Population structure and rejuvenation potential of *Schoenus nigricans* in coastal wet dune slacks

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SUMMARY

Populations of *Schoenus nigricans* L. in (formerly) wet dune slacks of the Wadden Island of Schiermonnikoog and the coastal dunes in North-Holland were analysed. The diameter of tussocks, as an indicator of plant age, was normally distributed only in areas with a periodic disturbance (Wadden Island), but strongly skewed in areas with strong soil fixation (coastal dunes). Rejuvenation was only observed after perturbation.

Damage of fruits by the larvae of the microlepidopteran *Glyphipteryx schoenicolella* was low in brackish and high in freshwater sites. Defoliation by rabbits was strongest in dry sites.

Nuts of *S. nigricans* germinated after a dormancy period of several months, under field conditions in April and May. Seedling growth was very slow, with two leaves after 3 months. The survival of seedlings was low during the first year (12%) and followed a Deevy Type III curve. First flowering was observed in experimental populations after 3 years.

The decrease and local extinction of the *S. nigricans* population is discussed in relation to dune management and to the facilitation model of Connell & Slatyer (1977).

Key-words: defoliation, germination, *Glyphipteryx schoenicolella*, herbivory, *Schoenus nigricans*, wet dune slacks.

INTRODUCTION

A decrease and local extinction of a plant population in number and/or area are often correlated with the impact of man on the abiotic environment (Blab *et al.* 1984, Mennema *et al.* 1985). Natural processes, however, may be underestimated in judging a decrease in population (Miles 1987), such as lack of population renewal by seedlings due to vegetation succession. To understand the factors that govern the numerical changes, especially the decrease in plant populations, is of direct concern to vegetation managers (Ernst 1985).

Schoenus nigricans L. is a plant species with a decreasing population and local extinction in The Netherlands. It is typical of wet dune slacks (Sparling 1968, Thalen 1971, Ketner 1971, Schat 1982), acid and alkaline peats (Newbould & Gorham 1956, Newbould 1960, Ranwell 1960, Boatman 1962, 1972, Sparling 1967a,b, Tyler 1979, 1981) and calcareous wetlands (Zobrist 1935, Poore 1956). From 1950 to 1985, *S. nigricans* lost at least

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Abbreviations: NHD: North-Holland Dune Reserve, RGR: Relative growth rate, ROL: Radial oxygen loss.
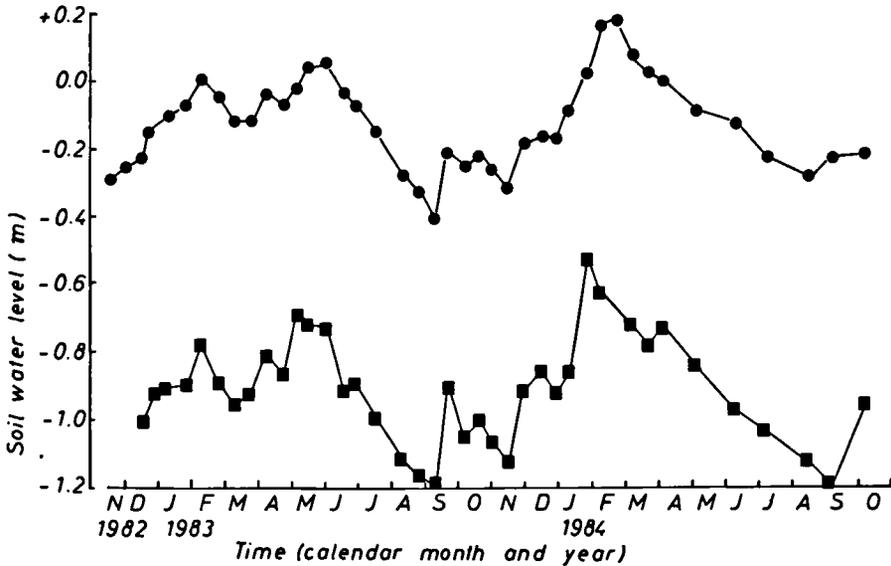
Fig. 1. Soil water level in a dry (■—■) and a wet (● - ●) dune slack in the Reggers and Sanders Valley (North-Holland Dune Reserve) from November 1982 to October 1984.

25 of its 76 sites, i.e. a decrease of 33% in The Netherlands, mainly in the wet heathlands and to a lesser extent in the coastal dunes (Heukels in Mennema *et al.* 1985). Heukels has correlated this decrease with the extraction of drinking-water from the dunes and with reclamation of heathlands.

In the present study we investigated the population structure, population dynamics, and rejuvenation potential of *S. nigricans* in order to provide recommendations for an appropriate management of the remnant populations on dune sites in the future, when the change of water table management in coastal dunes, due to legislation, may give new possibilities for restoration of wet dune slacks.

MATERIAL AND METHODS

Study sites

Populations of *S. nigricans* L. were studied in a dune slack on the beach plain of the Wadden Island of Schiermonnikoog, established from 1964 onwards (Schatt 1982), and in several (formerly) wet dune slacks along the coast of the Province North-Holland in the North-Holland Dune Reserve (NHD) (The Netherlands), with obviously long-living individuals. Contrary to the statement made by Heukels (in Mennema *et al.* 1985) that *S. nigricans* "has become rare in the Dune District due to the extraction of drinking-water from the dunes", the greatest number of populations in The Netherlands is present in the NHD in a 16-km long zone of various dune slacks along the coast from Bergen aan Zee to Wijk aan Zee. In this area we studied three populations, isolated by great dune ridges, in more detail. The first NHD site, Reggers and Sanders Valley, is a wet dune slack (Stuijfzand & Moberts 1987), in agreement with the definition given by Ranwell (1960), in which the free water table never falls below 1 m in any season (Fig. 1). In addition to the natural dune slacks at this site, an area of 20 m² was excavated up to the sand layer in the

autumn of 1976 for a re-establishment experiment with wet dune slack vegetation. The second NHD site, the Kil, is a 1-km long dune valley, that parallels the coast of the North Sea behind the first great dune ridge, where the water table during periods of water extraction and dry weather falls 1 m below the ground surface. The third NHD site, the Oceaan, consists of two small, nearly circular dune valleys (each nearly 50 m in diameter). Site Oceaan A was heavily grazed by rabbits and site Oceaan B was ungrazed. In both sites the water table falls 1 m below the ground surface during periods of longer dry spells and water extraction.

A population from a dune slack at Salin de Giraud (Camargue, France) was taken for comparison of seed quality, seed infestation by insects and germination behaviour.

Population structure

At each Dutch field site the following data were collected for *S. nigricans*: (i) tussock-diameter; (ii) maximum length of the leaves; (iii) number of inflorescences produced; (iv) number of fruits produced; (v) evidence of defoliation by rabbits (*Oryctolagus cuniculus* L.); (vi) evidence of damage of inflorescence by grazing of an unidentified noctuid caterpillar; (vii) evidence of fruit damage by the larvae of the microlepidopteran *Glyphipteryx schoenicolella* Stainton (Bradley 1953). Plants were primarily classified by size and inflorescence number and not age (see Discussion). Seedlings are distinguished by a single cotyledon and one primary leaf during the first 2 months of the growing season. The number of inflorescences per tussock was classified in a semilog-scale: 1: one inflorescence; 2: 2–5 inflorescences; 3: 6–10 inflorescences; 4: 11–25 inflorescences; 5: 26–50 inflorescences; 6: 51–100 inflorescences; 7: 101–250 inflorescences; 8: 251–500 inflorescences.

Fruit quality and quantity

Infructescences were collected from each field site in autumn 1984 from the sites in NHD. They were also collected in the autumn and spring between 1985 and 1987. Between 25 and 50 infructescences, each with 4–30 spikelets, were analysed for the mean number of fruits set per infructescence determined. Healthy, i.e. non-infested white nuts (100–150), were weighed individually on a Mettler ME30 balance.

Germination experiments

To test after-ripening and dormancy, nuts sampled from plants in the Reggers and Sanders Valley (NHD) were tested monthly from the time of harvest, and bi-weekly from March onwards. They were tested by imbibition on moist filter paper in closed Petri-dishes, filled with distilled water at 20°C day/5°C night, 14/10 hours light/dark. Each experiment was performed with 100 nuts and replicated twice. Nuts that had germinated were counted twice a week and then used for growth experiments.

Germination experiments were carried out on three repeated sets of 100 nuts, collected from the populations at Schiermonnikoog, the Kil and Reggers and Sanders Valley in NHD and at the Salin de Giraud. Experiments started in April 1985.

To test germination under field conditions, 360 fruits from each population were sown in a plastic container of 25×12 cm^2, filled with a 3-cm layer of dune sand and wetted with demineralized water. After sowing, the water-table was brought 5 mm above the sand layer. In another experiment the 3-cm thick layer of dune sand was replaced by leaf litter of *S. nigricans*, collected from mature tussocks in February 1986. These plastic containers were covered by a transparent plastic cap and placed in the dune slack of the Kil. Germination was controlled bi-weekly from 15 April to 15 June. At the same time, 100

nuts of each population were kept on moist filter paper in Petri dishes at $20° \pm 2°C$ in the laboratory with natural illumination.

For an analysis of germination and seedling establishment under field conditions, two groups of 300 fruits were sown in a plot from which the organic soil layer had been removed and in a plot with dense vegetation consisting of *Calamagrostis epigejos* (L.) Roth, *Molinia caerulea* (L.) Moench, *Salix repens* L. and *Schoenus nigricans* with tussocks of 25 cm diameter, both at Reggers Valley. After sowing in early March, germination was recorded in May, June and July, and established seedlings were harvested in November.

For analysing the effect of nut weight on the germination process, 100 nuts were divided into five weight classes (<300, 301–400, 401–500, 501–600, >601 µg) and allowed to germinate in a temperature regime of $20°/5°C$ (light/dark), as described above.

Survival and growth of seedlings

Seedlings that emerged in May 1985 were transplanted in bottom-perforated plastic containers ($16 \times 16 \, cm^2$ surface, 9 cm depth), filled with dune sand from the C-horizon at Reggers and Sanders Valley, buried up to ground level and watered with demineralized water, as necessary, to maintain the water table at, or 1 cm above, the surface. To avoid the impact of rain, the containers were protected with glass plates positioned 1 m above the container. From June to July the water supply was terminated and the glass protection removed to simulate summer drought. From August onwards water was again supplied. The seedlings were monitored for 3 years.

In another experiment set up in the same way with 600 nuts, seedlings were harvested at 3, 6, 12 and 18 months after germination, weighed individually after drying at $80°C$ for 48 h, and separated in root, shoot and endosperm. Relative growth rate (RGR) was calculated by measuring the change of the mean dry weight between two harvest intervals.

Vesicular-arbuscular mycorrhizal infection is common in *S. nigricans* (Mejstrik 1972) and was analysed after clearing with hot KOH for 2 h and staining with trypan blue in lactophenol, according to the procedure of Phillips & Hayman (1970).

Chemical analysis

Plant material was wet-ashed (HNO_3HClO_4, 7:1, v/v). The elements Ca, Cu, Fe, Mg, Mn, and Zn were analysed by atomic absorption spectrometry (Perkin Elmer 4000). Ca and Mg were analysed after addition of 1% $LaNO_3$. K and Na were measured by flame emission spectrometry. Phosphorus was determined as a blue ascorbic acid complex by spectrophotometry (Chen *et al.* 1956) and N was determined after burning in a pure oxygen stream by column chromatography (Carlo Erba Elemental Analyser 1106).

Statistical methods

Experimental values were analysed by one-way ANOVA; skewness was tested by moment statistics (Sokal & Rohlf 1981).

RESULTS

Size and structure of the population

The population of the beach plain at Schiermonnikoog and that of the sod-cutting site in NHD contained non-flowering juvenile plants with tussock-diameters of <4 cm (Fig. 2). No juveniles were found at the other sites. The frequency distribution for individual plant
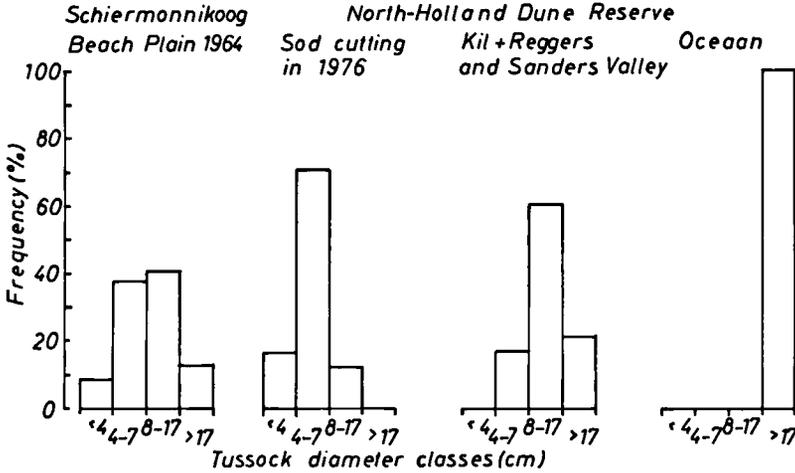
Fig. 2. Tussock diameter classes of *Schoenus nigricans* on the beach plain at Schiermonnikoog and several sites in the North-Holland Dune Reserve. The census was made in October 1984.

sizes of the beach plain population gave 8·5% for small and 28% for large tussocks; tussocks between 4 and 17 cm diameter made up the bulk of this population. Due to the relatively short period between sod-cutting and the start of this investigation, i.e. 8 years, plants with tussock-diameters above 17 cm were absent at the sod-cutting site. The predominant rosette size of most populations in NHD (Reggers and Sanders Valley, Kil) was that of 8–17 cm; 21·5% of the population had a tussock size greater than 17 cm, up to 35 cm. In the most southern population of NHD, i.e. the ungrazed population in the site Oceaan B, all tussocks had rosette-diameters above 17 cm, thus rejuvenation had not taken place for a long period.

As shown in Fig. 3a, production of inflorescences was correlated positively with tussock-diameter. The number of inflorescences per tussock increased from one in the third or fourth year after germination and three to five in the following year up to nearly 500 in plants with large tussocks. In the first year of reproduction, the number of spikelets per inflorescence is low, usually four, so that nut production of juvenile plants varies between 8 and 10.

Leaf length increased with the tussock diameter (Fig. 3b). In tussocks with less than 5-cm diameter, the longest leaf was shorter than 30 cm; in tussocks with more than 15-cm diameter, maximal leaf length was at least 35 cm with extremes up to 82 cm. In 2–4 year-old plants of the experimental population, maximum leaf length varied between 14 and 20 cm in tussocks with a diameter between 2 and 4 cm.

Impact of herbivores

Herbivores affected tussocks, inflorescences and fruits in a site-specific manner (Table 1). The lowest percentage of defoliation (0–3%) by rabbits was recorded at the brackish sites (Schiermonnikoog, Salin De Giraud), and at two sites in NHD, i.e. the sod-cutting area and the site Oceaan B. The heaviest defoliation occurred at the site Oceaan A, where all tussocks were defoliated during winter and spring and only a few tussocks developed inflorescences.

Other herbivores injured the inflorescences. The caterpillar of an unidentified noctuid moth defoliated the inflorescences from May to September. Aphids damaged the flower
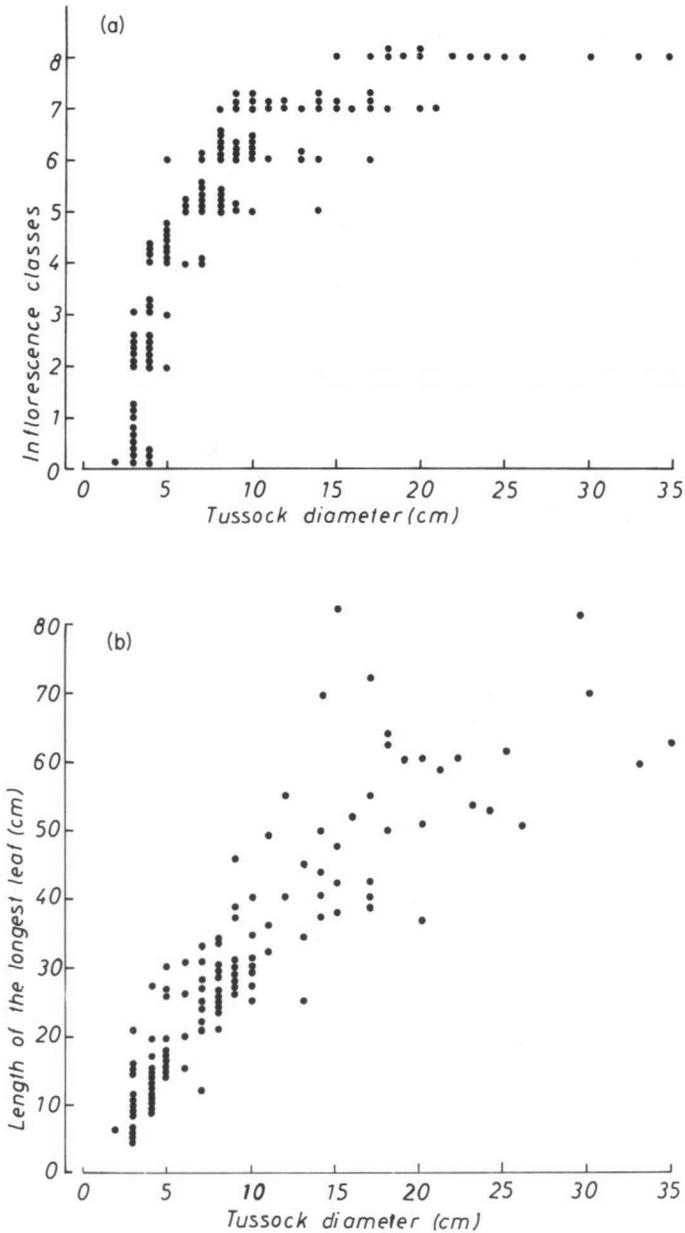
Fig. 3. (a) The relationship between tussock diameter and inflorescence classes (see Methods) and (b) between tussock diameter and the longest leaf per plant of *Schoenus nigricans* on the beach plain at Schiermonnikoog.

stalk beneath the inflorescence. The damage was small in the brackish sites and increased up to 78% of the inflorescences in NHD.

In those inflorescences that survived and produced fruits, the larvae of the microlepidopteran *Glyphipteryx schoenicolella* destroyed between 1·5% (Salin de Giraud) and 67·2% (North-Holland Dune Reserve) of the fruits. In the latter case 60% of the larvae were attacked by a parasite Hymenoptera and did not develop to pupae.

Table 1. The percentage of plants of *Schoenus nigricans* affected by herbivores

Site	Tussocks defoliated by rabbits (%)	Inflorescences grazed or damaged by insects (%)	Fruits damaged by *Glyphipteryx schoenicolella*	Number of investigated plants
Salin de Giraud	1·5	3·2	1·5	62
Schiermonnikoog	2·4	19·7	12·2	127
North-Holland Dune area				
Sod cutting area	0·0	41·7	3·7	24
Reggers and Sanders				
Valley and Kil	38·7	78·1	67·2	421
Oceaan A	100·0	3·2	No seeds	31
Oceaan B	0·0	66·1	38·5	124

Fruit quantity and quality

Nuts are dispersed mainly by strong wind so that, depending on the intensity and frequency of storms in the winter, up to 50% of the nuts can still be held in the infructescences until May, at least in the Dutch populations. In all populations, between 28 and 33% of all fruits did not develop to mature nuts; these underdeveloped nuts could be recognized by their brown colour.

The mean weight of healthy nuts collected in November and in May did not differ, either in mean nut weight or in the range of nut weights, indicating that nut shedding was not influenced by nut weight. Healthy nuts from populations in The Netherlands had a weight of 535 ± 107 μg (mean ± 1 SE), those from the Mediterranean population at the Salin de Giraud were heavier by 26% (Fig. 4) with a mean of 722 ± 124 μg in agreement with a negative relationship between seed weight and either altitude or geographical latitude (Baker 1972). With the exception of the nuts from the population in Reggers and Sanders Valley, the frequency distribution of nut weights was bell-shaped and not skewed.

The chemical composition of the nuts was similar in plants from the Dutch sites, with the exception of the increased iron content in nuts from the Wadden Island of Schiermonnikoog (Table 2), but differed strongly from that in the Mediterranean population. The latter had three times the concentration of sodium and twice that of potassium but lower concentrations of calcium, magnesium, phosphorus, and zinc.

Productivity and reproductive effort

The number of fruits per tussock depended on the number of infructescences. Fruit production per plant could increase up to a thousand but most mature tussocks produced between 400 and 700 fruits if they were not heavily grazed or damaged by aphids. There was no significant difference in fruit production of plants from the various sites. The reproductive effort, measured as the percentage of the biomass allocated to infructescences and fruits, was independent of tussock size and biomass, and varied from 3·1 to 4·0%. Manganese and phosphorus were allocated to the reproductive organs in the same percentage as the biomass, whereas the percentage of total nitrogen was slightly higher, all other nutrients were lower by a factor of nearly two.

Germination

Nuts were kept wet at a daily temperature regime of 20°/5°C (14 h light/10 h dark) and tested at various periods after harvesting in late October. They did not start germination
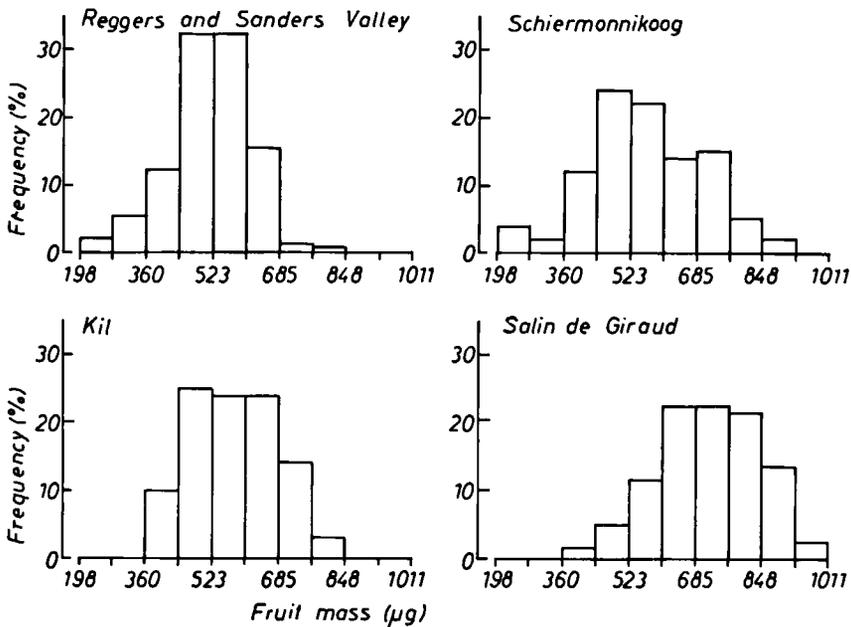
Fig. 4. Frequency distribution of fruit weights of *Schoenus nigricans* on two sites in the North-Holland Dune Reserve (Reggers and Sanders Valley, Kil), on the beach plain of Schiermonnikoog and in a wet dune slack at Salin de Giraud (Camargue).

Table 2. Concentration of nutrients in nuts of *Schoenus nigricans*, collected on the Wadden Island of Schiermonnikoog, the coastal dunes of North Holland and the dunes at Salin de Giraud (Camargue). The data are based on 100-mg samples

Site	Nutrient concentration (μmol g^{-1})									
	N	P	K	Na	Ca	Mg	Fe	Mn	Zn	Cu
Schiermonnikoog	2700	18	28	6	45	75	0·90	0·55	2·53	0·21
North Holland dune	3090	24	28	8	54	70	0·33	0·54	2·29	0·26
Salin de Giraud	2850	14	51	24	33	59	0·38	0·47	1·06	0·22

until mid-January, i.e. 78 days after fruit harvest. The percentage of germination remained below 5% and did not increase for a further 6 months, when the experiments were finished due to nut infection by fungi and slime moulds (Fig. 5). A similar result was achieved for nuts imbibed for the first time in December, January and February. Nuts imbibed in March and early April germinated after 18–19 days with a final percentage of 40%. With increasing periods of after-ripening, nuts germinated within 10 days after imbibition in May and had the highest percentage of germination (up to 90%). Up to 8% of nuts kept at a nearly constant room temperature (20 ± 2°C) germinated over a period of 14 months. Repetition of these experiments with nuts, stored for up to 4 years, did not change the rate and percentage of germination. Up to 96% of nuts exposed to natural conditions in
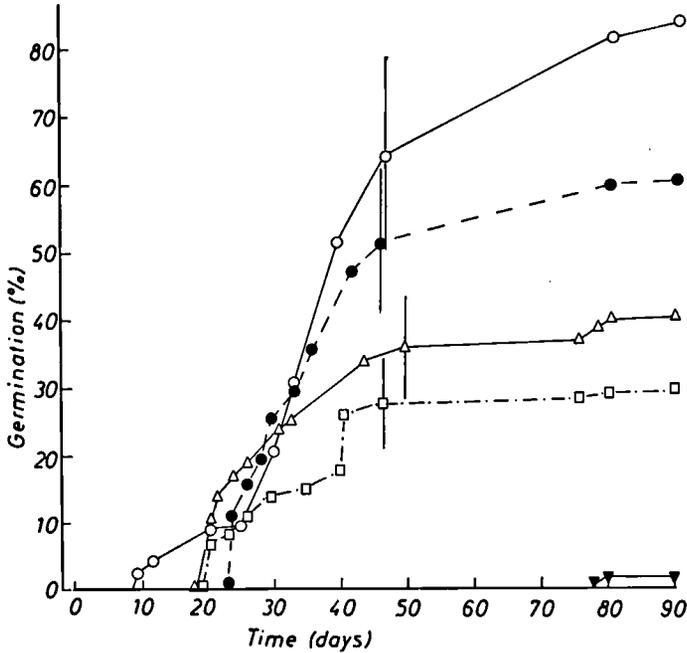
Fig. 5. Germination of fruits of *Schoenus nigricans,* collected in October 1984 in the North-Holland Dune Reserve, and imbibed at different periods after harvest at 20°/5°C (14 h light/10 h dark). The presented experiments were started on: 1 January 1985 (▼ — ▼), 1 March 1985 (□ — □), 1 April 1985 (△—△), 15 April 1985 (● – ●) and 1 May 1985 (○ – ○).

February germinated in May. A comparison of the germination behaviour of nuts collected from populations at Schiermonnikoog, NHD and Salin de Giraud and imbibed in late April, i.e. 6 months after harvest, showed no differences in the percentage and germination rates. Only up to 8% of nuts sown on leaf litter of *S. nigricans* germinated; most nuts were affected by fungi. If three days after germination seedlings were transplanted on such a litter, 70% were able to survive.

Nut weight may influence germination behaviour. Fifty per cent of the nuts derived from a population at Reggers and Sanders Valley in NHD, weighing between 200 and 400 μg, germinated within 10 days, followed by nuts weighing between 401 and 700 μg. Very heavy nuts did not germinate within 30 days after imbibition. After a further period of 45 days, all heavy nuts ($n = 10$) died by lysis.

In another experiment, germination and seedling establishment was compared on bare sandy soil and in adjacent dense vegetation. In both microsites *S. nigricans* was able to germinate ($20.3 \pm 3.9\%$); the low germination percentage may be due to seed loss by animals, negative interaction with other species or water transport. Whereas seedlings on bare soil were able to establish themselves and achieved a mean weight of 12.7 ± 8.3 mg ($n = 6$) in November, there was no seedling survival in the dense vegetation.

Seedling establishment and growth

Eleven days after germination the sheath of the seedling was fully developed and the cotyledon emerged. The dry weight of 11-day-old seedlings was only 170 ± 47 μg, that of the root was 25 ± 7 μg, whereas the remnant endosperm weighed 104 ± 60 μg ($n = 50$). Three months after germination 50% of the plants had developed one or two primary
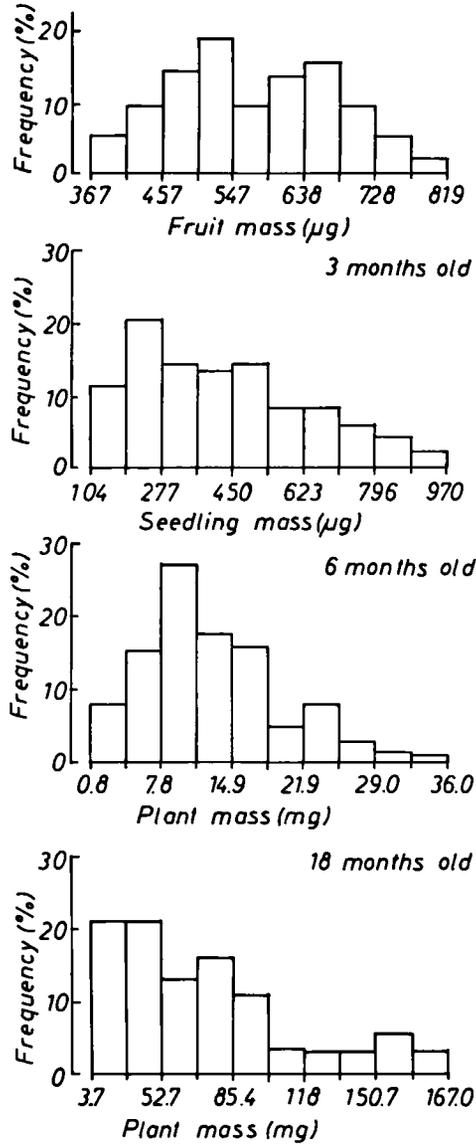
Fig. 6. Frequency distribution of dry weight of fruits, seedlings and juvenile plants at various periods after germination.

leaves. Plants with one leaf had a weight of $268 \pm 93\,\mu g$, those with two leaves had $589 \pm 162\,\mu g$ (Fig. 6). The shoot:root ratio was 8.02 ± 2.77, and the RGR was 0.0546 mg week^{-1} g^{-1}.

In the late autumn (November), i.e. 6 months after germination, plant dry weight had increased to 13.4 ± 7.0 mg with the heaviest plants weighing 36.0 mg. At this time the frequency distribution of dry weight was slightly skewed. The number of green leaves varied between 6 and 17; one to two leaves were dead. RGR had increased to 0.277 mg week^{-1} g^{-1}. The shoot:root ratio had decreased to 2.20 ± 0.79, thus indicating a change in the biomass allocation in favour of roots.
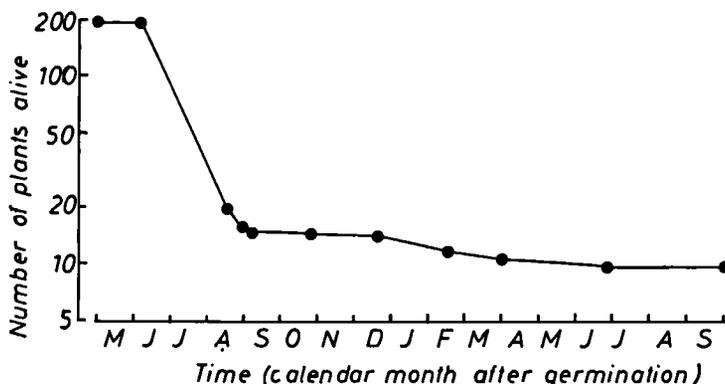
Fig. 7. Seedling survival of *Schoenus nigricans* in an experimental site in the North-Holland Dune Reserve, for 17 months after germination.

After a further growing season, the dry weight distribution of 2-year-old plants is strongly skewed. RGR during the second growing season decreased to 0.05 mg week^{-1} g^{-1}. The shoot:root slightly increased to 2.77 ± 1.83.

The fate of cohorts of seedlings was followed for the first 2 years (Fig. 7). Seedlings had a survival curve that could be described as Deevey Type III (Harper 1977), i.e. initially an extremely hazardous juvenile stage with a mortality of 88%, and with a mortality risk that declined with age. There was no mortality in the remnant plants from the summer of the second year to the spring of the fourth year. The percentage of biomass for plants in the fourth year, with 1588 ± 217 mg dry weight allocated to the roots, was 22.5%, 12.1% was allocated to the dead leaves, 3.1% to the inflorescences and 62.3% to the green leaves. The shoot:root ratio was 3.3, thus once more slightly increased in comparison with previous years.

With regard to the turnover of leaf biomass, at the end of the first growing season the ratio of living to dead leaf biomass was 2.5 ± 0.7, at the end of the winter it decreased to 1.9 ± 0.9. At the end of the second growing season the number of leaves alive increased from 5.5 ± 1.9 to 58.0 ± 10.0 with a ratio of living to dead leaf biomass of 1.7 ± 0.7. During the third year there was a doubling of the leaf production from 46 ± 6 in spring to 119 ± 13 leaves in autumn. The ratio of living to dead leaf biomass was 8.38 ± 1.45; this decreased after the winter to 5.15 ± 1.03.

With an increase in tussock diameter and age, the sheath of dead leaves with a low decomposition rate can make up for more than 50% of the biomass of a mature tussock (32 cm tussock diameter). The biomass of living leaves and roots was nearly the same, 16.3 and 15.9%, respectively. The laminae of dead leaves contributed 7.3% to tussock phytomass.

Plants were infested by vesicular-arbuscular mycorrhizal fungi at all sites. The degree of infection did not differ from that described from a fen in Central Europe (Mejstrik 1972) and from the infection percentage of the co-occurring *Calamagrostis epigejos* (Ernst *et al.* 1984).

DISCUSSION

The results of this study show that the population structure of *S. nigricans* in the coastal dune sites of The Netherlands is characterized by a lack of renewal by seedlings and a

dominance of very mature tussocks at sites that were first colonized some 20–30 years ago. In contrast, recently colonized wet dune slacks have more seedlings and small-sized tussocks. The calibration of plant age with tussock diameter and production of inflorescences can be made by using the tussock size of sites with a known history. The tussock diameter of 3-year-old plants from the experimentally grown population was a maximum of 4 cm; their first production of inflorescences fits well with the first reproductive age given for a *S. nigricans* population on the British Isles (Sparling 1968). Eight-year-old (in 1984) and 11-year-old plants (1987) in the sod-cutting experiment, initiated in 1976, had the greatest tussock diameter of 17 and 19 cm, respectively. Plants from the beach plain in Schiermonnikoog, which was established between 1962 and 1966 (Schat 1982), had the greatest tussock diameter (34 cm) and were less than 22 years old (in 1984). This calculation indicates that there is a reasonable relationship between plant age and tussock diameter. Based on this calculation, the most mature population investigated in this study was that at the site 'Oceaan' with tussocks of over 17 cm diameter; this population had no chance of rejuvenation, at least during the last 20 years. Sparling (1968) reported an annual extension of the rhizome from less than 1 cm under dry conditions. From the data on the soil water level, collected regularly from 1950 onwards in NHD (Stuifzand Moberts 1987), it can be deduced that the years of high water tables that had ensured the presence of a wet dune slack, and thus germination of *S. nigricans,* were 1951, 1962 and 1966. In this context it is interesting that Doing (1964) has already mentioned that the plant community with *S. nigricans* (Schoenetum nigricantis) was in a late stage of succession. Therefore, it seems to be more obvious that the tussocks at the site 'Oceaan' were established as seedlings in 1951 or earlier, and thus are at least 37 years old (in 1988). This latter age is in good agreement with an estimation of over 30-year-old tussocks of *S. nigricans* in the British Isles (Sparling 1968).

Although we would like to correlate the lack of rejuvenation and thus decrease in the populations of the Dutch coastal dunes with the lowering of the soil water table caused by the extraction of drinking water from the dunes, as proposed by Heukels (in Mennema *et al.* 1985) and Bakker *et al.* (1979); for a more correct judgement we should consider the interaction of several ecological factors. If a lack of rejuvenation may be a consequence of vegetation succession, we can confront our results with the succession models, as described by Connell & Slatyer (1977). Because there is general agreement on the pioneer character of *S. nigricans* (Westhoff & Den Held 1969), the behaviour of this species should fit into Connell & Slatyer's facilitation model, which describes the primary succession following perturbation. With regard to natural perturbation of dune sites, until now it is prescribed by Dutch legislation that moving sand in the coastal dunes must be immediately fixed by biological or technical means. Therefore, aperiodic perturbation by wind or water, which denudes the soil surface, is restricted to the Wadden Island of Schiermonnikoog (Rozema 1978, Schat 1982) and cannot occur in the coastal dunes of North-Holland. Therefore, perturbation can only be due to man, and will affect rejuvenation, as indicated by the sod-cutting experiment.

This facilitation can be realized by stabilization of moving substrates as in dunes (Olson 1958) or changes in the chemical speciation of minerals nutrients (Ernst 1987). How does *S. nigricans* facilitate the establishment of late-successional species? A very important factor in flooded soils is the supply of oxygen. Armstrong (1982) has shown that *S. nigricans* has a high radial oxygen loss (ROL) from its roots ($128–190\ \text{ng}\ O_2\ \text{cm}^{-2}\ \text{min}^{-1}$) compared to later successional species, e.g. *Molinia coerulea* with $14\ \text{ng}\ O_2\ \text{cm}^{-2}\ \text{min}^{-1}$. Other species in wet dune slacks can endure prolonged submergence only in the presence

of species with a high ROL (Schat 1984). Another aspect of facilitation may be the accumulation of organic matter as part of a general contribution to pedogenesis (Miles 1987); this diminishes the frequency of flooding of those plants that grow on the decaying tussocks of *S. nigricans.* One consequence of such a modification to the environment is the facilitation of the establishment of other species and the reduction of suitable sites for seedlings of its own species, if it has a narrow niche. Due to the very slow decomposition of the leaf sheaths, tussocks with a 15-cm diameter enabled less flood-resistant species, e.g. *Festuca rubra* (Rhebergen 1985) to establish themselves in the tussock of *S. nigricans.* Therefore, enhanced invasion of later-successional species is a consequence of facilitation but not a modifying factor, as suggested by Pickett *et al.* (1987).

Facilitation of the establishment of other plant species may hamper the rejuvenation of the initial population. Germination and establishment of *S. nigricans* has been postulated to occur only in wet dune slacks (Sparling 1968). During the past decade, however, the water table was sometimes at such a height (Fig. 1) that germination may have been possible at least in the Reggers and Sanders Valley, as demonstrated on the sod-cutting site. Fenner (1987) has postulated that a pioneer seed, once it arrives at the appropriate site, needs to have a 'gap-detecting mechanism' to inform the seed about its favourable position for germination. One such mechanism requires a fluctuation in temperature to break dormancy. In the case of *S. nigricans,* fruits germinate better if there is a daily fluctuation in the temperature rather than a constant temperature, as already known for Mediterranean populations of *S. nigricans* (Bocchieri *et al.* 1987). This temperature interval, however, can easily be realized at the Dutch dune sites independent of the water table. The establishment of *S. nigricans* on the sod-cutting site, and the absence of juvenile plants in adjacent sites with a closed vegetation comprising *Calamagrostis epigeios, Molinia caerulea* and *Salix repens,* indicates that a rejuvenation of the population is only possible if, in addition to a favourable water table, open microsites are available. Thus *S. nigricans* demands a regeneration niche *sensu* Grubb (1977). The necessity of an open site for the establishment of seedlings can be argued from the sensitivity to leaf litter and/or the associated micro-organisms, and a very low RGR of *S. nigricans* (cf. Boatman 1972), which is the lowest measured for perennial plant species in Europe (Grime 1979). The presence of only two very small leaves of 3-month-old seedlings prohibits a successful establishment in dense vegetation, as shown in the field experiment. The development of a skewed dry weight distribution without competition, within 1 year after germination, indicates that *S. nigricans* will undergo rapid selection in competitive sites. The strong size hierarchy of most populations in NHD supports the unbalanced population structure, as shown for other grassland plant species (Ernst *et al.* 1987). Whereas plant species with a broad niche can persist during succession by a change in the genetic structure of their population, which replaces less adapted genotypes by better adapted ones (Ernst 1976), *S. nigricans* presents itself as a species with a narrow ecological range, which persists only as mature individuals with a low, but constant, reproductive effort. This aspect is not seriously considered in modelling the dynamics of plant populations (for a review see Blom 1988).

Water extraction from the dunes may have enhanced the succession process in wet dune slacks. The strong impact of rabbits on the defoliation of the tussocks during winter may have severely hampered the further development of inflorescences which were, as in the population of the British Isles (Sparling 1968), initiated in September and were up to 6 cm long at the start of winter. The lack of inflorescences, as found in the severely grazed population at the site Oceaan A, support the statement made by Boatman (1972) that herbivorous mammals can lead to extermination of *S. nigricans* populations. The rabbits'

well-known distaste for wet paws, may however, indicate that a high water table, and thus a wet dune slack, during winter will prevent severe grazing and enhance the survival of seedlings. The small effect of rabbits on the beach plain at Schiermonnikoog may be due to regular flooding of this site during winter (Rozema 1978, Schat 1982).

The strong impact of aphids and noctuid moth larvae on inflorescences and *Glyphipteryx schoenicolella* on fruits, however, was as high as that reported for *S. nigricans* from the British Isles (Sparling 1968). The exceptions were the populations in the brackish sites of Schiermonnikoog and Salin de Giraud. Thus, the sensitivity of these insects to an increased concentration of sodium chloride in the inflorescences or in the soil may be the decisive factor that regulates insect damage in *S. nigricans*. The damage of nuts by *Glyphipteryx schoenicolella*, and its impact on rejuvenation, may not be influenced by the soil water table.

In conclusion, by ensuring rejuvenation, a successful management of populations of *S. nigricans* demands the following manipulations: (1) a high water table (just above ground surface) during late spring to ensure germination; (2) an annual fluctuation (not surmounting 1 m (Ranwell 1972)); (3) an area with a low vegetation cover, either by management of the remnant vegetation or by natural perturbation (wind, water); and (4) a high water table (centimetres above the surface) during winter to diminish the defoliation by rabbits.

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