Journal of Coastal Conservation 3: 87-94, 1997

Nutrient deficiency in dune slack pioneer vegetation: a review

Lammerts, E.J.[1*] & Grootjans, A.P.[2]

[1]*Ministry of Agriculture, Nature Management and Fisheries, P.O. Box 30032, NL-9700 RM Groningen, The Netherlands;* [2]*Laboratory of Plant Ecology, P.O. Box 14, NL-9750 AA Haren, The Netherlands; Tel. +31 50 3632229; Fax +31 50 3632273;*
[*]*Corresponding author; Tel. +31 50 5992312; Fax +31 50 5992399; E-mail e.j.lammerts@lnvn.agro.nl*

Abstract. A review of results of fertilization experiments in wet dune slacks is presented. In most cases the above-ground biomass appeared to be limited by nitrogen availability. Primary phosphorus limitation was assessed only once in a dune slack where sod cutting had been applied very recently. In most other case studies phosphorus limits biomass production after nitrogen deficiency was lifted. Potassium availability is of minor importance for biomass production in this type of ecosystem. Singular nitrogen additions led to increased dominance of *Carex* and *Juncus* species as well as perennial grasses, such as *Agrostis stolonifera* and *Calamagrostis epigejos*. A combined addition of nitrogen and phosphorus led to total dominance of grasses, while the characteristic basiphilous pioneer species (including mosses) decreased or even disappeared. Certain mechanisms are considered which may maintain nutrient availability in slacks with basiphilous pioneer vegetation at a low level, despite of the accumulation of nutrients in the developing organic soil layer. Some implications for management and further research are discussed.

Keywords: Fertilization experiment; *Junco baltici-Schoenetum nigricantis*; Succession.

Nomenclature: van der Meijden et al. (1990) for vascular plants; Schaminée et al. (1995) for plant communities.

Introduction

The number of dune slacks harbouring basiphilous pioneer species has rapidly been declining during the last decades in The Netherlands. Shrubs and tall grasses have taken over most of the dune area and the dunes themselves have been fixed. This dune fixation is mainly caused by afforestation and by prevention of sand blowing. Succession may have been accelerated by atmospheric deposition of nitrogen compounds from (bio-)industrial areas (e.g. ten Harkel & van der Meulen 1996). Abstraction of groundwater for drinking water production and drainage added to the decline of wet pioneer stages in dune slacks (van der Meulen 1982; van Dijk & Grootjans 1993). As a consequence many species such as *Schoenus nigricans, Parnassia palustris, Dactylorhiza incarnata* and *Epipactis palustris* are now endangered in most of the Dutch dune areas. These species survive only in nature reserves in pioneer stages of mainly three dune slack types: (1) primary beach plains; (2) secondary blowout slacks; (3) slacks in seepage areas of large hydrological systems (Lammerts et al. 1992).

In order to preserve endangered species, many restoration projects are being carried out. These include sod cutting, mowing and adjusting hydrological systems to the requirements of basiphilous species (Jungerius et al. 1995; Geelen et al. 1995; Ernst et al. 1996). These measures all aim at reducing biomass production of late successional stages. In most cases, however, it is unknown which macro-nutrients are primary limiting factors for plant growth in the various successional stages.

The present paper discusses the results of several fertilization experiments in coastal areas, focusing on wet and moist dune slacks.

Much research has been done on the nutrient conditions in dry dune ecosystems. Low nutrient pools were found in pioneer stages compared with older successional stages (Kellman & Roulet 1990; Olff et al. 1993; Gerlach et al. 1994). Fertilization experiments in pioneer stages showed that nitrogen was a limiting factor in dry dune soils; additions of only nitrogen or of nitrogen together with phosphorus and potassium led to increased biomass production (Lux 1964; Willis 1963; Boorman & Fuller 1982; Pemadasa 1983; Kachi & Hirose 1983). Phosphorus additions only hardly stimulated plant growth in young successional stages. These results suggest a primary nitrogen limitation in dry dune pioneer stages. Some authors suggest that this primary N-limitation may be followed by a secondary P-limitation in later successional stages (Walker & Syers 1976; Vitousek & Walker 1987).

Much less is known on the nutrient limitation of wet and moist dune slacks, where only a few fertilization experiments have been carried out (Willis 1963; Dougherty et al. 1990; Koerselman et al. 1992; Olff et al. 1993; Verhoeven et al. 1994). Recently, nutrient fertilization experiments were carried out in different successional stages in a wet dune slack on the barrier island of Terschelling, situated in the Dutch Wadden Sea (E.J.

Lammerts et al. submitted). Also data from two experiments in undisturbed dune slacks in the southwestern Netherlands (Koerselman & Meuleman 1994) could be used.

With these data we will try to present a synthesis on patterns in nutrient limitation in dune slacks.

Review of case studies

All fertilization experiments selected have been carried out in dune slacks which were never fertilized before and which have not been disturbed by direct anthropogenic influences such as drainage. They were all executed in the field and were aimed to assess the type of nutrient limitation influencing phytomass production.

Experimental designs

In early spring nitrogen, phosphorus and potassium were added, alone or in combination, on plots ranging from 0.25 to 1.5 m^2. Control plots, without nutrient addition, were also established. In each plot biomass was harvested in late summer. Only the effects on above-ground biomass are considered here – only in one case (Dougherty et al. 1990) below-ground biomass was sampled. Dougherty et al. (1990) and Olff et al. (1993) only measured *total* above-ground biomass. In all other studies species responses were also considered. Willis (1963) and Lammerts et al. (subm.) measured the above-ground biomass of all species with a high abundance, while in the remaining studies only species cover or abundance were recorded. When a treatment gave a significantly higher biomass than the control plot, the added nutrient(s) were considered to limit biomass production under natural conditions.

Willis (1963) did not present statistics on the experimental results from Braunton Burrows, but because of the detailed analyses of species responses, this study has been included in this review. In all other studies the experiments have been analysed as One-way Analysis of Variance where all additions of nutrients and combinations of nutrients were considered as separate treatments. For the Koegelwieck also Three-way Analysis of Variance has been applied considering the additions of N, P and K as independent variables, the effects of which add up in the effects of combined additions.

Table 1 summarizes the authors' conclusions of each experiment based on the results of the statistical analyses performed. Soil data, when available for the experimental sites, are summarized in Table 2.

Braunton Burrows (UK: Willis 1963)

Willis (1963) was the first to carry out fertilization experiments in dune slacks. Two experiments were established in a secondary dune slack covered by basiphilous vegetation. This vegetation type had much in common with the *Junco baltici-Schoenetum nigricantis* association, which is a basiphilous pioneer community occurring along the West-European coast (Schaminée et al. 1995). Two experiments were carried out, which will be further referred to as BB I and BB II. In BB I only a full NPK treatment was applied (in 1959-1960). In BB II a full factorial fertilization, with all possible combinations of N, P and K, was carried out (in 1960-1961) at a slightly wetter site of the same slack. No significance levels were given for different responses in the above-ground biomass.

In BB I the NPK treatment resulted in a considerable increase in above-ground biomass. This was mainly caused by vigorous growth of grass species, *Trifolium repens* and tall herbs such as *Pulicaria dysenterica* (Table 1). The decrease in biomass of the mosses was striking. Many characteristic basiphilous pioneer species also decreased.

In BB II full factorial fertilization gave similar results as in the first experiment. The singular nutrient additions showed that the vegetation was mainly N-limited (Table 1). *Agrostis stolonifera* increased in biomass after N- as well as P-addition. From the total set of treatments it appeared that vegetation biomass responded to P-addition only when also N was added. Willis concluded that the vegetation of the slack was primarily N-limited and secondarily P-limited. Table 1 also shows that *Carex* and *Juncus* species responded positively on sole N-addition and that the decline of the moss layer and of *Anagallis tenella* after full NPK-addition also occurred after sole N-addition.

The mineral soil appeared to be very calcareous with a $CaCO_3$-content of ± 16% (Willis et al. 1959). No further data were available for the organic top soil.

Elmers's Island (USA: Dougherty et al. 1990)

Dougherty et al. (1990) carried out a full factorial fertilization experiment in 1980 in a primary dune slack on Elmer's Island, Louisiana. The brackish dune slack was covered by a vegetation dominated by *Scirpus americanus* and *Spartina patens*.

Only the effects of nutrient addition on total above-ground biomass were assessed here. The results of the full NPK and the sole treatments are presented in Table 1. Dougherty et al. found that the full NPK treatment and singular supplies of N gave a significantly higher biomass than the control treatment. A more thorough analysis of N and P-additions, considering also the stepwise increased additions of both nutrients in various combinations, showed that P-addition only led to significant responses of the vegetation if given together

Table 1. Summary of the results of nutrient addition experiments in dune slack case studies. +,-: the effect of the added nutrient(s) is (are) positive or negative (for Braunton Burrows I and II no significancies are given, for the other cases +,- represent significant effects, $P < 0.05$, resulting from one-way Analyses of Variance); 0: no effect of nutrient addition; ns: no significant effect of nutrient addition. * For Koegelwieck I and II the results of N, P and K-additions are derived from three-way Analyses of Variance.

Site	Site information	Vegetation / Species	Effects of the addition of				Reference
			NPK	N	P	K	
Braunton Burrows I; Devon, UK	Secondary dune slack. Age and start of vegetation development unknown. No active management.	*Junco baltici-Schoenetum nigricantis* *Agrostis stolonifera* *Poa pratensis* *Pulicaria dysenterica* *Trifolium repens* Moss layer Remaining species	+ + + + + + +				Willis (1963)
Braunton Burrows II; Devon, UK	See above. Experimental site BB II is somewhat wetter than BB I.	*Junco baltici-Schoenetum nigricantis* *Agrostis stolonifera* *Poa pratensis* *Carex flacca* *Carex serotina* *Juncus gerardii* *Anagallis tenella* Moss layer	+ + + 0 0 0 - -	+ + + + + + - -	0 + + 0 0 0 0 0	0 0 0 0 0 0 0 0	Willis (1963)
Elmer's Island; Louisiana, USA	Primary dune slack, regularly flooded with salt water. Period of vegetation development is unknown. No active management.	Community of *Scirpus americanus* and *Spartina patiens*	+	+	ns	ns	Dougherty et al. (1990)
Strandvlakte I, plain; Barrier island of Schiermonnikoog, NL	Primary dune slack, regularly flooded with salt water. The experimental site had been vegetated for 20 yr. No active management.	*Juncetum gerardii*	+	+	ns	ns	Olff et al. (1993)
Strandvlakte II, dune slope; Barrier island of Schiermonnikoog, NL	See above.	*Centaurio-Saginetum moniliformis*	+	+	ns	ns	Olff et al. (1993)
Verklikkervallei; Schouwen Duiveland, NL	Primary desalinated dune slack, where vegetation development started around 1940. Mown once a year.	*Junco baltici-Schoenetum nigricantis* *Agrostis stolonifera* *Eleocharis pal.* ssp. *uniglumis* *Parnassia palustris* Moss layer	+ + ns - -	+ ns + ns -	ns ns ns ns ns	ns ns ns ns ns	Koerselman & Meuleman (1994); Croese (1995)
Reggers Sandervlak; Egmond, NL	Secondary dune slack which originated around 1700. Mown once a year.	*Junco baltici-Schoenetum nigricantis* *Festuca rubra* ssp. *arenaria*	+ +	+ ns	ns ns	ns ns	Koerselman & Meuleman (1994); Croese (1995)
Koegelwieck I; Barrier island of Terschelling, NL	Secondary dune slack. Vegetation development started ca. 1910. Sod-cutting led to different successional stages, which have not been managed. Koegelwieck I represents a 2 years old stage.	Community of *Juncus* species and *Samolus valerandi* *Juncus alpinoarticulatus* Remaining species	+ + ns	ns + ns	ns + +	ns ns ns	Lammerts et al. (submitted)
Koegelwieck II; Barrier island of Terschelling, NL	See above. Koegelwieck II represents a 6-yr old stage.	*Junco baltici-Schoenetum nigricantis* *Schoenus nigricans* *Juncus alpinoarticulatus* *Agrostis stolonifera* *Carex* spp. *Oxycoccus macrocarpos* *Calamagrostis epigejos* Remaining species	+ ns + + ns ns + ns	ns ns + + + + + +	ns ns ns + ns ns + ns	ns ns ns ns ns ns ns ns	Lammerts et al. (1997)

with a certain quantity of N.

Dougherty et al. concluded that N was the primary and P the secondary limiting nutrient. A relatively high pH was measured in the dune slack studied (Table 2), while $CaCO_3$ contents were very low. Apparently the pH was buffered by brackish groundwater or surface water. Total P-content was very low.

Beach plain Schiermonnikoog (NL: Olff et al. 1993)

The Beach Plain on the barrier island of Schiermonnikoog is one of the largest primary dune slacks in The Netherlands. Vegetation development started in the late 1950s, when the bare sand flat was largely separated from the North Sea by the construction of a sand dike. Since then flooding only occurred at high tides, inundating practically the whole beach plain. Nowadays different successional stages can be distinguished in the slack. The young stages occur close to the gap in the sand dike, the older ones occur in more sheltered places at the edges of the slack (Olff et al. 1993).

Fertilization experiments were carried out in 1991 in a vegetation of 20 yr old. The vegetation of the site was dominated by *Juncus gerardii* in which halophytic species, such as *Glaux maritima* and *Atriplex prostata* were present. *Agrostis stolonifera* was often co-dominant in the lower parts. The dune slope was covered by a sparse vegetation of *Festuca rubra* with glycophytic pioneer species, as *Centaurium littorale*, *Linum catharticum*, *Odontites verna* and *Sagina nodosa*. Fertilization experiments were laid out in both vegetation types, referred to as Strandvlakte I and Strandvlakte II. Only the effects on above-ground biomass were measured.

Combined NPK-addition as well as sole N-additions gave a significantly higher biomass than the control plots in both vegetation types (Table 1). No significant differences were found between a full NPK fertilization and sole N-additions. Olff et al. concluded that nitrogen was the limiting nutrient in this early successional stage.

The soil of the beach plain has a relatively high $CaCO_3$-content and a corresponding high soil pH (7.2). Only small amounts of organic matter had accumulated and consequently the nutrient pools were low (Table 2).

Verklikkervallei (NL: Koerselman & Meuleman 1994)

The Verklikkervallei is a primary dune slack, situated on the island of Schouwen-Duiveland in the southern part of The Netherlands. Vegetation development started ca. 50 yr ago (Doing-Huis in 't Veld 1977). The fertilization experiment was carried out in 1992 and 1993 in a community belonging to the *Junco baltici-Schoenetum nigricantis* association, although *Schoenus nigricans* itself was not present. The vegetation was subjected to an annual mowing regime.

Significant increases in above-ground biomass occurred after a full NPK fertilization and also as a result of sole N-addition (Table 1). This points to primary N-limitation. Sole N-addition led to a significant increase in cover of *Agrostis stolonifera* and *Eleocharis palustris* and to a decrease in the cover of mosses. Sole P- and K-additions had no significant effects on plant biomass nor on the species composition of the vegetation. After NPK-addition the cover values of *Agrostis stolonifera* and mosses increased resp. decreased further. *Parnassia palustris* decreased significantly after full NPK-addition (Croese 1995). These responses confirm the supposed primary N-limitation and suggest some secondary P-limitation. *Eleocharis palustris* did not show an increase in cover after the full NPK-addition despite its positive reaction to sole N-addition. The growth of this species is probably strongly suppressed by the growth of *Agrostis stolonifera* which is very competitive under these circumstances.

Data in Koerselman & Stuyfzand (1993) show that the top soil layer in the Verklikkervallei still was calcareous and the pH was above 7 (Table 2). The organic matter content as well as the content of major nutrients in the soil were very low.

Reggers Sandervlak (NL: Koerselman & Meuleman 1994)

The Reggers Sandervlak is a large secondary dune slack in the North Holland Dune Reserve. It originated ca. 300 - 250 yr ago (Jelgersma 1983). Different vegetation types occur with fragments of the *Junco baltici-Schoenetum nigricantis* association in parts of the slack.

Table 2. Measured soil factors in the dune slack case studies.

Site	Organic matter %	pH-KCl	N-tot. %	P-tot. %	$CaCO_3$ %	Reference
Elmer's Island		7.5		0.009	< 0.1	Dougherty et al. (1990)
Strandvlakte	4.0	6.8	0.13	0.059	3.4	Olff et al. (1993)
Verklikkervallei	2.2	8.2	0.03	0.007	2.3	Koerselman & Stuyfzand (1993)
Reggers Sandervlak	8.0	6.2	0.33	0.016	1.0	Koerselman & Stuyfzand (1993)
Koegelwieck I	0.5	7.0	0.01	0.011	< 0.1	Lammerts et al. (1997)
Koegelwieck II	7.1	6.4	0.18	0.040	< 0.1	Lammerts et al. (1997)

It is unknown when vegetation development has started. The actual presence of basiphilous species largely depends on the (annual) mowing regime executed since about 1976. A fertilization experiment was set up in 1992 and repeated in 1993.

A significant increase of above-ground biomass occurred after NPK and N-addition (Table 1). Except for *Festuca rubra*, none of the component species reacted significantly to NPK-addition (Croese 1995).

The top soil layer in the Reggers Sandervlak was still calcareous but the pH and the organic matter content were comparable to Koegelwieck I, where the top soil was completely decalcified (Table 2). The total N-content was high while the total P-content was very low.

Koegelwieck (NL: Lammerts et al. subm.).

The Koegelwieck is a large secondary dune slack on the barrier island of Terschelling in the Dutch Wadden Sea. The slack was blown out between 1825 and 1865 (van Dieren 1934) and became vegetated in ca. 1910 (Westhoff & van Oosten 1991). Sod-cutting experiments have been carried out in this slack in 1956, 1959, 1986 and 1990 (for details: see Lammerts et al. subm.). Only in the youngest two stages basiphilous pioneer species were present. The results of the fertilization experiments, executed in these two stages in 1992, will be discussed here.

Koegelwieck I, the youngest (2 yr old) stage, was practically unvegetated in 1992. Only a sparse growth of *Juncus articulatus, Juncus alpinoarticulatus* and *Samolus valerandi* occurred. After a combined addition of N, P and K total above-ground biomass increased. N- as well as P-addition contributed significantly to this effect. The most dominant species, *Juncus alpinoarticulatus*, clearly suffered a co-limitation of N and P, while the remaining species were mainly limited by P.

Koegelwieck II, the 6 year old stage, was situated in a well developed *Junco baltici-Schoenetum nigricantis* community, which was dominated by *Schoenus nigricans* and where many basiphilous pioneer species were found between the *Schoenus* tussocks. The moss layer was also well developed. Species of late successional stages such as *Calamagrostis epigejos, Salix repens* and *Oxycoccus macrocarpos* were already present, though with a low cover.

Table 1 shows that the grasses *Agrostis stolonifera* and *Calamagrostis epigejos* responded to both N- and P-addition. Lammerts et al. (1997) also found a clear interaction of N- and P-addition for these two productive species, which suggests a co-limitation for N and P. This explains the significant increase in total above-ground biomass after a full NPK-addition (Table 1). *Schoenus nigricans* did not react on the addition of any of the macronutrients.

Addition of only nitrogen led to a significant, though much smaller increase in biomass of the grass species and yet to a significant increase in total biomass. This latter response appears to be caused also by a significant increase in biomass of many other component species of the vegetation : *Carex* species (mainly *Carex flacca*), *Juncus* species, several characteristic *Schoenetum* species and even a late successional species such as *Oxycoccus macrocarpos*.

The soil-pH values in these youngest two Koegelwieck stages were relatively high, which is remarkable since the top soil was completely decalcified. The near neutral pH conditions were maintained here by occasional discharge of base-rich groundwater (Sival 1996). The organic matter content and the nutrient pools measured in this stage were comparable to the values found in the Reggers Sandersvlak (Table 2).

Discussion

The experimental designs

Though the experimental designs differ considerably between fertilization experiments, the results give a consistent picture. Except for the study of Willis (1963) the conclusions of the experiments had a sound statistical basis deduced from the application of One-way Analyses of Variance on treatments.

Willis (1963), Dougherty et al. (1990) and Lammerts et al. (subm.) applied a full factorial design with all possible combinations of nutrient addition. This is more informative on co-limitation of different nutrients because multiple limitations can be tested statistically by performing a three-way Analysis of Variance on the N, P and K-additions (Lammerts et al. 1997).

To explain vegetation development in relation to nutrient limitation it appears to be important not only to measure the response of total biomass but of individual species as well. In this respect the studies from Dougherty et al. (1990) and Olff et al. (1993) were less informative than the other studies.

Nutrient limitation in wet dune slacks

All fertilization experiments in the species-rich pioneer communities of the *Junco baltici-Schoenetum nigricantis* association showed a significant increase in total above-ground biomass after a combined NPK-addition. Basiphilous pioneer species tended to decrease or even disappeared.

Single N-additions in the species-rich pioneer stages led to an increase of several *Carex* and *Juncus* species, sometimes together with an increase of other basiphilous pioneer species. Willis (1963) explained such a response by pointing to the very low P-requirement of, for instance, *Carex flacca*. This gives the species a competitive advantage above species with higher P-requirements. Most case studies, however, also showed an increase of grasses when only N is added. In the long run these grasses will be more competitive towards some of the smaller basiphilous pioneer species. Conclusively, it may be expected that a temporarily increase of basiphilous pioneer species, followed by a decrease, will occur when only N-limitation is lifted, for instance by an increased atmospheric deposition of NO_3 and NH_4.

Significant effects of P-addition have only been demonstrated as a result of the Three-way Analysis of Variance in the Koegelwieck experiments. In the youngest stage, Koegelwieck I, total biomass production increased, while in the Koegelwieck II experiment there was a significant increase of grass species. This again indicates that a complete replacement of basiphilous pioneer species by grasses in the course of successional change may be retarded when P-limitation continues.

Single K-additions had no effect on total aboveground biomass nor was any significant response of individual species observed.

From these results the picture emerges that a simultaneous increasing availability of N and P, as usually occurs in young dune slacks, will accelerate vegetation succession. Under such conditions the moss layer decreases and most small character species of basiphilous vegetation types disappear, probably due to increased competition for light and nutrients by more productive grass species (Tilman 1988; Olff et al. 1993).

Nutrient pools and nutrient deficiency

The above described patterns in N- and P-deficiencies during dune slack succession can only partly be explained by differences in nutrient pools in the soil.

The N- and P-contents found in the youngest stage (2 years old) of the Koegelwieck, the site where the effects of P-limitation were most obvious, are extremely low. The percentage of organic matter is less than 0.5 %. Nitrogen which is organically bound is most likely in very short supply (ca. 0.01 %). Total phosphorus contents are equally low (0.011 %). Most of it is chemically bound (Walker & Syers 1976) and the availability of phosphates is expected to be very low, especially at a high pH (Ponnamperuma 1972).

Most other case studies discussed in this paper showed organic matter contents of less than 10 %, with N-contents less than 0.2 % and P-contents less than 0.02 %. These values are intermediate (N) or at the lower end (P) of the ranges given by Etherington (1982) for natural dune slack soils (N: 0.01 - 0.25%, P: 0.02 -0.5 %), which stresses the pioneer character of most of the sites. Despite their low P-contents all these sites were primarily N-limited, although the majority showed secondary P-limitation.

Influence of plant species on nutrient limitation

In natural dune slacks the nutrient status is predominantly controlled by water table fluctuations (Armstrong 1975). High water tables keep the mineralisation of organic matter at a low level, leading to suitable conditions for dune slack plants with low N and P requirements. Nutrient contents in soils supporting very similar vegetation types may, however, vary enormously. Lammerts et al. (1995) found that stands dominated by *Schoenus nigricans* occurred in dune slacks within a wide range of organic matter percentages in the topsoil (5 - 40 %). Under natural conditions some mechanisms apparently keep the nutrient availability within a more or less stable range, although the nutrient pools in the soil may differ considerably. The observation that nutrient additions do not always lead to the expected increases in soil concentrations (Boorman & Fuller 1982) corroborates this idea.

The low nutrient availability may partly be the result of chemical interactions in the soil, but there is growing evidence that several dune slack plants with specific adaptations to waterlogging play a crucial role in keeping the nutrient availability for basiphilous pioneer species at a low level (Schat 1982; van Beckhoven 1995). *Schoenus nigricans*, for instance, which is often abundant in pioneer stages of calcareous dune slacks, can establish under very nutrient-poor conditions and yet produce a high biomass. This may lead to a high retention of nutrients. Yet *Schoenus nigricans* appears to be facilitating small basiphilous dune slack species instead of competing them (Schat 1982). At the same time *Schoenus nigricans* seems to counteract the establishment and growth of more productive species, especially grasses (van Beckhoven 1992, 1995).

Competition for light will not play an important role. Due to the narrow leaves and stems even large tussocks of *Schoenus nigricans* do not intercept much light. Moreover, a decrease in light fall on the surface would favour tall grasses when outcompeting small pioneer plants. It is probably more important that *Schoenus nigricans* is capable of radial oxygen loss (ROL) under waterlogged conditions (Armstrong 1975; Schat 1982; Ernst & van der Ham 1988; van Beckhoven 1995). This keeps the redox potential in the rooting zone high and may be an advantage for basiphilous pioneer species without special adaptations to waterlogging (Schat 1982). Furthermore van Beckhoven (1995) suggested that radial oxygen loss by *Schoenus nigricans* will decrease phosphate availability because of the high redox potential it creates (Patrick & Khalid 1974). This could also be the reason that *Schoenus nigricans* facilitates the growth of basiphilous pioneer species.

The adverse conditions for grasses (especially *Calamagrostis epigejos*) may also be caused by the low phosphate availability. For *Schoenus nigricans* itself this is not a problem because it has most of its phosphate supply in its tussock (Ernst 1991). Furthermore, unlike *Calamagrostis*, *Schoenus* has a low P-requirement (Ernst 1991), so a decrease in phosphate availability is very disadvantageous for *Calamagrostis*. Whatever the reasons are, in experimental waterlogged conditions *Schoenus nigricans* appeared to dominate over *Calamagrostis epigejos*, while this species under the same conditions became very dominant in the absence of *Schoenus* (van Beckhoven 1992, 1995).

Lammerts et al. (1997) found that *Schoenus nigricans* did not show a significant reaction on nutrient addition in any of the experiments. Neither is there an indication that its abundance interferes in any way with the effects of nutrient additions. *Calamagrostis epigejos* responded vigourously to N and P-additions. Probably, the conditions which are supposed to suppress the growth of productive grasses when *Schoenus nigricans* is present, are changed by the addition of mineral nutrients.

Implications for management and research

Natural succession will always bring basiphilous pioneer stages to an end eventually. However, the results of fertilization experiments stress the importance of nutrient-poor conditions in dune slacks when basiphilous pioneer species are to be maintained as long as possible.

Nowadays the increased atmospheric deposition brings nitrophilous species to dominance in an earlier stage of succession. On the level of nature management little can be done to solve this problem. However, the fact that P-limitation appears to be capable to slow down the development of productive grasses, while it, at least temporarily, stimulates basiphilous pioneer species, is important from a management point of view. When the latter species are still present, it will be crucial to maintain P-limitation. A yearly mowing regime may then be a good measure. Also the maintenance of a high pH by buffering is important because this keeps P-availability on a relatively low level (Etherington 1982; Lammerts et al. subm.). For this purpose any interference with the hydrological system, especially lowering water tables, should be prevented, because in dune slacks hydrological regimes often control buffer mechanisms in the top soil (Stuyfzand 1993; Sival 1996).

When nutrient accumulation has proceeded so far that it has resulted in the development of a closed layer of grasses, then a basiphilous pioneer vegetation can only be regenerated by the complete removal of the organic layer.

For management purposes a more detailed knowledge of the responses of individual basiphilous species on P-limitation is of interest. Experimental research as well as further fertilization experiments, especially when directed to species responses on full-factorial treatments, may contribute hereto. Probably, research on nutrient concentrations in plant tissue (cf. Koerselman 1992), measured per species, also generates more insight in this respect.

References

Armstrong, W. 1975. Waterlogged soils. In: Etherington, J.R. (ed.) *Environment and plant growth*, pp. 181-218. Wiley, London.

Boorman L.A. & Fuller, R.M. 1982. Effects of added nutrients on dune swards grazed by rabbits. *J. Ecol.* 70: 345-355.

Croese, T.H.M. 1995. *Reacties van duinvalleivegetaties op het aanbod van voedingsstoffen*. Kiwa-rapport SWE 94.044, Nieuwegein.

Doing-Huis in 't Veld, C.J. 1977. *Literatuuronderzoek naar het ontstaan en de geschiedenis van de duinen op het eiland Schouwen.* Deltadienst Rijkswaterstaat, Middelburg.

Dougherty, K.M., Mendelssohn, I.A. & Montferrante, F.J. 1990. Effect of nitrogen, phosphorus and potassium additions on plant biomass and soil nutrient content of a swale barrier strand community in Louisiana. *Ann. Bot.* 66: 265-271.

Ernst, W.H.O. 1991. Ökophysiologie von Pflanzen in Küstendünen Europas in einem Gradienten von der Nordsee zum Mittelmeer. *Ber. R. Tüxen Ges.* 3: 157-172.

Ernst W.H.O. & van der Ham, N.F. 1988. Population structure and rejuvenation potential of *Schoenus nigricans* in coastal wet dune slacks. *Acta Bot. Neerl.* 37: 451-465.

Ernst, W.H.O., Slings, A.L. & Nelissen, H.J.M. 1996. Pedogenesis in coastal wet dune slacks after sod cutting in relation to revegetation. *Plant Soil* 180: 219-230.

Etherington, J.R. 1982. *Environment and plant ecology.* 2nd ed. John Wiley, Chichester.

Geelen, L.H.W., Cousin, E.F.H. & Schoon, C.F. 1995. Regeneration of dune slacks in the Amsterdam Waterwork Dunes. In : Healy, M.G. & Doody, J.P. (eds.) *Directions in European coastal management*, pp. 525-532. Samara Publishing Limited, Cardigan.

Gerlach, A., Albers, E.A. & Broedlin, W. 1994. Development of the nitrogen cycle in the soils of a coastal dune succession. *Acta Bot. Neerl.* 43: 189-203.

Jelgersma, S. 1983. The Bergen inlet, transgressive and regressive holocene shoreline deposits in the northwestern Netherlands. *Geol. Mijnbouw* 62: 471-486.

Jungerius, P.D., Koehler, H., Kooijman, A.M., Mücher, H.J. & Graefe, U. 1995. Response of vegetation and soil ecosystem to mowing and sod removal in the coastal dunes

"Zwanewater", The Netherlands. *J. Coast. Cons.* 1: 3-16.
Kachi, N. & Hirose, T. 1983. Limiting nutrients for plant growth in coastal sand dune soils. *J. Ecol.* 71: 937-944.
Kellman, M. & Roulet, N. 1990. Nutrient flux and retention in a tropical sand dune succession. *J. Ecol.* 78: 664-676.
Koerselman, W. 1992. The nature of nutrient limitation in Dutch dune slacks. In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington, M.J. (eds.) *Coastal dunes*, pp. 189-199. Balkema, Rotterdam.
Koerselman, W. & Meuleman, A.F.M. 1994. *Groeibeperkende voedingsstoffen in verschillende duinvalleitypen*. Kiwa-rapport SWE 94.020, Nieuwegein.
Koerselman, W. & Stuyfzand, P.J. 1993. *Chemie van ondiep grondwater en bodem in relatief ongestoorde natte en vochtige duinvalleien*. Kiwa-rapport SWE 93.010, Nieuwegein.
Lammerts, E.J., Sival, F.P., Grootjans, A.P. & Esselink, H. 1992. Hydrological conditions and soil buffering processes controlling the occurrence of dune slack species on the Dutch Wadden Sea islands. In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington, M.J. (eds.) *Coastal dunes*, pp. 265-272. Balkema, Rotterdam.
Lammerts, E.J., Grootjans, A.P., Stuyfzand, P.J. & Sival, F.P. 1995. Endangered dune slack plants; gastronomers in need of mineral water. In: Salman, A.H.P.M., Berends, H. & Bonazountas, M. (eds.) *Coastal management and habitat conservation*, pp. 355-369. EUCC, Leiden.
Lux, H. 1964. Die biologische Grundlagen der Strandhaferpflanzung und Silbergrasansat im Dünenbau. *Angew. Pflanzensoz.* 20: 6-53.
Olff, H., Huisman, J. & van Tooren, B.F. 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *J. Ecol.* 81: 693-706.
Patrick, W.H. & Khalid, R.A. 1974. Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science* 186: 53-55.
Pemadasa, M.A. 1983. Effects of added nutrients on the vegetation of two coastal grasslands in the dry-zone of Sri Lanka. *J. Ecol.* 71: 725-734.
Ponnamperuma, F.N. 1972. The chemistry of submerged soils. *Adv. Agron.* 24: 29-96.
Schaminée, J., Weeda, E.J. & Westhoff, V. 1995. *De vegetatie van Nederland*. *Deel 2*. Opulus Press, Uppsala, Leiden.
Schat, H. 1982. *On the ecology of some Dutch dune slack plants*. Doctoral Thesis, Free University of Amsterdam.
Sival, F.P. 1996. Mesotrophic basiphilous communities affected by changes in soil properties in two dune slack chronosequences. *Acta Bot. Neerl.* 45: 95-106.
Stuyfzand, P.J. 1993. *Hydrochemistry and hydrology of the Coastal Dune area of the western Netherlands*. Doctoral Thesis, Free University of Amsterdam. KIWA, Nieuwegein.
ten Harkel, M.J. & van der Meulen, F. 1996. Impact of grazing and atmospheric deposition on the vegetation of dry coastal dune grasslands. *J. Veg. Sci.* 7: 445-452.
Tilman, D. 1988. *Dynamics and structure of plant communities*. Princeton University Press, Princeton.
van Beckhoven, K. 1992. Effects of groundwater manipulation on soil processes and vegetation in wet dune slacks. In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington, M.J. (eds.) *Coastal dunes*, pp. 251-263. Balkema, Rotterdam.
van Beckhoven, K. 1995. *Rewetting of coastal dune slacks: effects on plant growth and soil processes*. Doctoral Thesis, Free University of Amsterdam.
van Dieren, J.W. 1934. *Organogene Dünenbildung, eine geomorphologische Analyse der westfriesischen Insel Terschelling mit pflanzensoziologischen Methoden*. Doctoral Thesis, Amsterdam. Nijhoff, The Hague.
van Dijk, H.W.J. & Grootjans, A.P. 1993. Wet dune slacks: decline and new opportunities. *Hydrobiologia* 265: 281-304.
van der Meulen, F. 1982. Vegetation changes and water catchment in a Dutch coastal dune area. *Biol. Conserv.* 24: 305-316.
van der Meijden, R., Weeda, E.J., Holverda, W.J. & Hovenkamp, P.H. 1990. *Heukels' Flora van Nederland*. 21st. ed. Wolters-Noordhoff, Groningen.
Verhoeven, J.T.A., Wassen, M.J., Meuleman, A.F.M. & Koerselman, W. 1994. Op zoek naar de bottleneck; N- en P-beperking in venen en duinvalleien (English summary). *Landschap* 11: 25-39.
Vitousek, P.M. & Walker, R.W. 1987. Colonization, succession and resource availability: Ecosystem-level interactions. In: Gray, A.J., Crawley, M.J., & Edwards, P.J. (eds.) *Colonization, succession and stability*, pp. 207-223. Blackwell, Oxford.
Walker, T.W. & Syers, J.K. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15: 1-19.
Westhoff, V. & van Oosten, M.F. 1991. *De plantengroei van de Waddeneilanden*. Natuurhistorische bibliotheek KNNV, Utrecht.
Willis, A.J., Folkes B.F., Hope-Simpson, J.F. & Yemm, E.W. 1959. Braunton Burrows: the dune system and its vegetation, Part I. *J. Ecol.* 47: 1-24.
Willis, A.J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.* 51: 353-374.

Received 16 January 1996;
Revision received 20 January 1997;
Accepted 3 February 1997.