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Vegetation dynamics in a wet dune slack I: rare species decline on the Waddenisland of Schiermonnikoog in The Netherlands

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SUMMARY

Vegetation changes in a wet dune slack complex have been studied over a period of 23 years, including some dry (1973–1977) and wet (1983–1987) periods. The vegetation was recorded in 1964, 1977, 1983 and 1987 in permanent quadrats.

Additional information was derived from vegetation maps and distribution maps of rare species. It was observed that several species shifted up and down a height gradient in response to wet and dry periods. The recent surveys show a dramatic decline in the occurrence of calciphilous species, which is thought to be related to a process of accumulation of organic matter in the wet sites and decalcification in the dryer parts of the dune slack. The causes of the rapid vegetation change are discussed and measures to preserve the calciphilous species recommended.

Key-words: Dactylorhiza incarnata, decalciphication, dune slack, *Epipactis palustris, Pedicularis palustris*, permanent plots, *Schoenus nigricans.*

INTRODUCTION

Most marshplants of alkaline habitats in the Netherlands have tended to become restricted to the coastal area of the Dune- or Wadden districts, due to the fact that most of their habitats on the mainland have been destroyed in the course of the last two or three decades, as a result of fertilization, drainage and the extraction of groundwater (Mennema *et al.* 1985). Examples are: *Schoenus nigricans, Dactylorhiza incarnata, Sagina nodosa, Epipactis palustris* and *Parnassia palustris.* The decrease in these species outside the coastal area is roughly two and four times that of the Dune and Wadden districts, respectively (Table 1). Within the Dune district the decrease in the calciphilous species is most pronounced between Egmond and The Hague, because of intense extraction of groundwater and the artificial infiltration of polluted surface water (Van Zadelhoff 1981) and the fixation of coastal dunes (Ernst 1984). The natural formation of young dune slacks, especially on the Frisian islands, the Voorne dune area and Goeree (Van Zadelhoff 1981) is now probably the main force which is preventing these species from becoming extinct in the course of this century.

Table 1. Changes in the occurrence (% decline) of some calciphilous species before and after 1950, as recorded in a grid of 5 × 5 km (Mennema *et al.* 1985). Changes in the Dune- and Wadden districts are compared to those on the mainland

	Percentage decline in:		
Species	Wadden district	Dune district	Mainland
Dactylorhiza incarnata	0	−11	−70
Pedicularis palustris	−17	−53	−58
Liparis loeseli	−20	−71	−61
Parnassia palustris	−33	−46	−74
Anagallis tenella	−38	−71	−83

Since Westhoff's thesis (1947), our knowledge on the vegetation succession in primary (developed from former beach plains) and secondary (wind blown) dune slacks has increased considerably. The establishment of the aforementioned calciphilous marsh-plants starts after sufficient desalinization of former salt plains or, in the case of secondary dune slacks, as soon as the groundwater table has reached the surface. As the valleys grow older, decalcification and accumulation of organic material occurs and acidophilous dune forests, heath or grasslands eventually become the dominant vegetation types (Doing 1983).

Factors that stimulate the acidification and accumulation of organic matter in dune slacks are: (1) lowering of the groundwater table and (2) acid rain. Factors that retard the process are: (1) renewed outblowing of dune valleys, (2) sod cutting, (3) grazing and trampling, which stimulates sand blowing, and (4) mowing. Probably most important of all, is the geomorphological setting of the dune complex (Bakker *et al.* 1981). The process of acidification is most retarded in regularly mown or grazed dune slacks surrounded by young dunes (high lime content) and situated in natural seepage areas which are occasionally flooded by seawater. Unfortunately, most Dutch dune slacks are situated in areas where sand blowing and flooding by the sea is prevented, where grazing has stopped, and where groundwater is extracted (Van Dijk 1984; Van Dorp *et al.* 1985).

Despite the increasingly unfavourable conditions for calciphilous species (Van Zadelhoff 1981; Pruyt 1984; Van Dorp *et al.*, 1985) there is a great lack of quantitative data on, for instance, the process and rate of decalcification (Rozema *et al.*, 1985). Similarly monitoring studies, in which the vegetation has been recorded regularly, are very rare despite numerous ecological studies in the Dutch coastal area. The only studies that give detailed information on vegetation change in dune slacks over a period of 10–30 years are those of Sykora (1978), Van der Laan (1978, 1979), Van Tooren *et al.* (1983) and Slings (1986).

This paper analyses the vegetation changes in a wet dune slack on the island of Schiermonnikoog over a period of 23 years. Special interest is given to the influence of prolonged wet and dry periods on the vegetation of a wet/dry gradient. Succession and fluctuation are discussed in relation to natural and anthropogeneous influences.

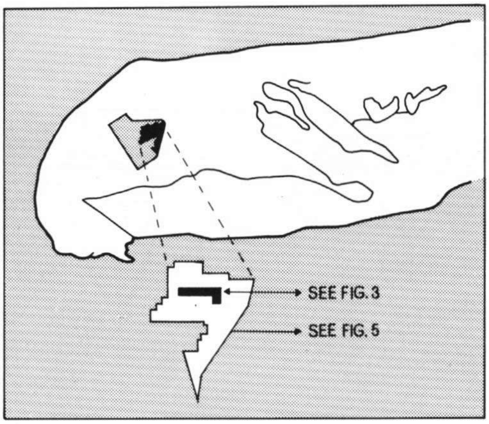

Fig. 1. Location of the study area on the Waddenisland of Schiermonnikoog.

MATERIALS AND METHODS

Description of the study area

The dune slack complex "Kapenglop" is situated in the central part of the island of Schiermonnikoog and is enclosed by three dune ridges of greatly differing ages (150–400 years; Isbary 1936). The Kapenglop was originally a sandy salt plain, which was later influenced by freshwater due to enclosing of the dune masses. Wind blowing in the northern "Kooiduinen" has had a major effect on the adjacent part of the "Kapenglop" (De Graaf 1978), and probably for a very long time prevented the topsoil from being leached. Considering the pattern of many small dunes and slacks, windblowing probably also occurred in the Kapenglop area itself. This could have been promoted by grazing, which was practised until 1955 (De Graaf 1978). The present study deals with vegetation changes in exclusively the eastern part of the Kapenglop (Fig. 1).

Vegetation recording

The distribution of species in the eastern part of the Kapenglop was registered for the first time by H. Frijlink (unpublished) in 1964 in a 10 × 10 m grid, which covered about half the dune slack complex (see Engelmoer & Hendriksma 1979). Permanent plots (2 × 2 m or 3 × 3 m) were laid out in certain areas that represented the variation in vegetation types of the Kapenglop area. Relevés were made according to the Braun-Blanquet approach (Braun-Blanquet 1928, Londo 1975). In order to compare the relevés of different years, rescaling was applied according to Engelmoer & Hendriksma (1979).

Vegetation maps were made in a transect of 20 × 120 m which included most of the permanent plots. In 1977 and 1987 some species were mapped again in the 10 × 10 m grid. Vegetation maps were made in 1964 and 1985. The permanent plots were recorded in 1964, 1977, 1983 and 1987.

Weather conditions

The precipitation surplus (precipitation minus evaporation) over the period 1954–1987 (Koninklijk Nederlands Meteorologisch Instituut. *Maandelijkse overzichten van het veer in Nederland.* 84 e'jaargang, de Bilt) was calculated for each vegetation period from March to August (Fig. 2). The picture that emerges from these data is that the period 1960–1964 was normal (deviation of the mean of 1954–1987: −5 mm). The 5-year period preceeding

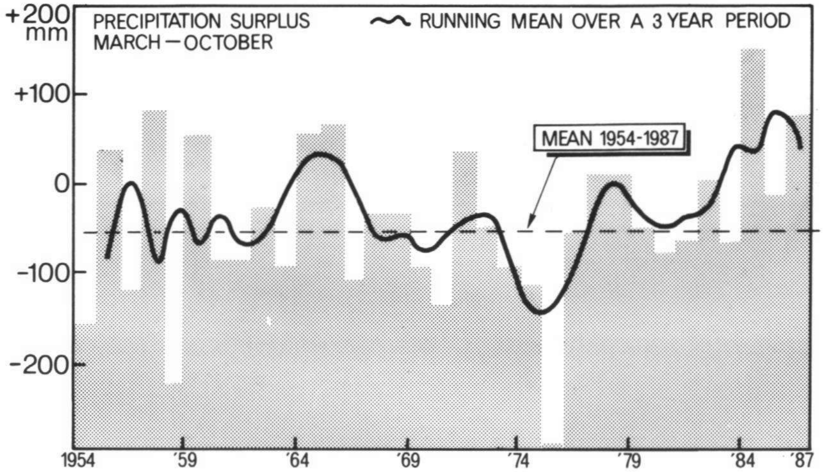

Fig. 2. Precipitation surplus of the period 1954–1987 according to data of the weather station Schiermonnikoog (KNMI 1987).

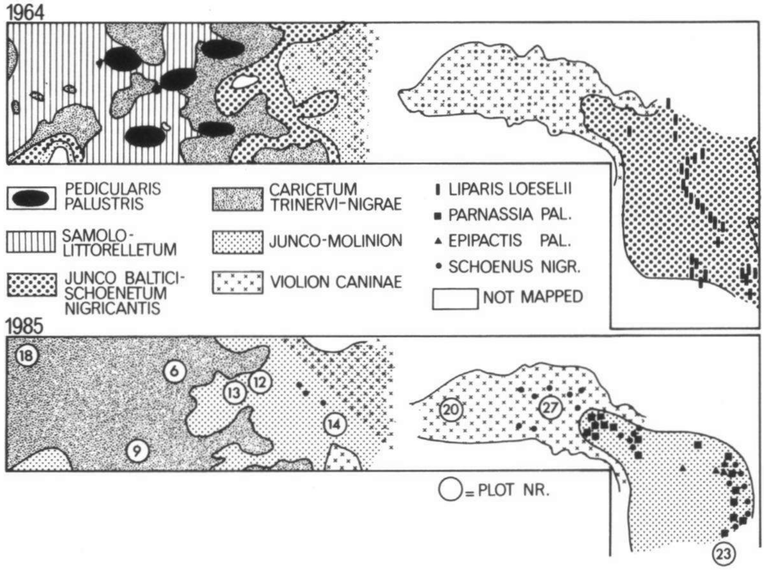

Fig. 3. Results of repeated vegetation mapping in a transect across a height gradient in the central part of the study area (see also Fig. 1).

1977 was very dry (deviation of the mean: −70 mm). This was particularly true for the last 3 years (1975, 1976 and 1977; deviation of the mean: −109 mm). The 5-year period preceeding 1987 was very wet (deviation of the mean: +81 mm). Again the last 3 years were extreme (deviation of the mean: +121 mm).

RESULTS

Vegetation change along a height gradient (1964–1985)

A comparison of vegetation maps from 1964 and 1985 (Fig. 3) of a representative gradient in the Kapenglop area, that had been mown regularly since 1977, shows a rapid decrease

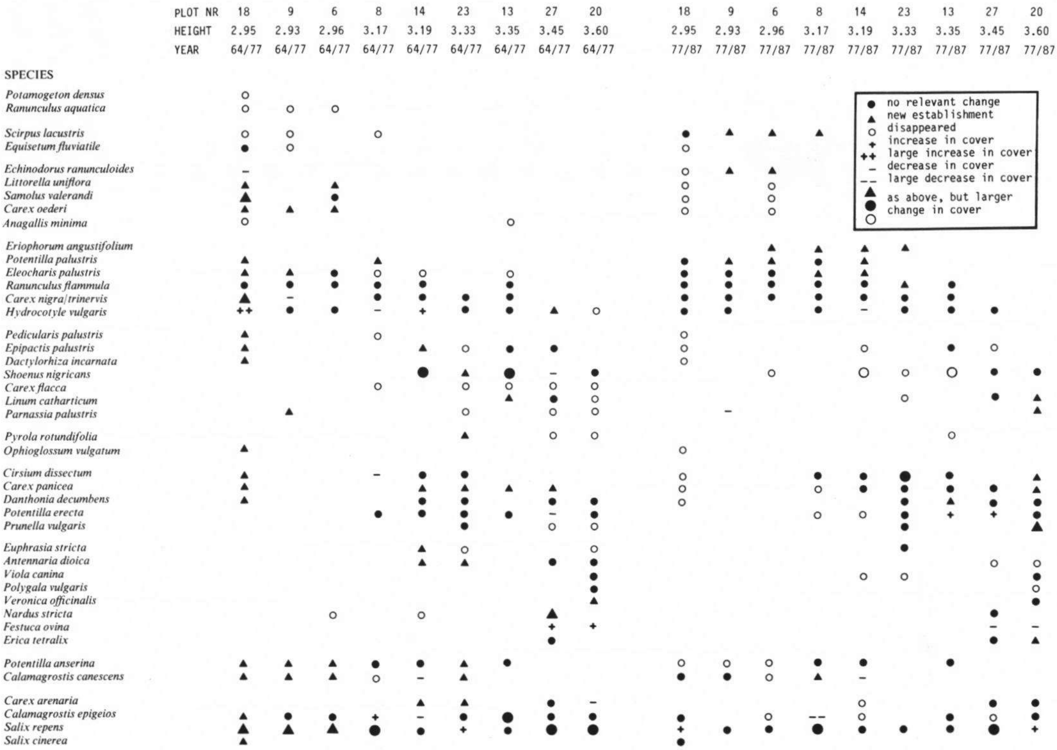

Fig. 4. Changes in the vegetation of nine permanent plots situated in a height gradient in the Kapenglop dune slack complex. The species response is indicated for two periods; 1964–1977 (relatively dry) and 1978–1987 (relatively wet). For exact location of the permanent plots see Fig. 3. Increase and decrease in cover is indicated when the changes surpassed two scale units.

in the pioneer vegetation (Samolo–Littorelletum) within a period of less than 20 years. This seems to be associated with the decline of the large populations of *Pedicularis palustris*.

The increase in the vegetation type belonging to the Caricetum trinervi–nigrae is accompanied by an increase in *Salix repens* and *Calamagrostis canescens*.

The vegetation dominated by (flowering) *Schoenus nigricans* in 1964 disappeared between 1977 and 1985. In 1985 just a few individuals were again found on the higher parts of the gradient. This was particularly clear in the valley further to the east, where a well developed Junco baltici-Schoenetum nigricantis stand with *Liparis loeselli* changed into a poorly developed Junco–Molinion vegetation with some affinity to the Caricetum trinervi–nigrae, while individuals of *Schoenus nigricans*, *Epipactis palustris* and *Parnassia palustris* were only found, in small numbers, along the valley flank.

In the highest part of this transect a more acidophilous variant of the Violion caninae developed between 1964 and 1985, although some calciphilous species, such as *Schoenus nigricans* and *Parnassia palustris*, still remained. They even increased slightly in numbers between 1985 and 1987.

Detailed vegetational changes between 1965 and 1987 in this particular gradient are illustrated in Fig. 4, showing the response of the vegetation to wet and dry periods monitored in nine permanent plots (see also Fig. 3).

Fig. 5. Distribution of *Pedicularis palustris, Epipactis palustris, Dactylorhiza incarnata* and *Antennaria dioica* in 1964, 1977 and 1987 in a 10 × 10 m grid. The height classes are based on the lowest sites within each grid.

In the period between 1964 and 1977, species of dune ponds, such as *Ranunculus aquatilis* and *Potamogeton densus*, disappeared and were never found again in this particular gradient. In 1977 a large number of species had colonized the bare sand (plot 18), but they disappeared again between 1977 and 1987. Only *Salix repens, Calamagrostis* spp. and species of the Caricion curto–nigrae maintained a high cover here. Species can be observed shifting up and down the slope as a response to several very wet and dry periods. Examples are *Eleocharis palustris, Schoenus nigricans*, and *Parnassia palustris. Pedicularis palustris, Linum catharticum* and *Pyrola rotundifolia* were lost after the rise of the water-table in the wet period 1983–1987, while *Schoenus and Parnassia* only remained in small numbers in the highest plot (20). Furthermore, acidophilous species, such as *Potentilla palustris, Eriophorum angustifolium, Carex panicea, Nardus stricta* and *Erica tetralix* showed a steady increase in various parts of the gradient.

Distribution of some rare species

The changes in the distribution patterns of several rare species in the eastern part of the Kapenglop area are illustrated in Fig. 5, which shows the results of the repeated mapping of four species in a 10 × 10 m grid.

The decline of *Pedicularis palustris, Epipactis palustris* and *Dactylorhiza incarnata* is particularly striking. In 1977 these dune slack species had disappeared in 68, 29 and 7% of the squares respectively, but in 1987 these had increased to 97, 95 and 97% respectively.

A dramatic decline was also observed in the dryer part of the study area where *Antennaria dioica* disappeared in 75% of the squares between 1964 and 1977. No quantitative data are available for 1987, but the species has become very rare by now.

Ophioglossum vulgatum, which was practically absent in 1964, appeared in approximately 30 new localities in 1977, but was not found again in 1987. *Pyrola rotundifolia* also showed a temporary increase in 1977. Some orchid species were counted individually in 1964: *Liparis loeselii* (100–200), *Gymnadenia conopsea* (2), Herminium monorchis (45), *Listera ovata* (1) and *Epipactis helleborine* (1). None of them were found again in 1977.

Pedicularis palustris disappeared in most of the central part of the valley as a result of the development of a very dense vegetation of *Phragmites australis, Calamagrostis canescens* and *Salix repens.* In the mown northern part, however, the decline was even more pronounced, since *Pedicularis* was most abundant here in 1964. The (remaining) individuals in the western part of the dune slack showed a stronger preference to the low lying areas in 1977 compared to 1964. In 1964, 79% of the *Pedicularis* sites were found in squares which had their lowest spot below 3·05 m + NAP (Dutch Ordnance Level), while in 1977 this figure was 94%.

Dactylorhiza incarnata, Ophioglossum vulgatum and, to a lesser extent, also *Pyrola rotundifolia* showed a similar "shift" to lower areas between 1964 and 1977.

New establishments of *Epipactis palustris* in 1977 and 1987 occurred almost exclusively along the slopes of the sand dunes bordering the main valley. The decline of the species was most pronounced in the low centre of the large dune slack and in the small slacks at the periphery of the study area.

DISCUSSION

Influence of wet and dry years

Many species established themselves in the lower quadrats and disappeared in the higher ones after a dry period (1964–1977). After a period with high water levels (1983–1987) some species were able to expand to higher areas (*Eleocharis palustris* and *Carex panicea*), but the calciphilous species either disappeared almost completely or were found high up in the valley boundaries (Fig. 6). With regard to the observed up and downward shifting of perennial species in the height gradient, we must make the restriction that certain species probably did not necessarily establish or disappear, but showed marked differences in phenology. Many perennials have dormant meristematic tissues, by means of which harsh periods can be survived (Schat 1982). *Schoenus nigricans,* for instance, can easily be overlooked when no flowering occurs. The up and downward shifting of such perennials can, therefore, be regarded as an indication of vitality under the prevailing conditions, rather than renewed establishment or ultimate perishing of the species. We have only limited information on year to year fluctuations, but the available information (A. P. Grootjans, unpublished) indicates that species showing considerable annual fluctuations in numbers are almost exclusively short-lived species, such as *Linum catharticum, Euphrasia stricta* and *Parnassia palustris.* The populations of perennial species appear to be much more indifferent towards short-term environmental fluctuations (Van Tooren

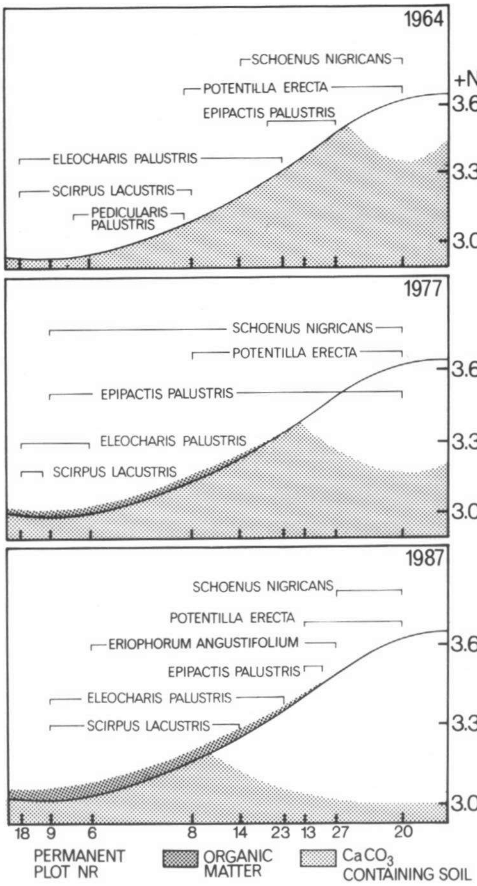

Fig. 6. Occurrence of plant species on a height gradient from dune slack to dune in three different years on the Waddenisland of Schiermonnikoog.

et al. (1983) but they may show the phenomenon of "shuttling" along a height gradient over a longer period.

The disappearance of the Samolo–Littorelletum in this part of the Kapenglop points to accumulation of organic material in the lowest parts and this might also have occurred in the sites previously occupied by *Schoenus nigricans*. These sites were only slightly flooded and accumulated organic matter may have kept large quantities of rain water to the surface, preventing a rapid enrichment with $Ca(HCO_3)_2$ in the rooting zone (Jasnowski *et al.* 1972). The occurrence of such a process would account for the distribution of calciphilous species, such as *Schoenus nigricans* and *Epipactis palustris* in Violion caninae sites on mineral soil. It was also observed, however, that *Antennaria dioica, Euphrasia stricta* and *Carex flacca* disappeared from these sites, while *Erica tetralix* expanded, indicating increased decalcification here. With respect to *Schoenus nigricans*, we are therefore dealing with a non-optimal, "compromise" habitat (Barkman 1972) here, where it might be able to maintain itself as long as the decalcification is restricted to the upper layers. *Schoenus* is a relatively deep-rooting species on mineral soils (De Vries 1961), which is very long lived and can persist for long periods of lowering the water level (Van der Ham 1985).

The process of decalcification in the higher parts and humification in the lower parts was expressed most clearly in the vegetation some 12–20 years after the original survey in 1964.

Vegetation change and decalcification rates

From the literature we gathered information on the rate of vegetation change in Dutch dune slacks (Table 3). We found that stands belonging to the Samolo–Littorelletum can change into a Caricetum trinervi–nigrae within 25 years (Van Dorp *et al.* 1985). In our case it took about half that time. The disappearance of a Junco baltici–Schoenetum nigricantis may take 12–30 years, and is dependent on the initial lime content of the location. On the island of Schiermonnikoog, with relatively low lime contents, the decline of this community took 13–20 years, which is faster than in the Dune-District, but comparable to Terschelling. It is very interesting, however, that between 1952 and 1964 no relevant changes had occurred in both the Samolo–Littorelletum and the Junco baltici–Schoenetum (compare Westhoff 1954). The total life span of these communities in the Kapenglop area, therefore, will be approximately 25–32 years, which is comparable to the data presented by De Vries (1961) for a Junco baltici–Schoenetum nigricantis stand (28–30 years).

The lime content of the Kapenglop area is somewhere between 0·6 and 0·1% (Leertouwer 1967). A sharp decrease in soil pH can be expected to occur between 0·5 and 0·1% $CaCO_3$ (Rozema *et al.* 1985). The data presented in this paper, in fact, allow the conclusion to be drawn that the pH(H_2O) is practically always lower than 6 in the layer of 10–30 cm when the $CaCO_3$ content is lower than 0·3%. Unpublished results from Schiermonnikoog (Leertouwer 1967) show the same pattern; pH(KCl) values are always lower than 5·5 at $CaCO_3$ values lower than 0·3%. Boerboom (1963) also pinpoints this "bend" at 0·3% $CaCO_3$. It can be calculated from the data of Rozema *et al.* (1985) that a drop in lime content from 0·3 to 0·2% will occur in the 10–20 cm soil layer after about 50 years.

These figures may illustrate that, although the process of decalcification is itself very slow (Stuyfzand 1984), rapid changes in the vegetation can be expected within 50 years, if the lime content has dropped below 0·3%. Further research on lime contents in the profile, might shed some more light on the actual decalcification rates in our study area.

Natural succession?

The question remains whether the relatively rapid changes in the calciphilous vegetation types are part of a natural succession or whether other factors enhance this process. The natural succession in wet dune slacks on the Frisian islands has been modelled in Fig. 7, showing the vegetation change in a height gradient at different stages of the dune slack development. This diagram is mainly based on the work of Westhoff (1947, 1971) on the islands of Terschelling, Vlieland and Texel. The changes observed in our permanent plot match those observed by Westhoff rather well, except that the Junco baltici–Schoenetum nigricantis on Schiermonnikoog changes into the Junco–Molinion instead of the Ophioglosso–Calamagrostietum epigeji. Furthermore, well developed stands of the Empetro-Ericetum, which are common on Vlieland and Terschelling, for instance, are not present in our study area.

The Violion caninae is the most acidophilous vegetation type here and has shifted towards a variant with *Erica tetralix*.

Despite the similarities with the succession series presented by Westhoff (1971), we cannot conclude that the observed vegetation changes in the Kapenglop are completely

Table 2. Changes in species composition of three permanent plots in a height gradient (see Fig. 4)

Species	Plot	18	18	18	18	23	23	23	23	20	20	20	20
	Height	2·95	2·95	2·95	2·95	3·33	3·33	3·33	3·33	3·60	3·60	3·60	3·60
	Year	1964	1977	1983	1987	1964	1977	1983	1987	1964	1977	1983	1987
Littorellion													
Echinodorus ranunculoides		2	p1										
Littorella uniflora			m2										
Samolus valerandi			m2										
Carex oederi			p1			+							
Anagallis minima		+				+							
Pragmiton													
Alisma plantago aquatica		1		a1	r1								
Equisetum fluviatile		+	a1	p1									
Scirpus lacustris		1	a1	m1	a1								
Lycopus europaeus			p1			+	r1	r1					
Caricion curto-nigrae													
Potentilla palustris			p1	m1	a2								
Eleocharis plaustris			m1	m4	m1	1		m1					
Ranunculus flammula		+	a1	m2		1	a1	m1	r1				
Mentha aquatica		+	p1	m1		2	m1	a1	a1				
Galium paulstre			m1	p1	a1	+	a1	m1	p1				
Carex nigra/trinervis			m1	m2	m2	2	a1	1	1+			p1	
Hydrocotyle vulgaris		+	2	m2	m1	2	m2	1	1	+			
Caricion davallianae													
Epipactis palustris			a1				a1	r1	p1	r			
Shoenus nigricans						2	2			1	a2	a1	p1
Carex flacca						1				+			
Linum catharticum							p1			+			p1
Parnassia palustris										1			a1
Junco-molinion													
Cirsium dissectum			r1			2	a2	p1	p1				p1
Carex panicea			p1				m2	m1	1			m1	m2
Danthonia decumbens			p1					a1	m2	1	m2	m2	m2
Potentilla erecta						+	a1	a1	m2	1	m2	m4	m4
Prunella vulgaris						+				1		m2	m2
Violion caninae													
Euphrasia stricta							m1			1		p1	
Antennaria dioica										1	a2		
Veronica officinalis										1	p1		
Polygala vulgaris										+	p1		
Viola canina							r1			1	p1	m2	a1
Nardus stricta													
Festuca ovina										1	2	2	1
Erica tetralix												m2	a1
Betula pubescens							r1			+	r1	p1	p1
Remaining species													
Salix cinerea			r1	p1	p2								
Agrostis stolonifera		r	1	m1		+		a1					
Potentilla anserina			a1			+	p1	m1	a1				
Calamagrostis canescens			m2	2	4	+			m1				
Vicia cracca			p1					r1	p1			p1	
Holcus lanatus			p1			+				1	p1	m2	m1
Agrostis capillaris							a4		m1		r1	p1	m1
Carex arenaria						+	p1			1	a1	m1	m1
Anthoxanthum odoratum										1	a1	m1	
Lotus corniculatus										+		a1	
Hieracium pilosella										1	p1	p1	
Luzula campestris										1	r1	a1	
Juncus alpinoarticulatus			p1	m1	m1	2		m1	m1	+		a1	a1
Calamagrotis epigeios			m2	1		2	1	1	0	1	p1	p1	a1
Salix repens			2	1	3	1	1	2	1+	2	1	2	3

Additional species: *Glaux maritima:* p1 (6/1977); *Centaurium vulgare:* + (20/1964); *Eriophorum angustifolium:* r (6/1987); *Pedicularis palustris:* r (18/1977); *Dactyorhiza incarnata:* p1 (18/1977); *Pyrola roundifolia:* 1 (20/1964); *Ophioglossum vulgatum:* p1 (18/1977); *Juncus articulatus:* p1 (6/1987), r (20/1983); *Cardamine pratensis:* p1 (18/1977); *Trifolium pratense:* + (20/1964); *Trifolium dubium:* + (20/1964); *Leontodon nudicaulis:* 1 (20/1964); *Poa pratensis:* 1 (20/1964); *Hypochaeris radicata:* + (20/1964).

Table 3. Degeneration time (years) of two plant communities in relation to the initial lime content of the dune complexes

Community	Author(s)	Locality	Duration (years)	Initial lime content (%)	Shift to
Samolo-Littorelletum	Van der Laan (1979)	Voorne dunes	8	5–15	Samolo–Littorelletum with dominant moss layer (*Campylium polygamum*)
Samolo–Littorelletum	Van Dorp *et al.* (1985)	Voorne dunes	25	5–15	Caricetum trinervinigrae/*Salix* spp.
Junco baltici–Schoenetum nigricantis with *Pedicularis palustris*	Westhoff (1947)	Terschelling	12	<1	Ophioglosso–Calamagrostietum epigeios
Junco baltici–Schoenetum nigricantis	De Vries (1961)	Vlieland	28–30	1–5	Idem with *Erica tetralix*
Junco baltici–Schoenetum nigricantis (typ.)	Pruyt (1984)	North-Holland	22	3–5	
Junco baltici–Schoenetum nigricantis with *Molinia caerulea*	Slings (1986)	North-Holland	30	3–5	*Molinia caerulea* community
Junco baltici–Schoenetum nigricantis with *Pedicularis palustris*	Grootjans *et al.* (1988)	Schiermonnikoog	25–32	1·1–1·3	Caricetum trinervinigrae/ Junco–Molinion

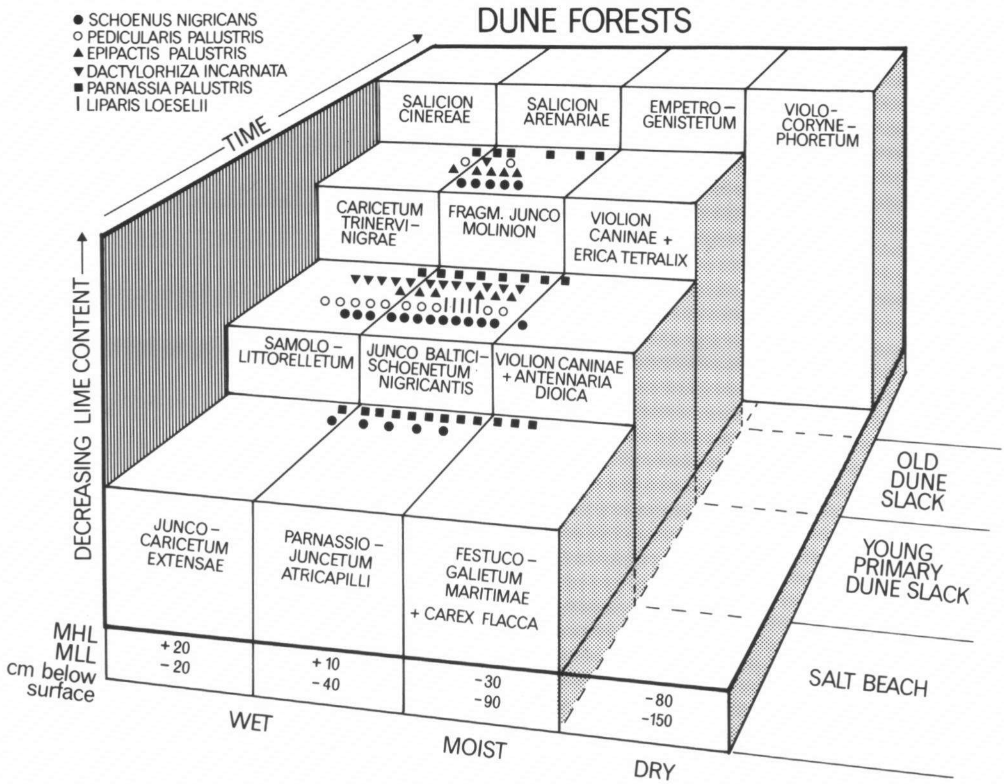

Fig. 7. Succession scheme for primary dune slacks on the Frisian islands, based on Westhoff (1947), Westhoff (1971), and the results of the present study. The distribution of some calciphilous species over the vegetation types is based on Westhoff (1947). MHL = mean highest level, MLL = mean lowest level.

natural. A possible influence of groundwater extraction from a nearby well field, for instance, cannot be excluded, but probably does not exceed 10–20 cm (Bakker 1981). The main reason for the decline of the rare species in this particular dune area is probably that renewed outblowing of dune slacks has stopped. Before 1940, cattle grazed in this dune complex and even ornamental flowers were grown here. Such activities must have stimulated sandblowing. Now fixation of the dunes is the dominant process. Sandblowing is permitted, however, in the northern part of the dune complex and many species that have been lost in the Kapenglop survive in the newly formed secundary dune slacks.

Officials of the nature management on Schiermonnikoog have attempted to retard the process of acidification and accumulation of organic matter by applying a mowing regime in certain parts of the dune slack. These attempts failed, however, to preserve most of the pioneer and calciphilous vegetation types. Well developed stands of the Samolo–Littorelletum only survived in the western part of the Kapenglop where sod cutting had been applied until the early sixties. The factors that stimulate the acidification and accumulation of organic matter were apparently stronger in the eastern part.

In order to prevent a further decline of the rare calciphilous species, sod cutting in the wet and moist parts, which are still influenced by calcium-rich groundwater, is recommended.

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