

6 Why Young Coastal Dune Slacks Sustain a High Biodiversity

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6.1 Introduction

Dune slacks are depressions within coastal dune areas that are flooded during the rainy season, which in Europe is during winter and spring (Boorman et al. 1997; Grootjans et al. 1998), but in the tropics during the summer (Vázquez, Chap 12). During the dry season the water table may drop far below the surface. Young dune slacks that have been formed in a natural way, by sand blowing or natural dune formation (Piotrowska 1988; Zoladeski 1991), are very poor in nutrients and at the same time very species-rich. Various life and growth forms can be present in such slacks: annuals, biennials, perennials, young shrubs and trees (Crawford and Wishart 1966; Ranwell 1972). Dune slack soils are usually calcareous, since they normally originate from recently deposited sands that contain much shell fragments. Dune slacks with acid soils occur in areas where sand has been deposited at the beach with a low initial lime content. Examples are dune areas in parts of Poland (Piotrowska 1988) and the Dutch, German and Danish Wadden Sea Islands, where initial lime contents are low (less than 2 % CaCO₃; Petersen 2000) and where precipitation dominates over evaporation. This leads to prominent decalcification processes in the top layer and to rapid acidification (Stuyfzand 1993). In dryer areas where evaporation dominates over precipitation, decalcification processes are less evidently expressed in the vegetation. Flooding frequencies during the wet period are decisive for the plant species composition in such dune areas (Zunzunegui et al. 1998; Munoz-Reinoso 2001).

Although many species are now restricted to the coastal area, dune slacks have very few endemic species (Van der Maarel and Van der Maarel-Versluys 1996). Many typical dune slack species can also occur in calcareous fens, fen meadows, and other types of inland wetlands. The restriction of many wetland species to the coastal area is no doubt related to the intensive land use in the mainland areas.

In the following, we will discuss the complex interactions between dune slack vegetation, hydrological conditions, and management in dune slacks in order to conserve or restore these ecosystems for future generations. The examples discussed will be mostly from the NW European dune areas, where dune areas have been affected very negatively by human activities, such as mass recreation, abstraction of drinking water for large cities, increased atmospheric nitrogen deposition from industrial and agricultural areas, and large-scale afforestation (Van Dijk and Grootjans 1993). This destruction of what is seen by many as the last remnants of natural ecosystems led to much societal opposition during the last decades and many restoration projects were initiated to restore dune ecosystems with a high biodiversity (Kooijman, Chap. 15).

6.2 The Dune Slack Environment

Since dune slacks are in fact temporary wetlands, most typical dune slack species have to be adapted to both wet and dry conditions. Consequently, plants that grow in dune slacks may experience severe anoxic conditions, which can be followed by sometimes very dry conditions.

6.2.1 Hydrological System

Dune slacks are not just temporary dune ponds filled with water during the wet season and evaporate water during the dry season. Although such slacks exist they are very rare. Most dune slacks are fed by various water sources. This can be precipitation water, surface water or groundwater. The latter two sources are usually calcareous while the first is acid. The hydrological situation can be more complicated, since the groundwater may come from different hydrological systems (Munoz-Reinoso 2001; Grootjans et al. 2002). In most cases the maintenance of dune slack ecosystems depends on both the amount of precipitation and groundwater discharge. Dune slacks fed by calcareous groundwater are usually situated at the low-lying periphery of the dune system, where most of the groundwater of the main hydrological system discharges. However, seepage slacks can also be found close to the top of the main hydrological system when thick clay or peat layers prevent infiltration to deeper layers and give rise to local groundwater flow towards adjoining dune slacks. Such slacks function as 'flow-through lakes' with groundwater discharge in one part of the slack and infiltration of surface water in another (Stuyfzand 1993). In a dune area with several dune slacks lying close together, slight differences in water level between the slacks may initiate groundwater flow from one slack to another (Kennoyer and Anderson 1989; Grootjans et al.

1996). Under such conditions calcareous groundwater from deeper layers can flow towards the up-gradient parts of the slack. The influx of calcareous groundwater stimulates mineralisation of organic matter and consequently the accumulation of organic matter is lower here than at the infiltration sites (Sival and Grootjans 1996).

6.2.2 Adaptations to Flooding and Low Nutrient Supply

Plant species with well-developed aerenchyma such as *Schoenus nigricans* and *Littorella uniflora* can counteract anoxia by actively leaking oxygen from the roots into the surroundings. This phenomenon is called radial oxygen loss (ROL) (Armstrong 1975). Anoxic conditions, therefore, may prevent the establishment of late-successional species without ROL capabilities. Such species are not adapted to high concentrations of reduced iron, manganese and sulphide that can occur in the rooting zone under anoxic conditions (Studer-Ehrensberger et al. 1993). Sulphide in particular can be very harmful for plant species if it remains in a reduced state (Lamers et al. 1998).

In addition to anoxia, dune slack species have to cope with nutrient-poor conditions (Schat et al. 1984). Many species, such as *Littorella uniflora*, *Centaureum pulchellum*, and *Radiola linoides*, have a very low nutrient demand because they are very small. Others, such as *Schoenus nigricans*, form large and long-lived tussocks. The tussock as such, is not an adaptation to nutrient poor conditions, but this particular species can very efficiently recycle nitrogen and phosphorus from senescent to juvenile shoot tissue (Ernst and Van der Ham 1988). In this way, it can capture nutrients in the tussock, making them unavailable for fast growing grasses and herbaceous species (Van Beckhoven 1995).

6.3 Succession in Dune Slacks

Natural succession in dune slacks starts with a pioneer phase in which small pioneer species establish on an almost bare soil. This wet soil is usually covered with a thin layer of green algae and laminated microbial mats (Van Gernerden 1993; Grootjans et al. 1997), and only a few phanerogamous species are adapted to the very low nutrient availability in this phase. In a later stage, where some organic matter has accumulated, pleurocarpic bryophytes and small dune slack species can establish. In this stage, the accumulation rate of organic matter increases and after 10–15 years tall grasses and shrubs appear, which eventually leads to the decline of pioneer species that require nutrient-poor and base-rich habitats. Red list species, such as *Dactylorhiza incarnata*, *Epipactis palustris* and *Liparis loeselii* represent such basiphilous species,

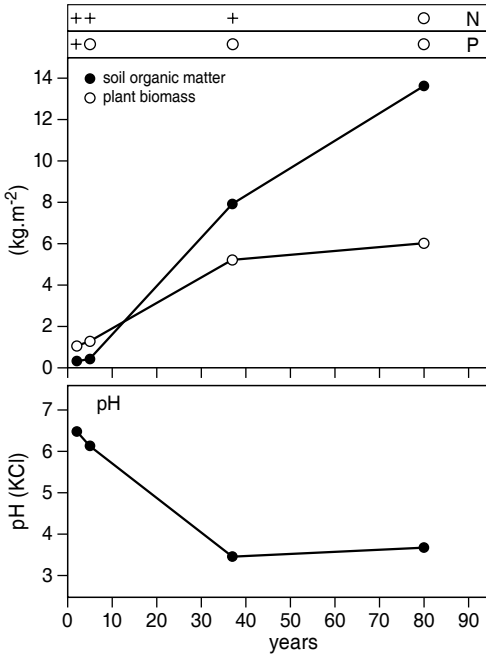


Fig. 6.1. Plant biomass, soil organic matter and soil pH measured in a chronosequence on the Dutch Wadden Sea island of Terschelling, representing various succession stages (2, 5, 37 and 80 years). Responses of the plant biomass to the addition of nitrogen and phosphorus fertilizer (quantity=16 g/m²) are indicated above

which are most abundant in the intermediate phases, where they receive nutrients from soil mycorrhizas (Smith 1966).

The shift from pioneer stage to more mature stages usually takes place between 20–30 years (Van der Maarel et al. 1985). In some dune slacks, however, pioneer stages may last for at least 30–60 years (Petersen 2000; Adema et al. 2002). The rate of vegetation succession in dune slacks is largely controlled by the productivity of the ecosystem, the decomposition of organic matter and the recycling of nutrients within the ecosystem (Koerselman 1992; Olff et al. 1993). To monitor factors governing vegetation succession over a period of more than half a century is almost impossible to carry out. However, sod-cut experiments, in which the organic top layer is removed, are available in some dune slacks where nature managers have tried to restore pioneer stages at various time intervals. Such a spatial representation of supposed successional stages is called a chronosequence. An analysis of vegetation development in such a chronosequence (Berendse et al. 1998) showed that during the first 10 years most of the organic matter was stored in the living plants, particularly in the root system (Fig. 6.1). After about 15 years the amount of soil organic matter increased, while the pH dropped steeply, and a thick (c. 10 cm) organic layer developed. This drop in pH only occurred in dune slack which were poor in CaCO₃, not in calcareous soils with lime contents above 0.3 % CaCO₃ (Ernst et al. 1996).

6.3.1 Nutrient Limitation During Succession

Fertilisation experiments in the same chronosequence showed that the growth of the aboveground biomass was limited by both nitrogen and phosphorus in the youngest (2-year-old) sod-cut experiment (Fig. 6.1; Lammerts et al. 1999). In the 5-year-old stage and in the 37-year old stage only nitrogen was limiting, most likely because many pioneer species have a very low phosphorus demand (Willis 1963; Van Beckhoven 1995). The sedge species *Schoenus nigricans* showed no response at all to either nitrogen or phosphorus additions. This implies that, as long as phosphorus limits the growth of tall grasses, basiphilous pioneer vegetation can persist for quite some time, even when nitrogen availability increases. Buffer mechanisms that keep the soil above pH 6 appear to be crucial for maintaining low phosphorus availability.

Due to increased accumulation of organic material in later successional stages, the N-mineralisation also increases, leading to a higher availability of mineral nitrogen (Berendse et al. 1998). The phosphorus availability is also relatively high in older dune slacks on the Dutch Wadden Sea islands because soils are poor in iron here and the phosphorus is, therefore, only loosely bound to iron-organic compounds (Kooijman and Besse 2002). Tall growing, late successional grass species, such as *Calamagrostis epigejos*, rapidly increase in cover after the nitrogen and phosphorus limitations have been lifted (Ernst et al. 1996).

In the 80-year-old stage the aboveground biomass was no longer limited by nitrogen. The most likely explanation for this lack of response to nutrient addition in this old successional stage is that competition for light has become a dominant factor. Willow (*Salix repens*) and heathland species (*Empetrum nigrum*, *Erica tetralix*) invest in supportive, non-productive tissue and lift their photosynthetically active parts to the top of the vegetation. In this way they can in some stage overgrow the small pioneer species.

Atmospheric input of nitrogen may accelerate the accumulation of organic matter in the topsoil considerably, because the growth of most pioneer and mid-successional species is N-limited and therefore, responsive to additional supply of nitrogen.

6.3.2 Seed Banks and Succession

Seed bank research (Bekker et al. 1999) showed that most pioneer species, such as *Centaureum pulchellum*, and several *Juncus* species had long-term persistent seed banks and that many late successional species, such as *Salix repens*, *Eupatorium cannabinum* and *Calamagrostis epigejos* had transient seed banks (Thompson et al. 1997). The species that had long-term persistent

seed banks were also the species that appeared immediately after sod cutting, even if the original pioneer vegetation had disappeared since several decades. Figure 6.2 clearly shows that the group of dune slack pioneer species as a whole had long-term persistent seed banks with seeds surviving at least 5 years but often for longer periods. The longevity index in Fig. 6.2 (after Bekker et al. 1998) was constructed from records of longevity in the database of Thompson et al. (1997). It indicates the 'average' period of seed survival in the soil. An index of 0–3 means that the seeds are transient; they cannot survive in the soil longer than 1 year. The range 4–7 indicates that seeds can survive for 1–5 years, and from 8–10 seeds survive for more than 5 years. The group of late successional species had short-lived or transient seed banks, while the seed longevity of the group of mid-successional species was intermediate. However, no data are available with respect to most typical dune slack species such as orchid species, which are critically endangered in NW-

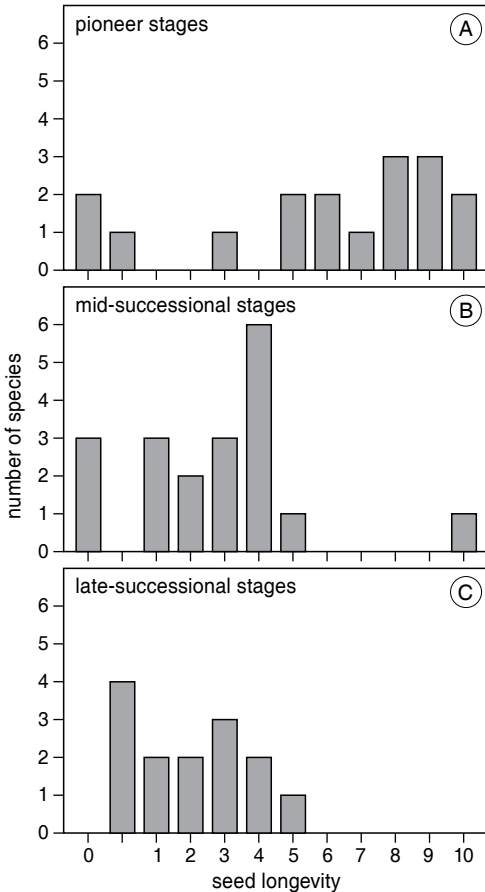
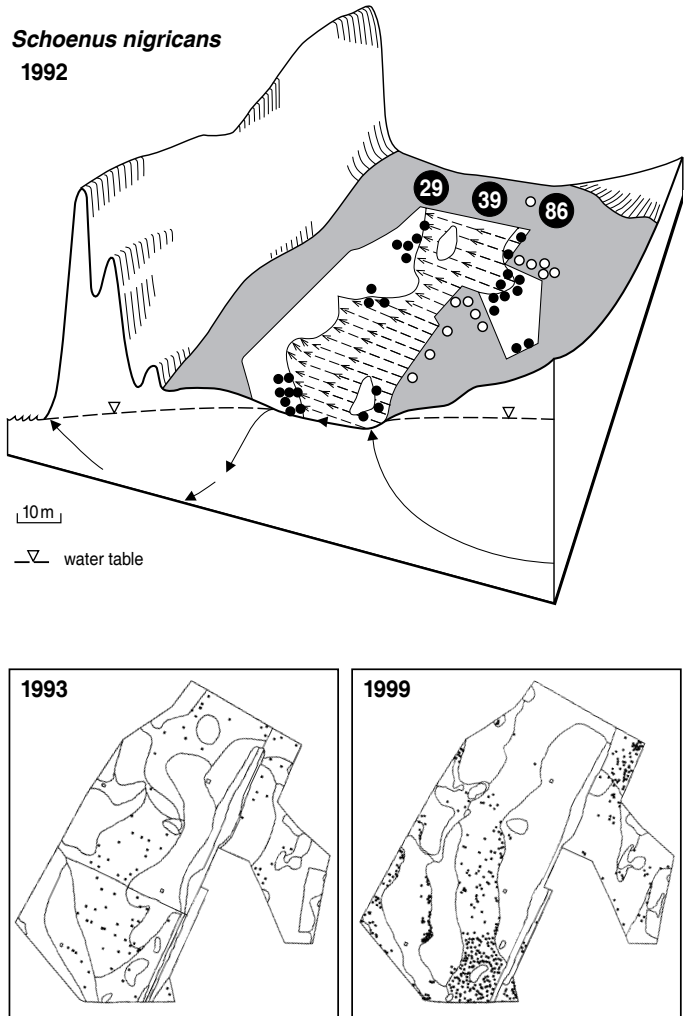


Fig. 6.2. Seed longevity of dune slack species of pioneer stages (A), mid-successional stages (B), and late-successional stages (C)

Europe. This means that we cannot rely on the presence of living seeds in sites where these species were found and have disappeared recently during vegetation succession.

The establishment of a new population of an endangered sedge species (*Schoenus nigricans*) can be illustrated in a recent sod-cut experiment in the dune slack Koegelwiek on the island of Terschelling. This slack is fed by calcareous groundwater that enters at the southern border. The water proceeds as surface water and becomes less calcareous due to dilution by precipitation water. When the surface water infiltrates again at the northern boundary, the water has become very calcium poor. *Schoenus nigricans* did not appear to have a long-term persistent seed bank, but had to establish new populations

Fig. 6.3. Distribution of the pioneer species *Schoenus nigricans* in 1992, 1993 and 1999 in a sod-cut dune slack (Koegelwiek) on the Wadden Sea island of Terschelling. This part of the slack had been sod cut in 1991. Mature plants in 1992 are indicated by open dots, juveniles in 1992 and 1993 by closed dots. Encircled numbers indicate the calcium concentration (mg/l) measured in the surface water in May 1992. The arrows represent water flow (both groundwater and surface water flow)



from scarcely distributed individuals in the close vicinity of the sod-cut area (Fig. 6.3). One of the target species, for instance, *Schoenus nigricans*, established small populations, within 1 year after sod cutting, although no viable seeds were found in the soil, not even in the stage where *Schoenus nigricans* was abundant. So, apparently *Schoenus nigricans* had to establish a new population from the limited number of adult plants surviving in the uncut vegetation which was more than 75 years old (Lammerts et al. 1999). The distribution of young *Schoenus* plants in the slack suggests that the young plants establish themselves either close to the mature plants at the exfiltration side of the slack or were transported by surface water flow to the infiltration part of the slack. One year later, the distribution of juvenile *Schoenus* plants is more or less random in the sod-cut area, except for the very wet and the very dry parts. After 8 years the distribution of *Schoenus* plants has changed considerably. The species is now most abundant in the western part of the slack with slightly less wet conditions. The sites that were favourable for germination in 1991/1992 were evidently not the sites that are favourable for more adult plants.

6.3.3 Stability of Pioneer Stages

The influx of anoxic and iron-rich groundwater is important for vegetation succession in yet another way. Lammerts et al. (1995) showed that pioneer stages were much more stable in groundwater-fed dune slacks compared to slacks that were situated in infiltration areas. They hypothesised that the discharge of groundwater in spring and early summer keeps the soil moist so that laminated microbial- and algal mats do not dry out (Van Gernerden 1993). It was already known that algal mats can stabilise sandy substrates during the very early stages of dune slack formation (Pluis and De Winder 1990). When growth leads to the formation of visible layers these are called microbial mats. Prerequisites for the growth of microbial mats are the availability of water, much light, and the absence of excessive erosion and consumption by animals. Optimal growth conditions occur on bare soils that are regularly flooded or attain sufficient moisture by capillary water supply. Cyanobacteria in microbial mats can fix nitrogen (Stal et al. 1994) and the mats may develop in a relatively short period. They may, therefore, assist in the colonisation by phanerogams.

Photosynthesis is concentrated in the algal layer of the microbial mat. Respiration by heterotrophic bacteria rapidly depletes oxygen that is produced in this top layer. Consequently, oxygen penetration in microbial mats is shallow ranging from less than 2-mm depth in the dark to 5–6 mm during active photosynthesis (Van Gernerden 1993). In the absence of oxygen, alternative electron acceptors, such as sulphate, are used by heterotrophic bacteria, which use organic matter as carbon source. Well-developed mats in sulphate-rich envi-

ronments are therefore characterised by an intense sulphur cycling. Sulphate-reducing bacteria produce sulphide which is partly oxidised again by either phototrophic sulphur bacteria in the presence of light or by colourless sulphur bacteria when sulphide diffuses to the oxic layer. Sulphide concentrations may reach toxic levels for higher plants depending on the amount of available sulphate and the amount of sulphide-fixing iron minerals.

Adema et al. (2002) measured sulphide and oxygen concentrations in a dune slack on the Wadden Sea island Texel in the Netherlands, using micro-electrodes (Fig. 6.4). They found that on the infiltration side of the slack where the topsoil had been decalcified, the sulphide concentrations reached toxic levels (30–90 $\mu\text{mol/l}$) for some higher plants, in particular sedges (Lamers et

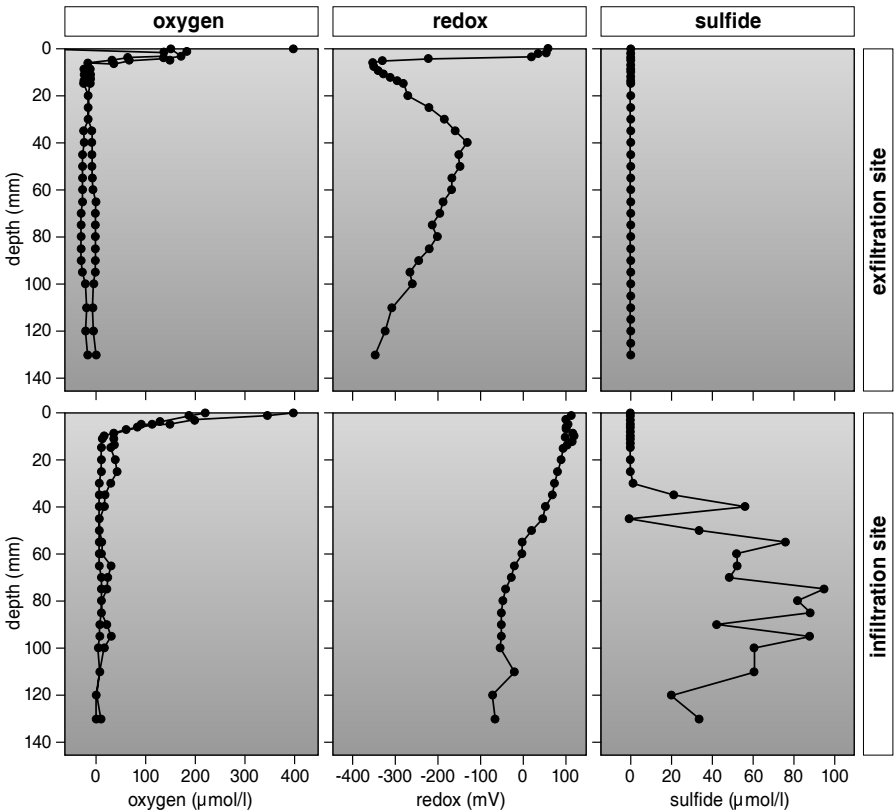


Fig. 6.4. Oxygen content, redox-potential, and sulfide concentrations measured in soil profiles in exfiltration and infiltration sites of ‘De Buiten Muy’ on the island of Texel in The Netherlands (after Adema 2002). No free sulfide was measured in the exfiltration despite lower redox potentials. Apparently, the toxic sulfide is bound by regular supply of iron in the discharging groundwater

al. 1998). Plants that could grow at the infiltration side of the slack were common reed (*Phragmites australis*) and small pioneer species, such as *Samolus valerandi* and *Littorella uniflora*. At the exfiltration side, no sulphide was measured, although the redox potentials were much lower than in the infiltration site, due to continuous inflow of anaerobic and iron-rich groundwater (Fig. 6.5). The authors argued that the iron-rich groundwater fixed the free sulphide produced by the microbial mats by forming FeS. At the infiltration side, however, no iron was present any more and free sulphide could accumulate. These relatively high sulphide concentrations did not harm common reed, nor the pioneer species, since they are capable of oxidising sulphide to sulphate by releasing oxygen from their roots (radial oxygen release). The sulphide production in the infiltration areas can, however, release phosphates in the iron-depleted topsoil due to binding of sulphides with iron (Lamers et al. 1998). The infiltration side of such a slack, therefore, would not be able to maintain a pioneer vegetation for a long time and tall reed vegetation would soon take over.

A stable pioneer vegetation existed for over 60 years between the exfiltration and central parts of the slack because the pH is buffered here; sulphide production is neutralised by iron and acidification is prevented by discharge of calcareous groundwater. Sival et al. (1998) found that in exfiltration sites of dune slacks also secondary, in situ, carbonate deposition occurred in early

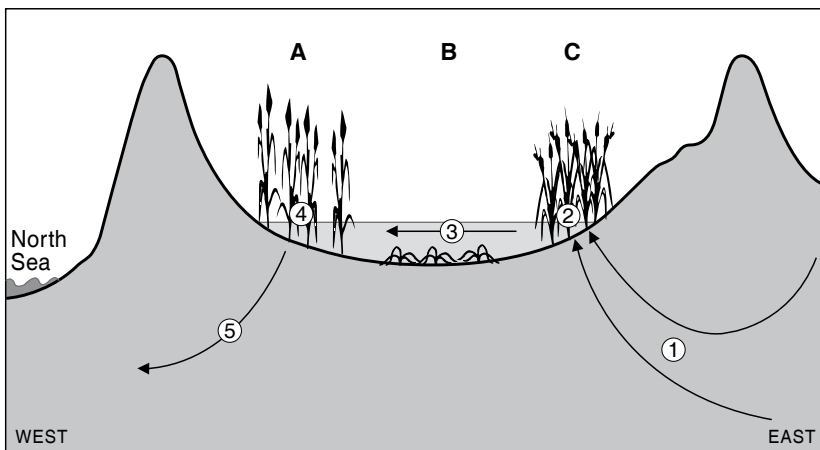


Fig. 6.5. Schematic presentation of a flow-through dune slack on a Dutch Wadden Sea island. In this particular case the vegetation zonation was derived from the dune slack 'De Buiten Muy' on the island of Texel. A Stand of common reed (*Phragmites australis*); B pioneer stage with *Littorella uniflora*; C tall sedges with *Carex riparia*. 1 Incoming calcium and iron-rich groundwater; 2 exfiltration of groundwater; 3 precipitation of iron and calcium; 4 infiltration of iron- and calcium-poor surface water; 5 sulfate reduction during infiltration. (After Adema 2002)

stages of dune slack succession. The carbonate was deposited in a very thin layer on the mineral soil. Loss of CO_2 from the calcareous groundwater resulted in carbonate precipitation at the soil-air interface (Chafetz 1994), thus counteracting soil acidification in a very significant way. Such carbonate precipitation occurs when water tables remain and temperatures are also high. Under such conditions CO_2 escapes from the discharging calcareous groundwater or is taken up by algae, mosses or small water plants. Calcium carbonate is then deposited as a thin silty layer on the soil or even on the leaves of plants. At the exfiltration side of the slack, therefore, the groundwater discharge contributes to maintaining a high pH, low nutrient availabilities, in particular phosphate, and preventing toxic sulphide conditions.

Summarising, the hydrological regime of a dune slack is essential for a good functioning of the dune slack ecosystem. Factors that stabilise the longevity of pioneer stages comprising many Red List species are always associated with a regular supply of groundwater.

6.4 Impact of Human Disturbances on Ecosystem Functioning

The high biodiversity noticed shortly before World War II often marked the beginning of a recovery process after a period of over-exploitation of the dune environment. Sod cutting of slacks occurred frequently but little documentation is available on the reasons why the slacks were sod cut. Fertilisation of gardens, were mentioned, roof material (Beinker 1996), but no real historical evidence has been presented. One reason for sod cutting during World War II appears to be clear: the material was used to cover the fortifications of the German Atlantic Wall. These activities served one purpose very well. Dune slack succession was set back on a large scale and this is one of the reasons why many pioneer and typical dune slack species can still be found along the NW European coast.

Factors that contributed to the dramatic decline of biodiversity in wet dunes during the second half of the 20th century were lowering of the water levels in the adjacent polder areas, reclamation for agricultural use and afforestation with pine plantations. In the Netherlands large-scale disturbances of dune slack environment started around 1853 when the vast stock of fresh dune water became a major source of drinking water production for the large cities. Large dune areas actually became drinking water catchments. The exploitation of dune water resulted in a large-scale lowering of the water table by 2–3 m on average (Bakker and Stuyfzand 1993). At the same time, large parts of the dune area were saved as a landscape in a time of rapid industrialisation and rapid urbanisation in this densely populated area. Munoz-Reinoso (2001) also reported on the negative effects of groundwater abstraction in the

Doñana National Park in Spain. He found that the impact of a groundwater abstraction facility near a large tourist resort, was obscured by large fluctuations in precipitation from year to year. Using aerial photographs he assessed a clear increase of scrubs and trees (notably *Pinus pinea* from surrounding pine plantations) along the shores of dune ponds over a period of 23 years. He suggested that the following mechanism is responsible for this increase in trees: The invasion of trees and large shrubs, under natural conditions, is prevented by the occurrence of exceptionally high floods during the spring, killing most of the tree and shrub species from dryer habitats. This flooding frequency stabilises the open grassy and heath vegetation that is adapted to temporary very wet conditions. The abstraction of groundwater from the main aquifer prevents some discharge of groundwater in the dune ponds, thus preventing the exceptional high flood even in areas situated more than 5 km away (González Bernáldez et al. 1993).

The very negative effects of drinking water extraction in the Dutch dune areas led to the development of new production techniques. To increase the water tables in the dried out dune areas, surface water from the rivers Rhine and Meuse was transported into the dunes and through an extensive network of ponds and canals was infiltrated in the soil. For nature conservation this technique was disastrous. The input of polluted river water led to increased water tables in the dune slacks, but at the same time promoted eutrophication in practically all dune slacks (Van Dijk and Grootjans 1993).

In less-affected dune areas, as the Wadden Sea coast, 70 years of dune fixation, in which every spot of bare soil had to be covered with branches or hay due to legislation, this resulted in an almost complete stop in natural dune formation. This has led to rapid vegetation succession in dry dunes, but also in slacks. For economical reasons grazing by cattle has stopped in most of the European coastal areas. This has led to enhanced grass encroachment (Veer 1997) and the development of woodland. A positive feedback mechanism exists between increased biomass production and decreased groundwater levels. Tall vegetation types, such as shrubs and forests intercept more nutrients from atmospheric deposition than relatively open and short vegetation types, which leads to increased growth and a higher evapotranspiration. The result is an increased drop in water tables during the summer and consequently in a decreased discharge of groundwater in the dune slacks (Stuyfzand 1993). If the supply of groundwater decreases, shrubs and tall grass species invade the site and pioneer communities lose the competition due to increased availability of nutrients. The succession was stimulated even more by increased atmospheric N-deposition during the last 50 years. The total amount of nitrogen which was deposited on the vegetation via precipitation and dust particles increased from ca. 10 kg N ha⁻¹ year⁻¹ in 1930 to ca. 25 kg N ha⁻¹ year⁻¹ in 1980 (Stuyfzand, 1993) and has stabilised between 25 and 35 kg N ha⁻¹ yr⁻¹ in the late 1990s (Ten Harkel and Van der Meulen 1996; Van Wijnen 1999). All these human disturbances during the

last 50 years have led to enormous loss of biodiversity along the European coasts.

At present, the pioneer stages in dune areas are rare in most parts of western Europe. Large blowing dune systems still occur in, for instance, Spain in the Coto Doñana, in Poland in the Wolinski National Park, in France near Bordeaux, on the German Wadden Sea island of Sylt, in Denmark and on the Dutch Wadden Sea island of Texel.

6.5 Restoration of Dune Slacks

During the last decade many restoration projects have been initiated to restore the biodiversity in European dune slacks. The first attempts, some 40–50 years ago, were not very successful. Ponds with rather steep slopes were dug in some convenient site to compensate for lost species-rich dune slacks. The number of target species establishing in such sites was rather low (Fig. 6.6). Better results were obtained by sod cutting in already existing dune slacks where relics of target species were still present in the grass- or shrub-dominated vegetation. Actually, the best results were obtained unintentionally. Very species-rich pioneer slacks developed behind the artificial sand dikes on large sand flats. These dykes were constructed for coastal defence purposes. The reason for these unexpected developments is that this situation resembles the natural dune slack formation by enclosure of sandy beaches by growing dune ridges. The vegetation development starts under near-natural conditions here. Usually, endangered pioneer species can easily colonise such areas since small populations are practically always present in older stages nearby, and dispersal mechanisms (wind, water, animals) appear to be very effective. If a well-developed soil seed bank is present, the pioneer stages are rich in Red List species immediately after the restoration measures.

In dune slacks, where the top soil has not yet been decalcified, mowing or grazing are also suitable restoration measures to restore or maintain species-rich dune slacks. However, when old dune slack soils have been decalcified mowing and grazing will not suffice to conserve the basiphilous dune slack species, because the acidification will proceed and organic material accumulates in the topsoil rapidly. These accumulated nutrient stocks in the soil compartment appear to act as a threshold. First, an endo-organic layer is formed in the top soil, but in decalcified soils also ecto-organic layers are formed on top of the surface. The surface is elevated in this way, preventing a good contact with the calcareous groundwater. Under such conditions basiphilous Red List species are no longer able to establish new populations. The soil seed bank underneath the organic layer may still be rich in Red List species, but when time passes the soil seed bank becomes depleted due to viability loss. When buffer mechanisms (blowing sand or groundwater fluxes) can be

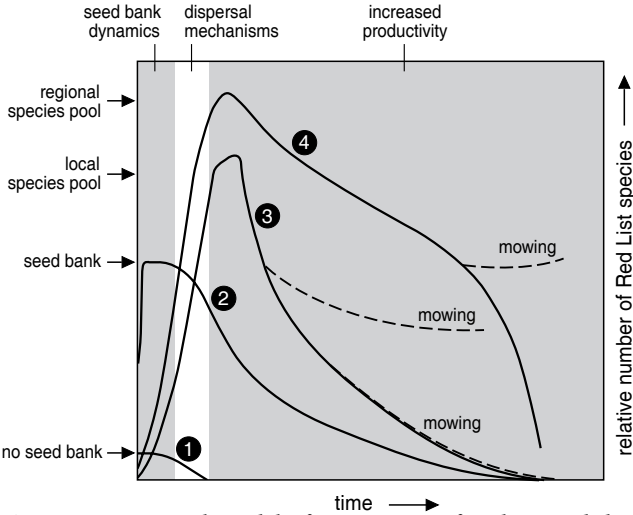


Fig. 6.6. Conceptual model of occurrence of endangered dune slack species (Red List species) after restoration measures have been carried out. 1 Unsuccessful projects where measures were carried out in unsuitable sites and where seed banks are depleted. 2 Temporary success, followed by rapid decrease in target species is encountered in slacks where environmental conditions are unfavourable, but where seed banks were still present. 3 Successful, but short-lived, reconstruction of pioneer vegetation with many Red List species. Dispersal mechanisms are effective, but environmental conditions are sub-optimal. Mowing may sometimes retard a rapid spread of later successional species and a rapid decline in Red List species. 4 Very successful projects where many typical dune slack species establish in large numbers and persist for many decades. Natural processes retard the succession towards late successional stages. A mowing regime may stabilise the pioneer stage even longer. (After Grootjans et al. 2002)

restored in acidified slacks, sod cutting is the best option here, since it removes the organic layer entirely.

Apart from man-made dune slacks there should be room for stimulating dynamic natural processes (action of wind and water) that form and sustain natural dune slacks. In this way endangered species can survive without human interference.

References

- Adema EB (2002) Alternative stable states dune slacks succession. Thesis, University of Groningen
- Adema EB, Grootjans AP, Petersen J, Grijpstra J (2002) Alternative stable states in a wet calcareous dune slack in The Netherlands. *J Veg Sci* 13:107–114
- Armstrong W (1975) Waterlogged soils. In: Etherington JR (ed) *Environment and plant growth*. Wiley, London, pp 181–218
- Bakker TWN, Stuyfzand PJ (1993) Nature conservation and extraction of drinking water in coastal dunes. In: Vos CC, Opdam P (eds) *Landscape ecology of a stressed environment*, Chapman and Hall, New York, pp 224–260
- Beinker O (1996) Zur Vegetationskunde der Dünen im Listland der Insel Sylt. *Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein und Hamburg* 25/26:128–166
- Bekker RM, Bakker JP, Grandin U, Kalamees R, Milberg P, Poschod P, Thompson K, Willems JH (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Funct Ecol* 12:834–842
- Bekker RM, Lammerts EJ, Schutter A, Grootjans AP (1999) Vegetation development in dune slacks: the role of persistent seed banks. *J Veg Sci* 10:45–54
- Berendse F, Lammerts EJ, Olf H (1998) Soil organic matter accumulation and its implication for nitrogen mineralisation and plant species composition during succession in coastal dune slacks. *Plant Ecol* 137:71–78
- Boorman LAG, Londo G, Van der Maarel E (1997) Communities of dune slacks. In: Van der Maarel, E. (ed) *Dry coastal ecosystems, part C. Ecosystems of the world*, Elsevier, Amsterdam, pp 275–293
- Chafetz HS (1994) Bacterially induced precipitates of calcium carbonate and lithification of microbial mats. In: Krumbein WE, Paterson DM, Stal LJ (eds) *Biostabilisation of sediments*. BIS Verlag, Oldenburg, pp 149–163
- Crawford RMM, Wishart D (1966) A multivariate analysis of the development of dune slack vegetation in relation to coastal accretion at Tentsmuir Fife. *J Ecol* 54:729–744
- Ernst WHO, Van der Ham NF (1988) Population structure and rejuvenation potential of *Schoenus nigricans* in coastal wet dune slacks. *Acta Bot Neerl* 37:451–465
- Ernst, WHO, Slings QL, Nelissen HJM (1996) Pedogenesis in coastal wet dune slacks after sod-cutting in relation to revegetation. *Plant Soil* 180:219–230
- González Bernáldez F, Rey Benayas JM, Martínez A (1993) Ecological impact of groundwater extraction on wetlands (Douro Basin Spain). *J Hydrol* 141:219–238
- Grootjans AP, Sival FP, Stuyfzand PJ (1996) Hydro-geochemical analysis of a degraded dune slack. *Vegetatio* 126:27–38
- Grootjans AP, Ernst WHO, Stuyfzand PJ (1998) European dune slacks: strong interactions between vegetation, pedogenesis and hydrology. *Trends Evol Ecol* 13:96–100
- Grootjans AP, Van den Ende FP, Walsweer AF (1997) The role of microbial mats during primary succession in calcareous dune slacks: an experimental approach. *J Coastal Conserv* 3:95–102
- Grootjans AP, Geelen, Jansen AJM, Lammerts EJ (2002) Dune slack restoration in the Netherlands; successes and failures. *Hydrobiologia* 487:181–302
- Kennoyer GJ, Anderson MP (1989) Groundwater's dynamic role in regulating acidity and chemistry in a precipitation lake. *J Hydrol* 109:287–306
- Koerselman W (1992) The nature of nutrient limitation in Dutch dune slacks. In: Carter RWG, Curtis TGF, Sheehy-Skeffington MJ (eds) *Coastal dunes*. Ballgame, pp 189–199
- Kooijman AM, Besse M (2002) On the higher availability of N and P in lime-poor than in lime-rich coastal dunes in the Netherlands. *J Ecol* 90:394–403
- Lamers LPM, Tomassen HBM, Roelofs JGM (1998) Sulphate induced eutrophication and phytotoxicity in freshwater wetlands. *Environ Sci Technol* 32:199–205

- Lammerts EJ, Grootjans AP, Stuyfzand PJ, Sival FP (1995) Endangered dune slack gastromonomers in need of mineral water. In Salman AHPM, Berends H, Bonazountas M (eds) Coastal management and habitat conservation. EUCC, Leiden, pp 355–369
- Lammerts EJ, Pegtel DM, Grootjans AP, Van der Veen A (1999) Nutrient limitation and vegetation change in a coastal dune slack. *J Veg Sci* 10:11–122
- Munoz-Reinoso JC (2001) Vegetation changes and groundwater abstraction in SW Doñana, Spain. *J Hydrol* 242:197–209
- Oloff H, Huisman J, Van Tooren BF (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. Diss Univ Hannover, Husum Verlag (English summary)
- Piotrowska H (1988) The dynamics of the dune vegetation on the Polish Baltic coast. *Vegetatio* 77:169–175
- Pluis JLA, De Winder B (1990) Natural stabilisation. In: Bakker TWM, Jungerius PD, Klijn PA (eds) Dunes of the European coasts. *Catena (Suppl)* 18:195–208
- Ranwell DS (1972) Ecology of salt marshes and sand dunes. Chapman and Hall, New York
- Schat H, Bos AH, Scholten M (1984) The mineral nutrition of some therophytes from oligotrophic dune slack soils. *Acta Oecol Oecol Plant* 5:119–131
- Sival FP, Grootjans AP (1996) Dynamics of seasonal bicarbonate supply in a dune slack: effects on organic matter, nitrogen pool and vegetation succession. *Vegetatio* 126:39–50
- Sival FP, Mûcher HJ, Van Delft SPJ (1998) Carbonate accumulation affected by hydrological conditions and their relevance for dune slack vegetation. *J Coastal Conserv* 4:91–100
- Smith SE (1966) Physiology and ecology of orchid mycorrhizal fungi with reference to seedling nutrition. *New Phytol* 65:488–499
- Stal LJ, Villbrandt M, De Winder B (1994) Nitrogen fixation in microbial mats. In: Krumbein WE, Paterson DM, Stal LJ (eds) Biostabilisation of sediments, BIS Verlag, Oldenburg, pp 384–399
- Studer-Ehrensberger K, Studer C, Crawford RMM (1993) Competition at community boundaries: mechanisms of vegetation structure in a dune slack complex. *Funct Ecol* 7:156–168
- Stuyfzand PJ (1993) Hydrochemistry and hydrology of the coastal dune area of the western Netherlands. PhD Thesis, Free Univ of Amsterdam
- Ten Harkel MJ, Van der Meulen F (1996) Impact of grazing and atmospheric deposition on the vegetation of dry coastal dune grasslands. *J Veg Sci* 7:445–452
- Thompson K, Bakker JP, Bekker RM (1997) Soil seed banks of north west Europe. University Press, Cambridge
- Van Beckhoven K (1995) Rewetting of coastal dune slacks: effects on plant growth and soil processes, PhD Thesis, Free Univ of Amsterdam
- Van Dijk HWJ, Grootjans AP (1993) Wet dune slacks: decline and new opportunities. *Hydrobiologia* 265:281–304
- Van der Maarel E, Van der Maarel-Versluys M (1996). Distribution and conservation status of littoral vascular plant species along the European coasts. *J Coastal Conserv* 2:73–92
- Van der Maarel E, Boot RGA, Van Dorp D, Rijntjes J (1985) Vegetation succession on the dunes near Oostvoorne, The Netherlands: a comparison of the vegetation in 1959 and 1980. *Vegetatio* 58:137–187
- Van Gernerden H (1993) Microbial mats: a joint venture. *Mar Geol* 113:3–25

- Van Wijnen H (1999) Nitrogen dynamics and vegetation succession in salt marshes. PhD Thesis, Univ of Groningen
- Veer MAC (1997) Nitrogen availability in relation to vegetation changes resulting from grass encroachment in Dutch dry dunes. *J Coastal Conserv* 3:41–48
- Willis AJ (1963) Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *J Ecol* 51:353–374
- Zoladeski CA (1991) Vegetation zonation in dune slacks on the Leba Bar, Polish Baltic Sea coast. *J Veg Sci* 2:255–258
- Zunzunegui M, Diaz Barradas M, García Novo F (1998) Vegetation fluctuation in mediterranean dune ponds in relation to rainfall variation and water extraction. *Appl Veg Sci* 1:151–160