

Alternative stable states in a wet calcareous dune slack in The Netherlands

Adema, Erwin B.^{1*}; Grootjans, Ab P.¹; Petersen, Jörg² & Grijpstra, Johan³

¹Laboratory of Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA, Haren, The Netherlands;

²Institut für Geobotanik der Universität Hannover, Nienburger Str. 17, D-30167 Hannover, Germany;

³Kiwa Onderzoek en Advies, P.O.Box 1072, 3430 BB Nieuwegein, The Netherlands;

*Corresponding author: Fax +31503632273; E-mail e.b.adema@biol.rug.nl

Abstract. Evidence is presented for the occurrence of alternative stable states in a wet calcareous dune slack on the Frisian island of Texel, The Netherlands. An early pioneer stage (0.5 kg m⁻² total standing crop) and a more productive later successional stage (2.9 kg m⁻²) occur side by side, with sharp boundaries between them. The pioneer vegetation has been recorded at the site for more than 62 yr. These features indicate the occurrence of a positive-feedback mechanism that has led to alternative stable states.

Analyses of ground and surface water composition, and decalcification depths, indicated that hydrologically the study site can be characterized as a flow-through slack, with exfiltration of calcareous groundwater on one side and infiltration of surface water on the other side of the slack. These differences in hydrological conditions have led to distinct differences in environmental conditions within the dune slack. The occurrence of the two successional stages can, however, not be explained by differences in hydrological conditions since both stages occur side by side in the centre of the dune slack. It is, therefore, more likely that biotic interactions are the cause of the vegetation pattern. Three possible mechanisms for feedback processes are discussed: (1) enhanced nitrogen loss; (2) sulfide toxicity and (3) nutrient accumulation in internal cycle.

Keywords: Hydrology; Microbial mat; Multiple stable state; Pioneer species; Succession; Sulfide.

Nomenclature: van der Meijden (1996) for phanerogams; Schaminée et al. (1995) for syntaxa.

Introduction

In the past decades, theoretical and empirical work has been done on the occurrence of alternative stable states in ecology, mainly focusing on the occurrence of alternative stable states caused by plant-animal interactions (Noy-Meir 1975; May 1977). Plant-plant interactions can also induce alternative stable states (Wilson & Agnew 1992). We report a situation where there is *prima facie* evidence that alternative stable states exist in vegetation succession of wet calcareous dune slacks.

Calcareous dune slacks show large variation in the persistence of low-production early successional pioneer stages (Lammerts et al. 1995). Pioneer stages may be very short-lived in some slacks, while in others they can persist for many decades. Lammerts et al. (1995) and Sival (1996) related these differences in succession rate to differences in the hydrological functioning of the slack. Alkaline groundwater at surface level, at least during wintertime, is necessary for the stable persistence of pioneer vegetation. If the groundwater level is lower and never reaches the surface level, the topsoil will acidify and organic matter can start to accumulate. The nutrient availability will increase (Olf et al. 1993), which favours later successional stages. This may explain some of the variation between different dune slacks but it does not explain the variation within one dune slack where comparable hydrological conditions are present. The occurrence of the two successional stages indicates the presence of positive-feedback mechanisms that stabilize the pioneer stage (Wilson & Agnew 1992).

A positive-feedback switch can occur if one or both vegetation types contain species that modify their environment to their own advantage (Wilson & Agnew 1992). These positive-feedback mechanisms may lead to alternative stable states and this may have large consequences for nature management. It means that successful restoration or development of early successional stages will need much more effort than simply restoring the abiotic conditions (Scheffer 1998).

Alternative stable states may cause hysteresis and research in the last decades reveals that this phenomenon is not uncommon in nature (May 1977; Rietkerk & van de Koppel 1997; van de Koppel et al. 1997; Wilson & Agnew 1992). The problem is how to recognize alternative stable states in the field.

Since alternative stable states occur only if a positive-feedback mechanism is operating, we can recognize possible alternative stable states in the field by those switches. A positive-feedback switch leads to

increasing differences between states, and consequently to a bimodal distribution of the system states (Fig. 1). Wilson & Agnew (1992) mention four possible outcomes of positive-feedback switches, all resulting from the bimodal distribution: (1) occurrence of a stable vegetational mosaic in a previously uniform environment, or (2) intensification of a vegetational gradient leading to sharp boundaries, (3) delay or (4) acceleration of succession by displacement or sharpening of temporal boundaries. A fifth outcome is the fact that coexistence is not possible and therefore intermediate states are lacking in the field (Scheffer 1998).

This study investigates whether alternative stable states occur in dune slack succession and how these may be related to the hydrological regime.

Study area

The ‘Buiten Mui’ on the Frisian island of Texel (53° 07' N 5° 47' E; Fig. 2) originates from a beach plain that was separated from the sea by a dune ridge between 1920 and 1925 (Westhoff & van Oosten 1991). The ‘Buiten Mui’ is part of the ‘De Mui’ nature reserve, which was established in 1908. The study area in the ‘Buiten Mui’ can be divided in three areas. 1. The southwestern part (1; Fig. 2) that is yearly mown in order to maintain rare species such as *Anagallis tenella*, *Epipactis palustris* and *Ophioglossum vulgatum*. 2. The unmanaged central part (2; Fig. 2) in which a pioneer stage (*Samolo-Littorelletum*) with a well-developed microbial mat is still present, despite more than 70 yr of undisturbed succession. 3. The northeastern part (3; Fig. 2) where the top soil was removed in 1994. Most of the unmanaged area consists of tall *Scirpo-Phragmitetum* dominated by *Phragmites australis* or *Carex riparia*, which represents a late successional stage.

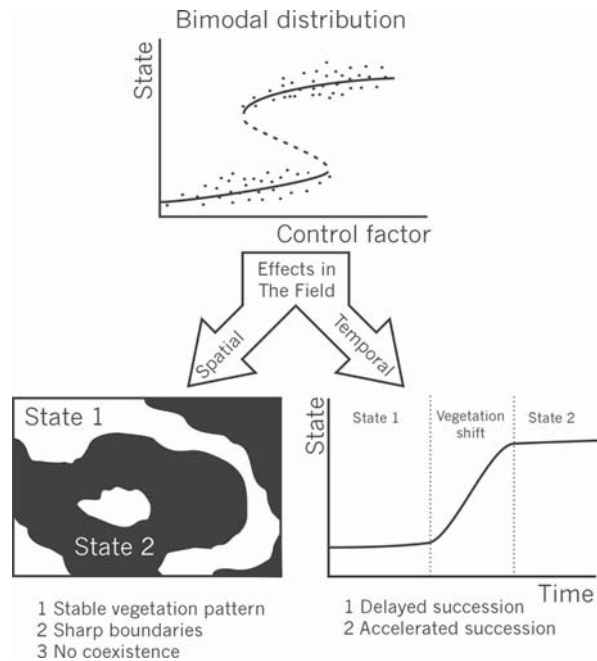


Fig. 1. Effects of a positive-feedback mechanism on the vegetation pattern in the field. The possible outcomes in the field are all based on the principle that a positive-feedback mechanism creates a bimodal distribution in the system states.

Methods

Three transects, running from southeast to northwest, were established across the slack (T1, T2 and T3; Fig. 2). On each transect 3 plots were situated: an inward plot (i), a seaward plot (s) and a plot in the middle of the transect (m). Two extra plots, i' and s' were added to the first transect (T1) in the *Samolo-Littorelletum* stand. The transects, T1, (low-productive state, *Samolo-*

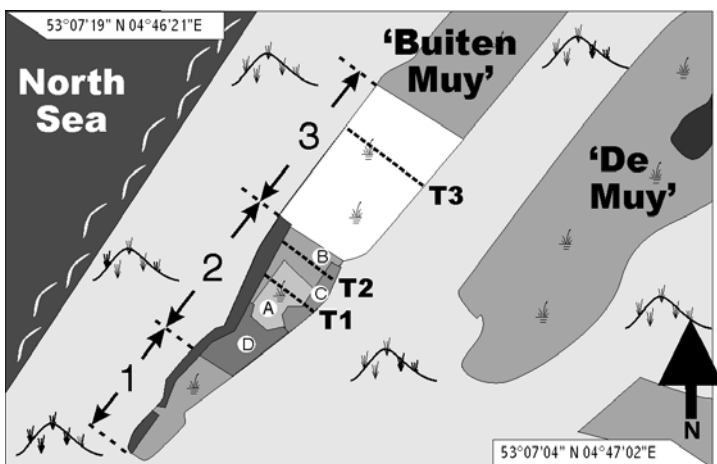


Fig. 2. Overview of the ‘Buiten Mui’ with surrounding area. 1. mown area; 2. unmanaged area; 3. sod-cut area. A = *Samolo-Littorelletum* with microbial mat; B = *Scirpo-Phragmitetum*; C = *Caricetum ripariae*; D = *Caricetum trinervinigræ* dominated by *Salix repens*. T1, T2, and T3 are the transects.

Littorelletum) and T2 (highly-productive state, *Scirpo-Phragmitetum*) lie in the unmanaged part of the slack, whereas T3 is situated in the sod-cut area. Height of the surface was measured on each plot at the transects using an automatic level.

Vegetation

The vegetation of the 'Buiten Mui' was sampled in the summers of 1996 and 2000 and classified into vegetation types according to Braun-Blanquet (1964). These data were supplemented by older data from this area (Petersen 2000).

Replicate samples ($n = 5$) of 25 cm \times 50 cm were harvested in T1 and T2 to determine above-ground biomass, standing crop, separated in dead and alive. Root biomass ($n = 5$) were taken with soil cores (diameter = 7 cm; depth = 10 cm) after harvesting the litter.

Soil parameters

Calcium (Ca) content and pH (H₂O) were measured in all transects at different depths up to 1 m. Total Ca content was measured after extraction with 1 M HCl by atomic adsorption spectrometry. pH (H₂O) (glass electrode), bulk density, thickness of the organic layer, moisture content, and percentage organic matter (by loss on ignition at 550°C) were determined in the topsoil of all plots. All soil parameters were collected in the spring of 1997.

Oxygen saturation, redox potentials and sulfide (S²⁻) were measured in the soil profile using specific needle electrodes (van Gernerden 1993). The amount of free sulfide was calculated from S²⁻ and pH measurements. Profiles were measured up to 130 mm depth using a micromanipulator for accurate depth positioning. The measurements were carried out using step sizes of 1 mm (0-15 mm), 5 mm (15-100 mm), or 10 mm (100-130 mm). These profile measurements were carried out in May 1998 in the inward and seaward parts of the slack – the central part was inaccessible due to the high water level.

Groundwater parameters

Groundwater tubes were installed in each plot at three different depths to measure the groundwater composition and water level. Water levels were measured on 27-8-1997, 28-8-1997 (after a shower), and 10-10-1997. Soil water samples were taken in October 1997, and analysed for electric conductivity (EC₂₅), and pH (H₂O) directly in the field. The concentrations of bicarbonate and carbon dioxide were measured by pH titration within 24 hr after sampling. Chloride and sulfate were measured by using an auto analyser (Skalar Analytical) directly after sampling. The samples for analyses of the cations: Na, K, Ca, Mg, and Fe were adjusted to pH 2 using 4% HCl and stored in the dark at

4 °C prior analysis. The cations were analysed by using AAS. For each plot saturation indices for Ca were calculated after Stuyfzand (1989).

Data analysis

Detrended correspondence analysis (DCA) was applied to detect successional trends in the *Samolo-Littorelletum* stand. All relevés of this site were analyzed with log transformed species cover-abundance. Vegetation samples of the *Scirpo-Pragmitetum* and *Caricetum ripariae* stands were included to indicate local successional stages.

Results

Vegetation

The DCA of the plots of the three vegetation types, (Fig. 3) shows a clear difference in the species composition. All the *Samolo-Littorelletum* plots lay on the left section of the graph, while the plots in the *Caricetum ripariae* lay at the right side. The vegetation plots where *Phragmites* dominates occurred in between these two on the first axis. This separation on the first axis of the DCA is very stable. The different years of the *Samolo-Littorelletum* vary on the second axes of the DCA.

The highly productive *Scirpo-Phragmitetum* stands had higher values with respect to living and dead standing crop, as well as root and litter biomass, compared to the low-production *Samolo-Littorelletum* stands (Table

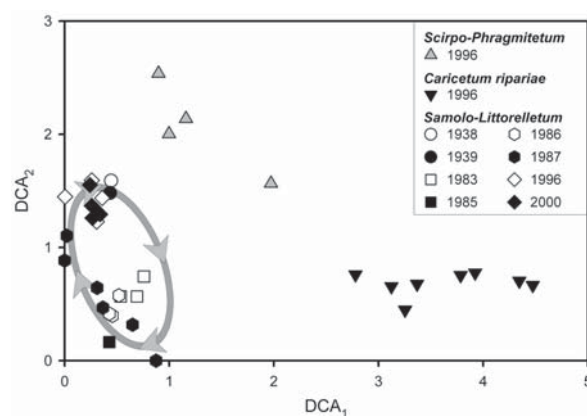


Fig. 3. The first two axes of the DCA showing the position of relevés of the three vegetation types distinguished; \blacktriangle = *Scirpo-Phragmitetum*; \blacktriangledown = *Caricetum ripariae*; all other symbols = *Samolo-Littorelletum* at different times. The *Samolo-Littorelletum* data shows a circular tendency in time. This is an indication that this vegetation state is in equilibrium and therefore stable in time. (Eigenvalues of $DCA_1 = 0.75$ and $DCA_2 = 0.26$) The analysis is carried out with log transformed species cover-abundance.

Table 1. Plant biomass divided into live and dead standing crop, root biomass, and litter biomass. Values are mean and standard error in $g\ m^{-2}$ from 5 samples. Asterisks mark plots that significantly differ from T1-m in a non-parametric *a priori* multiple comparison (Zar 1984), * = $P < 0.05$ ** = $P < 0.01$; $n = 5$.

Plot	Standing crop live ($g\ m^{-2}$)	Standing crop dead ($g\ m^{-2}$)	Root ($g\ m^{-2}$)	Litter ($g\ m^{-2}$)
T1-s	235.4*	403.6**	1186	198
T1-s'	206.5*	53.4*	666	85**
T1-m	92.9	0.0	382	0**
T1-i	316.0**	515.1**	4140**	500
T2-s	253.9*	713.5**	3895**	281**
T2-m	339.9**	85.4*	2195**	322**
T2-i	430.3**	383.9**	4181**	383**
T3-s	147.2	74.4*	439	0**
T3-m	19.2	0.0	174	0
T3-i	39.6	6.1	74	0

Table 2. Soil parameters: pH, organic matter content (OM %) of the top 5 cm of the soil and the thickness of the organic matter layer. Asterisks mark plots that significantly differ from T1-m in a non-parametric *a priori* multiple comparison (Zar 1984), * = $P < 0.05$ ** = $P < 0.01$.

Plot	pH (H_2O) $n = 2$	OM% (mass) $n = 7$	OM layer (cm) $n = 15$
T1-s	7.92	1.9	0.9
T1-s'	7.83	3.1 *	0.7
T1-m	7.93	1.3	0.4
T1-i	7.61 **	23.9 **	8.2 **
T2-s	6.23 **	7.0 **	12.3 **
T2-m	7.55 **	20.2 **	7.3 **
T2-i	7.53 **	24.7 **	10.0 **
T3-s	8.22 **	0.8 *	0.0 **
T3-m	8.03 *	0.8	0.1
T3-i	8.38 **	0.4 **	0.0 **

1). Litter and dead standing crop were not detectable in the *Samolo-Littorelletum* stand.

Soil parameters

The height difference of the two vegetational states within the unmanaged transects at soil surface level were less than 6 cm, the sod-cut area is ca. 15 cm lower due to topsoil removal. We found no differences in ground water level between the different sites. The sod-

cut area, however, is more frequently inundated due to the lower surface level (Fig. 4). The pH of the topsoil ranged from 6.23 to 7.93 in the unmanaged sites and from 8.03 to 8.38 in the sod-cut area (Table 2). Large differences existed between the sites in organic matter content and thickness of the organic layer (Table 2). These two parameters were highest in the site with *Phragmites australis*. The higher organic matter contents were also reflected in lower bulk density values for this site.

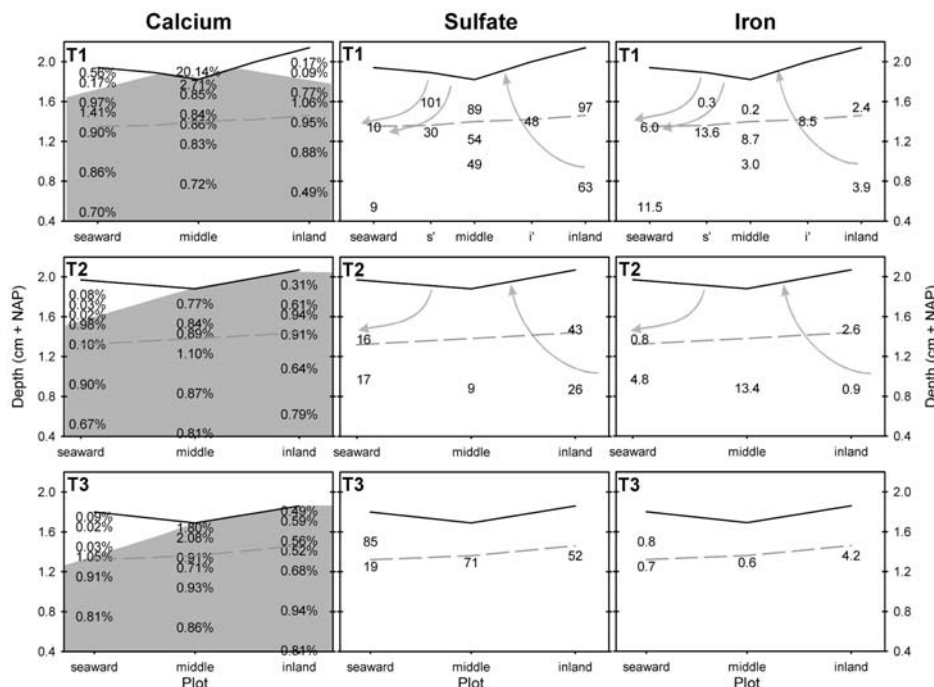


Fig. 4. Soil analyses of the three transects. Solid lines represent the soil surface and dashed lines the water table. The graphs at the left show the calcium content. The grey area marks the $CaCO_3$ containing soil, $CA > 0.3\%$. Numbers refer to the calcium content in percentage of soil dry weight at the measurement locations. The graphs give the content of sulfate (middle) and iron (right) of the groundwater (mg/l). The arrows mark the direction of the groundwater flow.

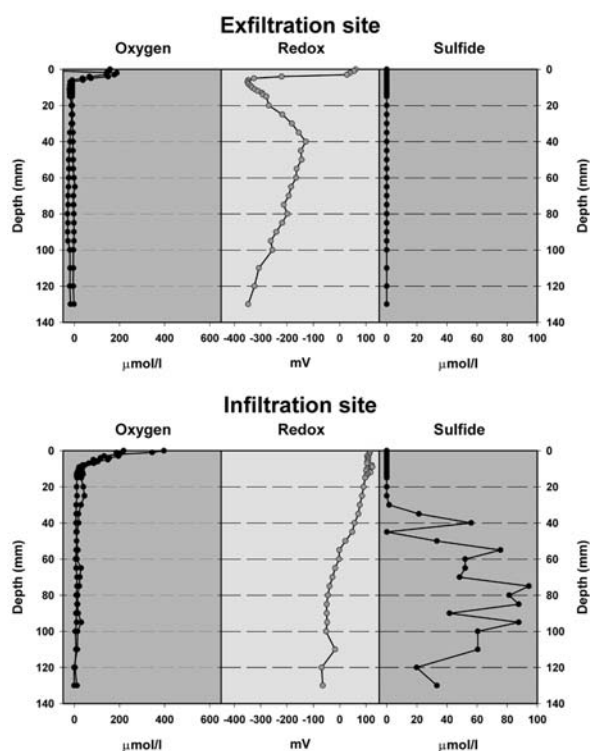


Fig. 5. Oxygen content, redox potential, and sulfide concentrations measured in soil profiles in exfiltration and infiltration sites of the ‘Buiten Muy’. No free sulfide was measured in the exfiltration site despite of the lower redox potential.

Ca concentrations of the soil are markedly lower at the top of the profiles at the seaward side than in the rest of the dune slack. The highest value, more than 20% is found in the middle of T1 at the soil surface (0-2 mm), due to calcium precipitation.

In contrast to the oxygen profile, the profiles of redox potential and sulfide show significant differences between the two sides of the dune slack (Fig. 5). Redox potential was much higher on the seaward side than on the inland side but sulfide is only found at the seaward side.

Table 3. Composition of the surface water in the ‘Buiten Muy’ on 26 May 1997.

		Seaward	Middle	Inward
EC	µS/cm	1035	1036	1245
pH (H ₂ O)		9.9	9.6	7.8
CO ₂	mg/l			9.15
HCO ₃ ⁻	mg/l	64.3	76.1	273.8
CO ₃ ²⁻	mg/l	27.6	19.6	
Cl ⁻	mg/l	230	274	232
SO ₄ ²⁻	mg/l	12.8	13.5	9.7
Na ⁺	mg/l	148	144	125
K ⁺	mg/l	5.1	5.4	9.7
Ca ²⁺	mg/l	27.3	29.5	88.8
Mg ²⁺	mg/l	15.7	15.5	17.6
Fe ²⁺ +Fe ³⁺	mg/l	1.2	0.9	7.1

Groundwater parameters

Irrespective of the low calcium concentrations in the soil at the seaward side Ca saturation indices (SI_c) are all between -0.5 and +0.5, indicating that the groundwater is in equilibrium with Ca.

Depth distribution of sulfate and iron in the groundwater differed between the three transects (Fig. 4). The amount of sulfate in the groundwater was distinctly higher at the inland side in all transects except for one measurement in T3. The pattern for iron was somewhat less distinct, but the highest iron concentrations were also found at the inland side. The lowest concentrations were found nearby the surface at the seaward sides for T2 and T3 but closer to the middle for T1.

The surface water on the inland side of the slack mainly consists of exfiltrated groundwater diluted by some rainwater. The surface water on the inland side of the slack differs from the surface water in the middle and on the seaward side. In particular the concentrations of Ca, iron, and bicarbonate are much higher at the inward side. Chloride and sulfate concentrations in the surface water did not differ (Table 3).

Discussion

Hydrological system

The results from the water analyses indicate that the ‘Buiten Muy’ is a dune slack containing a flow-through dune lake (Stuyfzand 1993; Stuyfzand & Moberts 1987) during a substantial part of the year (Fig. 6). The surface water data in particular conform this idea. Furthermore,

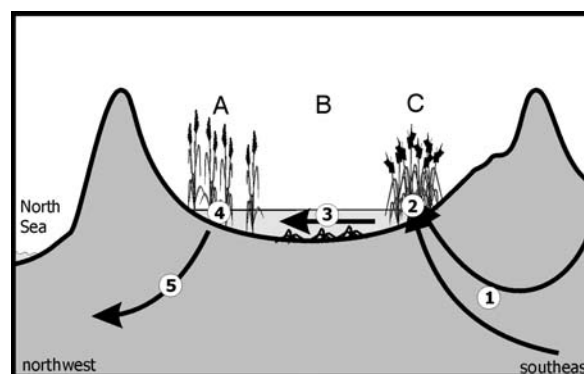


Fig. 6. Schematic presentation of the hydrological system in the ‘Buiten Muy’ A = *Scirpo-Phragmitetum*; B = *Samolo-Littorelletum*; C = *Caricetum ripariae*. 1 = Incoming calcium and iron rich groundwater; 2 = Exfiltration of groundwater; 3 = Precipitation of iron and calcium; 4 = Infiltration of surface water; 5 = Outgoing calcium- and iron-poor infiltration water.

the concentrations of Ca^{2+} , HCO_3^- , and iron ($\text{Fe}^{2+} + \text{Fe}^{3+}$) in the groundwater and surface water were higher at the inland side of the slack, due to the discharge of Fe- and Ca-rich groundwater here. Exfiltrated anoxic groundwater that originates from adjoining infiltration areas contains reduced iron (Fe^{2+}). At the surface, this soluble iron will be oxidized to Fe^{3+} , which precipitates almost immediately at the soil surface, presumably as iron oxides.

The precipitation of Ca is caused by the release of CO_2 from the water at the surface. Algae in microbial mats also consume much CO_2 and therefore contribute to the precipitation of CaCO_3 (Chafetz 1994). The precipitation of iron and calcium carbonate can also be clearly observed in the field.

As a result, when the surface water infiltrates at the seaward side, most of the iron, calcium and bicarbonate has been lost. This can explain why sulfide was present in measurable quantities at the seaward side of the dune slack. At this infiltration side, the soil contains less iron and is completely decalcified. When sulfate reduction occurs at the infiltration side, neither iron nor calcium is available in sufficient amounts to bind the sulfide that is produced.

In summary, we found hydrological and ecological differences between the opposite sides of the slack, which were clearly expressed in the vegetation, with *Scirpo-Phragmitetum* on the seaward side of the *Samolo-Littorelletum* and *Caricetum ripariae* on the inland side. However, the hydrological regime did not differ clearly between pioneer, *Samolo-Littorelletum*, and the late successional stage, *Scirpo-Phragmitetum*, in the middle of the unmanaged parts of the slack. The groundwater analyses do reflect differences in management (between unmanaged and sod-cut areas) but the hydrological system along the three transects is very similar. It is, therefore, likely that at the start, more than 75 yr ago, the two successional stages in the centre of the slack had the same starting conditions.

Alternative stable states

A reconstruction of the past succession could be as follows. After the beach plain became separated from the influence of the sea, most of the vegetation of the slack was in a pioneer stage. In the course of time, parts of the slack started to develop towards a late successional stage dominated by *Phragmites australis* or *Carex riparia*. The difference between the two vegetation types, the pioneer type and the subsequent one, increased with time due to one or more positive-feedback mechanisms. This led to distinctly different stable vegetation states.

The 'Buiten Mui' shows 4 of the 5 possible vegetational results that can occur if a positive-feedback

mechanism is present. 1. The vegetation pattern has been stable for more than 60 yr (Petersen 2000). 2. There is a sharp boundary between the two vegetational states of the slack. 3. The normal succession, in which a late successional phase (dominated by *Phragmites* or *Carex*) will replace the pioneer phase (*Samolo-Littorelletum*) within a few decades, is obviously delayed. 4. There are no intermediate states in which both vegetation types coexist. This clearly indicates that alternative stable states, or at least positive-feedback switches, are operating in the 'Buiten Mui'. There are also indications for the occurrence of alternative stable states from other work on the Frisian Islands of Terschelling (Lammerts et al. 1995; Petersen 2000) and Schiermonnikoog (Sival & Grootjans 1996). In some dune slacks the succession was extremely slow (up to 80 yr), while in other slacks a vegetation shift occurred within 10 yr.

The theoretical consequences of alternative stable states are discussed by Saunders (1980) and Lockwood & Lockwood (1991) in their work on discontinuous phenomena in otherwise continuous systems (catastrophe theory). The theory predicts that small disturbances may induce rapid irreversible changes from a pioneer stage with low nutrient accumulation to a highly productive stage. Catastrophic events, such as prolonged inundation in summer or human drainage activities can trigger this irreversible shift.

A practical consequence is that dune slacks that have entirely shifted towards a more productive state due to a disturbance will not simply return to a stable pioneer stage again when the disturbing agent is removed. Extraction of drinking water and acid rainfall are examples of disturbances that can happen in dune slacks. To restore the desired early-successional vegetation, additional measures are necessary. For instance sod cutting can be applied to make sure that the abiotic conditions are suitable for the pioneer vegetation, which then suffers less from competition with the later species. Nevertheless, first of all the restoration of a stable low-productive dune slack vegetation requires a restored hydrological system.

Positive-feedback mechanisms

Our field observations and earlier research give evidence for three possible positive-feedback mechanisms that can occur in wet dune slacks. A first mechanism could be the adaptation of pioneer species to anoxic and nutrient-poor conditions. Ernst (1991) showed that *Schoenus nigricans* has a very low nutrient demand. The species is very efficient by withdrawing nutrients from the top to the base of the shoots, from where the shoots grow. Several pioneer species show radial oxygen loss (ROL) from the roots (Armstrong 1982; Roelofs

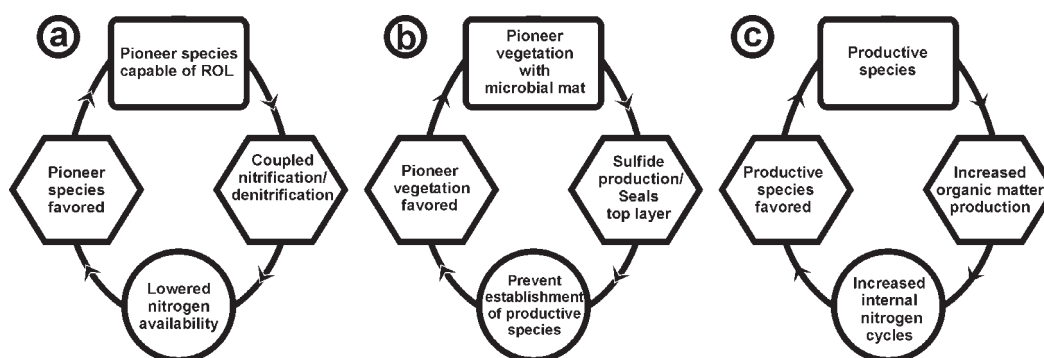


Fig. 7. Three possible feedback mechanisms that can occur in a calcareous wet dune slack: (a) Enhanced nitrogen loss; (b) Sulfide toxicity; and (c) Nutrient accumulation in internal cycle.

et al. 1984) which, in a calcareous environment, facilitates rapid decomposition of organic matter. Under such conditions nitrification may occur on a very local scale (Engelaar et al. 1991; Reddy et al. 1989; Vitousek & Walker 1987). Further away from the roots this can lead to denitrification and thus to nutrient losses from the system (Fig. 7a). If pioneer species are indeed capable of facilitating decomposition of their own litter or otherwise keep the nutrient accumulation at a low level by stimulating nutrient losses from the system, they could efficiently stabilize the pioneer phase.

In the second possible mechanism a microbial mat is involved. Microbial mats often cover the soil surface in open pioneer vegetation. Microbial mats are dominated by a few functional groups of microbes: cyanobacteria, colourless sulfur bacteria, purple sulfur bacteria, and sulfate-reducing bacteria. Their combined metabolic activities result in steep environmental micro-gradients, particularly of oxygen and sulfide (van Gernerden 1993).

Sulfide is toxic for most higher plants and inhibits the growth of most plant species. (Havill et al. 1985; Grootjans et al. 1997; Lamers et al. 1998). Therefore the vegetation remains open. However, some characteristic dune slack pioneer species can protect themselves against the toxic sulfide by releasing oxygen from their root system (Fig. 7b). Free sulfide will be detoxified by colourless sulfur bacteria in the oxic rhizosphere. This results in open stable pioneer vegetation with a microbial mat that cannot be invaded by later species not adapted to anoxic soils containing free sulfide.

A third possible feedback mechanism could be litter accumulation that increases the internal nutrient cycle. Later successional species grow on sites with higher nutrient pools (Olf et al. 1993; Lammerts et al. 1999). Berendse (1993) found that in wet heathlands the species of relatively nutrient-rich habitats had a higher nutrient turnover and produced litter that is more rapidly decomposable than species of poor habitats (Berendse & Elberse 1990). The situation appears to be

different in calcareous dune slacks. Van Beckhoven (1995) did not find significant differences in decomposition rates in litter formed by *Schoenus nigricans*, *Calamagrostis epigejos* and *Molinia caerulea*. Furthermore, litter of the pioneer species *Littorella uniflora* and *Samolus valerandi* decomposes very rapidly. Later successional species are more efficient in retaining nutrients (Ernst et al. 1996). They store nutrients in organic material and retrieve them the next growth season, so the internal nutrient cycle increases (Fig. 7c).

If one of the first two mechanisms coexists with the third mechanism we can explain the sharp boundaries. However, sharp boundaries can also exist if only one of the first two mechanisms occurs. Pioneer vegetation cannot invade the later successional stages because pioneer species suffer from shortage of light under the taller productive species.

Further research will address those possible positive-feedback mechanisms. This research shows that it is most likely that those mechanisms occur but more knowledge about the precise mechanisms is necessary for successful restoration and management of wet dune slack pioneer vegetation.

Acknowledgements. We wish to thank H. van Gernerden and J. van Aniel for their valuable comments on earlier versions of the manuscript.

References

- Armstrong, W. 1982. Waterlogged soils. In: Etherington, J.R. (ed.) *Environment and plant ecology*, pp. 290- 330. Wiley, Chichester, UK.
- Berendse, F. 1993. Ecosystem stability, competition and nutrient cycling. In: Schulze, E.D. & Mooney, H.A. (eds.) *Biodiversity and ecosystem function*, pp. 409- 431. Springer-Verlag, Berlin, DE.
- Berendse, F. & Elberse, W.T. 1990. Competition and nutrient availability in heathland and grassland ecosystems. In: Grace,

- J.B. & Tilman, D. (eds.) *Perspectives on plant competition*, pp. 94-116. Academic Press, New York, NY.
- Braun-Blanquet, J. 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer, Berlin, DE.
- Chafetz, H.S. 1994. Bacterially induced precipitates of calcium carbonate and lithification of microbial mats. In: Krumbain, W.E., Paterson, D.M. & Stal, L.J. (eds.) *Biostabilization of sediments*, pp. 149-164. BIS Verlag, Oldenburg, DE.
- Engelaar, W.M.H.G., Bodelier, P.L.E., Laanbroek, H.J. & Blom, C.W.P.M. 1991. Nitrification in the rhizosphere of a flooding-resistant and a flooding-non-resistant *Rumex* species under drained and waterlogged conditions. *FEMS Microbiol. Ecol.* 86: 33-42.
- Ernst, W.H.O. 1991. Ökophysiologie von Pflanzen in Küstendünen Europas in einem Gradienten von Nordsee zum Mittelmeer. *Ber. Reinhold Tüxen-Ges.* 3: 157-172.
- 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 Soil* 180: 219-230.
- Grootjans, A.P., van der Ende, F.P. & Walsweer, A.F. 1997. The role of microbial mats during primary succession in calcareous dune slacks: an experimental approach. *J. Coastal Conserv.* 3: 95-102.
- Havill, D.C., Ingold, A. & Pearson, J. 1985. Sulphide tolerance in coastal halophytes. *Vegetatio* 62: 279-285.
- Lamers, L.P.M., Tomassen, H.B.M. & Roelofs, J.G.M. 1998. Sulfate-induced eutrophication and phytotoxicity in fresh water wetlands. *Environ. Sci. Technol.* 32: 199-205.
- Lammerts, E.J., Grootjans, A.P., Stuyfzand, P.J. & Sival, F.P. 1995. Endangered dune slack plants; gastronomers in need of mineral water. In: Salman, A.H.P.M., Berends, H. & Bonazountas, M. (eds.) *Coastal management and habitat conservation*, pp. 355-369. EUCC, Leiden, NL.
- Lammerts, E.J., Pegtel, D.M., Grootjans, A.P. & van der Veen, A. 1999. Nutrient limitation and vegetation changes in a coastal dune slack. *J. Veg. Sci.* 10: 111-122.
- Lockwood, J.A. & Lockwood, D.R. 1991. Rangeland grasshopper (Orthoptera: Acrididae) population dynamics: Insights from catastrophe theory. *Environ. Entomol.* 20: 970-980.
- May, R.M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269: 471-477.
- Noy-Meir, I. 1975. Stability of grazing systems: an application of predator prey graphs. *J. Ecol.* 63: 459-481.
- Olf, H., Huisman, J. & van Tooren, B.F. 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *J. Ecol.* 81: 693-706.
- Petersen, J. 2000. *Die Dünenalvegetation der Wattenmeer-Inseln in der südlichen Nordsee. Eine pflanzensoziologische und ökologische Vergleichsuntersuchung unter Berücksichtigung von Nutzung und Naturschutz*. Husum Druck- und Verlagsgesellschaft, Husum, DE.
- Reddy, K.R., Patrick, W.H.J. & Lindau, C.W. 1989. Nitrification-denitrification at the plant root-sediment interface in wetlands. *Limnol. Oceanogr.* 34:1004-1013.
- Rietkerk, M. & van de Koppel, J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* 79: 69-76.
- Roelofs, J.G.M., Schuurkes, J.A.A.R. & Smits, A.J.M. 1984. Impact of acidification and eutrophication and macrophyte communities in soft waters. II. Experimental studies. *Aquat. Bot.* 18: 389-411.
- Saunders, P.T. 1980. *An introduction to catastrophe theory*. Cambridge University Press, Cambridge, UK.
- Schaminee, J.H.J., Weeda, E.J. & Westhoff, V. 1995. *De vegetatie van Nederland 2. Plantengemeenschappen van wateren, moerassen en natte heiden*. Opulus Press, Uppsala, SE.
- Scheffer, M. 1998. *The ecology of shallow lakes*. Chapman & Hall, London, UK.
- Sival, F.P. 1996. Mesotrophic basiphilous communities affected by changes in soil properties in two dune slack chronosequences. *Act. Bot. Neerl.* 45: 95-106.
- Sival, F.P. & Grootjans, A.P. 1996. Dynamics of seasonal bicarbonate supply in a dune slack: Effects on organic matter, nitrogen pool and vegetation succession. *Vegetatio* 126: 39-50.
- Stuyfzand, P.J. 1989. An accurate relatively simple calculation of the saturation index of calcite for fresh to salt water. *J. Hydrol.* 105: 95-107.
- Stuyfzand, P.J. 1993. *Hydrochemistry and hydrology of the coastal dune area of the western Netherlands*. Ph.D. Thesis, Vrije Universiteit, Amsterdam, NL.
- Stuyfzand, P.J. & Moberths, F.M.L. 1987. De bijzondere hydrologie van kwelplassen in duinen met kunstmatige infiltratie. *H₂O* 20: 52-57. (In Dutch, with summary.)
- van Beckhoven, K. 1995. *Rewetting of coastal dune slacks: effects on plant growth and soil processes*. Ph.D. Thesis, Vrije Universiteit, Amsterdam, NL.
- van de Koppel, J., Rietkerk, M. & Weissing, F.J. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol. Evol.* 12: 352-356.
- van der Meijden, R. 1996. *Heukels Flora van Nederland*. Wolters-Noordhoff, Groningen, NL.
- van Gernerden, H. 1993. Microbial mats: A joint venture. *Mar. Geol.* 113: 3-25.
- Vitousek, P.M. & Walker, L.R. 1987. Colonization, succession and resource availability ecosystem-level interactions. In: Gray A.J., Crawley M.J. & Edwards P.J. (eds.) *Colonization, succession and stability*, pp. 207- 223. Blackwell, Oxford, UK.
- Westhoff, V. & van Oosten, M. F. 1991. *De plantengroei van de waddeneilanden*. KNNV, Utrecht, NL.
- Wilson, J.B. & Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. *Adv. Ecol. Res.* 23: 263-337.
- Zar, J.H. 1984. *Biostatistical analyses*. Prentice-Hall, Englewood Cliffs, NJ.

Received 7 June 2001;

Revision received 16 November 2001;

Accepted 30 November 2001.

Coordinating Editor: J.B. Wilson.