oligotrophic wet dune slacks. Although waterlogging and prolonged flooding resulting from surface water can prevent productive species from becoming dominant (Bakker et al. 2006, Bakker et al. 2007), it is also possible that the nutrients brought in by surface water provide conditions for highly productive species, which may eliminate lowly productive species through competition. We, therefore, conclude that waterlogged conditions will sustain oligotrophic wet dune-slack species only when flooded by nutrient-poor groundwater.

The use of chronosequences could be risky

In this thesis, the application of chronosequences is a recurring theme (**Chapters 3-5**). A chronosequence consists of soils of different age, which lie close together but are influenced in a similar way by other environmental factors that influence soil formation, (Stevens and Walker 1970, Yaalon 1971, Hugget 1998). However, soil development processes and thus vegetation development may not always proceed as suggested in studies using the chronosequence approach. One basic assumption of this approach is that the spatial pattern of the studied sites results only from temporal changes in the vegetation. This means that the vegetation responds to a change in an environmental variable by becoming more similar to the vegetation in a site where the 'new' value of an environmental variable is already found (Van Dobben and Slim 2012). The underlying assumption is that habitats with similar environmental conditions will have similar species composition. Studies that use the chronosequence approach thus translate spatial differences in vegetation composition into temporal differences, in order to unravel the forces driving ecological processes such as vegetation succession. This involves the assumption that the soils in the identified sequence represent successive stages of one or several ecological processes, which further stipulates that soils pass through stages characterized by a preceding member of the successional sequence (Rode 1961, Vreeken 1975). In other words, the sequence is very predictable and random 'events' do not play an important role.

However, fluctuations in climate or weather conditions can be quite random 'events' and they greatly affect soil-development processes. Similarly, landscape variables such as hydrological setting, height, and connectivity to other landscape types could also affect the process of soil development (Van Diggelen et al. 1993, **Chapter 2**). For instance, vegetation development in dune slacks after sod cutting could follow divergent pathways in different areas of the slack, based on whether a given location in the dune slack is a seepage zone or an infiltration zone (Lammerts and Grootjans 1998). Processes such as species dispersal in time and in space can also affect the selection of early-colonizing plant species and thus have a larger impact on soil-development processes (Olff et al. 1993). Therefore, it could be difficult to stipulate that spatial pattern accurately reflects temporal change.

Factors affecting soil organic matter accumulation

We studied factors that affected accumulation of soil organic matter (SOM) over chronosequences, which in most cases were also monitored over time (diachronic chronosequence; **Chapters 4, 5**). Therefore, we could eliminate the above-mentioned risks of misinterpretations using a synchronic chronosequence approach. The questions we asked addressed: (i) the factors which regulate accumulation rates of SOM in wet dune slacks; (ii) and the length of time that pioneer species, such as *Littorella uniflora*, can retard the accumulation of organic matter in dune slacks.

We found that several dune slacks show high variability in SOM content among sites, despite being the same age. We also found that flooding duration and groundwater fluctuation were important factors for SOM accumulation, but above-ground biomass of the vegetation best explained differences in accumulation of SOM. Two species that resulted in very different amounts of SOM accumulation in dune slacks of similar age and flooding duration were *L. uniflora* and *Phragmites australis*. The first is a very low-productivity species and the latter is a very high-productivity species. We found three dune slacks on Dutch Wadden Sea islands that showed relatively stable Littorella-dominated pioneer stages over a period of 20-90 years.

Species, such as *L. uniflora* and *Schoenus nigricans*, are adapted to low availability of nutrients and high water levels (Ernst et al. 1988, Grootjans et al. 1996). Bakker et al. (2007) showed that the initial conditions following top soil removal impose a ‘narrow tolerance’ to waterlogged conditions for species during germination and establishment. Previous studies have demonstrated that the presence of a soil seed bank, although important, is not decisive compared to ongoing succession and dispersal from nearby populations (Bakker 2005). In some cases the seed bank is nearly depleted through top-soil removal and thus plays a minor role in the colonization of new areas (Bekkeret al. 2001, Grootjans et al. 2001). This is the reason why, vegetation is kept intact in some parts of the slack, during restoration of dune slacks by top soil removal, to provide seed sources for endangered plant species close to sod-cut areas.

The co-occurrence of low-productivity (*L. uniflora*) versus high-productivity species (*P. australis*) within the same slack could be the result of relatively small changes in flooding duration, causing shifts in SOM accumulation. Small changes in SOM accumulation are enhanced by productive species like *P. australis* in positive feedback loops. This species does not have a problem regarding seed distribution. *P. australis* propagules, which are dispersed by wind, are almost always present close to restoration sites. Once established, *P. australis* can rapidly build up organic matter. From these observations we conclude that the type of species that becomes dominant as well as the hydrology of the dune slacks involved are the two most important factors determining the amount of SOM in dune-slack habitats.

Weather fluctuations and vegetation development

In **Chapter 3** the focus was on effects of weather fluctuations (precipitation and evaporation) on long-term vegetation development. Earlier research on long-term vegetation response to changes in environmental conditions had been carried out on the island of Ameland, where gas abstraction had caused land subsidence, leading to an increase in wetness driven primarily by increased flooding frequencies and duration (Van Dobben et al. 2011) in the nearby dune slacks. In this chapter, we used long-term data sets on vegetation composition, precipitation and evaporation to model patterns in groundwater fluctuation over a period of 20 years. For some slacks on Ameland, we wished to assess whether large fluctuations in weather conditions or even global change could have interacted with the observed increase in wetness. Our long-term observational data of dune slacks originated from Terschelling (dune slack Koegelwieck), which is outside the sphere of influence of gas abstraction and associated soil subsidence risks.

Climatological models have predicted increased precipitation in coastal areas, particularly in the Wadden sea area (Allen and Ingram 2002, Christensen and Christensen 2003). Rain showers are expected to be more intense, particularly during summer. This would result in increased flooding in dune wetlands (Clarke and Rendell 2009, Clarke and Rendell 2011). The questions addressed in this chapter were: (i) how species composition is influenced by dry years versus wet years; and (ii) whether large weather fluctuations can trigger shifts in successional patterns. Our long-term hydrological modelling indeed indicated an increase in water level in the Koegelwieck dune slack during the past twenty years. This shows that changes in the hydrology of dunes and dune slacks can result from changes in weather fluctuation patterns or climate (precipitation and evapotranspiration). Our analyses of permanent plots, monitored for 17 years, also showed that a dry period (1995-1998) had a marked influence on the succession trajectory of early successional stages (1986 and 1995 in particular). This dry period apparently prevented some pioneer species from establishing, while late-successional species with capabilities of lateral spread or retrieving water from deeper soil layers became dominant in a very short period of time. This is an example of how the outcomes of restoration projects are sometimes strongly influenced (both negatively and positively) by cycles of weather fluctuations. Our results showed that a relatively short span of dry years can cause a shift in the vegetation of dune slacks from a pioneer stage to a late-successional stage. The effects of weather fluctuations on succession depend on the stage of vegetation development; the effects are much less in late-successional stages.

Stability of dune-slack vegetation

Several authors have pointed out the importance of hydrological factors on succession in dune-slack vegetation (Sival 1997, Lammerts et al. 2001, Davy et al. 2006, Bakker 2005). Some mechanistic explanations for the persistence of stable states in dune succession have been proposed by Adema et al. 2002 (see also **Chapter 1**). In **Chapter 4,** the questions addressed were: (i) whether alternative stable states in dune slacks really occur or whether successional stages always transitional; and (ii) which successional stages are most stable and why.

Analyzing vegetation changes over almost twenty years did not reveal strong evidence for the occurrence of alternative stable states in the dune slack under study. Although we observed that the dominance of *L. uniflora* under waterlogged conditions did indeed delay the establishment of other species in the chronosequence site of 1990, albeit after about 20 years, late-successional species such as *P. australis* eventually became dominant. Thus, *L. uniflora* and other species of wet dune slacks with radial oxygen loss can keep nutrient availability low for some time (Adema et al. 2003), but this may not always prevent the establishment of more productive species.

Functional role of wetland species adaptations

The early- and mid-stage successional species, L. uniflora and Schoenus nigricans respectively, can put oxygen into their rooting zone through radial oxygen loss (ROL) in dune slacks. By releasing oxygen into the soil, these earlier stage dune-slack species gain competitive advantages over later-successional species lacking this adaptation. For species under permanently waterlogged peat-forming conditions, ROL can be a vital adaptation for survival (Armstrong and Armstrong 1991, Armstrong et al. 1991, Joabsson et al. 1999, Aulakh et al. 2000, Jackson and Colmer 2005, Bergström et al. 2007, Erwin 2009, Askaer et al. 2011, Ma et al. 2012, Bhullar et al. 2013). In several species, this same adaptation found in wetland phanerogams promotes methane emissions from anoxic layers into the atmosphere. This is because the aerenchyma tissues in the plant, which allow oxygen to reach the root zone, also permit the transport of methane from the root zone to the atmosphere (Yavitt and Knapp 1998, Whiting and Chanton 2001). However, Fritz et al. (2011), who studied cushion plants in Tierra del Fuego (Argentina), reported a case in which a cushion plant with ROL capability (Astelia pumila) prevented the formation of methane in deeper layers, thus sustaining ‘zero methane’ emission from these cushion bogs.

In **Chapter 6** of this thesis, another example of ‘zero-methane’ emission is provided from the mountain wetlands of Ethiopia above 4000 m a.s.l. The cushion-forming plant Eriocaulon schimperi also prevents methane production by extreme oxygenation of its rooting zone via its capability of radial oxygen loss. Both E. schimperi and A. pumila have similar morphological characteristics: high root biomass compared to their above-ground biomass, high root porosity and high root density. They both form very dense cushions (see Photo 1 and 2), have leaves that can survive for several years (Phillips 1996), and oxygenate the rooting zone considerably, thus creating high CO_2 concentrations and low methane concentration in the soil water. However, the species grow in different peat systems; A. pumila sometimes dominates bogs, whereas E. schimperi is restricted to fens (groundwater-fed) in the Bale Mountains.

In conclusion, ROL adaptation of plant species under waterlogged conditions can be considered as an ecosystem function that can play some role, however small it may be, to reduce emissions of greenhouse gases, such as methane, into the atmosphere.

Photo 1. Eriocaulon schimperi.

Photo 2. Astelia pumila.

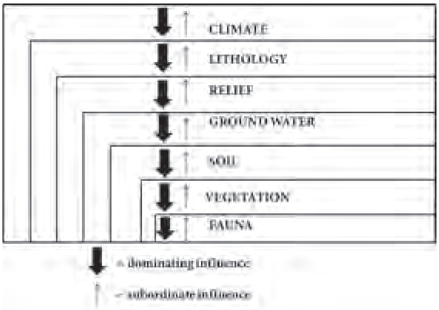

Figure 1. This conceptual model shows the environmental spheres of impacts on a dune system. The Figure shows that influences of environmental factors largely act top-down, but subordinate effects may occur in the opposite direction. Adopted from Van der Hagen et al. (2008), but originally based on a model by C.G. van Leeuwen & E. Van der Maarel (pers. comm.).

Implications for management

In many ecological studies, landscape processes and regional factors are not specified and disentangled from each other (Van der Hagen et al. 2008). Figure 1 presents a hierarchy of the abiotic and biotic spheres of influence operating on a dune system. The basic idea of this hierarchy stems from C.G. van Leeuwen and was internationally presented by Van der Maarel. Van der Hagen et al. (2008) suggested that restoration managers should intervene at the levels of relief and hydrology (groundwater). For instance, facilitating the development of blow-outs in dunes and altering the hydrology of a dune system could also initiate biotic processes if propagules of plant species occur in the landscape. While the level of intervention the authors put forward is viable and advisable, it can be inferred from this thesis that interventions at the level of soil development can also be an effective way to restore dune-slack vegetation. Processes at the landscape level, however, are still very important, because they determine the rate of soil development in terms of organic matter accumulation and nutrient availability and soil properties such soil basicity as well as acidity.

Summary

Bikila Warkineh Dullo

Wetlands are dynamic ecosystems that render mankind a great deal of direct and indirect services. Their resilience and structure are mostly dependent on their hydrology, which is affected by both landscape variables and regional climatic conditions. Most of the use of direct or indirect benefits from wetlands alter the hydrology or stimulate other factors that could lead to an altered hydrology. This direct or indirect alteration of wetland hydrology has led to losses of 'water-logged capital' worldwide (Maltby 2013).

This thesis presents the dynamics of temporal wetlands where hydrological cycles are dependent on seasonal weather patterns. The following quote elegantly captures this theme. *"Wetlands often are transient features in landscape development, and can be regarded in many cases as the authors of their own destruction. The inherent processes of natural change, such as sedimentation, peat growth and soil development lead to hydrologic changes that may be less favorable for existing plants and animals than competitors. So too, a plant assemblage may alter conditions in ways that make the habitats less favorable for survival of its component species, and more favorable for the development of a different community. Wetland ecosystems can pass through many such 'seral' stages, emphasizing their dynamic yet temporary character."* (Maltby 2009).

Dune slacks are temporal wetlands where hydrology plays a crucial role in determining the types of plant species that occupy them. The hydrology in dune slacks is dependent on weather patterns. This means that it is mainly governed by meteorological conditions of precipitation and evapotranspiration. Changes in the global climate may imply that the pattern of weather conditions, both at local and global levels, will become more and more erratic. Extreme events of torrential summer rains could lead to events of flooding, for instance in parts of Western Europe. On the other hand, winters could become wetter while summers could become drier. Besides, temporal wetlands are not limited to dune slacks, but they also occur from mountain tops to desert valleys all across the globe.

For instance, dune slacks on the Wadden Sea islands of the Netherlands have suffered severe desiccation due to water abstractions, expansion of agriculture, tourism, and pine plantations. In order to restore the natural dynamics of dune slacks, several restoration projects were initiated. These restoration projects often involved abandonment of water abstraction facilities as part of the hydrological restoration and removal of top soil from the aging dune slacks, in order to facilitate restart of vegetation succession. In such restoration activities in which millions of euros are invested, an assessment of long-term success is paramount. In order to investigate whether restoration of dune slack vegetation is successful over the long-run **(Chapter 2)**, vegetation records of long-term permanent plots were analyzed using multivariate statistics and studied changes in environmental variables such as soil organic matter accumulation and changes in soil acidity. Geomorphological positions (isolated and non-isolated) and hydrological conditions (fed by surface water vs. groundwater) affected the pattern and rates of species colonization in dune slacks. In the long run, these factors also determined the success of the restoration project. Isolated dune slacks generally accumulated a third of organic matter accumulated in non-isolated dune slacks and, in terms of changes in soil acidity, soil pH was lower in non-isolated dune slacks, which is expected to be basically due to humic acid in soil organic matter. In terms of species colonization patterns, there seemed to be no difference between isolated and non-isolated dune slacks but both the cumulative and actual species richness (numbers of species) were higher in non-isolated dune slacks. In general, hydrology plays a key role in keeping soil organic matter lower and soil pH higher, which was observed in isolated dune slacks where there is exfiltration of groundwater into the dune slacks. A high species richness in dune slacks is determined by occurrence of flooding by surface water, the proximity of a local species pool and the way the seeds are being dispersed.

Hydrology of dune slacks plays a key role **(Chapter 2),** but this is dependent on weather conditions. How hydrology affects species dynamics was studied in **Chapter 3.** Using bi-weekly measurements of water levels recorded for six years in the dune slack Koegelwieck on the Wadden Sea Island of Terschelling, long-term waterlevel fluctuation patterns were studied, using hydrological modelling software (Menyanthes). Long-term fluctuation patterns influenced by meteorology, site heights, and coastal expansion variables were simulated. It was found that at Koegelwieck, hydrology is governed by meteorology i.e. precipitation and evaporation. These two meteorological variables explained on average about 85% of the variance. With the computer model Menyanthes the mean summer groundwater level MSGL was calculated, which was then used as an explanatory variable in the vegetation analysis. In addition, measured environmental variables such as organic matter, soil pH and age of the vegetation were used as variables that determined changes in the vegetation. These results indicated that MSGL is a significant variable that affects the vegetation composition on most chronosequence sites at Koegelwieck. Soil organic matter, soil pH and age of the slack also affected the vegetation composition. However, the effect of dry years became pronounced on the recently sod-cut site of 1995 where the occurrence of two very dry years (1996/97) led to a shift in vegetation composition to an older successional stage with many shrub species. Prolonged wetness at the site of 1990 resulted in little accumulation of organic matter, and in a relatively high soil pH. The small dune slack species *Littorella uniflora* started to dominate and kept the vegetation in a pioneer stage.

Chapter 4 and Chapter 5 present studies on the stability of pioneer dune-slack vegetation and the conditions that are necessary to keep the pioneer stages stable in the long run. For this follow-up study on the possible existence of alternation stable states (ASS) in dune slacks **(Chapter 4)**, combinations of techniques such as multivariate analysis, calculations of similarity indices and statistical analysis were used on both permanent plot vegetation records and measurements of environmental variables. In general, despite the possible operation of positive feed-back mechanisms in dune slacks, the results indicate convergence of vegetation toward a homogenous community type within 12-14 years. Thus, it may be concluded that successional stages in dune slacks, including the pioneer stages, are states in transition. In addition, it was found that changes in vegetation preceded changes in soil conditions such as acidity and organic matter accumulation, which means that, when coupled with small perturbations of hydrology or meteorology, plant species can trigger a sudden shift in stages of succession. The study in **Chapter 5** led to the conclusion that the rate of soil organic matter accumulation is primarily determined by plant productivity. The results indicated that when dune slacks were flooded for the most part of the year, above-ground plant productivity and soil organic matter accumulation could remain very low since only species with the adaptive trait of radial oxygen loss were able to survive the flooding. Such species are often low-productivity species, such as *L. uniflora*, which are capable of maintaining vegetation succession at a pioneer stage.

It was concluded that the rate of soil organic matter accumulation in wet dune slacks is primarily controlled by above-ground biomass of the vegetation. Both above-ground biomass and SOM accumulation can remain very low over a long period of time when dune slacks are flooded during most of the year and plants with adaptive traits are able to maintain vegetation succession at a pioneer stage.

Radial oxygen loss (ROL) is an adaptation of several wetland species occurring in water-logged conditions. Using this adaptation, the plants put atmospheric oxygen into the soil surrounding their roots so that the roots can function under very harsh conditions. In dune slacks it was observed that species such as *L. uniflora* and *S. nigricans* use this adaptation to survive the conditions of high-water levels in which species without this capability cannot survive. In **Chapter 6** a comparative study on a cushion plant (*Eriocaulon schimperi*) occurring in groundwater fed mires on the Bale Mountains in Ethiopia was presented. *E. schimperi* has a root-bound strategy where it invest about 90% of its biomass underground and pumps oxygen into the soil in order to oxidize the anaerobic condition that surrounds its rooting zone. This root-bound strategy of *E. schimperi* also resulted in complete oxygenation of the peat layer well beyond its rooting zone reaching to about 60 cm below the surface. In an earlier study on the peatlands of the Patagonia region in Southern Argentina, it was found that another cushion plant, *Astelia pumlia*, performs a similar functional role preventing methane from deeper layer to reach the surface and escape to the atmosphere. What is unique about this species from the Bale Mountains is the fact that this species performs an identical functional role in a meso-eutrophic environment, unlike *Astelia pumlia*, which thrives in a very nutrient-poor bogs, mainly in competition with *Sphagnum* species, which are known for their efficiency in nutrient uptake.

Samenvatting

Bikila Warkineh Dullo

Translated by Ab Grootjans

Moerassen of in het engels "wetlands"zijn dynamische ecosystemen die voor de mensheid van heel veel nut zijn en zijn geweest, zowel direct of op een indirecte manier. Ze zijn echter heel sterk afhankelijk van de heersende waterhuishouding van het gebied. Op zijn beurt is de hydrologie afhankelijk van landschapsfactoren en klimaat. Het gebruik van wetlands door de mens kan echter de lokale waterhuishouding veranderen of ontwikkelingen in gang zetten die eveneens van invloed zijn op de lokale hydrologie. Zulke directe en indirecte veranderingen in de waterhuishouding van wetlands hebben op wereldschaal geleid tot verlies van zgn. 'water-logged capital' (Maltby 2013).

Dit proefschrift gaat in op temporele aspecten van met name wetlands in duingebieden. Hier is de waterkringloop sterk afhankelijk van veranderingen in weersomstandigheden gedurende het seizoen. Zoals Maltby (2009) het in zijn Wetlands Handbook uitdrukt: *"Wetlands zijn vaak tijdelijke verschijningen tijdens de ontwikkeling van een landschap. Ze zijn vaak zelf de aanzeggers van hun eigen ondergang. Inherente (natuurlijke) veranderingsprocessen, zoals sedimentatie, veenvorming of andere vormen van bodemvorming, kunnen leiden tot hydrologische veranderingen die minder gunstig zijn de aanwezige planten of dieren en deze veranderingen kunnen hun concurrenten bevoordelen. Dus ook een plantengemeenschap zelf kan de standplaats voor sommige van zijn eigen soorten ongunstig maken, en juist de ontwikkeling bevorderen van een andere vegetatietype. Veel ecosystemen in wetlands maken zulke ontwikkelingen door, en dit benadrukt dat ze heel dynamisch, maar ook heel tijdelijk kunnen zijn.*

Wetlands in duingebieden, ook wel duinvalleien genoemd zijn zulke tijdelijke wetlands, waarin de waterhuishouding een cruciale rol speelt en bepaalt welke vegetatietypen en soorten zich kunnen vestigen en handhaven. De hydrologie van een duinvallei wordt sterk bepaald door de weersomstandigheden ter plekke, zoals het patroon van de neerslag en de verdamping. Klimaatveranderingen op wereldschaal zijn er de oorzaak van dat weersveranderingen, zowel lokaal als op wereldschaal, onvoorspelbaarder worden. Extreme neerslag in de zomer, bijvoorbeeld, zou in delen van West-Europa kunnen leiden tot het veelvuldiger optreden van overstromingen. Maar het is ook mogelijk dat de winters natter worden en de zomers droger. En effecten van klimaatsveranderingen zijn niet beperkt tot duinvalleien. Droogvallende (temporal) wetlands komen wereldwijd voor, zowel in berggebieden als in woestijnen.

Duinvalleien op de Nederlandse Waddeneilanden zijn sterk verdroogd geraakt door onttrekking van grondwater, door uitbreiding van de landbouw, toerisme en door de aanplant van dennenbossen. Om de natuurlijke dynamiek van duinvalleien te herstellen werden in het verleden verschillende herstelprojecten uitgevoerd. Soms hield dat in dat grondwateronttrekkingen werden gestopt als onderdeel van hydrologisch herstel en in combinatie met plaggen van de bovenste bodemlaag om de successie weer op nieuw te laten beginnen. In dergelijke projecten werden in totaal miljoenen Euro's geïnvesteerd en het is dus van het grootste belang dat kon worden vastgesteld dat deze maatregelen ook op de langere termijn succesvol waren. In **Hoofdstuk 2** hebben werden daarom vegetatiebeschrijvingen op een reeks permanente waarnemingsplekken (permanente kwadraten) geanalyseerd, waarbij ook veranderingen in milieuomstandigheden zijn bestudeerd, zoals opbouw van organische stof en veranderingen in de zuurgraad van de bodem.

De positie in het landschap ((geïsoleerd of niet-geïsoleerd) en ook de hydrologische omstandigheden (voeding door oppervlaktewater of grondwater) zijn van invloed op de het patroon van vestiging en ook op de snelheid van vestigen van koloniserende soorten. Op de lange termijn bepalen dergelijke factoren ook het uiteindelijke succes van een herstelproject. Geïsoleerde en grondwater gevoede valleien stapelden veel minder organische stof dan niet geïsoleerde valleien die door oppervlaktewater waren beïnvloed, en de pH van de bodem was hoger. Wat betreft het patroon van kolonisatie van soorten was er weinig verschil tussen geïsoleerde en niet geïsoleerde valleien. Wel was de soortenrijkdom per oppervlakte hoger in niet geïsoleerde valleien. De hydrologie van een duinvallei en met name het optreden van kwel, is heel belangrijk voor het laag houden van de organische stof in de bodem en ook voor hoog houden van de pH.

Belangrijk voor een hoge soortenrijkdom van een duinvallei is het al dan niet overtomen met oppervlaktewater, de aanwezigheid van lokale zaadbronnen en ook hoe die verspreid worden.

Hoe de hydrologie van een duinvallei afhankelijk is van weersomstandigheden en hoe dit de soortensamenstelling van de vallei beïnvloedt, is het onderwerp van studie in **Hoofdstuk 3**. Hierbij werd gebruik gemaakt van tweewekelijkse waterstandsmetingen die zes jaar lang werden uitgevoerd in een Duinvallei (De Koegelwieck) op Terschelling. Om het langjarige fluctuatiepatroon van het grondwater te bepalen werd het computerprogramma Menyanthes gebruikt dat in staat is langjarige grondwaterstandsfluctuaties te simuleren op basis van gemeten waterstanden, neerslaghoeveelheden en de hoeveelheid water die door verdamping verdwijnt. Ook de hoogteligging van de waarnemingspunten en de afstand tot de zee werd in het model in beschouwing genomen. De lokale waterhuishouding van de Koegelwieck bleek sterk door de weersomstandigheden werd bepaald. Neerslag en verdampingsparameters verklaarden ongeveer 85% van de variatie.

De gemiddelde zomer grondwaterstand (MSGL) werd met het model voor alle waarnemingsplekken berekend en samen met de gemeten bodemfactoren (organische stof en pH) in verband gebracht met de veranderingen in de vegetatie. De resultaten wezen erop dat de gemiddelde zomerwaterstand een belangrijke variabele is die een grote invloed heeft op de gesignaleerde veranderingen in de soortensamenstelling van de vegetatie. Maar ook het organische stofgehalte, de pH en de leeftijd van een vallei waren van invloed op de soortensamenstelling. Het effect van droge jaren was het meest uitgesproken in het jongste successiestadium van de Koegelwieck. Het bleek dat twee opeenvolgende droge jaren (1996/1997) tot een plotselinge verandering in soortensamenstelling hebben geleid, die uitmondde in een snelle ontwikkeling naar een ouder vegetatiestadium met veel struiken. De daarop volgende periode van natte zomers leidde ertoe dat op de plekken die in 1990 werden geplagd pioniersstadia zich wisten te handhaven, en dat de stapeling van organische stof sterk geremd bleef, terwijl de pH niet zakte. Onder die omstandigheden bleef de vegetatie gedomineerd door Oeverkruid (*Littorella uniflora)*.

Hoofdstuk 4 en **Hoofdstuk 5** gaan in op de stabiliteit van duinvalleivegetaties en de condities die het mogelijk maken om pioneerstadia langere tijd in stand te houden. De vraag hierbij is of er in duinvalleien inderdaad zgn. 'alternative stable states' (ASS) bestaan. In **hoofdstuk 4** werd voor de beantwoording van deze vraag gebruik gemaakt van verschillende analysetechnieken om vegetatiewaarnemingen uit permanente kwadraten te analyseren en te interpreteren. Ook werden weer gemeten milieufactoren gerelateerd (met multivariate technieken) aan veranderingen in de vegetatie. De resultaten geven aan dat, hoewel er aanwijzingen zijn voor het optreden van positieve feedback mechanismen in duinvalleivegetatie, na verloop van tijd alle vegetatiestadia convergeren naar een en hetzelfde oudere successiestadium. Dit gebeurt veelal binnen 12-14 jaren. Dus werd de conclusie getrokken dat alle successiestadia, inclusief de pioniersstadia in feite overgangsstadia in de tijd zijn; ze zijn niet stabiel. Verder werd gevonden dat veranderingen in de bodem mbt organische stof gehalten en zuurgraad, voorafgegaan werden door veranderingen in de vegetatie. Hieruit kan worden afgeleid dat plantensoorten als reactie op relatief kleine weersveranderingen, of veranderingen in organische stofopbouw, vrij plotselinge verschuivingen in successiestadia kunnen veroorzaken.

Ook in **Hoofdstuk 5** werd de conclusie getrokken dat de snelheid van organische stofstapeling in duinvalleien vooral bepaald wordt door de bovengrondse biomassa van de vegetatie. Ook werd gevonden dat wanneer duinvalleien zeer langdurig onder water staan gedurende het groeiseizoen, de bovengrondse biomassa, en als gevolg daarvan ook het organische stofgehalte van de bodem heel laag kan blijven, zelfs gedurende vele tientallen jaren. Dit lijkt veroorzaakt te worden doordat laag-productieve soorten met special aanpassingen aan zuurstofloze omstandigheden (ze hebben mogelijkheden tot radiaal zuurstof verlies via hun wortels) in staat zijn de overhand in de vegetatie te behouden. Met name een soort als Oeverkruid (*L. uniflora*) is in staat de vegetatie op die manier langdurig in een pioniersstadium te houden. Radiaal zuurstofverlies (ROL) is aangetoond bij veel moerasplanten die langdurig onder water staan. Door deze aanpassing brengen deze soorten zuurstof uit de atmosfeer in de bodem, zodat hun wortels ondanks de ongunstige (zuurstofloze) omstandigheden goed kunnen blijven functioneren. In duinvalleien zijn het vooral Oeverkruid en Knopbies (*Schoenus nigricans*) die in staat zijn langdurig te overleven onder omstandigheden waaronder veel soorten zonder die aanpassing niet kunnen overleven.

In **Hoofdstuk 6** wordt een voorbeeld gepresenteerd van een moerasplant met ROL aanpassingen, maar in een geheel andere constellatie dan de Nederlandse duinvalleien. Deze plant (*Eriocaulon schimperi)* vormt zeer dichte vegetatiekussens in laagveenmoerassen in de Bale Mountains van Ethiopië. In tegenstelling tot Oeverkruid investeert *E. schimperi* ongeveer 90% van zijn biomassa in de wortels, die in staat zijn het hele bodemprofiel tot een diepte van ca. 60 cm te 'oxyderen'. De resultaten werden vergeleken met een eerdere studie over de kussentjesplant *Astelia pumula* die (hoogvenen) kan domineren in Patagonie in Zuid-Amerika. De beide kussentjesplanten *Eriocaulon schimperi* en *Astelia pumula* verhinderen op een zeer vergelijkbare wijze dat methaan uit diepere bodemlagen de toplaag bereikt en kan ontsnappen naar de atmosfeer. Een verschil met *Astelia pumula* is dat *Eriocaulon* voorkomt in een veel voedselrijker milieu dan *Astelia* die alleen gevonden wordt in extreem voedselarme spreihoogvenen.

Cited Literature

Abreu Z, Llambí L.D., Sarmiento L. 2009. Sensitivity of soil restoration indicators during Páramo succession in the high tropical Andes: chronosequence and permanent plot approaches. Restoration Ecology 17:619-627

Adema E.B., H. van Gemerden, and A.P. Grootjans. 2003. Is succession in wet calcareous dune slacks affected by free sulfide? Journal of Vegetation Science 14:153-162.

Adema E.B., Grootjans A.P., Petersen J., Grijpstra J. 2002. Alternative stable states in a wet calcareous dune slack in The Netherlands. Journal of Vegetation Science 13:107-114

Adema E.B., J. Van de Koppel, H.A.J. Meijer, and A.P. Grootjans. 2005. Enhanced nitrogen loss may explain alternative stable states in dune slack succession. Oikos 109:374-386.

Adema E.B. 2002. Alternative stable states in dune slack succession. Ph.D. Thesis, University of Groningen, Groningen, NL.

Aerts R., J.T.A. Verhoeven, and D.F. Whigham. 1999. Plant-Mediated Controls on Nutrient Cycling in Temperate Fens and Bogs. Ecology 80:2170-2181.

Allen M.R. and W.J. Ingram. 2002. Constraints on future changes in climate and the hydrologic cycle. Nature 419:224-232.

Alvarez R., Lavado R.S. 1998. Climate, organic matter and clay content relationships in the Pampa and Chaco soils, Argentina. Geoderma 83:127-141

Anderies J.M., M.A. Janssen, and B.H. Walker. 2002. Grazing Management, Resilience, and the Dynamics of a Fire-driven Rangeland System. Ecosystems 5:23-44.

Armstrong W. 1967. The Oxidising Activity of Roots in Waterlogged Soils. Physiologia Plantarum 20:920-926.

Armstrong W. 1975. Waterlogged soils. Environment and plant ecology 181:218.

Armstrong W. 1982. Waterlogged soils. In: Etherington JR (ed) Environment and Plant Ecology, Wiley, Chichester, UK, pp 290-330

Askaer L., B. Elberling, T. Friborg, C. Jørgensen, and B. Hansen. 2011. Plant-mediated CH4 transport and C gas dynamics quantified in-situ in a Phalaris arundinacea-dominant wetland. Plant and Soil 343:287-301.

Bakker C., P. Van Bodegom, H. Nelissen, W. Ernst, and R. Aerts. 2006. Plant responses to rising water tables and nutrient management in calcareous dune slacks. Plant Ecology 185:19-28

Bakker C., Rodenburg, J. and Van Bodegom, P.M. 2005. Effects of Ca- and Fe-rich Seepage on P Availability and Plant Performance in Calcareous Dune Soils. Plant and Soil 275: 111-122.

Bakker C. 2005. Key processes in retoration of wet dune slacks. Ph.D. Thesis, Vrije Universteit, Amsterdam, NL.

Bakker S.A., Jasperse C., Verhoeven J.T.A. 1997. Accumulation rates of organic matter associated with different successional stages from open water to carr forest in former turbaries. Plant Ecology 129: 113-120

Bakker, C., P.M. van Bodegom, H.J.M. Nelissen, R. Aerts, and W.H.O. Ernst. 2007. Preference of wet dune species for waterlogged conditions can be explained by adaptations and specific recruitment requirements. Aquatic Botany 86:37-45.

Basiliko N. and J. Yavitt. 2001. Influence of Ni, Co, Fe, and Na additions on methane production in Sphagnum-dominated Northern American peatlands. Biogeochemistry 52:133-153.

Beisner B.E, D.T. Haydon, and K. Cuddington. 2003. Alternative Stable States in Ecology. Frontiers in Ecology and the Environment 1:376-382.

Bekker R.M., E.J. Lammerts, A. Schutter, and A.P. Grootjans. 1999. Vegetation development in dune slacks: the role of persistent seed banks. Journal of Vegetation Science 10:745-754.

Berendse F., Lammerts E.J, Olff H. 1998. Soil organic matter accumulation and its implications for nitrogen mineralization and plant species composition during succession in coastal dune slacks. Plant Ecology 137:71-78

Berendse F. 1990. Organic Matter Accumulation and Nitrogen Mineralization During Secondary Succession in Heathland Ecosystems. Journal of Ecology 78:413-427.

Bergman I., B.H. Svensson and M. Nilsson. 1998. Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. Soil Biology and Biochemistry 30:729-741.

Bergman I, M. Klarqvist, and M. Nilsson. 2000. Seasonal variation in rates of methane production from peat of various botanical origins: effects of temperature and substrate quality. FEMS Microbiology Ecology 33:181-189.

Bergström I, S. Mäkelä, P. Kankaala, and P. Kortelainen. 2007. Methane efflux from littoral vegetation stands of southern boreal lakes: An upscaled regional estimate. Atmospheric Environment 41:339-351.

Bhullar G.S., P.J. Edwards, and H. Olde Venterink. 2013. Variation in the plant-mediated methane transport and its importance for methane emission from intact wetland peat mesocosms. Journal of Plant Ecology.

Bobbink R., Hicks K., Galloway J., Spranger T., Alkemade R., Ashmore M., Bustamante M., Cinderby S., Davidson E., Dentener F., Emmett B., Erisman J.-W., Fenn M., Gilliam F., Nordin A., Pardo L., De Vries W. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications 20:30–59

Bodegom P. M. v, M. d. Kanter, and C.B.R. Aerts. 2005. Radial oxygen loss, a plastic property of dune slack plant species. Plant and Soil 271:351.

Bodelier, P.L.E., M. Stomp, L. Santamaria, M. Klaassen, and H.J. Laanbroek. 2006. Animal–plant–microbe interactions: direct and indirect effects of swan foraging behaviour modulate methane cycling in temperate shallow wetlands. Oecologia 149:233–244.

Boedeltje G., Bakker, J.P. Bekker, R.M., Van Groenendael, J.M. and Soesbergen, M. 2003. Plant Dispersal in a Lowland Stream in Relation to Occurrence and Three Specific Life-History Traits of the Species in the Species Pool. *Journal of Ecology* 91: 855-866.

Cao M., K. Gregson, and S. Marshall. 1998. Global methane emission from wetlands and its sensitivity to climate change. Atmospheric Environment 32:3293-3299.

Cappers R.T.C. 1994. An ecological characterization of plant macro-remains of Heveskesklooster. Ph.D. thesis, University of Groningen, Groningen, NL.

Carpenter S.R. 2003. Regime Shifts in Lake Ecosystems: Pattern and Variation. Excellence in Ecology 15.133: 1539–1540.

Choi Y.D, V.M. Temperton, E.B. Allen, A.P. Grootjans, M. Halassy, R.J. Hobbs, M.A. Naeth, and K. Torok. 2008. Ecological restoration for future sustainability in a changing environment. Ecoscience 15:53-64.

Choi Y.D. 2004. Theories for ecological restoration in changing environment: Toward a futuristic restoration. Ecological Research 19: 75-81.

Choi Y.D., Temperton, V.M., Allen, E.B. Grootjans, A.P., Halassy, M. Hobbs, R.J., Naeth, M. A. and Torok, K. 2008. Ecological restoration for future sustainability in a changing environment. Ecoscience 15: 53-64.

Christensen J. H. and O.B. Christensen. 2003. Climate modelling: Severe summertime flooding in Europe. Nature 421:805-806.

Clarke M. and H. Rendell. 2011. Atlantic storminess and historical sand drift in Western Europe: implications for future management of coastal dunes. Journal of Coastal Conservation.

Clarke M.L. and H. M. Rendell. 2009. The impact of North Atlantic storminess on western European coasts: A review. Quaternary International 195:31-41.

Couwenberg J., A. Thiele, F. Tanneberger, J. Augustin, S. Bärisch, D. Dubovik, N. Liashchynskaya, D. Michaelis, M. Minke, A. Skuratovich, and H. Joosten. 2011. Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. Hydrobiologia 674:67-89.

Crawford R.M.M. and D. Wishart. 1966. A Multivariate Analysis of the Development of Dune Slack Vegetation in Relation to Coastal Accretion at Tentsmuir, Fife. The Journal of Ecology 54:729-743.

Dai W. Huang Y. 2006. Relation of soil organic matter concentration to climate and altitude in zonal soils of China. Catena 65:87-94

Davy A.J, Grootjans A.P., Hiscock K., Peterson J. (2006) Development of eco-hydrological guidelines for dune habitats – Phase 1. English Nature Research Reports, No 696, Peterborough

Day F.P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63:670–678

De Bakker N.V.J., Adema E.B., Everts F.H. 2004. Vegetation changes in the Kroon's Polders Vlieland (in Dutch). Report University of Groningen, NL.

De Leeuw J., H. Olff, and J.P. Bakker. 1990. Year-to-year variation in peak above-ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. Aquatic Botany 36:139.

De Vries V. 1961. Vegetatiestudie op de westpunt van Vlieland. PhD thesis, University of Amsterdam

Decleer K., Bonte D., Van Diggelen R. 2013. The hemiparasite Pedicularis palustris: 'Ecosystem engineer' for fen-meadow restoration. Journal of Nature Conservation 21:65-71

Dias A.C., B. Hoorens, R.P. Logtestijn, J. Vermaat, and R. Aerts. 2010. Plant Species Composition Can Be Used as a Proxy to Predict Methane Emissions in Peatland Ecosystems After Land-Use Changes. Ecosystems 13:526-538.

Ding W., Z. Cai, and H. Tsuruta. 2004. Diel variation in methane emissions from the stands of Carex lasiocarpa and Deyeuxia angustifolia in a cool temperate freshwater marsh. Atmospheric Environment 38:181-188.

Ding W., Z. Cai, and H. Tsuruta. 2005. Plant species effects on methane emissions from freshwater marshes. Atmospheric Environment 39:3199-3207.

Diserud O.H. and F. Ødegaard. 2007. A multiple-site similarity measure. Biology Letters 3:20-22.

Dobben H. and P. Slim. 2012. Past and future plant diversity of a coastal wetland driven by soil subsidence and climate change. Climatic Change 110:597-618.

Duan X., X. Wang, Y. Mu, and Z. Ouyang. 2005. Seasonal and diurnal variations in methane emissions from Wuliangsu Lake in arid regions of China. Atmospheric Environment 39:4479-4487.

Elmgren R. 2001. Understanding Human Impact on the Baltic Ecosystem: Changing Views in Recent Decades. Ambio 30:222-231.

Engelaar W.M.H. G., P.L.E. Bodelier, H.J. Laanbroek, and C.W.P.M. Blom. 1991. Nitrification in the rhizosphere of a flooding-resistant and a flooding-non-resistant Rumex species under drained and waterlogged conditions. FEMS Microbiology Letters 86:33-42.

Ernst W.H.O, Slings Q.L., Nelissen H.J.M. 1996. Pedogenesis in coastal wet dune slacks after sod-cutting in relation to revegetation. Plant and Soil 180:219-230

Farmer V.C., Morrison R.I. 1964. Lignin in sphagnum and phragmites and in peats derived from these plants. Geochimica et Cosmochimica Acta 28:1537-1546

Folke C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C.S. Holling. 2004. Regime shifts, reilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557-581.

Fritz C., G. van Dijk, A.J.P. Smolders, V.A. Pancotto, T.J.T.M. Elzenga, J.G.M. Roelofs, and A.P. Grootjans. 2012. Nutrient additions in pristine Patagonian Sphagnum bog vegetation: can phosphorus addition alleviate (the effects of) increased nitrogen loads. Plant Biology 14:491-499.

Fritz C., V.A. Pancotto, J.T.M. Elzenga, E.J.W. Visser, A.P. Grootjans, A. Pol, R. Iturraspe, J.G.M. Roelofs, and A.J.P. Smolders. 2011. Zero methane emission bogs: extreme rhizosphere oxygenation by cushion plants in Patagonia. New Phytologist 190:398-408.

Fukami T. and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? Ecology Letters 14:973-984.

Gibson N. 1990. The Environments and Primary Production of Cushion Species at Mt Field and Mt Wellington, Tasmania. Australian Journal of Botany 38:229-243.

Gibson N. and J.B. Kirkpatrick. 1985. A comparison of the cushion plant communities of New Zealand and Tasmania. New Zealand Journal of Botany 23:549-566.

Glenn-Lewin D.C. and Van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. Plant succession – Theory and Prediction, pp 11-59. Chapman-Hall.

Gorham E., Vitousek, P.M. and Reiners, W.A. 1979. The Regulation of Chemical Budgets over the Course of Terrestrial Ecosystem Succession. Annual Review of Ecology and Systematics 10: 53-84.

Grootjans A., E. Adema, R. Bekker, and E. Lammerts. 2006. Why Coastal Dune Slacks Sustain a High Biodiversity. Page 85 Coastal Dunes.

Grootjans A.P., E.B. Adema, W. Bleuten, H. Joosten, M. Madaras, and M. Janáková. 2006. Hydrological landscape settings of base-rich fen mires and fen meadows: an overview. Applied Vegetation Science 9:175-184.

Grootjans A.P, F.P. Sival, and P.J. Stuyfzand. 1996. Hydro-geochemical analysis of a degraded dune slack. Plant Ecology 126:27-38.

Grootjans A.P., Geelen L, Jansen A.J.M, Lammerts E.J. 2002. Restoration of coastal dune slacks. Hydrobiologia 478:181-203

Grootjans A.P., Hartog, P.S., Fresco, L.F.M, & Esselink, H. 1991. Succession and Fluctuation in a wet slack in relation to hydrological changes. Journal of Vegetation Science 2:545-554.

Grootjans A.P, W.H.O. Ernst, and P.J. Stuyfzand. 1998. European dune slacks: Strong interactions of biology, pedogenesis and hydrology. Trends in Ecology & Evolution 13:96-100.

Grootjans A.P., Everts, H., Bruin, K. and Fresco, L.F.M. 2001. Restoration of Wet Dune Slacks on the Dutch Wadden Sea Islands: Recolonization After Large-Scale Sod Cutting. Restoration Ecology 9: 137-146.

Gunderson L.H. 2001. South Florida: the reality of change and the prospects for sustainability: Managing surprising ecosystems in southern Florida. Ecological Economics 37:371-378.

Harris J.A., Hobbs, J., Higgs, E. and Aronson, J. 2006. Ecological Restoration and Global Climate Change. Restoration Ecology 14: 170-176.

Hedberg O. 1997. High-Mountain areas of Tropical Africa. Pages 185-197 in F.E. Wielgolaski, editor. Ecosystems of the World 3: Polar and Alpine Tundra. Elsevier, Amsterdam.

Heslenfeld P., P. D. Jungerius, and J.A. Klijn. 2008. European Coastal Dunes: Ecological Values, Threats, Opportunities and Policy Development. Pages 335-351 in M.L. Martínez and N. Psuty, editors. Coastal Dunes. Springer Berlin Heidelberg.

Hillman J.C. 1986. Bale Mountains National Park, Management Plan. Wildlife Conservation Organisation, Adis Abeba. 250 p.

Hillman J.C. 1988. The Bale Mountains National Park Area, Southeast Ethiopia, and Its Management. Mountain Research and Development 8:253-258.

Hillman J.C. 1990. The Bale Mountains National Park area, southeastern Ethiopia, and its management. Pp. 277-286. In. Messerli, B. and Hurni, H. (eds.). African Mountains and Highlands, Problems and Perspectives.. African Mountains Association, Walsworth Press, Missouri.

Hillman J.C. 1993. Ethiopia: Compendium of Wildlife Conservation Information, Report to Ethiopian Wildlife Conservation Organisation, Addis Ababa.

Hirota M., Y. Tang, Q. Hu, S. Hirata, T. Kato, W. Mo, G. Cao, and S. Mariko. 2004. Methane emissions from different vegetation zones in a Qinghai-Tibetan Plateau wetland. Soil Biology and Biochemistry 36:737-748.

Houston J.A. 2008. Management of Natura 2000 Habitats. 2190 Humid dune slacks. European Commission.

Huggett R.J. 1998. Soil chronosequences, soil development, and soil evolution: a critical review. Catena 32:155-172

Jackson J.B.C. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Jackson J.B.C. and K.G. Johnson. 2001. Measuring past Biodiversity. Science 293:2401-2404.

Jenny H. 1980. The Soil Resource: origin and behavior. Springer-Verlag, New York

Joabsson A., T.R. Christensen, and B. Wallén. 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends in Ecology & Evolution 14:385-388.

Joabsson A. and T.R. Christensen. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biology 7:919-932.

John D. 1988. Forest Vines to Snow Tussocks: the Story of New Zealand Plants Victoria University Press:183-184.

Jones L., Nizam M.S., Reynolds B., Bareham S., Oxley E.R.B. 2013. Upwind impacts of ammonia from an intensive poultry unit. Environmental Pollution 180:221-228

Jones M., Sowerby A., Williams D., Jones R. 2008. Factors controlling soil development in sand dunes: evidence from a coastal dune soil chronosequence. Plant and Soil 307:219-234

Jones M.L.M, Reynolds B., Brittain S.A, Norris D.A, Rhind P.M, Jones R.E. 2006. Complex hydrological controls on wet dune slacks: the importance of local variability. Science of the Total Environment 372: 266–277

Jones R. 1972. Comparative Studies of Plant Growth and Distribution in Relation to Waterlogging: VI. The Effect of Manganese on the Growth of Dune and Dune Slack Plants. The Journal of Ecology 60:141.

Kautsky N., H. Kautsky, U. Kautsky, and M. Waern. 1986. Decreased depth penetration of Fucus vesiculosus (L.) since the 1940s indicates eutrophication of the Baltic Sea. Marine ecology progress series 28:1-8.

Kelly R.D. and B.H. Walker. 1976. The Effects of Different Forms of Land Use on the Ecology of a Semi-Arid Region in South-Eastern Rhodesia. Journal of Ecology 64:553-576.

Kirschbaum M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic storage. Soil Biology and Biochemistry 27:753-760

Kleinebecker T., N. Hölzel, and A. Vogel. 2008. South Patagonian ombrotrophic bog vegetation reflects biogeochemical gradients at the landscape level. Journal of Vegetation Science 19:151-160.

Kleinebecker, T., N. Hölzel, and A. Vogel. 2007. Gradients of continentality and moisture in South Patagonian ombrotrophic peatland vegetation. Folia Geobotanica 42:363-382.

KNMI, the Royal Dutch Meteorological Institute. September 2003.

Kooijman A.M. 2008. Environmental Problems and Restoration Measures in Coastal Dunes in the Netherlands. Pages 243-258 in M.L. Martínez and N. Psuty, editors. Coastal Dunes. Springer Berlin Heidelberg.

Kooijman A.M. and M. Besse. 2002. The higher availability of N and P in lime-poor than in lime-rich coastal dunes in the Netherlands. Journal of Ecology 90:394-403.

Kooijman A.M, Dopheide J.C.R, Sevink J., Takken I., Verstraten J.M. 1998. Nutrient limitations and their implications on the effects of atmospheric deposition in coastal dunes; lime-poor and lime-rich sites in the Netherlands. Journal of Ecology 86:511–526

Laanbroek H. J. 2010. Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. Annals of Botany 105:141-153.

Lamers L.P.M, H.B.M. Tomassen, and J.G.M. Roelofs. 1998. Sulfate-Induced Eutrophication and Phytotoxicity in Freshwater Wetlands. Environmental Science & Technology 32:199-205.

Lammerts E.J., C. Maas, and A.P. Grootjans. 2001. Groundwater variables and vegetation in dune slacks. Ecological Engineering 17:33-47.

Lammerts E. J. 1999. Basiphilous pioneer vegetation in dune slacks on the Dutch Wadden Sea islands. PhD Thesis, University of Groningen, The Netherlands.

Lammerts E.J. and A.P. Grootjans. 1998. Key environmental variables determining the occurence and life span of basiphilous dune slack vegetation. Acta Botanica Neerlandica 47(3):369-392.

Lammerts E.J., Grootjans A.P. 1997. Nutrient deficiency in dune slack pioneer vegetation: a review. Journal of Coastal Conservation 3: 87-94

Lammerts E.J., Pegtel D.M.P, Grootjans A.P, van der Veen A. 1999. Nutrient limitation and vegetation changes in a coastal dune slack. Journal of Vegetation Science 10:111-122

Laurence R. Walker, and R. d. Moral. 2003. Primary succession and ecosytem rehabilitation. Cambridge University Press, 2003.

Lepš J. and Šmilauer, P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, New York.

Londo G. 1975. The Decimal scale for relevesof permanent quarats. Plant Ecology 33:61-64.

MacArthur R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton, N.J. Princeton.

Maltby E., S. Ormerod, M. Acreman, M. Blackwell, I. Durance, M. Everard, J. Morris, C. Spray, J. Biggs, and P. Boon. 2008. Freshwaters–Open waters, Wetlands and Floodplains.

Maltby E. 2009. The Changing Wetland Paradigm. The Wetlands Handbook. Blackwell Publishing Ltd:4.

Maltby E. 2013. Waterlogged wealth: why waste the world's wet places? Routledge.

Mark A.F. and L.C. Bliss. 1970. The high-alpine vegetation of Central Otago, New Zealand. New Zealand Journal of Botany 8:381-451.

Meyerson L.A., Saltonstall K., Windham L., Kiviat E., Findlay S. 2000. A comparison of Phragmites australis in freshwater and brackish marsh environments in North America. Wetlands Ecology and Management 8:89-103

Mohr P.A. 1963. The geology of Ethiopia. Univ. College of Addis Ababa:268.

Morecroft M.D., G.J. Masters, V.K. Brown, I.P. Clarke, M.E. Taylor, and A.T. Whitehouse. 2004. Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. Functional Ecology 18:648.

Moreno-Casasola P. and G. Vázquez. 1999. The Relationship between Vegetation Dynamics and Water Table in Tropical Dune Slacks. Journal of Vegetation Science 10:515-524.

Mukhortova L. 2008. The influence of high water table on carbon storage in the soil of forest ecosystems in the forest-tundra zone of central Siberia, Krasnoyarsk region. Peckiana 5:25-39

Munoz-Reinoso J.C. 2001. Vegetation changes and groundwater abstraction in SW Donana, Spain. Journal of Hydrology 242:197-209.

Nystrom M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol. Evol. 15:413-417.

Nystrom M. and C. Folke. 2001. Spatial resilience of coral reefs. Ecosystems 4:406-417.

Olff H., J. Huisman, and B.F.V. Tooren. 1993. Species Dynamics and Nutrient Accumulation During Early Primary Succession in Coastal Sand Dunes. The Journal of Ecology 81:693-706.

Ozinga W., Hennekens, S. Schaminée, J. Bekker, R., Prinzing, A., Bonn, S., Poschlod, P., Tackenberg, O., Thompson, K., Bakker, J. and Van Groenendael, J.M. 2005. Assessing the relative importance of dispersal in plant communities using an ecoinformatics approach. Folia Geobotanica 40: 53-67.

Ozinga W.A., Römermann, C., Bekker, R.M. Prinzing, A., Tamis, W.L.M. Schaminée, J.H.J., Hennekens, S.M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J.P. and Van Groenendael, J.M. 2009. Dispersal failure contributes to plant losses in NW Europe. Ecology Letters 12: 66-74.

Palm C.A, Sanchez P.A. 1991. Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. Soil Biology and Biochemistry 23:83-88

Parè D., Boutin R., Larocque G.R., Raulier F. 2006. Effect of temperature on soil organic matter decomposition in three forest biomes of eastern Canada. Canadian Journal of Soil Science 86:247-256

Peña-Ramírez V.M., Vázquez-Selem L., Siebe C. 2009. Soil organic carbon stocks and forest productivity in volcanic ash soils of different age (1835–30,500 years B.P.) in Mexico. Geoderma 149:224-234

Petraitis P.S. and S.R. Dudgeon. 2004. Detection of alternative stable states in marine communities. Journal of Experimental Marine Biology and Ecology 300:343-371.

Phillips S.M. 1996. Eriocaulon schimperi (Eriocaulaceae) and Some Related Species in Eastern Africa. Kew Bulletin 51:333-342.

Pitt M. D. and H.F. Heady. 1978. Responses of Annual Vegetation to Temperature and Rainfall Patterns in Northern California. Ecology 59:336.

Pollux B.J.A. 2007. Plant dispersal in rivers – A mechanistic and molecular approach. Ph.D, thesis, Radboud University Nijmegen, Nijmegen, NL.

Provoost S., M. Jones, and S. Edmondson. 2011. Changes in landscape and vegetation of coastal dunes in northwest Europe: a review. Journal of Coastal Conservation 15:207-226.

R development core team. 2010. R, a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, AT

Ranwell D. 1959. Newborough Warren, Anglesey: I. The Dune System and Dune Slack Habitat. The Journal of Ecology 47:571.

Ranwell D. 1960a. Newborough Warren, Anglesey: II. Plant Associes and Succession Cycles of the Sand Dune and Dune Slack Vegetation. The Journal of Ecology 48:117.

Ranwell D.S. 1960b. Newborough Warren, Anglesey: III. Changes in the Vegetation on Parts of the Dune System After the Loss of Rabbits by Myxomatosis. The Journal of Ecology 48:385.

Ranwell D.S. 1972. Ecology of Salt Marshes and Sand Dunes. Chapman & Hall Ltd, London UK.

Reddy K.R, W.H. Patrick, Jr., and C.W. Lindau. 1989. Nitrification-Denitrification at the Plant Root-Sediment Interface in Wetlands. Limnology and Oceanography 34:1004-1013.

Remke E., Brouwer E., Kooijman A., Blindow I., Esselink H., Roelofs J.G.M. 2009. Even low to medium nitrogen deposition impacts vegetation of dry, coastal dunes around the Baltic Sea. Environmental Pollution 157:792-800

Rundel P.W. 1994. Tropical alpine climates. Pages21-44 in P.W. Rundel, A.P. Smith, and F.C. Meinzer, editors. Tropical alpine environments: plant form and function.. Cambridge University Press, Cambridge.

Salisbury E.J. 1925. Note on the edaphic succession in some dune soils with special reference to the time factor. Journal of Ecology 13:322-328

Scheffer M., S. Rinaldi, A. Gragnani, L.R. Mur, and E.H. Van Nes. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. Ecology 78:272-282.

Scheffer M. and S.R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648-656.

Scheffer R.A., van Logtestijn R.S.P., Verhoeven J.T.A. 2001. Decomposition of Carex and Sphagnum litter in two mesotrophic fens differing in dominant plant species. Oikos 92:44-54

Schroeder K,A. Ribotti, M. Borghini, R. Sorgente, A. Perilli, and G.P. Gasparini. 2008. An extensive western Mediterranean deep water renewal between 2004 and 2006. Geophysical Research Letters 35.18: L18605

Sevink J. 1991. Soil development in the coastal dunes and its relation to climate. Landscape Ecology 6:49-56

Sival F.P. and A.P. Grootjans. 1996. Dynamics of seasonal bicarbonate supply in a dune slack: effects on organic matter, nitrogen pool and vegetation succession. Plant Ecology 126:39-50.

Sival F.P., Strijkstra-Kalk M. 1999. Atmospheric deposition of acidifying and eutrophicating substances in dune slacks. Water, Air, and Soil Pollution 116:461-477

Smith S.M., Hanley M., Killingbeck K.T. 2008. Development of vegetation in dune slack wetlands of Cape Cod National Seashore (Massachusetts, USA). Plant Ecology 194:243-256.

Sollins P., Spycher G., Topik C. 1983. Processes of soil organic-matter accretion at a mudflow chronosequence, Mt. Shasta, California. Ecology 64:1273-1282

Sparrius L.B. 2011. Inland dunes in The Netherlands: soil, vegetation, nitrogen deposition and invasive species. PhD thesis, University of Amsterdam

Stephens P.A., C.A. d'Sa, C. Sillero-Zubiri, and N. Leader-Williams. 2001. Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. Biological Conservation 100:307-322.

Studer-Ehrensberger K., C. Studer, and R.M.M. Crawford. 1993. Competition at Community Boundaries: Mechanisms of Vegetation Structure in a Dune-Slack Complex. Functional Ecology 7:156-168.

Stuyfzand P.J. 1993. Hydrochemistry and hydrology of the coastal dune area of the Western Netherlands. PhD thesis, Free University of Amsterdam

Suding K.N, K.L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19:46-53.

Sýkora K.V., J.C.J.M. van den Bogert, and F. Berendse. 2004. Changes in soil and vegetation during dune slack succession. Journal of Vegetation Science 15:209-218.

Tansley A.G. 1949. The British Islands and their vegetation. CUP Archive.

Ter Borg S.J. 1979. Some topics in plant biology. In: Werger MJA (ed) The study of vegetation. Dr. W. Junk bv Publishers, The Hage-Boston-London, pp 11 – 55

Ter Braak C.J.F. and P. Šmilauer. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Ithaca, NY, USA (www.canoco.com): Microcomputer Power.

Turner M.G., Baker, W.L. Peterson, C.J. and Peet, R.K. 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. Ecosystems 1: 511-523.

Valentine D.W., E.A. Holland, and D.S. Schimel. 1994. Ecosystem and physiological controls over methane production in northern wetlands. Journal of Geophysical Research: Atmospheres 99:1563-1571.

Van Bodegom P.M., De Kanter, M. and Aerts, C.B.R. 2005. Radial oxygen loss, a plastic property of dune slack plant species. Plant and Soil 271: 351-364.

Van Breemen N., Buurman P. 2002. Soil Formation, 2nd edn. Springer-Kluwer Academic Publishers, Dordrecht, Boston, London

Van Breemen N. 1995. How Sphagnum bogs down other plants. Trends in Ecology & Evolution 10:270-275

Van de Koppel Johan, Max Rietkerk, Frank van Langevelde, Lalit Kumar, Christopher A. Klausmeier, John M. Fryxell, John W. Hearne, Jelte van Andel, Nico de Ridder, Andrew Skidmore, Leo Stroosnijder, and Herbert H. T. Prins. 2002. Spatial Heterogeneity and Irreversible Vegetation Change in Semiarid Grazing Systems. The American Naturalist 159:209-218.

Van den Berg L.J.L., H.B.M. Tomassen, J.G.M. Roelofs, and R. Bobbink. 2005. Effects of nitrogen enrichment on coastal dune grassland: A mesocosm study. Environmental Pollution 138:77.

Van der Hagen, H.G.J.M., L.H.W.T. Geelen, and C.N. de Vries. 2008. Dune slack restoration in Dutch mainland coastal dunes. Journal for Nature Conservation 16:1-11.

Van der Laan, D. 1979. Spatial and temporal variation in the vegetation of dune slacks in relation to the groundwater régime. Plant Ecology **39**:43-51.

Van der Maarel E. and Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. Journal of Vegetation Science 4: 179-188.

Van der Maarel, E. 1981. Fluctuations in a coastal dune grassland due to fluctuations in rainfall: experimental evidence. Vegetatio 47: 259-265.

Van der Meijden, R. 1996. Heukels' flora of the Netherlands, 22nd edition. Wolters Noordhoff, Groningen.

Van Dieren J.W. 1934. Organogene Du¨nenbildung, eine geomorphologische Analyse der westfriesischen Insel Terschelling mit pflanzensoziologischen Methoden. Doctoral thesis, University of Amsterdam.

Van Dijk H. and A. Grootjans. 1993. Wet dune slacks: decline and new opportunities. Hydrobiologia 265:281-304.

Van Dorp D. 1996. Seed dispersal in agricultural habitats and the restoration of species-rich meadows. Ph.D. thesis, Agricultural University, Wageningen, NL.

Van Gemerden H. 1993. Microbial mats: A joint venture. Marine Geology 113:3-25.

Verhagen R., Klooker, J., Bakker, J.P., Van Diggelen, R. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. Applied Vegetation Science 4: 75–82.

Verhoeven J.T.A. 1986. Nutrient dynamics in minerotrophic peat mires. Aquatic Botany 25:117-137.

Verhoeven J.T.A, Toth E. 1995. Decomposition of Carex and Sphagnum litter in fens: effect of litter quality and inhibition by living tissue homogenates. Soil Biology and Biochemistry 27:271-275

Visser E.W. and G. Bögemann. 2003. Measurement of porosity in very small samples of plant tissue. Plant and Soil 253:81-90.

Von Asmuth J.R., Maas K., Knotters M., Leunk I. 2010. Menyanthes user manual, version 1.9.3

Walker L.R, and del Moral R. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge, UK

Walker L.R., Wardle D.A., Bardgett R.D., Clarkson B.D. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725-736

Walther G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Wassen M. and A. Grootjans. 1996. Ecohydrology: an interdisciplinary approach for wetland management and restoration. Vegetatio 126:1-4.

Wassen M.J. 1990. Water flow as a major landscape ecological factor in fen development. Ph.D. Thesis, Utrect University, Utrecht NL.

Westlake D.F. 1963. Comparison of plant productivity. Biological Reviews 38:385-425

Whiting G.J. and J.P. Chanton. 1993. Primary production control of methane emission from wetlands. Nature 364:794-795.

Whiting G.J. and J.P. Chanton. 2001. Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. Tellus B 53:521-528.

Wigginton J.D, Lockaby B.G., Trettin C.C. 2000. Soil organic matter formation and sequestration across a forested floodplain chronosequence. Ecological Engineering 15:141-155

Williams P.A. 1991. Subalpine and alpine vegetation of granite ranges in western Nelson, New Zealand. New Zealand Journal of Botany 29:317-330.

Wilson E.J., Wells T.C.E., Sparks T.H. 1995. Are calcareous grasslands in the UK under threat from nitrogen deposition? – an experimental determination of a critical load. Journal of Ecology 83:823-832

Wilson J. B. and A.D.Q. Agnew. 1992. Positive-feedback switches in plant community. Advances in Ecological Research 23. 263-336.

Wilson K. 1960. The time factor in the development of dune soils at South Haven Peninsula, Dorset. Journal of Ecology 48:341-359

Windham L, and Lathrop R. 1999. Effects of Phragmites australis (common reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. Estuaries and Coasts 22:927-935.

Yalden D.W. 1983. The extent of high ground in Ethiopia as compared to the rest of Africa. Sinet. Ethiop. J. Sci. 6:35-39.

Yalden D.W. and M.J. Largen. 1992. The endemic mammals of Ethiopia. Mammal Review 22:115-150.

Young T.P., Petersen, D.A. and Clary, J.J. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters 8: 662-673.

Zobel M. 1997. The relative role of species pools in determining plant species richness; an alternative explanation of co-existence? Trends in Ecology and Evolution 12: 266-269.

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The idea for this PhD project was born while I was working on a literature with Ab. First, the master program that I followed was basically designed to train and prepare students for further scientific career that normally begins with a PhD study, which means I was already thinking about finding a position as a PhD student. Ab knew the desire I had about pursuing a PhD to which he helped me in several ways already. He introduced me to new sites, taking me with him on several field trips including a trip to Western part of Poland in June 2007. While I did a literature study with him about vegetation succession after large scale sod-cutting, Ab told me about a possibility of me working on a PhD project that was going to be financed by NAM. He mentioned about a report produced by Alterra Institute on the effects of soil subsidence due to gas abstraction on Wadden Sea Island of Ameland and to which he argued against one of the basic findings of the report. According to Ab, soil subsidence that was caused by gas abstraction can only be assessed based on reference sites where there is no gas abstraction. Ab argued that a good evaluation of the effects of gas abstraction on the flooding frequency of coastal wetlands is complicated by another effect of global warming; increased precipitation during the winter and less precipitation, but more intense rainfall during short periods. Therefore, according to him it was not possible to conclude that from the report of Altera whether or not gas abstraction has affected dune slack vegetation. NAM on their side accepted the criticism and pledged to fund a research project that will focus on reference sites as well. In this way the funding for this project was acquired. In September 2008, I started working on this project. I thank NAM for providing this funding that has led to my PhD.

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Curriculum Vitae

Bikila was born 16th of April, 1982, in a remote village called Lokkoo located in the Western part of Ethiopia near Nekemte town. He graduated from high school in the summer of 2001 where he studied natural sciences. October 2001 he joined former Debub University, now called Hawassa University, department of Applied Biology. In July 2005, he graduated from Applied Biology with a great distinction. Bikila studied biological sciences initially with keen interest on subjects such as cell biology, genetics, biotechnology, microbiology and virology but later on he became more interested in studies of ecology, ecosystems and the environment.

From September 2005-August 2006, Bikila took a position as a graduate assistant in the department of Applied Biology where he studied. During this time he participated in teaching activities of several courses but also he served as an organizer for community based training program of the department. As an organizer of this program he worked with several public, private and international organizations to facilitate student placements in work places and on job trainings.

Bikila found about the scholarship program of University of Groningen on the internet and he applied for a 'top master program in evolutionary biology' in April 2006. He was accepted for this program and came to Groningen in September 2006. Between 2006 & 2008, he followed 'Top master' program in Evolutionary biology. Bikila's first thesis was on 'An internal nutrient transport in *Sphagnum* mosses', a study he conducted in the laboratory of plant physiology of University of Groningen under supervision of Prof. dr. Theo Elzinga and his then PhD student dr. Wouter Patberg. After that Bikila worked with his PhD promoter Prof. dr. A.P. Grootjans on the 'Dynamics of vegetation of dune slacks on Wadden Sea Islands of Schiermonninkoog'. Beginning from September 2008, Bikila continued with his PhD at the Center of Environmental and Energy Studies of University of Groningen.

Publications

Dullo, B.W., Grootjans, A.P. & van Dobben, H. 2011. Oorzaken van vernatting: bodemdaling of andere oorzaken? Een studie naar een referentiegebied (de Koegelwieck) op Terschelling. In: Audit Effecten van bodemdaling als gevolg van Gaswinning op Ameland- Oost, Hoofdstuk 4.5 (with English summary), pp. 584-595.

Grootjans, A.P., **Dullo, B.W**., Kooijman, A. & Aggenbach, C. 2013. *Restoration of dry dune vegetation and wet dune slacks in the Netherlands.* In. Martínez, M.L., Gallego-Fernández J.B. & Hesp, P.A. (eds). Restoration of coastal dunes, 235-253. Springer, Berlin.

Shahrudin Rohani, **Bikila Dullo,** Wilmer Woudwijk, Pieter de Hoop, Annemieke Kooijman, & Ab Grootjans. 2014. Accumulation rates of soil organic matter in wet dune slacks on the Dutch Wadden Sea islands. *Plant & Soil, Accepted Febr. 2014.*

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