15 Environmental Problems and Restoration Measures in Coastal Dunes in The Netherlands

A.M. Kooijman

15.1 Introduction

The more than 350-km-long coastal dune zone forms one of the last large semi-natural areas in The Netherlands and is home to some 70 % of the plant species occurring in this country, of which many are almost exclusive. The vegetation consists to a large part of open, species-rich dune grasslands belonging to the plant communities *Phleo-Tortuletum, Anthyllido-Silenetum, Taraxaco-Galietum, Festuco-Galietum* and *Violo-Corynephoretum* (Schaminee et al. 1996). However, during the last decades grass-encroachment has transformed the species-rich dune grasslands into monospecific stands of tall grasses (Weeda et al. 1994; Kooijman and de Haan 1995; Fig. 15.1). While increases in biomass and changes in species richness naturally occur in the course of succession, the loss of species diversity seemed unnaturally high. This was attributed, similar to other Dutch ecosystems (Aerts 1989; Bobbink 1989), to increased atmospheric deposition, which may amount to 30 kg N/ha annually (Dopheide and Verstraten 1995). However, since the effect of high N availability also depends on the availability of P, the ecosystem responses appeared to differ between dune districts and successional stages with different soil chemistry. The goal of this chapter is to give an overview of how grass-encroachment could have developed in the lime-rich and lime-poor dune areas of the Netherlands and which restoration measures are effective against it. Both aspects were studied as part of the larger Dutch restoration program 'Restoration plan forest and nature (OBN)'. Detailed methods and results are given in Kooijman and de Haan (1995), van der Meulen et al. (1996), Veer (1997, 1998), Veer and Kooijman (1997), Kooijman et al. (1998, 2000) and Kooijman and Besse (2002).

Ecological Studies, Vol. 171
M.L. Martínez, N.P. Psuty (Eds.)
Coastal Dunes, Ecology and Conservation

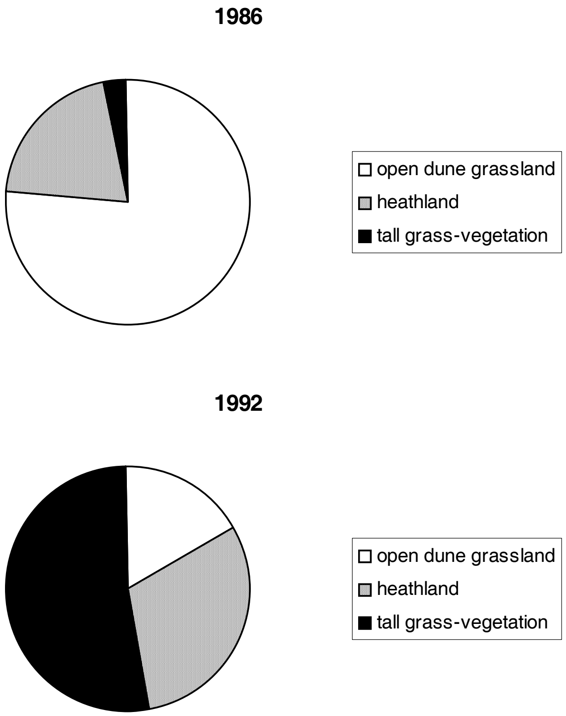

Fig. 15.1. The decrease in species-rich dune grassland from 1986 to 1992 in a 50 ha ungrazed part of the Zwanenwater area, Wadden district. Data from Kooijman and de Haan (1995)

15.2 Differences Between Renodunaal and Wadden Districts

The Dutch dunes are separated into two different districts: the lime-poor Wadden district in the north and the lime-rich Renodunaal district in the south. Both districts are representative of European coastal dune areas north and south of the Netherlands. Whereas in Chapter 6 (Grootjans et al.) the wet dune slacks are treated, the present study concentrates on the dry dunes, which comprise approximately 65 % of the total dune area.

The Renodunaal and Wadden district are distinguished on the basis of their differences in initial lime content, but also because of the mineral composition of the sand. In the Renodunaal district initial lime content ranges from 2–10 %, while in the Wadden district these values rarely exceed 1 % (Eisma 1968). The Renodunaal district has approximately 15-fold higher amounts of amorphic iron and aluminium (hydr)oxides than the Wadden district (Eisma 1968; Kooijman et al. 1998).

Apart from differences between districts, successional stages are important as well. In the lime-rich Renodunaal district three main soil types can be distinguished: (1) calcareous soils with high pH, (2) soils in which the topsoil has become decalcified, but part of the root zone is still calcareous and (3) soils decalcified to more than 1 m depth which have become acid. Because of the low initial lime content in the Wadden district the calcareous and partly decalcified soils are limited to a very small zone near the sea.

Several tall grass species are involved in grass-encroachment, each dominating under particular conditions (Weeda et al. 1994). In the Renodunaal district, *Elytrichia atherica* (Link) Carreras Mart. is a dominant species in calcareous soils and *Calamagrostis epigejos* (L.) Roth in decalcified soils. In the Wadden district, *Ammophila arenaria* (L.) Link is the main invading species.

15.3 Impact of Availability of P on Biomass Production and Successional Trends

15.3.1 Renodunaal District

In the lime- and iron-rich Renodunaal district plant biomass production seems to be primarily regulated by the availability of P (Kooijman et al. 1998; Kooijman and Besse 2002). Aboveground productivity, N-mineralization and P-mineralization values showed a peak around pH 5 (Fig. 15.2). The correspondence between N-mineralization and biomass production is not surprising, since these two factors can be closely coupled (e.g., Veer 1997; Neitzke 1998), but the peak at a particular pH is more difficult to explain. At high pH mineral N mainly occurs as nitrate and at low pH as ammonium, but both are highly soluble at all pH values.

The productivity peak at pH 5 corresponds very well, however, with the chemical behaviour of phosphate (Lindsay and Moreno 1966). In calcareous soils with pH>6.5 P-availability is low due to fixation in calcium phosphates, which is shown by the negative 'mineralization' values. In partly decalcified soils with pH 5 calcium phosphates have dissolved and become available to plant roots. This is indicated by the decrease in mineral-P from calcareous to partly decalcified soils (Kooijman et al. 1998), but especially by the high P-'mineralization' (Fig. 15.2). In decalcified soils P-availability is low again due to the chemical fixation in iron and aluminium phosphates.

This suggests that the biomass production in the Renodunaal district is primarily regulated by the P-availability. The peak in N-mineralization at pH 5 may be explained as a response to the increase in biomass production (and litter production) allowed by the higher P-availability. This increase in natural fertility corresponds with the large-scale formation of shrubland especially in this dune zone (e.g., Westhoff et al. 1970; Doing 1988). It also suggests that in this zone species-rich dune grasslands may not be a permanent stage, but be maintained only when the vegetation is kept short by grazers.

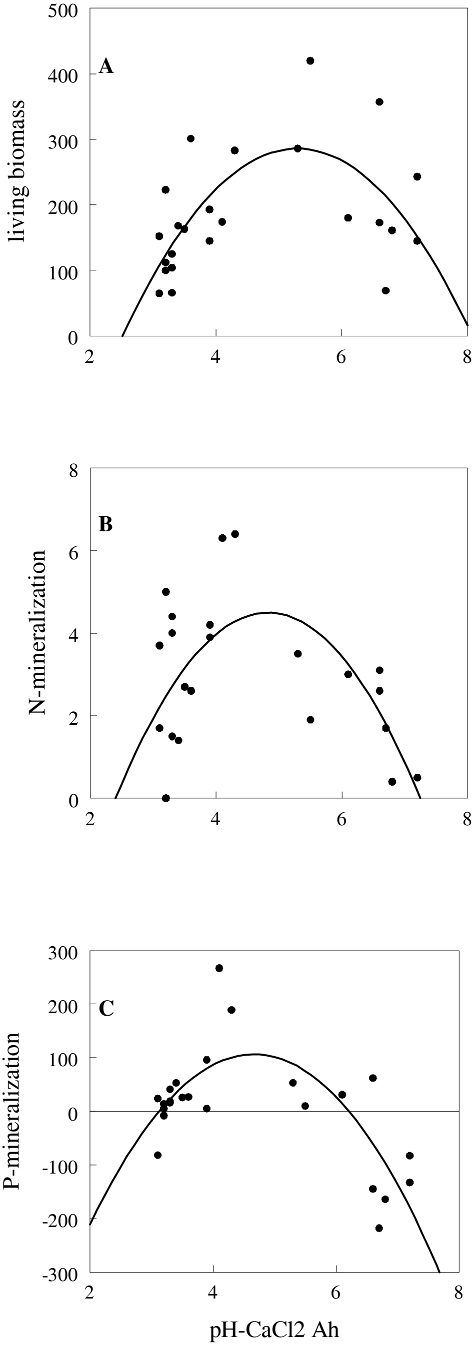

Fig. 15.2. Biomass production and nutrient availability in coastal dune grasslands over a pH-gradient in the Renodunaal district. **A** Aboveground biomass production (g m^{-2}) in July measured in exclosures (r=0.61), **B** in situ N-mineralization (g m^{-2}) measured over the period April–October(r=0.61) and **C** in situ P-mineralization (mg m^{-2}) over the same period (r=0.56). Data are derived from Kooijman and Besse (2002). All three correlations are significant (p<0.05)

Regulation of plant biomass production by the availability of P suggests that the Renodunaal district is not very sensitive to atmospheric deposition of N. However, increased atmospheric deposition is probably a very important factor when both acid and nitrogen deposition are taken into account. Acid deposition leads to increased decalcification and dissolution of calcium phosphates, whereas nitrogen deposition simultaneously increases N-availability. The higher availability of both nutrients stimulates biomass production. This in turn not only increases internal acidification of the soil through root exchange processes and higher litter decomposition, but also increases N-mineralization, thus further stimulating plant productivity. This implies that increased atmospheric deposition may not change the direction, but nevertheless accelerates succession from calcareous to decalcified dunes. Because many characteristic plant and animal species prefer open calcareous dune grasslands, this is a problem for nature conservation.

15.3.2 Wadden District

Although in a different way, the availability of P is also a key-factor in regulating biomass production and response to atmospheric deposition in the Wadden district (Kooijman et al. 1998; Kooijman and Besse 2002). Foliar N/P ratios, which are 11 for both open dune grassland and tall grass vegetation, suggest that the vegetation is limited by N instead of P (Koerselman and Meuleman 1996). This is also illustrated by the P-mineralization rates, which are about ten times higher than the values in the (equally acid) decalcified soils of the Renodunaal district. This can be partly ascribed to the very low levels of inorganic iron and aluminium (hydr)oxides. As a result, chemical P-fixation in iron and aluminium phosphates is limited. Instead, phosphate is basically bound to iron and aluminium-organic matter complexes, which are much more reversible bindings (Scheffer 1982). The high P-availability implies that the ecosystem is relatively N-limited and sensitive to atmospheric N-deposition.

15.4 Mineralization of Nitrogen

15.4.1 Impact of Litter Production

Cycling of N seems to be more rapid in the Wadden district: N-mineralization rates were two to four times higher than in the Renodunaal district. In theory, this can be attributed to a number of factors. N-mineralization may be regulated by the input of litter. In the Wadden district the relationship between N

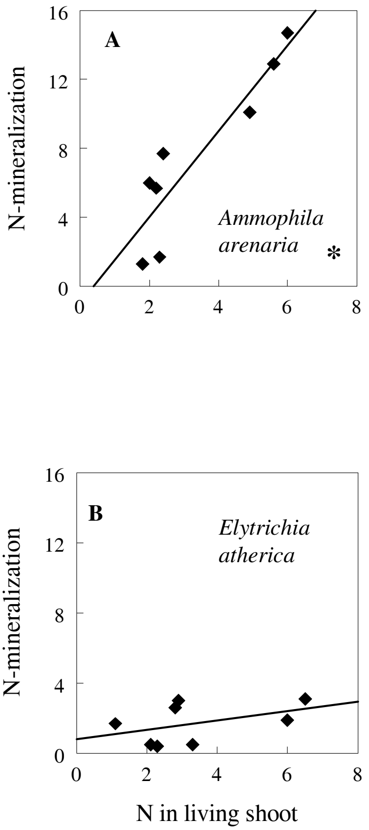

Fig. 15.3. Relationship between N in the living aboveground vegetation (g m^{-2}) in exclosures as indicator for plant performance and in situ N-mineralization over the period April–October (g m^{-2}) in coastal dune grasslands. **A** Wadden district with *Ammophila arenaria* (r=0.91); **B** calcareous soils in Renodunaal district with *Elytrichia atherica* (r=0.45). Data derived from Kooijman and Besse (2002). * Significant correlation (p<0.05)

in biomass and N-mineralization appeared to be very strong indeed (Fig. 15.3). However, the amount of N in litter cannot explain the higher N-mineralization compared to the Renodunaal district, since this was about the same in both districts.

Rates of N-mineralization have been reported to increase over a successional dune gradient, due to the accumulation of soil organic matter and the development of a N-cycle in the soil (Gerlach et al. 1994). However, this cannot explain the higher N-mineralization values in the Wadden district, since soil organic matter contents were about the same in both districts. N-mineralization may also increase with increased atmospheric deposition (Sjöberg and Persson 1998). However, this cannot explain the higher N-mineralization values in the Wadden district, because atmospheric N-deposition is lower instead of higher than in the Renodunaal district (Dopheide and Verstraten 1995).

15.4.2 Impact of Litter Decomposition

The key to the high N-mineralization rates in the Wadden district seems to lie in the mechanism of litter decomposition, although in a different way than usually assumed. In the 'common wisdom' low decomposition leads to low N-mineralization rates and vice versa (Swift et al. 1979, Lambers et al. 1998, Aerts and Chapin 2000). The reasoning behind this is that a high biological activity leads to a rapid turnover of carbon, and as such of nutrients. Also, differences in C/N ratio between litter and micro-organisms are smaller in highly degradable litter with high N-concentrations, which supposedly means that microbial N-need is satisfied earlier in the breakdown process and net N-mineralization rates are higher.

However, in the coastal dunes the relationship between litter decomposition and N-mineralization seems to be negative instead of, as expected, positive (Kooijman and Besse 2002). The lowest values for litter decomposition and highest for N-mineralization were found in the Wadden district, while the Renodunaal district showed the opposite (Fig. 15.4). The combination of low decomposition and high N-mineralization and vice versa does not seem to be unique for the Dutch coastal dunes, but has been reported from calcareous-acid fens as well (Verhoeven et al. 1988, 1990). Also, N-mineralization appeared to be four times higher in acid than in calcareous beech forests (Davy and Taylor 1974).

The above suggests that acid soils with low-degradable litter are characterized by a high instead of low N-availability to the vegetation. This may be due to a lower microbial N-demand because of the lower overall biological activity, but also because in low-degradable litter the C-limitation stage is reached

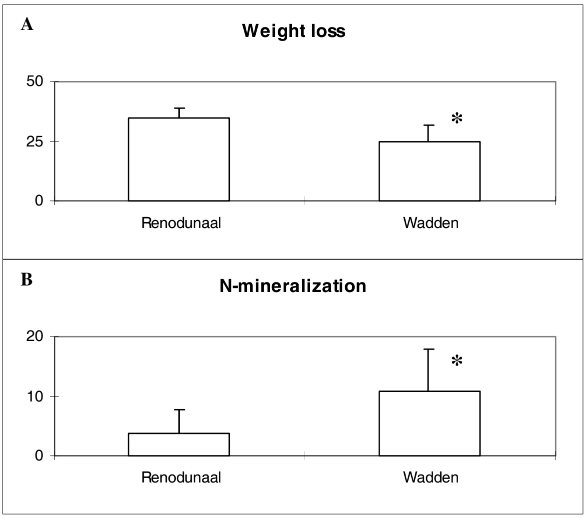

Fig. 15.4. Litter breakdown and N-mineralization in coastal dune grasslands dominated by tall grasses. **A** Weight loss after 1 year (%); **B** N-mineralization in the period April–October (g m^{-2}). Mean values (n=12 for Renodunaal and n=4 for Wadden district) and standard deviations. Data derived from Kooijman and Besse (2002). * Significant differences between dune districts

at higher C/N ratios (Berg and Ekbohm 1983; Berg and McClaugherty 1987), i.e., earlier in the decomposition process. In addition, microbial C/N ratios are higher (and N-demand lower) in soils unfavourable for decomposition (Hassink 1994; Hassink et al. 1993). A relatively large attribution of N to the vegetation instead of soil microbes may also explain the strong relationship between litter input and N-mineralization for *A. arenaria*, as opposed to the weak one for *E. atherica* (Fig. 15.3).

15.5 Role of *Ammophila arenaria* in the Wadden District

Grass encroachment, once started, follows its course driven by positive feedback mechanisms (Veer and Kooijman 1997). The large aboveground biomass of tall grasses increases root biomass and nutrient uptake capacity. The large biomass also increases litter input and therefore N-mineralization and nutrient availability. Both factors lead to enhanced nutrient uptake and even higher biomass production. The effect on smaller species in the vegetation is obvious: strongly reduced light availability and poor survival.

In the Wadden district these feedback mechanisms are aggravated by specific characteristics of *A. arenaria*. This species has low foliar N-levels and a high Nutrient Use Efficiency (Pavlik 1983), which means a relatively low N-need per unit biomass and thus a high biomass production. Its low N and high C content also lead to low-degradable leaves. As a result dead material stays on the plant for a relatively long time, thus further reducing light availability to smaller species. The low-degradable litter also seems to lead to a low microbial N-demand and a relatively high N-availability to plants. While in the Renodunaal district annual N-mineralization was estimated to be 1–5 % of total soil N, in the *Ammophila*-dominated plots in the Wadden district this amounted to 18 % (Kooijman et al. 2000).

In the Wadden district biomass production could already be high due to the relatively high P-availability and the response to increased atmospheric N-deposition. The low N-demand per unit biomass and the efficient recycling of N in the soil further contribute to the explosion of *A. arenaria* throughout most of the Wadden district.

15.6 Restoration

The effects of atmospheric deposition, grass-encroachment and enhanced succession may be counteracted by management practices. One way to accomplish this is directed towards removing aboveground biomass, e.g., by annual mowing and grazing by cattle. The second way is to develop new substrates, in order to set back succession of vegetation and soil, e.g. by sod-cutting and the stimulation of aeolian activity. Methods and results are briefly discussed below; the details are given in van der Meulen et al. (1996), Veer (1997, 1998) and Kooijman et al. (2000).

15.6.1 Effect of Grazing and Annual Mowing

A comparison of four Dutch coastal dune areas where mowing was applied for seven years and nine which were grazed by cattle for five years or more suggests that both measures are effective to counteract grass-encroachment (Fig. 15.5). Mean aboveground biomass was significantly reduced at all sites where mowing or grazing was applied. Available light at the soil surface was 3–5 % of full sunlight in the untreated tall-grass vegetation and increased significantly after mowing or grazing. Both measures increased species richness per square metre.

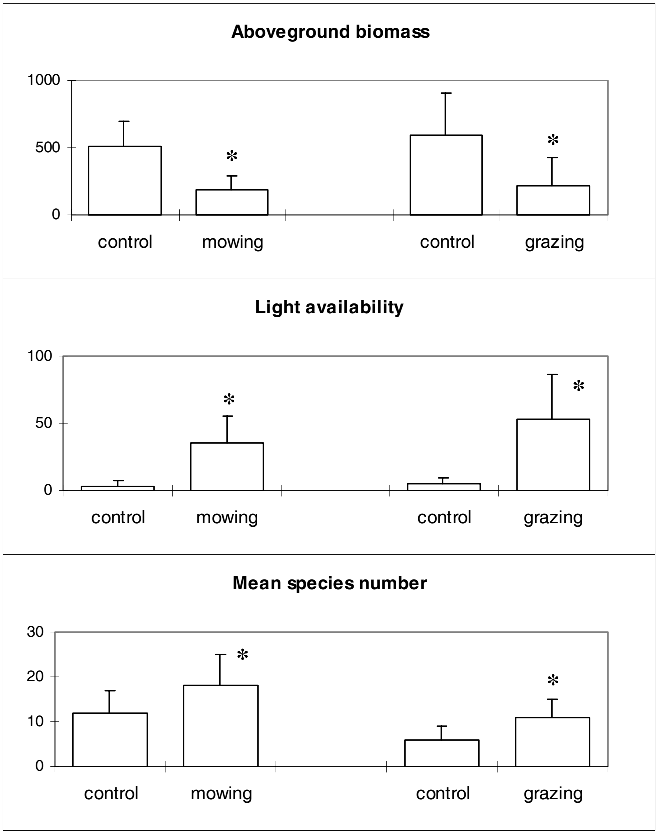

Fig. 15.5. Effect of annual mowing and grazing by cattle on aboveground biomass (g m^{-2}), light availability (% full daylight) and species number (mean number of plant species m^{-2}) in coastal dune grasslands dominated by tall grasses. Data derived from Kooijman et al. (2000). Mean values (n=4 for mowing and n=9 grazing) and standard deviations. * Significantly different from the associated control treatment (p<0.05)

The reduction in aboveground biomass thus clearly leads to improved conditions for small species in the understorey. However, for long-term ecosystem functioning and the development of management plans it is important to know whether this is only due to the temporary removal of biomass, or also due to a reduction in productivity as a result of reduced litter input. The latter would especially harm tall grasses, which have a higher nutrient demand (Veer and Kooijman 1997). Reduced input of litter and as such of nutrients to the soil would theoretically lead to a reduction in N-mineralization and biomass production. In this way competition between tall grasses and smaller herbs would change from light to nutrients (Olff and Ritchie 1998).

A reduction in N-mineralization and aboveground biomass production by grazing was indeed detected in the Wadden district (Fig. 15.6). Also, the area of tall-grass vegetation decreased in favour of species-rich dune grassland (ten Haaf 1999a). In the Renodunaal district, however, N-mineralization was only affected in decalcified soil and biomass production not at all. Also, the area of tall-grass vegetation did not decrease and development of shrubland continued despite the grazing regime in calcareous and partly decalcified

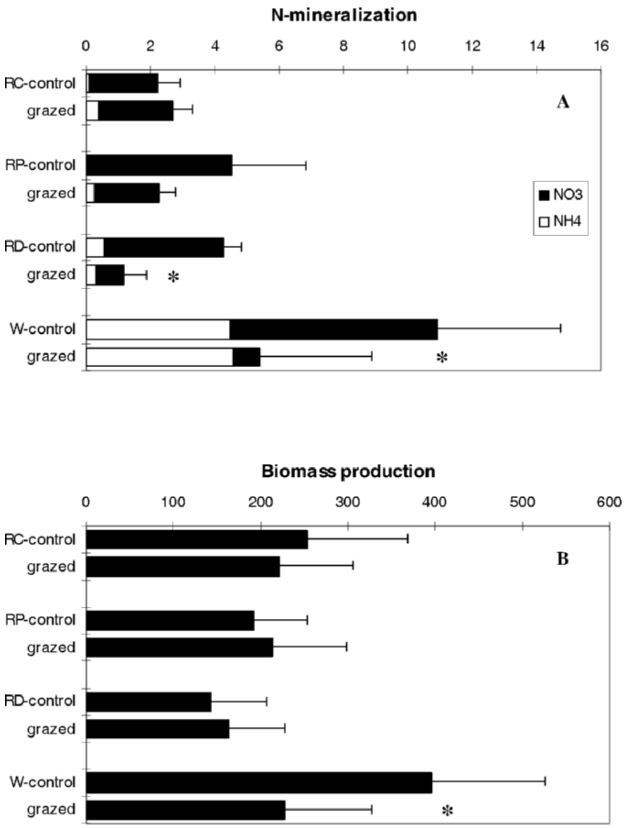

Fig. 15.6. The effect of grazing on nutrient availability and productivity in coastal dune grasslands dominated by tall grasses. **A** N-mineralization (NO_3+NH_4) from April–October (g m^{-2}) and **B** biomass production in July (g m^{-2}). *RC* Renodunaal district, calcareous soils; *RP* Renodunaal district, partially decalcified soils; *RD* Renodunaal district, soils decalcified to more than 1 m; *W* Wadden district. Data derived from Kooijman et al. (2000). Mean values (n=4) and standard deviations. * Significantly lower values in grazed plots (p<0.05)

dune zones (ten Haaf 1999b; Everts et al. 2000). Annual mowing, which was only studied in the Renodunaal district, did also not lead to changes in nutrient availability in calcareous and partly decalcified soils. In a decalcified site with high P-availability due to former agricultural practices, however, the mown treatment strongly indicated N-limitation. The above suggests that acid soils with low-degradable litter respond more strongly to management practices than calcareous soils.

While annual mowing and grazing by cattle are primarily applied to counteract grass-encroachment, they may reduce succession in calcareous and partly decalcified soils, because soil acidification is higher in highly productive systems. Over a seven year-period soil pH values had decreased in the tall-grass control treatments with 0.5–1 in calcareous and partially decalcified soisl respectively, but were about the same as before in the mown treatments. This suggests that removal of aboveground biomass retards soil acidification and further succession at least to some degree.

15.6.2 Effect of Sod-Cutting

Sod-cutting naturally leads to a decrease in soil organic matter and nutrient stocks and an increase in soil pH. It also led to a decrease in nutrient availability and biomass production. After seven years vegetation cover was still below 100 %, mean light availability at the soil surface (41 %) was higher than in the tall-grass control treatments (3 %) and the total number of species had increased from 27 to 42 (Fig. 15.7). However, not all results were positive. In the calcareous soils the establishment of the shrub *Hippophae rhamnoides* L. may give rise to the development of shrubland instead of dune grasslands. In the partly decalcified soil calcicole species, which were still present in the grass-dominated control treatments, did not re-establish. Thus, because of these potentially unfavourable side effects, sod-cutting should be applied with some care.

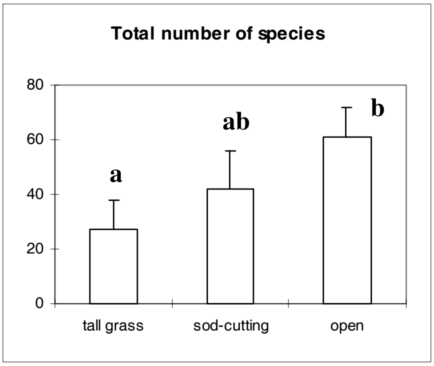

Fig. 15.7. Effect of sod-cutting on total species number in dune grasslands. *Tall grass* Untreated control plots in tall-grass vegetation; *sod-cutting* plots where sod-cutting was applied seven years earlier; *open* open, species-rich dune grassland used as reference vegetation. Data derived from Kooijman et al. (2000). Mean values (n=4) and standard deviations. *Different letters* indicate significant differences (p<0.05)

15.6.3 Effect of Increased Aeolian Activity

Until very recently, blow-outs in coastal dunes were stabilized as much as possible and since the 1950s the area of aeolian dynamic dunes have strongly decreased. During the last decades nature management organisations, however, began to realize that the loss of aeolian dynamics and lack of rejuvenation may be a loss for the dune ecosystem as a whole.

Monitoring of blow-outs over the past twenty years suggests that they do not expand very rapidly, which is in line with van der Meulen and Jungerius (1989). Two dune areas in the Renodunaal district where fixation practices were abandoned around 1980 showed an increase in aeolian activity from 1980 to1990, indicated by the increase in bare sand area from 3–6 % in one and from 7–12 % in the other location (Kooijman et al. 2000). However, in the following decade aeolian activity decreased again. These changes were ascribed to some large storms in the first period and wet years in the second. Blow-outs reactivated by buldozers showed some expansion in surface area over a seven year period in the Renodunaal district, but in the Wadden district the area of bare sand also strongly decreased.

Thus, on a landscape scale expansion of blow-outs seems to be limited. This may be partly due to increased atmospheric N-deposition. Natural stabilization of blow-outs occurs through algae (Pluis 1993), which need water and nutrients to grow. Early successional stages appeared to be N-limited in both the Wadden and Renodunaal district, as indicated by the foliar N/P ratios ranging from 9–11. This suggests that increased N-input results in enhanced growth of algae and blow-out stabilization.

Although aeolian activity clearly leads to an increase in pioneer vegetation, it does not seem to arrest grass-encroachment. Nineteen years after succession started in a Renodunaal district site the vegetation still consisted of (tall) pioneer vegetation. It is not known how long it takes for dune grassland to develop, but these results suggest that it requires much more than twenty years. Also, in a second site the area of species-rich dune grassland decreased from close to 50 % in 1979 to less than 20 % in 1997, due to burial by sand or continuing grass (and shrub) encroachment. A particular problem in the Wadden district may be that aeolian activity especially favours *Ammophila arenaria*, which is the main species in the grass-encroachment process.

Despite the (short-term) negative effects on the areas of species-rich dune grasslands, aeolian activity seems to be a very effective measure against enhanced acidification of the soil and thus vegetation succession (Table 15.1). In all areas, values in pioneer vegetation were higher than pH 7. Even in the control vegetation further away, which was supposedly outside the direct reach of the blow-outs, pH values were (much) higher than in comparable dune zones. In dune zones decalcified to some depth, blow-out development may bring calcareous sand to the surface, which is hardly possible with sod-cutting.

Table 15.1. Differences in pH between coastal dune grasslands with different aeolian activity in Renodunaal district (R) and Wadden district. Data derived from Kooijman et al. (2000). Mean values (n=4) and standard deviations. Different letters indicate significant differences within a column (p<0.05)

	R-calcareous soils	R-partly decalcified soils	R-decalcified soils	Wadden district
Pioneer vegetation in blow outs	8.3 (0.3) b	7.9 (0.2) c	8.4 (0.3) c	7.6 (0.5) c
Reference vegetation in surroundings of blow outs	7.8 (0.1) a	7.5 (0.8) b	7.8 (0.3) b	6.6 (1.2) b
Reference vegetation in the same dune zone	7.4 (0.3) a	5.0 (0.5) a	4.1 (0.1) a	4.2 (0.3) a

Aeolian activity also leads to changes in nutrient availability. As said, the pioneer stages are clearly N-limited. This may be due to the low organic matter content and low litter input, as well as the high pH, which all contribute to low N-mineralization. However, the high pH also leads to low P-availability, which suggests that biomass productivity will be limited for some time, probably until values have dropped below pH 6.5. This may mean that, in spite of the negative short-term effects on the areas of species-rich dune grasslands, the long-term prospects are much better.

15.7 Concluding Remarks

The results are based on dunes in a small country, but they suggest that the availability of nutrients and sensitivity to increased N-deposition is regulated by more general factors such as lime and iron contents in the soil. This implies that the mechanisms behind grass-encroachment have a wider application. There are unfortunately no data on N and P-availability and soil chemistry in other European dune areas to confirm this, but some indirect indications and personal observations are in line. Grass-encroachment has not (yet) been reported from the calcareous dunes in England, possibly due to a low availability of N and P at high pH. The northern part of the dunes in Denmark is low-productive, possibly due to a combination of low pH and high iron levels and thus low P-availability. However, on the Wadden isles of Germany and Denmark with soils low in lime and iron grass-encroachment is becoming a serious problem.

This study suggests that in (initially) lime- and iron-rich soils plant productivity can be limited by P-fixation at high and low pH. The ecosystem seems less responsive to N, which may mainly be a secondary factor responding to the productivity allowed by P. Management practices can affect light availability and increase chances for survival of small species, but hardly seem to alter nutrient availability and biomass production. Increased atmospheric deposition seems to be a problem mainly because of the simultaneous impact on both N and P, leading to more rapid succession of soil and vegetation. Stimulation of aeolian activity may be the best way to counteract this.

In lime- and iron-poor soils P does not seem to be a limiting factor, because of the absence of P-fixation. These ecosystems may instead strongly respond to increases in N-availability. This is aggravated by the strong relationship between litter input, N-mineralization and plant productivity, due to low rates of decomposition and thus low microbial N-demand and high N-mineralization per unit litter input. However, the strong relationship between litter input and N-mineralization also means that the ecosystem is sensitive to management practices. Removal of biomass not only leads to improved light conditions to small species, but also to lower nutrient availability and productivity, which are important responses in the longer term.

References

Aerts MAPA (1989) Plant strategies and nutrient cycling in heathland ecosystems. PhD Thesis, Univ of Utrecht

Aerts MAPA, Chapin III FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of process and patterns. Adv Ecol Res 30:1–67

Berg B, Ekbohm G (1983) Nitrogen immobilisation in decomposing needle litter at variable carbon:nitrogen ratios. Ecology 64:63–67

Berg B, McClaugherty C (1987) Nitrogen release from litter in relation to the disappearance of lignin. Biogeochemistry 4:219–224

Bobbink R (1989) *Brachypodium pinnatum* and the species diversity in chalk grasslands. PhD Thesis, Univ of Utrecht

Davy AJ, Taylor K (1974) Seasonal patterns of nitrogen availability in contrasting soils in the chiltern hills. J Ecol 62:793–807

Doing H (1988) Landschapsecologie van de Nederlandse kust. Stichting Duinbehoud en Stichting Publikatiefonds Duinen, Leiden

Dopheide JCR, Verstraten JM (1995) The impact of atmospheric deposition on the soil and soil water composition of the coastal dry dunes. Rep Lab Phys Geogr and Soil Sci 54, Univ of Amsterdam

Eisma D (1968) Composition, origin and distribution of Dutch coastal sands between Hoek van Holland and the island of Vlieland. PhD Thesis, Rijksuniversiteit Groningen

Everts FH, Fresco LMF, Pranger DP, Berg GJ, Til M van (2000) Beweiding op het Eiland van Rolvers; analyse permanente kwadraten 1983–1999. Rapport Everts & de Vries e.a., ecologisch advies en onderzoek. EV 00/17

Gerlach A, Albers EA, Broedlin W (1994) Development of the nitrogen cycle in the soils of a coastal dune succession. Acta Bot Neerl 43:189–203

Haaf C ten (1999a) Zwanenwater Slahoek 1998–1999; Monitoring van effectgerichte maatregelen tegen verzuring in open droge duinen. Referentie projekt begrazing. Ten Haaf en Bakker ecologisch en hydrologisch adviesbureau, Alkmaar

Haaf C ten (1999b) Duin en Kruidberg Zuidervlak 1998–1999; Monitoring van effectgerichte maatregelen tegen verzuring in open droge duinen. Referentie projekt begrazing. Ten Haaf en Bakker ecologisch en hydrologisch adviesbureau, Alkmaar

Hassink J (1994) Effects of soil texture and grassland management on soil organic C and N and rates of C and N mineralization. Soil Biol Biochem 26:1221–1231

Hassink J, Bouwman LA, Zwart KB, Bloem J, Brussaard L (1993) Relationships between soil texture, soil structure, physical protection of organic matter, soil biota, and C and N mineralization in grassland soils. Geoderma 57:105–128

Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33:1441–1450

Kooijman AM, Besse M (2002) On the higher availability of N and P in lime-poor than in lime-rich coastal dunes in the Netherlands. J Ecol 90:394–403

Kooijman AM, Haan MWA de (1995) Grazing as a measure against grass-encroachment in Dutch dry dune grasslands: effects on vegetation and soil. J Coastal Conserv 1:127–134

Kooijman AM, Dopheide J, Sevink J, Takken I, Verstraten JM (1998) Nutrient limitation and their implications on the effects of atmospheric deposition in coastal dunes: lime-poor and lime-rich sites in the Netherlands. J Ecol 86:511–526

Kooijman AM, Besse M, Haak R (2000) Effectgerichte maatregelen tegen verzuring en eutrofiering in open droge duinen, Eindrapport fase 2, 1996–1999. Report Univ of Amsterdam, 120 pp

Lambers H, Chapin III FS, Pons TL (1998) Plant physiological ecology. Springer, Berlin Heidelberg New York

Lindsay WL, Moreno EC (1966) Phosphate phase equilibria in soils. SSSA Proc 24:177–182

Meulen F van der, Jungerius PD (1989) Landscape development in Dutch coastal dunes: the breakdown and restoration of geomorphological and geohydrological processes. In: Gimingham CH, Ritchie W, Willetts BB, Willis AJ (eds) Coastal sand dunes. Proc R Soc Edinb (Sect B) 96:219–229

Meulen F van der, Kooijman AM, Veer MAC, Boxel JH van (1996) Effectgerichte maatregelen tegen verzuring en eutrofiëring in open droge duinen; eindrapport fase 1. Fysisch Geografisch en Bodemkundig Laboratorium, Univ of Amsterdam

Neitzke M (1998) Changes in nitrogen supply along transects from farmland to calcareous grassland. Z Pflanzenernähr Bodenk 161:639–646

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. Tree 13:261–265

Pavlik BM (1983) Nutrient and productivity relations of the dune grasses *Ammophila arenaria* and *Elymus mollis* I. Blade photosynthesis and nitrogen use efficiency in the laboratory and field. Oecologia 57:227–232

Pluis JLA (1993) Algae in the spontaneous stabilization of blow-outs. PhD Thesis, Univ of Amsterdam

Sjöberg RM, Persson T (1998) Turnover of carbon and nitrogen in coniferous forest soils of different N-status and under different $^{15}NH_4$-N application rate. Environ Pollut 102:385–393

Scheffer F (1982) Scheffer/Schachtschabel; Lehrbuch der Bodenkunde. Enke Verlag, Stuttgart

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell, Oxford
Veer MAC (1997) Nitrogen availability in relation to vegetation changes resulting from grass-encroachment in Dutch dry dunes. J Coastal Conserv 3:41–48
Veer MAC (1998) Effects of grass-encroachment and management measures on vegetation and soil of coastal dry dune grasslands. PhD Thesis, Univ of Amsterdam
Veer MAC, Kooijman AM (1997) Effects of grass-encroachment on vegetation and soil in Dutch dry dune grasslands. Plant Soil 192:119–128
Verhoeven JTA, Kooijman AM, Wirdum G van (1988) Mineralization of N and P along a trophic gradient in a freshwater mire. Biogeochemistry 6:31–43
Verhoeven JTA, Maltby E, Schmitz MB (1990) Nitrogen and phosphorus mineralization in fens and bogs. J Ecol 78:713–726
Weeda EJ, Westra J, Westra Ch, Westra T (1994) Nederlandse oecologische flora, wilde planten en hun relaties 5. IVN, Amsterdam
Westhoff V, Bakker PA, Leeuwen CG van, Voo EE van der (1970) Wilde planten; flora en vegetatie in onze natuurgebieden. Deel 1. Vereniging tot behoud van natuurmonumenten in Nederland. 's-Graveland