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Published in:
Journal of Ecology

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1993

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

OLFF, H., VANTOOREN, B. F., & Tooren, B. F. V. (1993). SPECIES DYNAMICS AND NUTRIENT ACCUMULATION DURING EARLY PRIMARY SUCCESSION IN COASTAL SAND DUNES. *Journal of Ecology*, 81(4), 693-706.

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Source: *Journal of Ecology*, Vol. 81, No. 4 (Dec., 1993), pp. 693-706

Published by: [British Ecological Society](#)

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Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes

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Summary

1 The present study reports on a primary succession series which started on bare soil on the Dutch island of Schiermonnikoog after the building of a sand dike. Vegetational changes were studied for 18 years by means of permanent transects along a topographic gradient from a moist plain to dry dunes. Soil development and vegetation structure were reconstructed using a chronosequence. A fertilizer experiment was set up in an intermediate successional stage in the plain and on the dune, in order to determine which soil resources limited productivity.

2 Differences in salinity, flooding and moisture content were important determinants of the differences in species composition along the topographic gradient. In addition, year-to-year fluctuations of these factors seem to be responsible for the year-to-year fluctuations in frequency of occurrence of many short-lived species. These factors did not, however, show a consistent long-term trend over time.

3 From soil analyses and the nutrient addition experiment, it is concluded that nitrogen limited above-ground biomass production. Over a period of about 16 years the total amount of nitrogen in the organic layer of the soil increased from 7 to 50 g N m⁻² in the plains and from 1 to 15 g N m⁻² on the dunes.

4 The accumulation of nitrogen during the successional series is accompanied by an increased biomass, a decreased light penetration to the soil surface, a decreased root/shoot ratio, increasing dominance of tall species, and a decreasing abundance of small, short-lived species. These data suggest that the importance of light competition is increasing during succession.

5 The importance of plant height versus light reduction at the soil surface in determining the outcome of light competition is discussed.

Keywords: fluctuations, nitrogen accumulation, sand dunes, succession, vegetation structure

Journal of Ecology 1993, **81**, 693–706

Introduction

Although succession has been intensively studied by plant ecologists since the beginning of this century, a single theoretical framework has not yet emerged (Miles 1987). Several attempts at such a synthesis have been made (e.g. Clements 1916; Connell & Slatyer 1977; Peet & Christensen 1980; Tilman 1985). These studies revealed many important elements of succession; e.g. resource competition, tolerance to extreme conditions, plant dispersion, species effects on nutrient cycling and vegetation structure.

Tilman's (1985, 1988) resource ratio hypothesis

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of plant succession focused on plant competition for limiting resources. This hypothesis predicts that when nutrients are short in supply during early succession, competition for nutrients will be more important than competition for light. This will favour small species with high investments into roots. With the accumulation of nutrients in the ecosystem, plant biomass is expected to increase (at least at low levels of herbivory). Increased biomass will lead to increased light interception, and thereby to reduced light availability at the soil surface. As a consequence, competition for light may be more important than competition for nutrients during the later successional stages. This will favour tall species with high investments into stems and leaves. Accordingly, species replacement during succession can be explained

by changing availabilities of nutrients and light (Tilman 1985, 1988).

If, however, physical and chemical stress factors such as high salinity, anaerobic conditions or very low pH prevail, other plant traits might be important for dealing with constraints on plant productivity. Investments in physiological and morphological traits which enable a plant to tolerate 'extreme' conditions might cause stress-adapted species to be weak competitors in situations where these stress factors are unimportant (Grime 1979; Taylor 1989). Therefore, it should be expected that a change in the intensity of such stress factors will also lead to changes in species composition.

Primary successions can be initiated after sand-dune formation, the retreat of glaciers, volcanic eruptions, or in other situations where new substrates are formed. A joint analysis of vegetation composition, biomass distribution, soil changes and nutrient limitation during the course of primary succession has so far been published for only a few ecosystems, e.g. Glacier Bay (Crocker & Major 1955; Crocker & Dickson 1957; Lawrence *et al.* 1967; Bormann & Sidle 1990), Lake Michigan sand dunes (Olson 1957; Robertson & Vitousek 1981; Robertson 1982) and china clay wastes (Roberts *et al.* 1981; Marrs *et al.* 1981).

In this paper, we report on the species dynamics, biomass distribution, soil changes and nutrient limitation during early primary succession in a coastal sand-dune area. The data are discussed in the light of the aforementioned conceptual models.

Study area

The study area (a 'Beach Plain') is located on the Wadden Sea island of Schiermonnikoog, the Netherlands (53°29'N, 6°12'E). Up to the late 1950s, the area was a nearly bare sand flat, with scattered young dunes (up to 2 m high). These dunes were sparsely vegetated with the perennial grasses *Elymus farctus* and *Ammophila arenaria*. (Nomenclature follows Van der Meijden *et al.* 1983.) The lower parts were bare, or sparsely covered with the annuals *Salicornia stricta*, *Spergularia marina* and *Suaeda maritima*. In 1959, with the construction of a sand dike, the area was protected from the direct influence of the North Sea, and the vegetation succession started (Fig. 1). However, heavy storms in 1972 created a large opening in the dike which is still present. In a 1-km² area around this gap, vegetation succession has started repeatedly, after the vegetation and top soil were removed by severe winter storms. This enabled us to sample sites where succession had proceeded for shorter periods. In most winters, when the water table is higher than 1.8 m above NAP (Dutch Ordnance Datum), the entire area is flooded by sea water coming through the opening. This sea water may remain fully saturating the soil of the

Beach Plain for several months because the relatively low position of the area prevents it from flowing out again. The water table in the lower parts usually falls below the soil surface by April or May. It normally reaches a depth of about 30–50 cm at the end of the summer although a depth of 1 m may be reached in extremely dry summers. Fluctuations in the length of the inundation period and in the precipitation/evaporation balance result in a strongly fluctuating salinity of the upper soil layers (van Tooren *et al.* 1983).

At present, the small dunes and their slopes in the undisturbed area (30 years of succession) are densely covered with *Hippophae rhamnoides*, a nitrogen fixing shrub, while the lower plain is dominated by *Juncus gerardi*, *Scirpus maritimus* and *Phragmites australis*.

Methods

Changes in species composition were studied from 1972 to 1989 in permanent transects along a topographic gradient from a moist plain to dry dunes. In 1990, changes in biomass composition, soil factors and canopy structure were reconstructed by a spatial comparison of three sites which closely resembled three different stages of our primary succession series. Nutrient limitation was investigated by fertilizer addition at one of these locations (a single successional stage).

THE PERMANENT TRANSECTS

Set-up and recording

The course of succession in the undisturbed area was recorded from 1972 to 1989 in a grid consisting of 12 permanent transects, each 20 m long, separated by a distance of 1 m. Each year in August, the presence (not abundance) of every species was recorded in adjacent 1-m × 0.4-m plots along the 12 transects, resulting in data from 12 × 20 = 240 plots. Since succession started in 1960, the permanent transects comprised a period of 12 to 29 years of succession. In some years, mainly before 1979, part of the transects and/or some species were not recorded, but in all cases it was noted which parts and which species were not recorded. Further details on the recording and on species replacement during the first 8 years are given in Van Tooren *et al.* (1983). The transects comprised a flat low part, a dune slope with a northern exposure, and a dry dune. Because the main scope of our study was to analyse succession under different sets of physical and chemical constraints, the transect-area was subdivided into five topographic positions according to elevation and electrical conductivity of the soil moisture (Table 1; Fig. 1). The data from the Plain, Slope and Dune plots will be presented here. The data thus contained information on both topographic variation (Plain, Slope, Dune)

Table 1 Criteria used for the division of the permanent transects area in five topographic positions

Topographic position	Number of plots	Height above NAP (cm)	Electrical conductivity ($\mu\text{S}/\text{cm}$)
'Creek'	17	130 – 155	2200 – 17000
'Plain'	132	155 – 185	750 – 6300
'Foot'	21	155 – 185	180 – 1200
'Slope'	38	185 – 230	50 – 200
'Dune'	32	230 – 320	12 – 200

and temporal variation (from 12 to 29 years of succession).

Analysis of the data

The data from the permanent transects were analysed following the response analysis approach developed by Huisman *et al.* (1993). A successional trend derived from the presence/absence data can be interpreted as the probability (p) to find a certain species in a plot (0.4 m^2) as a function of time (t). Thus when $p(t) = 1$ the species was found in all plots at time t . $p(t)$ will be referred to as the probability of occurrence of a species. For each species at each topographic position – provided that the species was found at that topographic position for at least 4 years – the data were fitted to the following general response model

$$p(t) = \frac{1}{1+e^{a+bt}} \frac{1}{1+e^{c+dt}},$$

where a , b , c and d are the parameters to be estimated. A parameter was only included in the model when addition of this parameter provided a signifi-

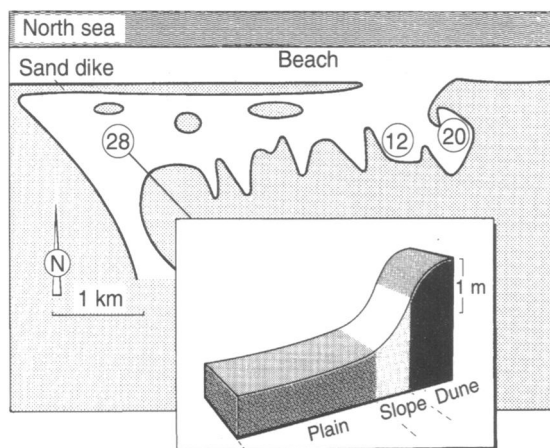


Fig. 1 The study area with the different research locations. The primary succession was initiated after the building of a sand dike in 1959. Permanent transects were recorded from 1972 until 1989; a sketch of the three topographic positions is indicated in the box ('Creek' and 'Foot' are omitted, since they were not used for the succession analysis). A reconstruction of soil development and vegetation structure was based on locations where the vegetation showed close resemblance to the vegetation of the permanent transects after 12, 20 and 28 years of succession.

cantly better fit. The parameters were estimated by logistic regression, with the parameter selection based on a χ^2 -test (Jongman *et al.* 1987; McCullagh & Nelder 1989; Huisman *et al.* 1993). As an indication of the goodness of fit of the response model, R^2 was calculated on basis of the observed probability of occurrence in each year and the probability of occurrence 'predicted' by the model. See Huisman *et al.* (1993) for further details on the fitting and testing of these models, with several examples.

Species may exhibit considerable variation around the successional trend (low R^2). This may be due to sampling errors or to some stochasticity in the studied phenomena, but also to effects of independent variables not included in the model. In order to investigate the possible causes of fluctuations around the successional trend, the influence of the trend should first be eliminated. For this purpose, the standardized residuals (SR) were calculated (Huisman *et al.* 1993):

$$SR = \frac{\text{residual}}{\sqrt{p(1-p)}},$$

where p represents the probability of occurrence predicted by the response model. For each species at each topographic position, a multiple regression was performed with SR as the dependent variable, and rainfall deficit over the period April–June and annual maximal height of the sea level (related to depth of flooding) as independent variables. Meteorological data, collected 2 km west of the permanent transects, were provided by the Geological Institute of the Free University of Amsterdam. Rainfall deficit was calculated as precipitation minus evaporation according to Penman (1948). There were marked year-to-year differences of the rainfall deficit in spring, but a long-term change was not observed (linear regression: $R^2 = 0.02$, $n = 18$, $P > 0.1$). Data on the sea level, collected 3 km to the south, were derived from the annual reports of Rijkswaterstaat, The Hague. The annual maximal height of the sea level fluctuated considerably, but no long-term change could be detected (linear regression: $R^2 = 0.01$, $n = 18$, $P > 0.1$).

The response models were also used for computations on the occurrence of groups of species with different life-forms and maximal heights. By using the calculated trends instead of the observed values for each year, the patterns were not obfuscated by annual fluctuations and missing values. The classification of Raunkiaer (1934) of life forms was used and maximal heights of the species were taken from the Dutch botanical database (Anonymous 1986). Life-form spectra per year per topographic position were calculated by weighting each species by its probability of occurrence. The six species which could behave both as hemicryptophyte and geophyte were assigned to a separate group. The weights of the three other species able to exhibit more than one life-form were divided equally among their life-form groups. Mean maximal

plant height for each topographic position and each year was calculated using log-transformed maximal heights weighted by the probability of occurrence of each species.

The importance of plant height was investigated further by relating the occurrence of several plant species to the occurrence of *Hippophae rhamnoides* shrubs of several heights. This is the first shrub which enters the succession on the Slope and Dune, and could therefore play an important role in the disappearance of other species through shading. During the recording of the plots, no direct measurements of the height of the *Hippophae* shrubs were made. Therefore, the height of this species was estimated from a regression between plant age a (measured by counting growth rings) and plant height h (in cm.). This relationship was derived from 25 individuals, and was $h(a) = 278a/(7.83 + a)$ (nonlinear regression, $R^2 = 0.81$, $n = 25$). Since it was known when the shrubs invaded the plots, their height could be estimated for every plot in each year.

RECONSTRUCTION

Within our research area, we searched for locations where the vegetation showed close resemblance to the vegetation in the permanent transects after 12, 20 and 28 years of succession, for the three topographic positions (Fig. 1). Near the gap in the sand dike, about 2.5 km from the permanent transects, we found such locations where the soil had been cleared by storm floods about 12 and 20 years ago, respectively, as could be seen on older aerial photographs. For each combination of successional stage and topographic position, we established three experimental plots at locations where the vegetation showed the closest possible resemblance (checked by percentage dissimilarity) to the permanent transects after 12 and 20 years of succession. The plots representing the last successional stage were located near the permanent transects, and showed closest resemblance to the permanent transects after 28 years of succession. By this procedure, we situated 3 replicate plots in each of three successional stages (12, 20 and 28 years) at each of the three topographic positions (Plain, Slope and Dune), yielding a total of $3 \times 3 \times 3 = 27$ experimental plots.

With this experimental design the problem of pseudoreplication cannot be avoided, since the factor successional stage cannot be truly replicated (a problem arising in most studies which use chronosequences). However, we have strong indications from the vegetation development in the permanent plots and from the aerial photographs that the different locations reflect the different successional stages.

The combinations of topographic position and successional age will be called Plain-12, Plain-20, Plain-28 (succession on the Plain), Slope-12, Slope-20, Slope-28 (succession on the Slope) and

Dune-12, Dune-20, Dune-28 (succession on the Dune). Sampling of soil and biomass from the experimental plots was done from 1 to 15 July 1990.

Biomass and light profiles

The above-ground standing crop, root biomass, vertical light profile and percentage cover were measured for all 27 plots ($n = 3$ for each combination of successional stage and topographic position). The above-ground standing crop, without the shrub *Hippophae rhamnoides*, was sampled by clipping areas of 0.4 m \times 0.4 m. These samples were sorted to species and litter, dried to constant mass at 70°C and weighed. The above-ground biomass of *Hippophae* was estimated by a nondestructive procedure, sampling over a larger area. For this, we measured the above-ground fresh weight (B , in g), above-ground dry weight, height (h , in cm) and diameter at the bottom of the stem (d , in cm) of 13 *Hippophae* shrubs in the Beach Plain, ranging in height from 30 to 250 cm. The above-ground biomass of each individual shrub could be estimated by $B = 2.815(d^2h)^{0.9094}$ ($R^2 = 0.98$, $n = 13$). Dry weight of the shrub was calculated by multiplying the fresh weight by 0.478 ($R^2 = 0.97$, $n = 7$). Average total above-ground biomass (dry-weight) of *Hippophae rhamnoides* was estimated from these relationships by taking an area around each plot of at least 15 m² in which we estimated the dry-weight of each individual shrub by measuring h and d .

Roots were collected by taking two soil cores per plot (20 cm deep, 38.5 cm² area). Only a few roots, mainly of *Hippophae rhamnoides* and *Ammophila arenaria*, were observed deeper than 20 cm. The roots were rinsed free of soil under a fine water spray. Rhizomes were separated from the fine roots, and all fractions were dried at 70°C and weighed. For each plot, on bright sunny days, the vertical light profile in the vegetation was measured at 5-cm intervals, using a PAR collector (400–700 nm) with a measuring surface of 1 m \times 0.01 m. The light intensity at each height was expressed as a fraction of the ambient light intensity above the vegetation.

Soil development

The thickness of the organic layer was measured at 10 randomly chosen spots in each experimental plot. The dark brown organic layer showed a sharp boundary with the underlying yellow to greyish sand, which will be referred to as the mineral layer. At least five cores were taken from both the organic layer and from the mineral layer (depth 10–15 cm). These cores were pooled by layer and mixed until at least 700 g per sample was collected, resulting in one organic layer sample and one mineral layer sample per plot. These samples were analysed in duplicate for NaCl (water solution), CaCO₃ (titration with 1

mol l⁻¹ HCl), pH (KCl) (1 volume soil with 5 volumes 1 mol l⁻¹ KCl), organic matter content (loss on ignition at 550°C), total carbon (Carmomat analyser with correction for CaCO₃), total nitrogen (destruction with phenol-H₂SO₄ + Se, colorimetric analysis of NH₃ using endophenol blue with salicylate) and total phosphorus (destruction with H₂SO₄ + HNO₃, colorimetric analysis of PO₄³⁻ using ammonium molybdate). The moisture content and bulk volume (volume per weight) were measured immediately after sampling for each layer using 100-ml volumetric rings. The bulk volume was used in all area-based calculations.

The effects of successional age (12, 20 and 28 years) and topographic position (Plain, Slope and Dune) on biomass and on soil characteristics of the organic and of the mineral layer were statistically tested using two-way analyses of variance with Student–Newman–Keuls contrasts among means. All cell means were compared when the interaction effect was significant; when only main effects were significant then the means were compared over the factor levels of each significant main effect. The dependent variable was log-transformed prior to the analysis if this improved the homogeneity of variances (as tested by Cochran's *C* test).

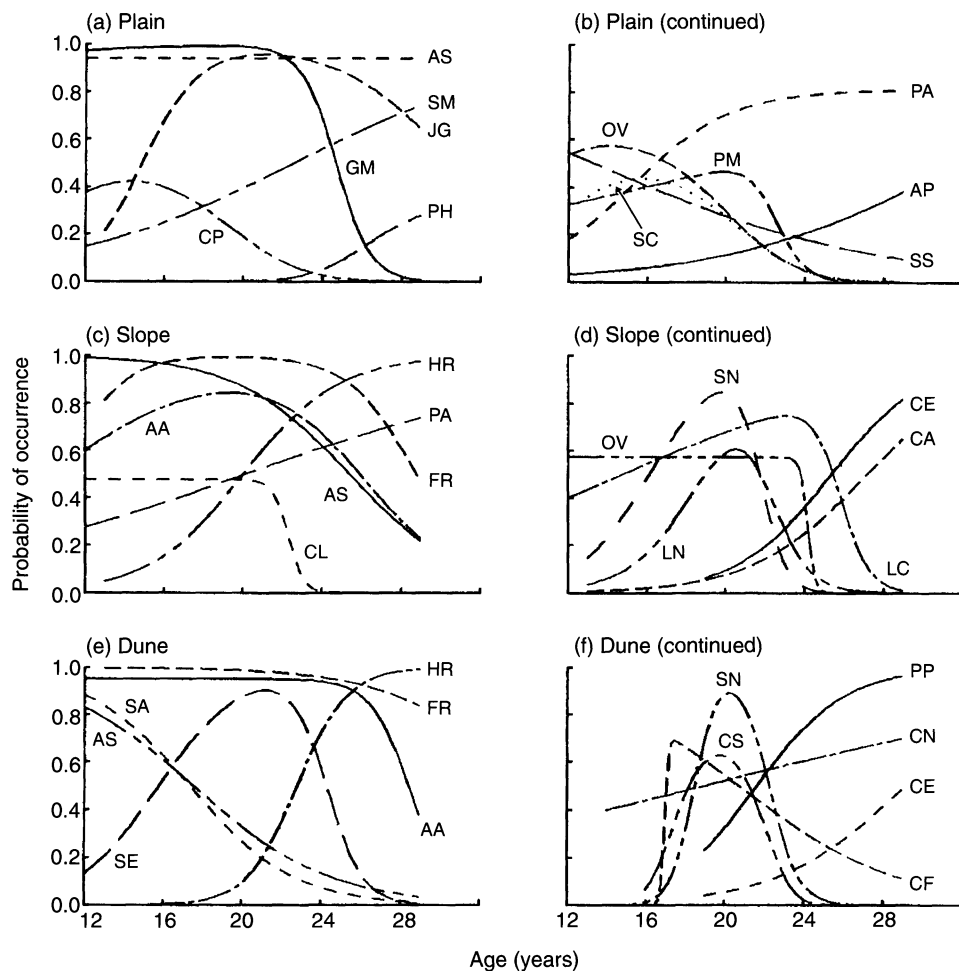


Fig. 2 Fitted changes in probability of occurrence during primary succession in a coastal sand dune area, for three different topographic positions (Plain, Slope, Dune). Data were recorded in permanent transects from 1972 (age = 12) to 1989 (age = 29). Only the 12 most frequently occurring species per topographic site are shown. Species abbreviations (with R^2):

PLAIN: AP, *Atriplex prostrata* (0.19); AS, *Agrostis stolonifera* (-); CP, *Centaurium pulchellum* (0.40); GM, *Glaux maritima* (0.95); JG, *Juncus gerardii* (0.96); OV, *Odontites verna* ssp. *serotina* (0.59); PA, *Potentilla anserina* (0.81); PH, *Phragmites australis* (0.98); PM, *Plantago maritima* (0.96); SC, *Salicornia* sp. (0.45); SM, *Scirpus maritimus* (0.93); SS, *Spergularia* sp. (0.40).

SLOPE: AA, *Ammophila arenaria* (0.74); AS, *Agrostis stolonifera* (0.89); CA, *Cirsium arvense* (0.85); CE, *Calamagrostis epigejos* (0.88); CL, *Centaurium littorale* (0.58); FR, *Festuca rubra* (0.87); HR, *Hippophae rhamnoides* (0.90); LC, *Linum catharticum* (0.44); LN, *Leontodon nudicaulis* (0.94); OV, *Odontites verna* ssp. *serotina* (0.63); PA, *Potentilla anserina* (0.70); SN, *Sagina nodosa* (0.98).

DUNE: AA, *Ammophila arenaria* (0.73); AS, *Agrostis stolonifera* (0.74); CE, *Calamagrostis epigejos* (0.56); CF, *Cerastium fontanum* (0.74); CN, *Chamerion angustifolium* (0.33); CS, *Cerastium semidecandrum* (0.80); FR, *Festuca rubra* (0.27); HR, *Hippophae rhamnoides* (0.98); PP, *Poa pratensis* (0.90); SA, *Sonchus arvensis* (0.88); SE, *Sedum acre* (0.95); SN, *Sagina nodosa* (0.97).

All presented response models were significant, as tested by a χ^2 -test based on logistic regression (see text).

To investigate which soil resource limited plant productivity during early succession in these sand dunes, we added inorganic nitrogen, phosphate, potassium and water to the Plain-20 and Dune-20 stages of succession on 4–5 May 1991. Since we hypothesized from the 1990 soil measurements that nitrogen would be limiting, we used four levels for this nutrient, and one level for P, K and water. The nutrients were added as solution (4 l) to each 2-m × 2-m plot, with five replicate plots per site. After addition of the nutrient solutions, another 4 l of water was added to each plot, to rinse the nutrient solution from the vegetation. The treatments were: C (control, no addition), W (addition of water, 1 l m⁻²), N₁ (2 g N m⁻² N as NH₄NO₃ solution), N₂ (4 g N m⁻²), N₃ (8 g N m⁻²), N₄ (16 g N m⁻²), P (16 g P m⁻² as Na₂HPO₄ solution), K (16 g K m⁻² as KCl) and N–P–K (16 g N m⁻², 16 g P m⁻², 16 g K m⁻²). These nine treatments were arranged in a randomized block design with five blocks per site, where each treatment occurred once in each block. This yielded a total of 9 × 5 × 2 = 90 plots.

The total above-ground vegetation (including standing dead) was harvested at 9 September 1991 in 10-cm × 100-cm strips in each plot, dried at 70°C, and weighed.

Results

ANALYSIS OF PLANT SPECIES DYNAMICS

The Plain

During the first years, the hemicryptophytes *Glaux maritima* and *Agrostis stolonifera* were very abundant in the Plain (Fig. 2A,B). The therophytes (annuals) *Salicornia* spp., *Odontites verna* ssp. *serotina* and *Centaurium pulchellum* also occurred frequently

during these early stages of succession. After a few years, the rhizomatous monocots *Juncus gerardii* and *Juncus maritimus* and the stoloniferous *Potentilla anserina* increased gradually, whereas *Glaux maritima*, *Limonium vulgare*, *Plantago maritima* and the aforementioned therophytes decreased. At the end of the research period, annual forbs, mainly *Atriplex prostrata* and *Spergularia* sp. could still be found. *Juncus gerardii* had passed its peak abundance, while *Agrostis stolonifera* was still very common and the tall rhizomatous monocots *Scirpus maritimus* and *Phragmites australis* were still increasing (Fig. 2A).

In general, the therophytes had a lower *R*² than the perennial species (Fig. 2A,B), which indicates that the therophytes fluctuated more severely. For four halophytic summer annuals, these fluctuations were positively correlated with the annual maximal sea level (Table 2). The fluctuations of *Centaurium pulchellum* and *Centaurium littorale* were negatively correlated with rainfall deficit in spring. Long-term changes in life forms can be observed, therophytes being replaced by geophytes, while hemicryptophytes remained rather constant in frequency (Fig. 3A). The weighted maximal plant height increased slightly, but significantly, with time (Fig. 4).

The Slope

The perennial grasses *Agrostis stolonifera*, *Ammophila arenaria* and *Festuca rubra* initially occurred with high frequency on the Slope, as did the therophytes *Centaurium littorale*, *Linum catharticum* and *Odontites verna* ssp. *serotina* (Fig. 2C,D). Small hemicryptophytes like *Leontodon saxatilis*, *Sagina nodosa*, *Armeria maritima*, *Trifolium repens* and *Trifolium fragiferum*, as well as the monocots *Juncus alpino-articulatus* and *Carex distans* increased quickly. The stoloniferous *Potentilla anserina* was present from the beginning and increased during the

Table 2 Standard partial regression coefficients of a multiple regression of standardized residuals against annual maximal height of the sea level ('flooding'), and rainfall deficit over the period April–June ('rainfall'). Only those therophytes are shown which showed at least one significant response

Species	Plain		Slope		Dune	
	Flooding	Rainfall	Flooding	Rainfall	Flooding	Rainfall
Halophytes						
<i>Salicornia</i> sp.	0.61**	NS	–	–	–	–
<i>Spergularia</i> sp.	0.68**	NS	–	–	–	–
<i>Suaeda maritima</i>	0.63*	NS	–	–	–	–
<i>Atriplex prostrata</i>	0.54*	NS	NS	NS	–	–
Glycophytes						
<i>Odontites verna</i>	NS	NS	NS	NS	NS	–0.60*
<i>Centaurium pulchellum</i>	NS	–0.57*	NS	NS	–	–
<i>Centaurium littorale</i>	NS	–0.63*	NS	NS	NS	NS
<i>Linum catharticum</i>	–	–	NS	–0.55*	–0.72**	NS
<i>Arenaria serpyllifolia</i>	–	–	NS	NS	NS	–0.77**

– = no trend calculated, because species occurred in less than 4 years.

NS = *P* > 0.05; **P* < 0.05; ***P* < 0.01.

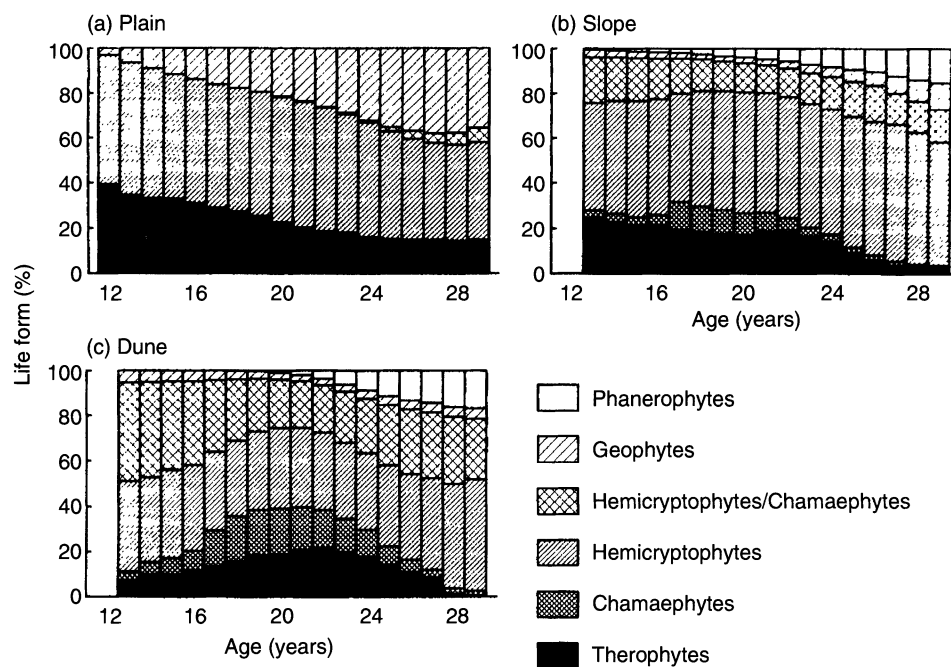


Fig. 3 Changes in the life-form spectra in the Plain (A), on the Slope (B) and on the Dune (C) during primary succession. Each species was weighted for its probability of occurrence.

whole study period. From 1981 onwards all the earlier mentioned therophytes and monocots started decreasing. In contrast, the shrub *Hippophae rhamnoides*, the tall forbs *Cirsium arvense* and *Chamerion angustifolium* and the tall grasses *Calamagrostis epigejos*, *Poa pratensis* and *Holcus lanatus* strongly increased during the latter half of the study period (Fig. 2C,D). Fluctuations of *Linum catharticum* were negatively correlated with rainfall deficit in spring (Table 2). Hemicryptophytes were the dominant life form on the Slope during the whole study period. The therophytes were gradually replaced during succession by both geophytes and phanerophytes. Chamaephytes reached their maximum frequency in the intermediate successional stage (Fig. 3B). The weighted maximal plant height increased concordantly from 1980 onwards (Fig. 4).

The Dune

Agrostis stolonifera, *Festuca rubra*, *Ammophila arenaria* and *Sonchus arvensis* were the abundant species in the early successional stage on the Dune. Therophytes were almost absent in this stage (Figs 2E,F & 3C). *Sonchus arvensis* and *Agrostis stolonifera* decreased during the whole study period. The therophytes *Euphrasia stricta*, *Cerastium semidecandrum* and *Aira praecox* entered the Dune after a few years and increased in frequency. The small chamaephytes *Cerastium fontanum*, *Sedum acre* and *Sagina nodosa* reached their maximal frequency around 1980. From 1981 onwards, all therophytes and small chamaephytes disappeared, and the perennial grasses *Festuca rubra* and *Ammophila arenaria* decreased as well. At the same time, the shrub *Hippophae rham-*

noides, the tall forb *Chamerion angustifolium* and the tall grasses *Poa pratensis*, *Calamagrostis epigejos* and *Elymus pycnanthus* increased. Two glycophytic annuals, *Odontites verna* and *Arenaria serpyllifolia*, were only found on the Dune in years with much rainfall in spring (Table 2). Fluctuations of *Linum catharticum* were negatively correlated with the annual maximal sea level. Small species, especially chamaephytes and therophytes, occurred most frequently during the intermediate successional stages (Figs 3C & 4). The average maximal plant height was rather high in 1972, then decreased towards 1980, and subsequently increased to the end of the study period (Fig. 4).

The increase in occurrence of *Hippophae rhamnoides* on the Slope and the Dune seemed to be correlated with the decrease of several grass and forb species (Fig. 2). To quantify this effect further, we plotted the observed probability of occurrence of these decreasing species against the probability of occurrence of *Hippophae* with a minimal height comparable to the maximal height of each species (Fig. 5). This analysis revealed that the upper limit of occurrence of these species was determined by the occurrence of *Hippophae* shrubs taller than the maximal height of these species. In other words, these species disappeared as soon as they were over-topped by the *Hippophae* shrubs.

RECONSTRUCTION OF BIOMASS AND LIGHT PROFILES

The total biomass increased significantly with time at each topographic position, although at different rates (Fig. 6A). Especially at the early successional stages,

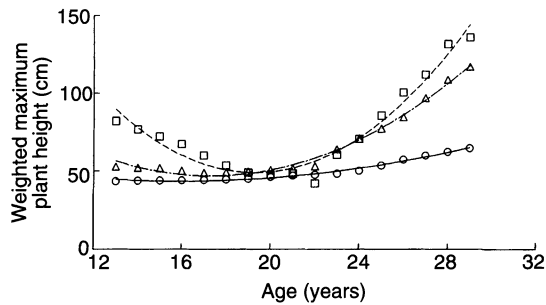


Fig. 4 Average maximal plant height per year, weighted for the probability of occurrence of each species in each year, in the (○) Plain ($R^2 = 0.98$, $P < 0.001$), (△) Slope ($R^2 = 0.98$, $P < 0.001$) and (□) Dune ($R^2 = 0.96$, $P < 0.001$) primary succession.

a very large fraction of the total biomass was found below ground. After 28 years of succession, the total biomass at each topographic position was about the same, but with a quite different distribution over the different plant parts.

The above-ground biomass was dominated by only a few species (Fig. 6B). *Juncus gerardii* was important during the later stages in the Plain. *Ammophila arenaria* dominated the early stages on the Dune. During the later stages on the Slope and Dune most above-ground biomass consisted of the woody structures of *Hippophae rhamnoides*. *Chamerion angustifolium* was only important during the late stages on the Dune. The total root biomass increased in the Plain and on the Dune, but did not change on the Slope (Fig. 6C). In the Plain, this increase was partly due to the appearance of rhizomes of *Juncus gerardii* and *Scirpus maritimus*, and on the Dune to the appearance of woody roots of *Hippophae rhamnoides*.

The profile of light extinction in the Plain, on the Slope and in the later Dune stages showed similar changes; the canopy height increased during succession, with less light penetrating to the soil (Fig. 7). The vegetation of the Dune-12 plots was rather open, but quite tall compared with the Plain-12 and Slope-12 plots.

RECONSTRUCTION OF SOIL DEVELOPMENT

The Dune plots were much drier than the Plain and Slope. No major differences between successional stages in soil moisture were found, except a small increase on the Dune (Fig. 8A,B). The NaCl content of the soil decreased in the sequence Plain > Slope > Dune, with again no consistent differences between successional stages (Fig. 8C,D). The CaCO₃ concentration of the organic layer also decreased in the sequence Plain > Slope > Dune. The organic layer was very low in CaCO₃ after 28 years (Fig. 8E), probably due to the strong increase in organic matter concentration. The pH(KCl) of the organic layer decreased with time in the Plain and on the Dune, but remained unchanged on the Slope (Fig. 8G). The pH

of the mineral layer remained high, as could be expected from the high CaCO₃ concentration (Fig. 8F,H). In the Plain-20 plots, we observed high concentrations of CaCO₃ and NaCl in the organic layer.

Very low N concentrations were found in the mineral layer (Fig. 9B), with a slight but significant increase after 28 years. The P concentration of the mineral layer was comparable with the concentration found in the organic layer, with the highest levels found in the Plain (Fig. 9D). Both the N concentration and the P concentration of the organic layer increased significantly with time at each topographic position (Fig. 9A,C), with the exception of P on the Dune. The C/N ratio of the organic layer was some-

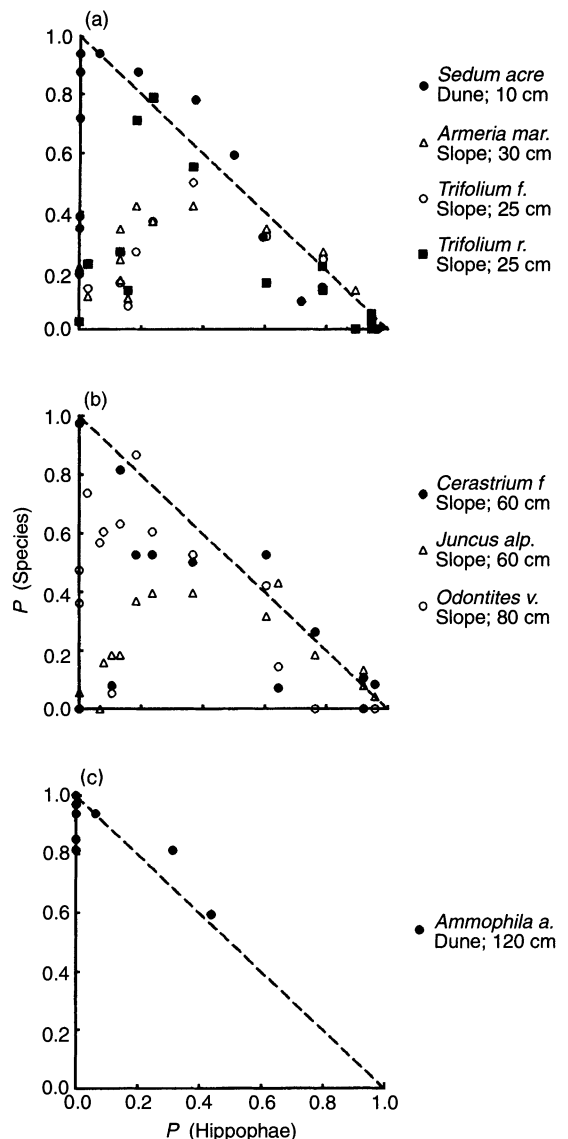


Fig. 5 Probability of occurrence of several early successional species plotted against the probability of occurrence of *Hippophae rhamnoides* of an estimated minimal plant height h . The broken lines indicate the relationship $P(\text{species}) = 1 - P(\text{Hippophae above height } h)$. Each species is plotted when its maximal height (see legend) was comparable with the minimal height h of *Hippophae*. Height h of *Hippophae*: (A) 31 cm (1 year old), (B) 57 cm (2 years old) and (C) 108 cm (5 years old).

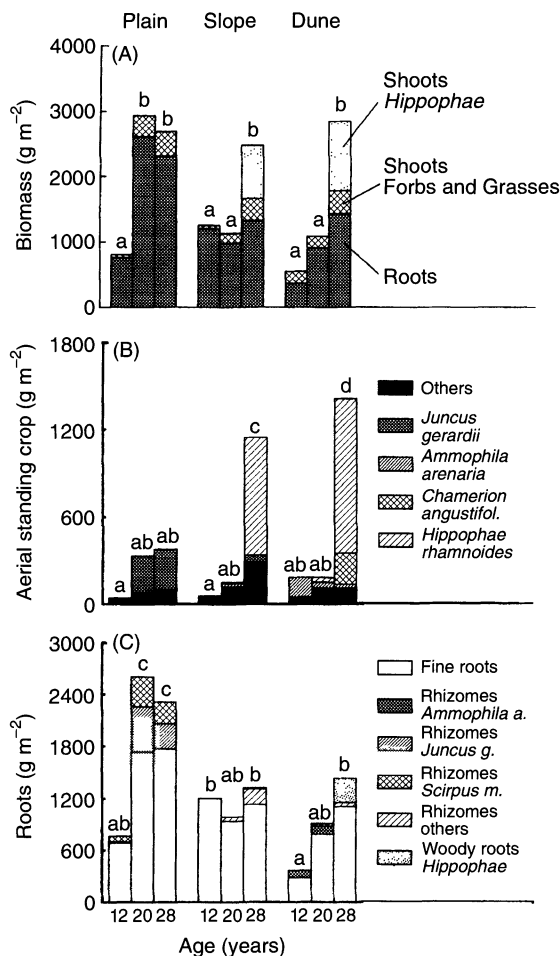


Fig. 6 Reconstruction of total biomass (A), above-ground biomass (B), and below-ground biomass (C) of different plant species in Plain, Slope and Dune at three stages of primary succession. Totals with the same letter within each subfigure were not significantly different.

what higher in the 28-year-old plots (Fig. 9E). Due to the very low C and N concentrations in the mineral layer, the C/N ratio of this layer was very variable, with no significant differences occurring (Fig. 9F). The C/P ratio of the organic layer increased strongly with time at each topographic position (Fig. 9G). The C/P ratio of the mineral layer remained low (Fig. 9H) which was due to the low organic matter content and the high P concentration of the mineral sand.

The thickness of the organic layer increased with successional age and varied between topographic positions (Fig. 10A). Hence, the accumulation of N and P in the organic layer was caused both by an increase in the thickness of this layer (Fig. 10A) and an increase in concentration (Fig. 9A,C). Because relatively high P concentrations were found in the mineral layer (Fig. 9D), the P accumulation in the organic layer was very small compared with the total pool of P in the underlying mineral layer. In contrast, the N accumulation in the organic layer was very large compared with the total amount of N in the mineral layer (Figs 9A,B & 10B). The accumulation rates of N in the organic layer were much higher in

the Plain and on the Slope than on the Dune (Fig. 10B). It should be noted that the total amounts of N are extremely low, especially during the earliest successional stage.

FERTILIZER APPLICATION

Analysis of variance of the effect of fertilizer application to the Plain-20 and the Dune-20 vegetation revealed that the block effect was not significant. Therefore, the experiment was analysed as a two-way ANOVA, with nine treatments and two sites. The variances of untransformed values were not significantly different between cells (Cochran's $C = 0.14$, $P = 0.65$). The sites were significantly different in total above-ground standing crop ($F_{1,72} = 17.56$, $P < 0.001$) which was higher on the Dune (Fig. 11). The treatment effect was also significant ($F_{8,72} = 6.29$, $P < 0.001$) while the site \times treatment interaction was not significant ($F_{8,72} = 0.93$, $P = 0.50$). Therefore, differences between treatments were tested using a-priori contrasts (planned comparisons) while pooling over both sites for each treatment. Only the treatments N_3 ($t = 3.42$, $P < 0.001$), N_4 ($t = 3.09$, $P = 0.003$) and N-P-K ($t = 5.07$, $P < 0.001$) were significantly different from the control, indicating that nitrogen lim-

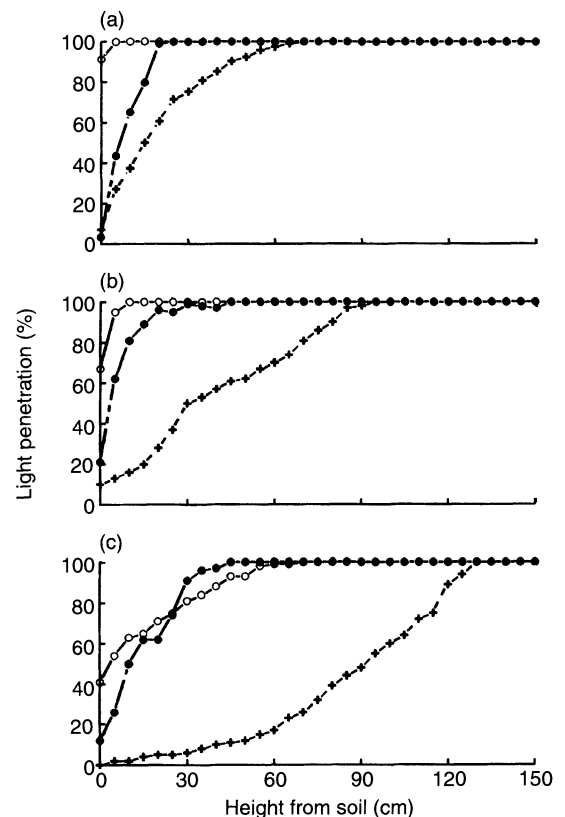


Fig. 7 Changes in vertical light profiles in (a) Plain, (b) Slope and (c) Dune during primary succession, as reconstructed using a chronosequence. The successional ages of the sites were 12 years (○), 20 years (●) and 28 years (+). The light penetration at each height was expressed as a percentage of the ambient light intensity above the vegetation.

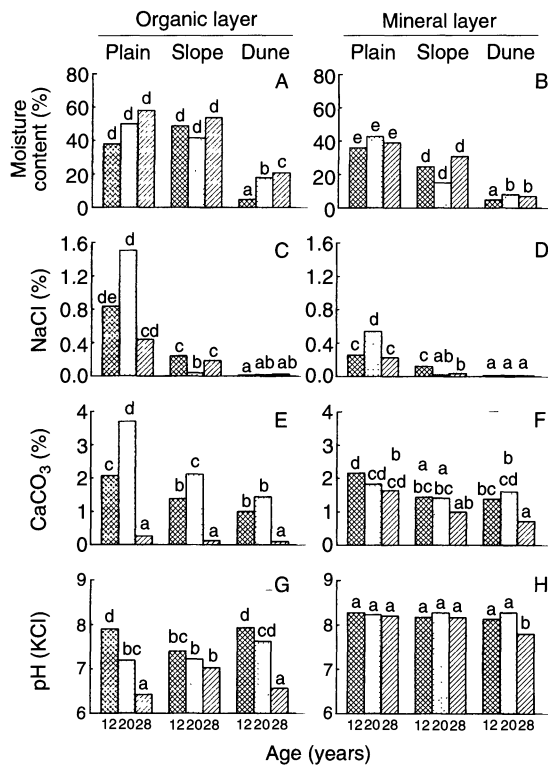


Fig. 8 Changes of various soil chemical and physical factors in the organic and mineral layer in Plain, Slope and Dune during primary succession, as reconstructed using a chronosequence. Bars with the same letter within each subfigure were not significantly different.

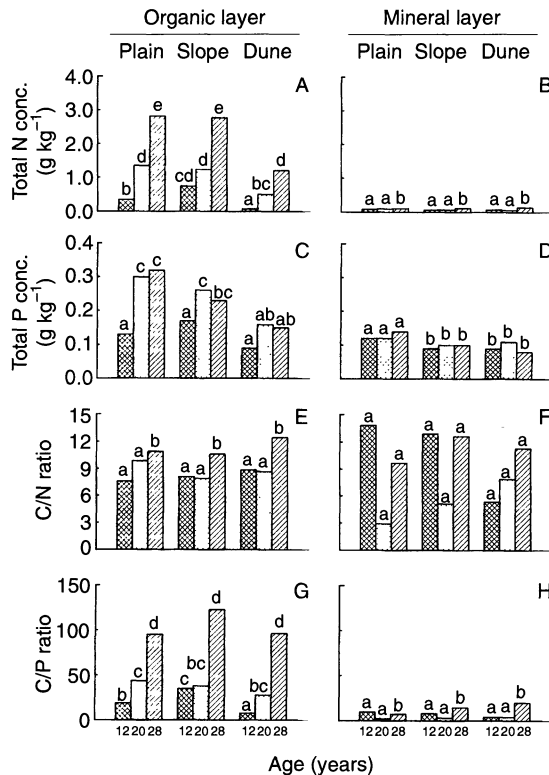


Fig. 9 Changes in total N content (A,B), total P content (C,D), C/N ratio (E,F) and C/P ratio (G,H) of the organic and the mineral layer of the soil in Plain, Slope and Dune during primary succession, as reconstructed using a chronosequence. Totals with the same letter within each subfigure were not significantly different.

ited shoot production in this successional stage on both topographic positions. The pairwise differences between the treatments N_3 , N_4 and $N-P-K$ were not significant ($P > 0.05$). There also seemed to be an effect of water on the Dune, but this effect was not significant.

Discussion

SALINITY, SOIL MOISTURE AND FLOODING

Species growing on the Plain have to cope with high salinity and with flooding in the winter period. Many species on the Plain are known as halophytes (tolerant to saline conditions). Most of the species occurring in this area have no above-ground biomass in winter. The therophytes occurring early in succession are almost all summer annuals. *Glaux maritima* has a special kind of hibernating buds (Rozema 1978). *Juncus gerardii*, *Scirpus maritimus* and *Phragmites australis* have extensive rhizomes for surviving the winter period when shoots die off. The high above-ground losses of biomass in the Plain during winter might imply that species which reduce these losses by storing nutrients and/or carbohydrates below ground will be better competitors for nutrients and/or light (Berendse & Jonasson 1992; De Kroon & Schieving 1990). Yet extremely high tides may result in the formation of large gaps in the perennial vegetation (personal observation). Several annual species, mainly halophytes, can establish in these gaps (Table 2). So far, we cannot offer a single explanation for the unexpected high values of $CaCO_3$ and $NaCl$ in the organic layer of the Plain-20 stage. High evapotranspiration rates in the summer period may cause secondary precipitation of these minerals in the topsoil (Schlesinger 1982, 1991), which might explain why the values in the organic layer were higher than in the underlying mineral layer. But this does not explain the difference from the Plain-12 and Plain-28 stages. Perhaps, this is due to a spatially deviant situation of the Plain-20 plots with respect to these variables.

The Slope is much less saline than the Plain, but still has a rather high moisture content. The species are mainly glycophytes (not tolerant to saline conditions). The later successional dynamics on the Slope are comparable to those on the Dune (both sites show invasion of *Hippophae*), while at the early stage the slope shows more resemblance to the Plain.

Salinity and soil moisture content are both low on the Dune. Winter annuals like *Cerastium semidecandrum*, *Arenaria serpyllifolia* and *Aira praecox* flower in spring, die after seed-setting in May–June and survive during the dry summer as seeds (Rozijn 1984); *Sedum acre* can reduce evaporation by closing the stomata at daytime (CAM metabolism); *Hippophae rhamnoides* and *Ammophila arenaria* can root rather deep; *Ammophila arenaria* and *Elymus pycnanthus*

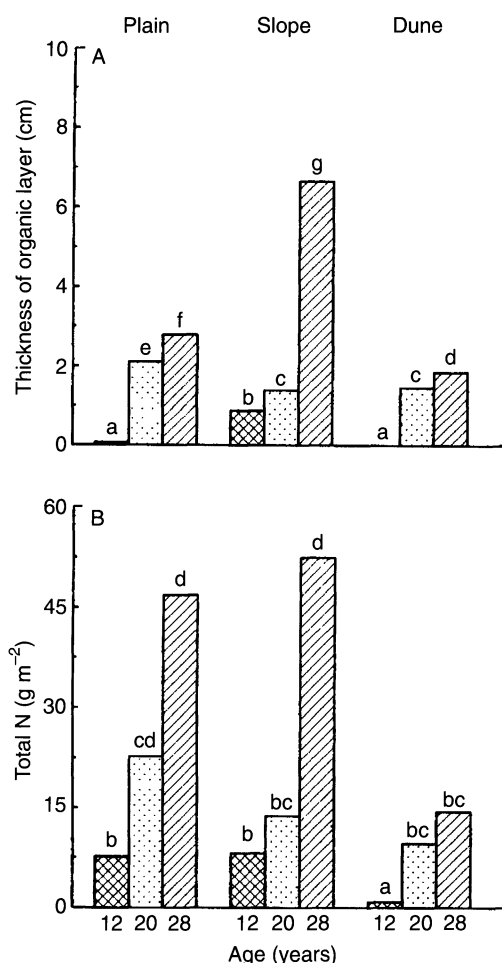


Fig. 10 Thickness of the organic layer (A) and total amount of nitrogen in the organic layer (B) of the Plain, Slope and Dune during primary succession, as reconstructed using a chronosequence. Bars with the same letter within each sub-figure were not significantly different.

fold their leaves when it gets dry, burying their stomata deeply between the ribs. Fluctuations of several short-lived glycophytes were negatively correlated with rainfall deficit in spring (Table 2). In this study area, a high rainfall deficit causes a low soil moisture content and, especially in the Plain and Slope, an increased salinity (van Tooren *et al.* 1983). Both low soil moisture content and high salinity have negative effects on the germination and establishment of most of these glycophytes (Schat 1982). Although we have not been able to prove that water limits the productivity, Fig. 11 suggests that further experiments might reveal that, in addition to nitrogen, water is also a limiting soil resource on the Dune.

Our results suggest that differences in salinity, water availability and flooding are important determinants of the differences in species composition along the topographic gradient. In addition, year-to-year fluctuations of these factors seem to be responsible for the year-to-year fluctuations of many short-lived species. However, none of these factors can be held responsible for the observed successional sequence. The NaCl content did not change consistently, except

for a slight decrease on the Slope. Similarly, van Tooren, Schat & Ter Borg (1983) did not observe any long-term trend in the soil moisture conductivity from 1973 to 1980. Soil moisture content increased only on the Dune, accompanied by an increased organic matter content (larger water holding capacity) and an increased above-ground standing crop (moist microclimate); so this might be rather a consequence than a cause of the observed succession. Long-term trends in the height of flooding or in the rainfall-deficit in spring did not occur.

NUTRIENT DYNAMICS

The total P content of the mineral layer was rather high, although this is probably mostly Ca-P which is not directly available for plant uptake. Potassium is usually deposited in high amounts through salt spray from the sea. Nitrogen was nearly absent from the soil during the early stages of succession. The total amount of nitrogen in the topsoil after 12 years seems too little to sustain the total biomass observed after 28 years. Addition of single nutrients revealed that only N significantly enhanced the above-ground biomass with respect to the control. The N content of the soil was strictly correlated with its organic matter content, suggesting that all N is organic N. A C/N ratio of about 11, as found in this study, was also found during early succession at both the dunes of Lake Michigan (Olson 1957) and the receding glaciers in Alaska (Crocker & Dickson 1957). The conclusion that nitrogen was an important limiting nutrient was also drawn by several other studies on nutrient limitation in sand dunes (Willis *et al.* 1959; Willis 1963; Kachi & Hirose 1983; Dougherty *et al.* 1990).

For the Plain and Slope we estimated an average increase in total soil nitrogen of $2.8 \text{ g m}^{-2} \text{ year}^{-1}$. This

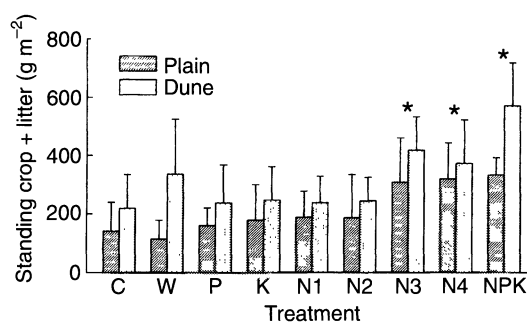


Fig. 11 Effect of application of various nutrient solutions on the aboveground biomass of (■) Plain-20 and (□) Dune-20 vegetation, representing mean values \pm SD. ($n = 5$). Since the site \times treatment interaction in a 2-way ANOVA was not significant, treatments were compared to the control over both sites, where pairs noted with an asterisk were significantly different from the control ($P < 0.05$). The treatments were: C (control, no addition), W (1 l m^{-2}), N1 (2 g N m^{-2}), N2 (4 g N m^{-2}), N3 (8 g N m^{-2}), N4 (16 g N m^{-2}), P (16 g P m^{-2}), K (16 g K m^{-2}) and NPK (16 g N m^{-2} , 16 g P m^{-2} , 16 g K m^{-2}).

is comparable with the rate of nitrogen accumulation during the first 30 years of succession after recession of glaciers in Alaska, which was 3–4 g m⁻² year⁻¹ (Crocker & Major 1955; Crocker & Dickson 1957). On the Dune, on average 0.9 g N m⁻² year⁻¹ accumulated in the soil, which is comparable with the accumulation rate during the early successional stages of the dry dunes of both Lake Michigan (Olson 1957) and the island of Spiekeroog, Germany (Gerlach *et al.* 1988). An accumulation of 1.0 g N m⁻² year⁻¹ was also found at the higher part of the salt marsh at Schiermonnikoog (Olf 1992b). The total increase in nitrogen in the ecosystem must have been larger, but we have not (yet) investigated the N content of the vegetation.

In our study area, the total rate of nitrogen input into the ecosystem is expected to be determined by the rate of atmospheric deposition, the abundance of nitrogen-fixing organisms and the input of N by flooding of sea water. On the East Frisian islands, Germany, the atmospheric input from dry and wet deposition is estimated at about 1.5 g N m⁻² year⁻¹ (Gerlach *et al.* 1989). On the Dutch mainland this input is estimated at about 4 g N m⁻² year⁻¹. Probably, in our study area the atmospheric input will be somewhere between these two estimates. Stewart (1965) estimates that nitrogen fixation by free-living bacteria in dune slacks is about 6 g N m⁻² year⁻¹. *Hippophae* shrubs can fix between 1.5 g N m⁻² year⁻¹ (Akkermans 1971) and 17.9 g N m⁻² year⁻¹ (Becking 1970). In the period 1973–89, the North Sea water near our study area had a mean (\pm SD) total N content of 1.33 \pm 0.95 mg l⁻¹ ($n = 95$, Rijkswaterstaat, personal communication). Thus evaporation of 20 cm of inundated North Sea water (as happens in spring) will add only about 0.26 g N m⁻² to the soil. The actual accumulation of N will be determined by the differences between these inputs, and all losses that occur. The magnitude of N losses from the soil organic matter pool (mineralization) and from the ecosystem (denitrification, leaching, or litter export during floodings) has not yet been measured for sites similar to our study area.

The vegetation itself is likely to be one of the main determinants of the observed nitrogen accumulation. Without storage of nitrogen in plants and soil organic matter, nitrogen easily leaches out of sandy soils (Schlesinger 1991). Moreover, as discussed above, N-fixation by plants and their associates may be one of the most important sources of N input to the ecosystem. This can result in a positive feedback when a species which is a superior competitor at high rates of N supply produces a type of litter which rapidly decomposes and therefore results in higher rates of N mineralization (Vitousek & Walker 1987; Berendse 1990). When these species have established high rates of N supply, they may in turn be out-competed for light by species which are taller. While discussing the primary succession at Glacier Bay,

Lawrence *et al.* (1967, p. 812) state: 'it is only the latter [the nitrogen fixing *Alnus*] that raises the nitrogen supply to a level enabling the spruce forest to achieve dominance'. These types of interactions between plant growth and nutrient supply come close to the facilitation hypothesis of Clements (1916) and Connell & Slatyer (1977).

SUCCESSION AND SYNTHESIS

The spatial variation in stress factors like salinity, drought and flooding has led to very different successional sequences, in terms of species composition. However, the general patterns of these successional sequences in terms of soil development, nutrient accumulation, plant height and biomass compartmentation were very similar. Nitrogen, which limited productivity, was nearly absent from the soil during the early stages of succession. The accumulation of soil nitrogen was accompanied by an increased biomass and, thereby, by an increased light interception by the vegetation. The root/shoot ratio decreased and small, short-lived species were replaced by taller grasses, forbs and shrubs. Only the earliest Dune stage deviated from this general pattern. In this early stage, the vegetation was composed of tall species, with relatively much above-ground biomass. Small species were absent although much light penetrated to the soil surface. This deviating stage might be explained as the result of drifting sand, which can lead to deposition of many centimetres of sand on the vegetation within a few days (personal observation). Small species would probably be buried under the sand in this early dune stage.

The general successional patterns in our study area, with the exception of the early dune stage, are in agreement with the patterns predicted by Tilman's resource ratio hypothesis of primary succession (e.g. Tilman 1988, p. 132). This hypothesis predicts a gradual change from nutrient competition during early, nutrient-poor successional stages towards light competition at later, nutrient-rich stages. However, a comparison between observed and predicted patterns can provide only weak support for such a mechanistic hypothesis. The resource ratio hypothesis is derived from a graphical isocline approach, in which superior nutrient competitors reduce limiting nutrients to low levels, while superior light competitors reduce light near the soil surface to low levels. It cannot yet be decided whether nutrient competition or colonization dynamics, or both, are important determinants of the community structure during the early successional stages in our study area. It may be that, although nutrient availability is low, the plants are not really able to compete effectively with each other so that the colonization characteristics of the plant species are more important than their competitive ability (e.g. Gleeson & Tilman 1990). This possibility needs further experimental investigation. The accumulation of

nitrogen led to an increased above-ground biomass and, thereby, to a reduced light availability at the soil surface. Furthermore, small species were replaced by taller species. In the case of *Hippophae rhamnoides*, the first shrub entering succession on Slope and Dune, it was shown that many of the early successional grass and forb species disappeared from the permanent transects as soon as they were overgrown by the shrubs. This suggests that the importance of light competition is increasing during this succession. However, it also indicates that plant height is an important determinant of the outcome of competition for light (e.g. Grime 1979; Givnish 1982; Olff 1992a). Light competition will of course be mediated by reducing the light availability for other plants, but, in addition to light reduction abilities (i.e. 'light near soil surface'), the position at which light is reduced (i.e. 'plant height') has to be taken into account. Information on plant height is not included in Tilman's graphical isocline approach. For this reason, Tilman's (1985, 1988) resource ratio hypothesis of primary succession is considered inadequate as soon as plant height becomes an important determinant of the outcome of competition for light. But our data cannot reject the more general hypothesis that species replacement in our study area was mainly governed by changing availabilities of nutrients and light.

In conclusion let us evaluate to which extent our results contribute to a more general theoretical framework for primary succession. It seems that, in our case, stress factors like salinity, drought, and flooding have provided the environmental setting in which a particular succession has taken place. Given that these stress factors did not show long-term changes, the observed species replacement may be attributed mainly to an increasing importance of light competition when nutrients accumulate in the system. This nutrient accumulation rate, in turn, is probably closely linked to the vegetation development itself. Within each successional stage however, the spatial variation in species composition along the topographic gradient seemed closely related to spatial variation in salinity, moisture content and flooding. This indicates that these stress factors may have considerable impact on species composition and on the pathway of succession. Accordingly, whenever stress factors exhibit long-term changes with time, the analysis of interspecific differences in ability to cope with such stress factors should be an important additional component of studies on primary succession.

Acknowledgements

We are grateful to Siny ter Borg, Peter-Jan Keizer and Titia Zonneveld for field assistance. J. van Andel, J. P. Bakker, F. Berendse, W. H. O. Ernst, the anonymous referees and the members of the Laboratory for Plant Ecology made valuable comments on an earlier draft.

We thank Albrecht Gerlach and David Tilman for discussions on the subject. Figure 1 was drawn by Evert Leeuwinga. The investigations were supported by the fund Cooperation Groningen-Oldenburg and by the Foundation for Biological Research (BION) which is subsidized by the Netherlands Organization for Scientific Research (NWO).

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Received 23 July 1992

Revised version accepted 21 April 1993