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Restoration of Wet Dune Slacks on the Dutch Wadden Sea Islands: Recolonization After Large-Scale Sod Cutting

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Abstract

The effects of sod cutting were studied in a dune area on the Dutch Wadden Sea Island of Texel. Sod cutting was carried out in a range of different dune slacks in order to restore dune slack vegetation with many endangered Red List species. Sod cutting removed approximately 96% of the soil seed bank. Species abundant in the seed bank, notably *Juncacea*, also had a high frequency in the vegetation that established during the first year after the restoration measures. Many other species not registered in the seed bank or in the former vegetation also appeared. Species richness in the monitored plots exceeded that of uncut reference plots after a few years. Colonization rates were higher than extinction rates in most plots, indicating that a stable state has not been reached after 5 years. Differences in species richness between slacks appeared to be related to the occurrence of source areas nearby and availability of dispersal agents, such as flooding and animals.

Key words: colonization, dune slack, hydrology, monitoring, permanent plots, seed bank, sod cutting, succession.

Introduction

Dune slacks are low-lying areas within the coastal dunes where the water table is near the surface with a high seasonal fluctuation. A century ago natural dune-forming processes were predominant on the Dutch Wadden Sea islands, and new dune slacks were regularly formed by enclosure of sandy beach plains by dune ridges, or by blowouts in older dune areas (Holkema 1870). Dune-slack soils can be calcareous or relatively acidic depending on the initial lime content of the dunes and on their hydrological position in the landscape. Young dune slacks are very nutrient-poor but show a large variability with respect to species composition, which reflects the characteristics of the groundwater regime (Grootjans et al. 1998). Due to natural succession, accumulation of organic matter takes place leading to the invasion of tall grasses and shrubs, which replace pioneer species (Jones & Etherington 1989; Olff et al. 1993). The rate of organic matter accumulation, however, appears to be influenced by the hydrological regime in a dune slack. In dune slacks fed by a regular supply of groundwater, the accumulation of organic matter in soil and vegetation can be very slow (Sival & Grootjans 1996), and pioneer stages can persist for many decades. Slacks predominantly fed by rainwater acidify rapidly in decalcified dune areas. The rate of accumulation of organic matter is rapid in such slacks and pioneer stages with many rare and endangered wetland species disappear within 10–15 years (Lammerts et al. 1995; Lammerts & Grootjans 1998). Nowadays the more mature stages (shrub and forest) prevail in dune slacks due to fixation of mobile dunes. Pioneer stages have become very rare (van Dorp et al. 1985; Grootjans et al. 1991). This loss of biodiversity in Dutch dune areas was promoted by fixation of moving dunes, by increased atmospheric deposition (5-fold increase in 50 years; Stuyfzand 1993), by interference with local hydrological systems (van Dijk & Grootjans 1993; Grootjans et al. 1996) and by stopping the traditional grazing regime (Westhoff 1989). These combined processes accelerated succession toward mature stages (van der Maarel et al. 1985). Invasion of non-native species is not the issue here, as it is in many other dune areas in the world (van der Maarel 1997; Pickart et al. 1998).

Conservation practices are needed to stop this decline of basiphilous pioneer communities by initiating restoration projects, usually sod cutting (Ernst et al. 1996; Sival 1996), which start the succession anew. Sod cutting is applied on an ever-increasing scale in Dutch dune areas, but deviates from natural dune slack for-

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mation in several ways. Firstly, the large-scale sod cutting is carried out within a very short time, usually in summer, when water levels are low. Natural formation of dune slacks, however, proceeds gradually. It may take many years before a beach plain is effectively cut off from the influence of the sea by enclosing dune masses or before intensive sand blowing stops when the local water table has been reached. Secondly, sod cutting removes the existing vegetation and may remove populations of endangered plant species.

The monitoring project discussed in this paper was set up to evaluate vegetation development after large-scale sod cutting. We examined whether the rate of species establishment is influenced by the geomorphologic (isolated, non-isolated) and hydrological features (groundwater, surface water influenced) of the slacks. Furthermore, we focused on the conditions favoring the establishment and survival of endangered Red List species.

Study Area

The study area consisted of approximately 250 ha of dunes and dune slacks and located at the southwestern part of the island of Texel (Fig. 1), where a large number of primary and secondary dune slacks are present in the area, locally known as "Moksloot area." This area originated circa 1770 when a long dune ridge enclosed a former beach plain. Around 1850, the largest slacks were rich in basiphilous pioneer and marsh communities (Holkema 1870). Since then the slacks have become drier due to: (1) retreat of the west coast; (2) digging of a ditch (Moksloot) in 1880; (3) drainage in nearby polder areas; and (4) extraction of groundwater in the slacks for drinking water purposes (since 1956). In 1991, a vegetation survey was carried out in order to assess the restoration prospects of the area. This survey showed that eutrophic reed beds with *Phragmites australis* (common reed), *Cladium mariscus* (great fen-sedge) and *Carex disticha* (sedge species) dominated the lower parts of the slacks, while the higher parts were covered by tall grasses such as *Calamagrostis epigejos* or creeping willow shrubs (*Salix repens*). Yearly mowing was applied in some areas to preserve nutrient-poor marsh vegetation and species-rich grasslands.

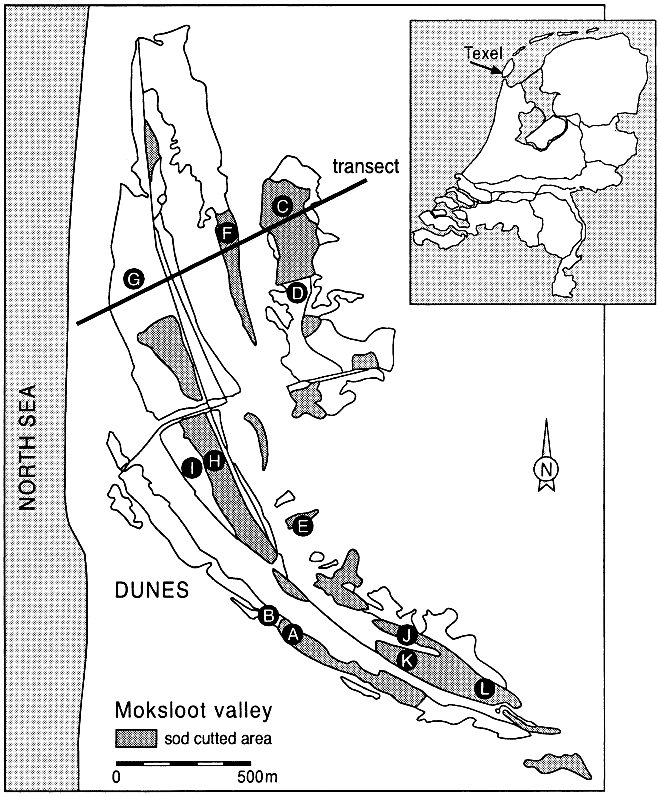

Figure 1. Location of monitoring plots (A–L), sod cut areas (shaded), and position of the transect where hydrological flow patterns were studied in the Moksloot area on the Wadden Sea Island of Texel.

Restoration of species-rich dune slack communities began after the termination of groundwater extraction in 1993. Sod cutting of the slacks began in July 1993 and continued through August 1993 until approximately 35 ha of dune slack vegetation had been removed. Depth of sod cutting varied between 10–40 cm depending on the thickness of the organic layer. During sod cutting, some organic material was spilled in the water in some valleys. This material of fine organic matter later deposited in small depressions. The topsoil material was piled up behind the foredunes and covered with dune sand, which was then planted with *Ammophila arenaria* (marram grass) to prevent sand blowing.

In 1995, a small herd of Highland cattle and Exmoor ponies was introduced to the area to prevent a rapid regrowth of the vegetation in the sod-cut areas. A small sand blown valley (E in Fig. 1) was fenced to prevent intensive trampling by cattle and horses.

Selection of Monitoring Sites

In May 1994, the electrical conductivity standardized to 25°C (EC_{25}) was measured in the surface water of all the slacks, using portable equipment. The electrical conductivity is a measure of the total amount of dissolved ions in the water. Calcium and chloride concentrations were measured in the laboratory. Based on these measurements, a distinction could be made between slacks influenced by calcareous surface water with EC values exceeding 600 μS/cm and slacks not influenced by surface water.

Precipitation of iron hydroxides on the valley margins provided another indication of the hydrological regime of the different slacks. We consider this a strong indication of discharge of calcareous and iron-rich groundwater.

Some slacks were completely sod cut, leaving no mature vegetation as sources of seed nearby, while others were only partly sod cut. In such cases, seed could be easily transported during flooding to the adjacent sod-cut areas.

Furthermore, some sod-cut slacks were markedly influenced by resting birds in spring and summer 1994. This could be judged by visual observation and by the development of green algae mats at these sites.

Grazing intensity also differed between slacks. Some slacks were heavily grazed, while others were not grazed at all. Grazing intensity was not measured directly, but estimated from the presence of dung and from direct field observations. Five slacks, differing in geomorphologic history, hydrology, presence of resting birds and impact of grazing, were selected for the purpose of the present study (Table 1).

Hydrological Modeling

The flow pattern of the groundwater was modeled in a cross-section through a series of parallel primary dune slacks (Fig. 1). The groundwater flow pattern during winter (when the slacks were flooded) and summer conditions was visualized with the computer program FLOWNET (van Elburg & Engelen 1986). This two-dimensional steady-state model generates flow lines and isochrones (lines of equal age) in a vertical plane. The results of the model are based on known permeability values of soil layers and on measured water levels along the boundaries of the model area. Values chosen for permeability (k) of the various layers are as follows: aquifer 1 (sand), $k = 8.3$ m/day; aquitard 1 (clay), $k = 0.002$ m/day; aquitard 2, $k = 0.01$ m/day; aquifer 2, $k = 48$ m/day. At 40–70m meters below the surface an impervious clay layer is present. Water tables used in the model were measured in May 1994.

Groundwater Composition

Groundwater tubes (PVC, 18-mm diameter) were placed near the sites where the soil samples were taken. In a transect of approximately 600 m across various dune slacks, additional piezometers were placed at three depths (20–30, 50–60, 90–100 and occasionally 140–150 cm). The tubes were emptied one day before sampling in order to allow for refilling with fresh groundwater. The samples were taken and stored in polyethylene bottles. All the samples were stored for 8 days at 4°C in a dark room. In the laboratory the samples were separated into two parts. 50 ml was brought to $pH = 2$ by the addition of 2.5 ml 4% HCl. Cation contents (Ca^{2+}, Mg^{2+}, Na^+, K^+, Fe_t) were measured in this subsample, using atomic absorption spectrometry (AAS). CO_2 and HCO_3^- were measured by titration methods. Cl^- and SO_4^{2-} were measured with an auto-analyzer (Skalar). To check the reliability of the analyses, the charge balance was computed as well as the electrical conductivity (EC_{25}). Unreliable analyses (deviation in the charge balance of more than 10% or a difference in computed versus measured EC_{25} of more than 15%) were not used.

Table 1. Characteristics of the five dune slacks, which were selected for more detailed monitoring purposes. Explanation of symbols: – = absent, + = present, ++ = present in large numbers.

	A	*E*	*F*	*H*	*K*
Influenced by calcareous surface water ($EC > 600\mu S/cm$)	–	–	+	+	+
Source area for seeds nearby	++	–	–	++	–
Iron precipitation along valley margin	–	+	+	–	–
Influenced by resting birds	+	–	–	+	++
Grazed by cattle/horses	+	–	+	++	+

Soil Sampling

Twenty-five soil samples were taken in the sod-cut slacks at regular intervals within the 10 × 10 plots in May 1994 and May 1997. The top 5-cm layer was sampled using 100-cm^3 volume rings. The samples were analyzed for pH (H_2O) after the addition of 20 ml of deionized water to 15 g fresh soil. Organic matter content was determined by loss-on-ignition of 10 g at 500°C for 3 hours.

Seed Bank Analysis

The seed bank was sampled in eight sites where the topsoil had been removed and in four sites where the vegetation had remained intact (Fig. 1). In each monitoring plot of 10 × 10 m, 16 subsamples were taken randomly from the topsoil (0–5cm) after which all samples were pooled. The soil cores (diameter 3.6 cm) were taken in spring 1994 when the water table had just dropped below the surface in the monitoring plots. Sampling in spring avoids effects of recent seed rain or lack of stratification. Seed concentration (ter Heerdt et al. 1996) was applied in each sample by washing over a fine sieve (mesh width 0.21 mm). The samples were then spread out in trays on sterile soil in a greenhouse at alternating temperatures (13-hour day temperature 25°C, night temperature 15°C). Seedlings were counted and removed as soon as possible. After eight weeks, only negligible numbers of seedlings were found and counting was stopped.

Vegetation Monitoring

The vegetation development after sod cutting was monitored both on the level of the individual dune slack and on the detailed level of monitoring plots of 10 × 10m. Qualitative monitoring of individual dune slacks was carried out during each summer and led to a species list of phanerogams occurring in each sod-cut slack. Quantitative monitoring included the collection of detailed vegetation data from 5 permanent plots of 100 m^2 situated across the mean high water level. This was done to reduce variation in soil wetness in the monitoring data. Species data were collected in July and August. Species presence and abundance were estimated in subplots of 1 × 1 m. Percent cover was estimated for individual species using a modified Braun-Blanquet cover-abundance scale (Londo 1975). Red List species were derived from Weeda et al. (1990).

Statistical Analyses of Plot Data

Statistical differences between pH and organic matter were tested using a non-parametric multiple comparison test. pH values were log-transformed. A canonical correspondence analysis (CCA) was carried out on species frequencies and corresponding values of water tables, pH and organic matter contents in 1994 and 1997, in order to analyze species responses to changing environmental conditions. The computer program CANOCO (ter Braak 1987) was used for this analysis in which species frequencies were square root transformed. We used the mean water table and the difference between highest and lowest water level during the measuring period (amplitude) as water table characteristics. In the CCA, water table measurements of 1994 were used.

Results

Hydrological Modeling

The simulation showed groundwater flow during the winter along an east–west transect through three parallel dune slacks (Fig. 2). Most of the infiltrating water in the up-gradient areas (slack C) is flowing downward, but several flow lines are directed toward the central slack (slack F). Seepage water enters this slack at the eastern side and infiltrates again at the western side. Then the groundwater proceeds to the exfiltration area (seepage area) of the lowest lying slack (G).

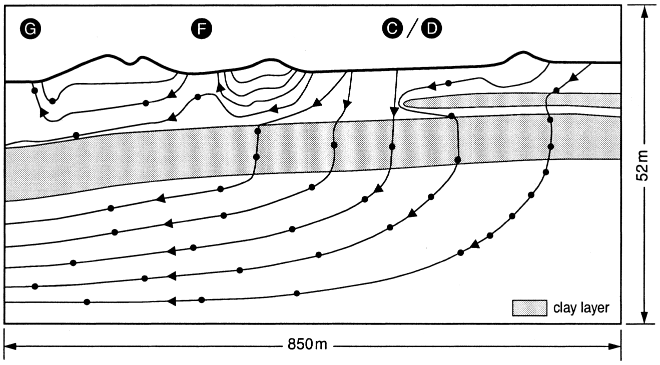

Figure 2. Simulated groundwater flow pattern calculated with the hydrological model FLOWNET, based on measured water tables and estimated values for permeability of the various geological strata. Distances between two solid dots along a flow line represents a period of 6 years.

Groundwater Composition

The macro–ionic composition of the shallow groundwater reflects this simulated flow pattern quite well (Fig. 3). The up-gradient infiltration area (slack C) and neighboring dune area have low values of calcium and chloride at depths between 30 and 60 cm below the surface. Deeper in the profile the filters are situated below the decalcification front, and the calcium values are consequently higher due to dissolution of $CaCO_3$. According to the simulation of water flows, the eastern part of slack F is an exfiltration (seepage) area. The calcium values confirm the idea that calcareous groundwater is present here. Calcium-poor groundwater is

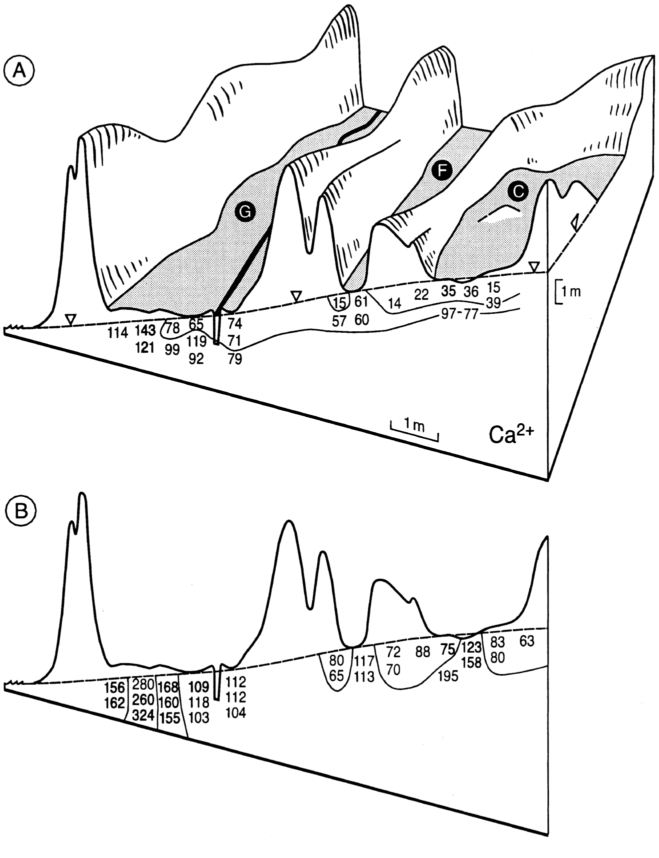

Figure 3. Concentrations of calcium in mg l^{-1} (Fig. 3A) and chloride (mg l^{-1}) (Fig. 3B) in groundwater sampled in a transect across three dune slacks.

present in the top layer of the western part of this slack. This points to infiltration of precipitation water. In slack G, which according to the model is an exfiltration area, the calcium values are high again in the whole profile. Further to the west the groundwater has even higher calcium values, which coincide with high chloride and sulfate values. This points to the presence of brackish groundwater here, which most likely originates from infiltrating brackish surface water from the Moksloot.

Soil Organic Matter and pH

The percentage organic matter was low in 1994 in all slacks and varied between 0.4 and 16.5%. In some slacks (H and K) the standard deviation was higher than the mean (Table 2), pointing to a large heterogeneity within the plots. These differences were the result of deposition of organic matter in depressions directly after sod cutting in 1993. In 1997 the percentage of organic matter was significantly lower than in 1994; in several plots less than half of the original percentage had remained. The lowest values were found in slacks F and K, which had a high pH. Higher values were found in the more acidic plots (A and E) and in plot H, which started with the highest organic matter values in 1994. Compared to 1994, pH values of 1997 were higher in plots A and E. In both years, slacks A and E had significantly lower values than the other slacks.

Table 2. Mean values and standard deviation of organic matter content and pH of the topsoil of the monitoring plots.

	Organic Matter (%)				*pH*			
	1994		*1997*		*1994*		*1997*	
slack	mean	SD	mean	SD	mean	SD	mean	SD
A	2.3	0.8	0.9	0.3	4.9	0.4	5.3	0.5
E	1.9	0.7	1.5	0.4	5.0	0.8	5.3	0.7
F	1.5	0.5	0.8	0.1	6.8	1.1	7.2	0.2
H	3.2	3.9	1.2	0.6	6.6	0.6	6.6	0.5
K	1.4	1.6	0.8	0.6	6.6	0.5	6.7	0.5

Soil Seed Bank

The number of species and the number of seeds encountered in the seed bank in the spring of 1994 were much lower in the plots where the topsoil had been removed than in the plots with intact vegetation (Table 3). In general, the number of species found in the seed bank of the intact vegetation was four times as high as the sod-cut plots, while the number of seeds/m^2 was 25 times higher. The effect of sod cutting was particularly striking in dune slack C in the up-gradient infiltration area (Fig. 1) where no seeds were found. The number of species that emerged later that year was also very low. In the other sod-cut plots, the number of species that established during the summer was not lower than in the plots with intact vegetation. Species that were abundant in the seed bank, notably *Juncacea*, also had a high frequency in the newly established vegetation in 1994. In most sod-cut plots, over 90% of the seeds belonged to either *Juncus articulatus* (jointed rush) or *J. alpino-articulatus*.

Table 3. Number of species and number of seeds present in eight dune slacks in spring 1994. The slacks had been sod cut in the summer of 1993. The seed bank was also analyzed in four plots where the vegetation had remained intact.

Slack	*No. of Species in Vegetation*	*No. of Species in Seed Bank*	*No. of Seeds/ m^2 in Seed Bank*
Sod cut			
A	22	1	298
C	9	0	0
E	18	4	6,266
F	42	3	199
H	40	6	1,690
J	50	6	596
K	28	6	1,789
L	41	8	747
mean	31	4	1,448
Control (not sod cut)			
B	12	8	7,311
D	24	17	43,913
G	39	18	52,023
I	35	23	40,190

Species Richness

Surprisingly, the species richness measured in the monitoring plots one year after sod cutting was approximately the same as in plots with a mature vegetation (Table 3). During the five years of monitoring the species richness showed a steady increase, both on the level of whole slacks and in the smaller monitoring plots. On the level of a whole dune slack (Fig. 4A), the species richness was almost twice as high as the smaller plots. In 1994, the first year after sod cutting, the large slacks (H and K), flooded by surface water, started with a much higher diversity than the smaller (E) or more isolated slacks (A, E and F). This was particularly clear in slack H, in which almost 90% of the species were already present in 1994. On the level of monitored plots, the increase in species richness followed the pattern observed in the whole valleys. The species richness in the sod-cut plots was higher than that of comparable sites with intact vegetation in 1994 (Table 3). Plot F started with a high species richness in 1994 and maintained high values. The species that contributed to the species richness belonged to plant communities ranging from dry dunes to eutrophic marshes (Fig. 4). In some plots even species of brackish sand beaches, such as *Juncus gerardi* (saltmarsh rush),

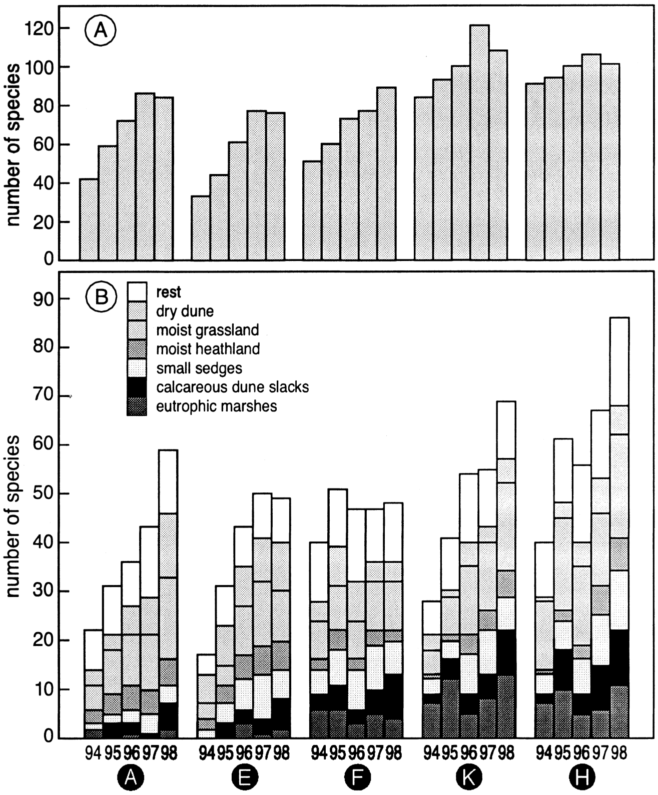

Figure 4. Changes in species richness between 1994 and 1998, measured in large sod cut parts of whole valleys (Fig. 4A) and in smaller monitoring plots of 10 × 10 m (Fig. 4B). Dune slacks A, E and F represent the isolated dune slacks, while K and H represent the non-isolated slacks. In the small monitoring plots the species have been grouped into ecological groups.

Glaux maritima (sea-milkwort), *Chenopodium rubrum* (red goosefoot) and *Carex distans,* were found; these were not present in the study area before sod cutting. Pioneer species of early successional stages were frequent in 1994 and increased in numbers during the monitoring period. The same was true, however, for species of later successional stages and even for species of eutrophic marshes, which established in 1994 on the extremely nutrient-poor sandy soil; many remained even after five years. Typical species of nutrient-poor calcareous dune slacks show a steady, but slow increase. Most of these species are placed on the Red List of endangered plant species in northwestern Europe.

Figure 5 illustrates the dynamic character of species establishment (I = immigration) and decline (E = extinction) of species during the five-year monitoring period. The number of new species in the plots was generally larger than the extirpated species (I−E>0).

Species Frequency

The changes in species frequency differed markedly among species, but between plots, the species show more or less the same pattern during the five-year monitoring period (Figs. 6A & B). Some pioneer species, such as *Juncus articulatus* and *J. ambiguus*, which had a high density in the seed bank directly after sod cutting, appeared with a high frequency in the plots and became abundant within two years. The annual rush species *J. ambiguus* disappeared in most plots within a few years, but the perennial species *J. articulatus* remained in all plots, with a high frequency.

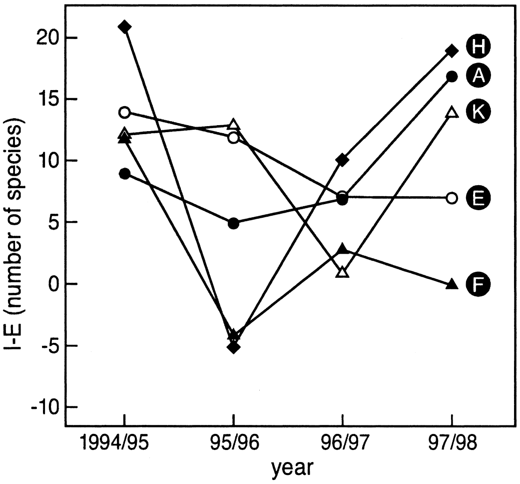

Figure 5. Changes in species establishment (I = immigration) minus species extinction (E) in five monitoring plots during 5 years.

Several species which were not encountered in the seed bank or had a low density did not appear in 1994, but appeared one year later with a low frequency. Their numbers steadily increased afterward in most plots. Examples are pioneer species, such as *Carex oederi* (green sedge) and *Anagallis tenella* (primrose family), but also species of late successional stages, such as *Salix repens, Calamagrostis epigejos* and *Phragmites australis*. *Salix repens* and *C. epigejos* showed the most rapid increase in frequency in all plots. *Carex oederi* and *P. australis* showed a rapid increase in some plots, but declined in other plots after two or three years.

A canonical correspondence analysis (CCA) was applied on species frequencies in 1994 and 1997 and corresponding data of pH, organic matter content, mean water table below the surface and its amplitude. Thirty-three percent of the cumulative variance of the species data was explained by the first two axes, while 64% of the species–environment relationship was explained. The pH and mean water table were clearly correlated, but organic matter content was independent of these factors. Differences between highest and lowest levels explained very little variance of the species composition. This analysis clearly shows that the percentage organic matter decreased between 1994 and 1997 (Fig. 7). Slacks F, H and K were characterized by a set of

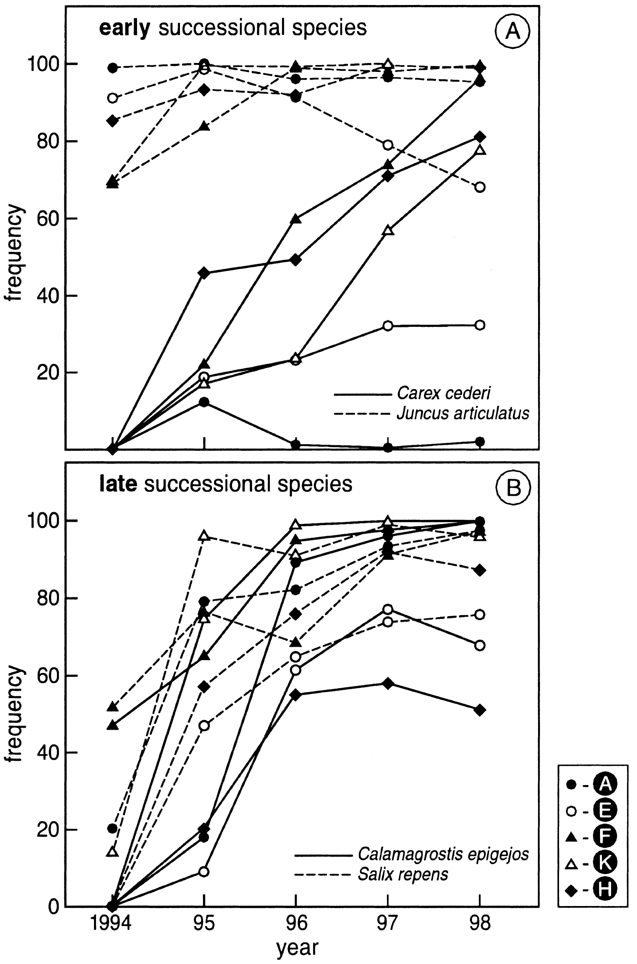

Figure 6. Changes in frequency of two early (Fig. 6A) and two late successional species (Fig. 6B), measured in monitoring plots of 10 × 10 m.

eutrophic marsh species, such as *Polygonum amphibium* (amphibious bistort) and *Ranunculus sceleratus* (celery-leaved buttercup), which had disappeared in 1997. The more acidic slacks A and E were characterized by relatively dry dune species such as *Festuca ovina* and by heathland species such as *Calluna vulgaris* and *Erica tetralix*. In 1997, slacks F, K and H were associated with many endangered dune slack species, such as *Anagallis tenella, Linum catharticum* (fairy flax), *Centaurium pulchellum* (lesser centaury: Gentianaceae) and *Schoenus nigricans* (black bog-rush: Cyperaceae).

Species Cover

Species cover values generally remained very low in the sod-cut areas throughout the monitoring period of five years. Most species present in the monitoring plots still had values of less than 1% in 1998. Only the late successional willow species *Salix repens* had a mean cover exceeding 10% in just two plots (A: 16.7% and K: 17.8%).

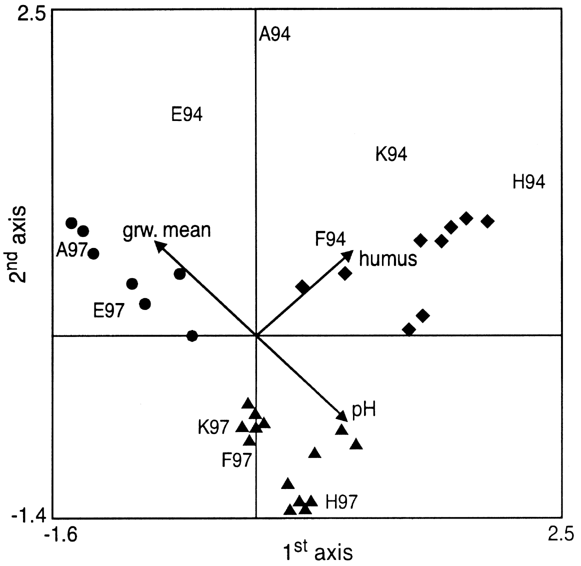

Figure 7. CCA analysis of plant species frequency in 1994 and 1997 in relation to measured environmental variables; pH, % organic matter, mean water table and its amplitude (highest minus lowest water table). Symbols are as follows: ▲ = endangered dune slack species, ● = species of acidic/dry dunes, ◆ = species of eutrophic marshes. Grw.mean = mean groundwater level.

Calamagrostis epigejos, which is also a late successional grass species, had the highest cover in the same plots (A: 1.8% and K: 2.5%). The total cover of all phanerogams steadily increased in most plots, but never exceeded 50%. In 1998 all but one plot had comparable values for total plant cover. Values remained low in plot F (between 10–20% cover) throughout the monitoring period.

Red List Species

The number of Red List species was low in all slacks in 1994 (Fig. 8). Almost no Red List species were recorded in the 10 × 10-m plots. After 3–4 years the number of Red List species increased rapidly in most slacks, and more or less followed the pattern that was revealed by monitoring whole slacks. Only in plot K, which was influenced by resting birds and where grazing intensity was low, did the number of Red List species remain relatively low. At the end of the observation period, the number of Red List species was highest in the larger slacks which were flooded by surface water. In the isolated and smaller slacks the number of Red List species was distinctly lower, except in the groundwater-fed slack F where the number of Red List species increased rapidly.

Discussion

The general objective of this large-scale restoration project was to restore species-rich stages of early dune

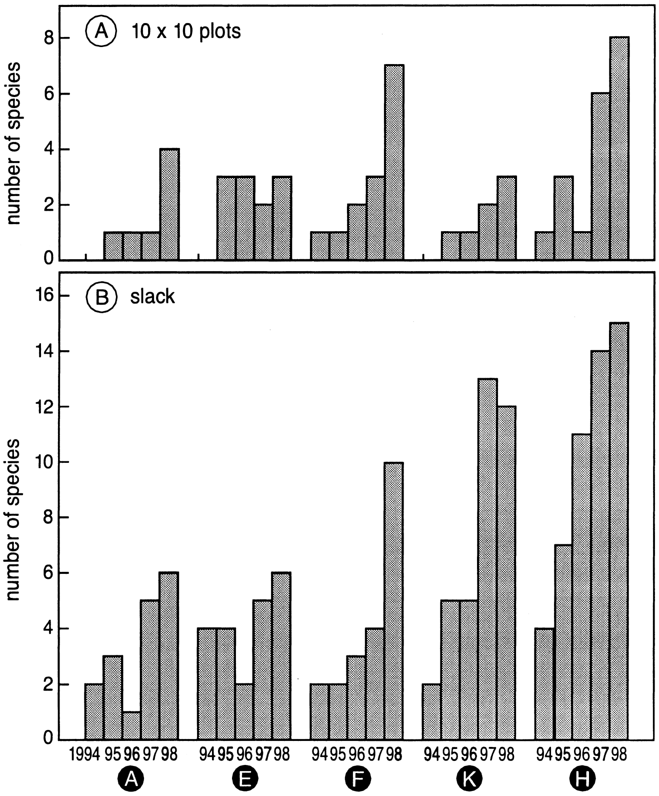

Figure 8. Changes in the number of Red List species, measured in sod cut dune slacks and in small monitoring plots of 10 × 10 m. between 1994 and 1998.

slack succession with special reference to endangered Red List species. A further objective was to create conditions in which the speed of recovery of late successional stages was slow in order to ensure a long lifespan of early successional stages with a high biodiversity. Parikh and Gale (1998) report on the successful creation of a dune slack, in which a rapid vegetation development occurred after spreading out the topsoil saved from destroyed donor wetlands. Cover values for species and total vegetation in these created wetlands were high within three years after construction. Spreading out the shallow topsoil from donor areas with a well-developed seed bank apparently ensures a rapid restoration of a species-rich wetland, but in our case, would encourage a rapid establishment of fast-growing late successional species.

The large-scale topsoil removal applied in the Moksloot area has depleted the seed bank almost completely. From the seed bank analysis we estimate that approximately 96% of all seeds had been removed. The analysis probably underestimated the number of species occurring in low densities, which might still be able to establish new populations. However, we found that species that were abundant in the seed bank, notably *Juncacea*, also had high frequencies in the newly established vegetation in 1994. Many other species not observed in the seed bank also appeared. Species richness in the sod-cut plots exceeded that of undisturbed vegetation types after 2–3 years. The conditions after sod cutting apparently had become suitable for colonization of species from a range of different environmental conditions. This colonization followed a pattern that was remarkably similar in all dune slacks studied, although environmental conditions differ considerably between slacks. Colonization rates were always higher than extinction rates, indicating that a stable state has not been reached after five years (MacArthur & Wilson 1967). This also indicates that the colonization process was not only influenced by the site conditions in the target area, but that dispersal processes between source and recruitment areas were important (Ehrlén & van Groenendael 1998). In our case the differences in species richness appears to be related to the occurrence of source areas nearby and availability of dispersal agents, such as flooding and animals. The most species-rich plot was regularly flooded, situated close to very species-rich mature vegetation and heavily grazed by cattle and geese. The more isolated plots (A and E) started with low species richness in 1994, but in the following years the number of species increased almost linearly. This rapid increase was unexpected in plot E, in particular, since no mature vegetation was left, no surface water could reach the area and grazing by cattle was prevented. Apparently other dispersal vectors, such as wind, birds or rabbits, were active as well. Plot F, which was also quite isolated, started with a high species richness and stayed at this level. It is unlikely that this high species richness originated solely from the seed bank. Most of the emerging species were not even present in the vegetation before sod cutting. About half of the species could have reached the sod-cut area from the surrounding dry dunes with mature vegetation. These dunes harbored many wind-dispersed species, such as *Calamagrostis epigejos, Salix repens* and several *Taraxacum* (daisy) species (Ridley 1930; De Vries 1940). Some species, such as *Rubus caesius* (dewberry) and *Carex arenaria* (sand sedge), originated from root remains in the sod-cut areas themselves. Species which came from the soil seed bank were probably more frequent than the ones actually sampled. Bekker et al. (1999) showed that pioneer species, such as *Juncus articulatus, Samolus valerandi* (brookweed: Primulaceae) and *Carex oederi* had persistent seed banks in dune slacks, and occurred at depths exceeding 10 cm. After sod cutting, these species reoccurred immediately, although some species (*C. disticha, C. flacca* [glaucus sedge], *S. valerandi*) were not found in the vegetation for more than 40 years. The most likely agent for long-distance seed dispersal in plot F appeared to be waterfowl or rabbits (De Vries 1940; Gilham 1974; Müller 1978), of which we found numerous droppings. De Vries (1940) studied dispersal by ducks on the Wadden Sea Island of Vlieland. He studied stomachs of over 279 ducks, in which he found seeds of over 30 salt marsh and dune slack species. Viable seed of 15 species was encountered in excrements of ducks, with *Carex oederi, Empetrum nigrum* (crowberry) and *Eleocharis palustris* (creeping spike-rush) as the most frequent species. Dispersal within the slacks is relatively easy, since all slacks are flooded in winter with slow-moving surface water. Therefore, as long as the seeds are able to float, many species can be dispersed by water (Skoglund 1990; Cappers 1994). In our study area, this was obvious, since we encountered massive establishment of species (*Iris pseudacorus* [yellow iris], *Salix repens, Carex oederi* and many *Juncus* species) along the flood marks of the valleys.

Differences in the total number of species and the number of Red List species among the slacks became more apparent at the end of the monitoring period, where slacks flooded by surface water had the highest species diversity and the highest number of Red List species. Differences between slacks also became evident in the mean cover of individual species and in the mean total cover of the vegetation in the plots. Some late successional species, such as *Calamagrostis epigejos* and *Salix repens,* showed a steady increase in slacks that had been influenced by resting birds or cattle, but were distinctly limited in growth in the more isolated groundwater-fed slacks and in slacks that were intensively grazed. These differences in species responses were not related to differences in soil organic matter. In all slacks, organic matter accumulation remained low. Organic matter content even decreased in most slacks. This was probably due to decomposition of organic material that had been spilled in the water during sod cutting in 1993. Nutrients that had become available were, apparently, stored in the living plants. Unfortunately, we had no means of quantifying differences in biomass, because grazing by cattle, geese and rabbits influenced biomass production in an unknown and varying way. Nevertheless, we conclude that nutrient availability was most restricted in the groundwater-fed dune slack F. Where total vegetation cover remained lowest throughout the monitoring period, late successional species were limited in growth and the number of Red List species was high. This slack, therefore, appears to be most suitable for long-term preservation of endangered basiphilous dune slack plants. It is still unclear why groundwater-fed valleys do not store many nutrients in the soil or in the vegetation, even after several decades (Lammerts et al. 1995; Sival & Grootjans 1996). Whatever the mechanism behind this retarded succession, groundwater-fed slacks provide good opportunities for low-competitive Red List species. Grazing combined with flooding by calcareous surface water can also provide opportunities for the establishment of many Red List species, but such conditions appear to be less stable. As soon as the grazing intensity decreases, later successional species that are already present in high frequencies will soon eliminate the Red List species.

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