PATTERN AND PROCESS IN COASTAL DUNE VEGETATIONS

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Mededeling nr. 10 van het Rijksinstituut voor Natuurbehoud

SUMMARY

A survey is given of types of pattern in the dunes: band-type, ribbon-type and lattice-type patterns. Examples are given on various pattern scales. The main processes in dune ecosystems are mentioned. The influences of animals and men, especially trampling and rabbit grazing, are discussed. The relations between pattern and process and the integration within ecosystems are discussed. An example of a quantitative approach of these relations is given.

1. INTRODUCTION

With WATT (1947) the relation between pattern and process in the plant community is considered as a fundamental object of ecological study. Coastal dunes are an environment par excellence for this approach (VAN LEEUWEN 1963; VAN DER MAAREL 1966a). The general relation theory by VAN LEEUWEN (1966b) is taken as a basis for this type of study, which may be carried out by yearly analysis of permanent quadrats and, still better, permanent transects (VAN DER MAAREL & VAN LEEUWEN 1967).

2. PATTERN

2.1. Types of pattern in the dunes

The vegetation map of the dunes near Oostvoorne (VAN DER MAAREL & WESTHOFF 1964) shows the main geomorphologically determined patterns:

a. *Band-type pattern* ("bandpatroon"). The coastal dunes as a whole form a band and many dune species, *e.g. Hippophaë rhamnoides* ssp. *maritimus* show this type of distributional pattern. Bands also occur within one dune system, partly because of a regular alternation of dune ridges and dune flats, as on Voorne, partly because of a zonation which may be determined by geomorphology and microclimate. Examples: *Cerastium atrovirens* forms a band of about 400 m width along the present coast line, *Crataegus monogyna* occurs in the landward zone of the middle dunes as a dominant species – bandwidth 300 m; from 700–1000 m from the coastline – (*cf.* DOING KRAFT 1958; BOERBOOM 1958; VAN DER MAAREL 1961).

b. *Ribbon-type pattern* ("lintpatroon"). This is a variant of type a with a very small width, *e.g. Elytrigia juncea* on the present coastal ridge, *Sambucus nigra* on older coastal ridges and on so-called stripe dunes ("streepduinen"), *i.e.* small dune ridges developed by secondary blowing from the Medieval coastal ridge.

c. *Lattice-type pattern* ("rasterpatroon"). This pattern consists of networks of ribbons and is found in the net-like structure of dune tops and hollows in areas with parabolic dune formation. Species like *Ammophila arenaria* (tops) and *Salix repens* (hollows) are examples in the seaward zone of the middle dunes. The same structure is found in the inner dunes with *Corynephorus canescens* as a typical top-species.

2.2 Underlying patterns in the environment

The main environmental patterns responsible for – and easily deducible from – the above-mentioned species patterns are the zonation and the topographical variation in height. This is treated in detail by ADRIANI & VAN DER MAAREL (1968).

2.3 Small-scale patterns of species

The same types of pattern mentioned in 2.1 also occur on a smaller scale, as *morphological* or *sociological pattern* (*cf.* VAN LEEUWEN 1960; KERSHAW 1964). These patterns are developed in close interaction between a species and its environment or between species, and thus they are a direct outcome of process.

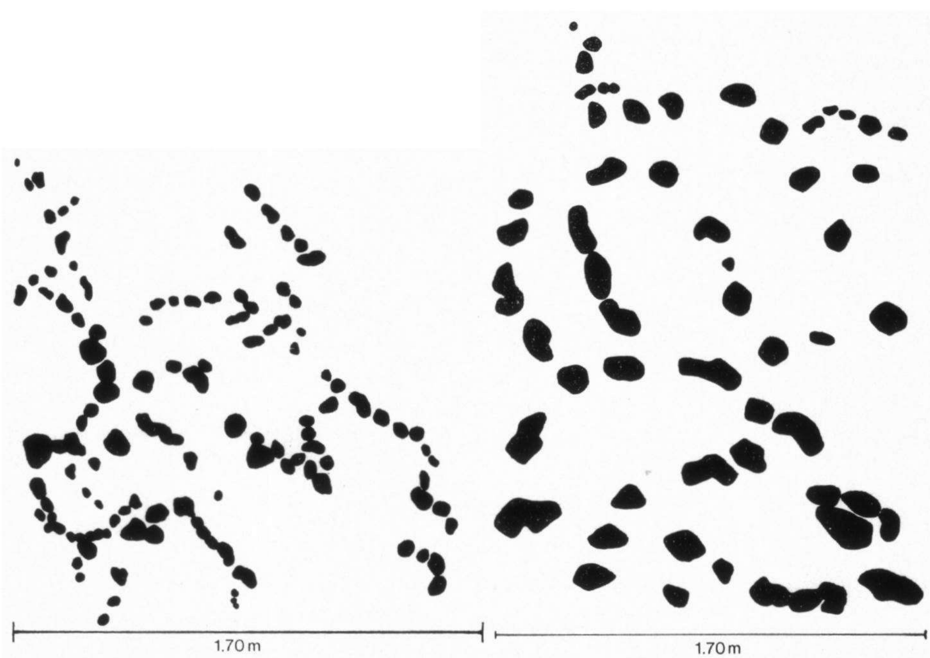

Fig. 1a. Growth pattern of *Corynephorus canescens* on a gentle slope in the dunes of Voorne.
Fig. 1b. Ibid. *Koeleria albescens*.

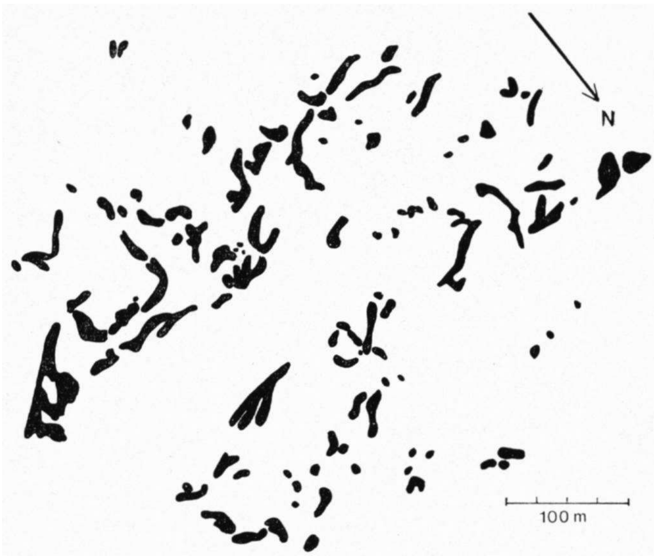

Fig. 1c. Distribution pattern of *Corynephorus canescens* in the dunes near Oostvoorne Note bands in W-E direction.

Example 1: *Lattice-type patterns of* Corynephorus canescens.

In *fig. 1a* and *b* the distributional pattern of the morphologically similar grass species *Corynephorus canescens* and *Koeleria albescens* is shown. The net structure is obvious in both cases.

Fig. 1c shows the pattern of the first species in a much larger area, also in the dunes near Oostvoorne. These illustrations are taken from VON KOENINGSWALD & DE ZWAAN (1965). The similarity between the two scales of pattern is obvious as well. In many cases the pattern of these species is superimposed on a lattice-type pattern of *Carex arenaria*, as is shown in *fig. 2* (from observations by van Leeuwen in the Terschelling dunes.)

The pattern of *Corynephorus* again determines the patterns of subsequent species such as *Polypodium vulgare* and, in later phases, *Empetrum nigrum*. In this sequence of species the space within the nets remains bare or becomes covered with mosses (*Hypnum cupressiforme* var. *elatum*) only.

Example 2: *The relation between size of pattern and topography.*

Fig. 3 shows the relationship between the size of the nets in a lattice-type pattern and the position within a topographical gradient from a North-facing slope via a hollow towards a South-facing slope in the dunes near Katwijk. The latter slope has a coarse-grained pattern with much bare sand and a high temporal variation (instability). Only a few species occur here, esp. *Artemisia lloydii* and *Festuca rubra* subvar. *arenaria*.

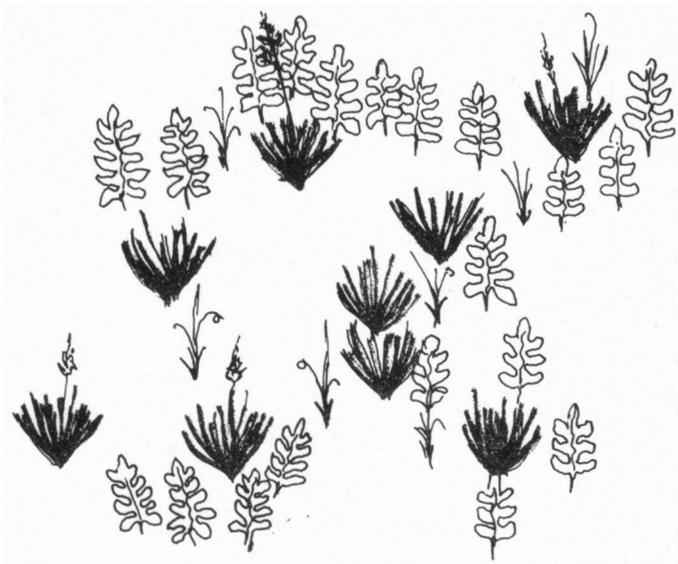

Fig. 2. Growth pattern of *Corynephorus canescens* in a open dry dune hollow in the dunes of Terschelling, preceded by *Carex arenaria* and succeeded by *Polypodium vulgare*.

The North-facing slope has a fine-grained pattern with up to 40 species, amongst which *Anacamptis pyramidalis*, *Silene nutans*, *Orobanche vulgaris*, *Galium verum*, and *Polygonatum officinale*. Here a well-developed moss and a humus-rich A_1 soil layer occur. The hollow in between has an intermediate position with very clear nets of *Carex arenaria* and *Koeleria albescens*, mixed with *Rubus caesius*, *Sedum acre*, *Leontodon nudicaulis* a.o.

3. PROCESS

3.1. Types of process

Processes responsible for the above mentioned patterns may be considered of two types: processes of *concentration* and those of *spreading*. The following environmental factors are involved in dune processes:

sand: accretion, "aanstuiving", versus decretion, "verstuiving"; salt: salination, "verzilting", vs. desalination, "ontzilting"; lime: calcification, "bekalking", vs. decalcification, "ontkalking"; nutrients: fertilisation, "bemesting", vs. defertilisation, "verschraling"; humus: humification, "humusvorming", vs. mineralisation, "mineralisatie".

These processes are all influenced by moisture conditions, esp. the seasonal fluctuations of the ground water table.

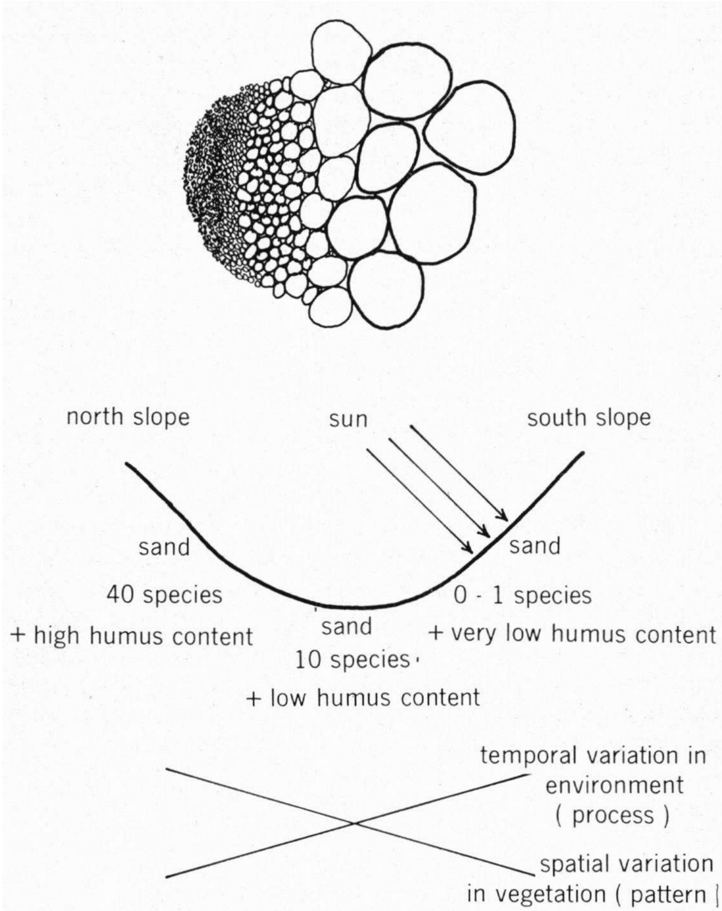

Fig. 3. Scheme of net-structure on North slope, hollow and South slope in the seaward dunes near Katwijk. See text.

3.2. Influences of animals and man.

These processes are also influenced by animals: rabbits, ants, moles, birds, and man, in such a way that these biotic effects lead to superimposition of small-scale patterns upon the already mentioned large-scale ones. Important examples are local blow outs, manuring and soil hardening. The effect upon vegetation depends on the position in the large-scale pattern and on the moisture conditions.

Example 3: The influence of rabbits on gradient patterns.

Fig. 4 shows the influence of rabbits on a gradual transition from dune grassland to dune scrub, a very common complex in the dunes rich in lime.

The dune grassland is extended with an open variant ending mostly with a short bare zone, and then abruptly turns into the scrub.
The dune grassland may consist of species like *Carex arenaria* and *Calamagrostis epigejos*, the open phase of species from the *Tortulo-Phleetum* association and the scrub of *Hippophaë rhamnoides*, *Ligustrum vulgare* or *Berberis vulgaris*. *Cynoglossum officinale* is very characteristic for the bare zone immediately bordering the scrub.
In dune slacks the influence of rabbits may have more differentiating effects: here minute differences in height may lead to subtile differences in vegetation composition, provided the vegetation as a whole is under a grazing regime of sheep, cattle or rabbits. – In the meanwhile VAN DER MAAREL & LEERTOUWER (1967) published an example of a species-rich gradient in a dune slack heavily grazed by rabbits. –
When rabbit grazing stops, e.g. after an outbreak of myxomatosis the differentiated pattern is replaced by a coarser one, dominated by *Salix repens* and *Hippophaë rhamnoides* or tall grasses (*cf.* RANWELL 1960).
Van Leeuwen followed a number of permanent plots in very young habitats in the former dune system De Beer which were partly fenced and thus kept free from rabbit grazing. The results of the observations of two double-quadrats were extensively discussed and illustrated in VAN DER MAAREL & VAN LEEUWEN (1967). The general conclusion was that the fenced places were richer in species during the first years of observation when all vegetations were still very open, but despite the severe rabbit grazing the unfenced places tended to get richer in species, at least in the dune slack areas.

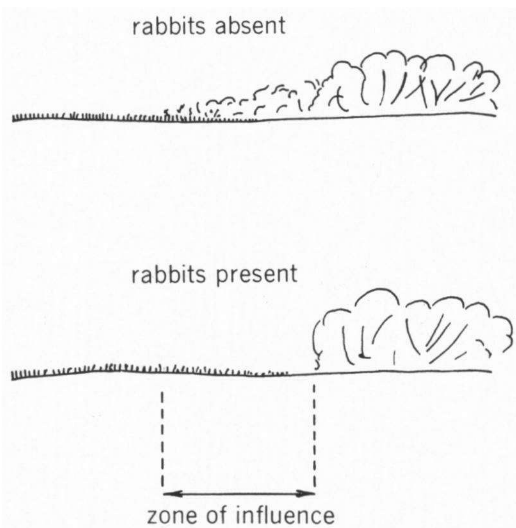

Fig. 4. Scheme of the influence of rabbits on the structural pattern in the grassland- scrub mosaic in the dunes. See text.

The first outbreak of myxomatosis in 1955 did not considerably change the diversity of comparable fenced and unfenced areas, but the differences in species composition were increased for some years.

Example 4: *The influence of trampling on patterns in a dune grassland.* This example is taken from a study of species diversity in a gradient-rich dune grassland complex (VAN DER MAAREL 1966b). A path is running across the area, partly along a dune slope, in a topographical gradient with high species diversity, partly in a flat semi-dry hollow with a lower species diversity (species numbers of 25–30 and 15–20 per sq.m. respectively). The zone directly bordering the path appeared to be richer in the species-rich area and poorer in the species-poor area. This demonstrates the dependance of the effect of human interference on the original pattern.

3.3 Stabilisation

The obvious dynamics of these processes are gradually fading in time, partly as a result of the relative constancy in some environmental processes, like prevailing wind direction and water table fluctuation cyclus, partly by the vegetation, which stabilises soil and microclimate. Human activities concerned with the management of dune areas can also exert a stabilising influence, e.g. yearly mowing in slacks and dune grasslands (VAN LEEUWEN 1965, 1966a, b).

4. INTEGRATION

Pattern and process are thus interrelated in a very complex way. (VAN LEEUWEN 1967). We are in need of system-theoretical methods of studying these relations. First suitable parameters are needed to describe spatial and temporal variation. Furthermore the study of permanent quadrats – the usual way of following changes – should be extended to the study of permanent transects, i.c. strips of vegetation covering gradient situations in the field which are described as series of permanent quadrats.

Example 5: *The relation between pattern and process quantitatively determined.* In the same dune grassland Van der Maarel followed the species composition and diversity in some permanent transects, covering most of the variation in the complex. A negative correlation could be observed between the initial diversity in stands, measured as the index of diversity α, and the rate of floristical change in these stands, measured as an average value of the information parameter I for floristic difference between samples of adjacent years. For figures and further discussion; see VAN DER MAAREL & VAN LEEUWEN (1967).

REFERENCES

ADRIANI, M. J. & E. VAN DER MAAREL (1968): *Voorne in de branding*. Oostvoorne, Sticht. Wet. Duinonderz. 104 pp.

BOERBOOM, J. H. A. (1957): Zonering van begroeiing en landschap in het Haagse duingebied. *De Levende Natuur* **60**: 247–259.

DOING KRAFT, H. (1958): Zonering in landschap en plantengroei van de duinen bij Bloemendaal en Velsen. *De Levende Natuur* **61**: 219–227.

KERSHAW, K. A. (1964): *Quantitative and Dynamic Ecology*. London, Edward Arnold. VIII + 183 pp.

KOENIGSWALD, F. VON & A. DE ZWAAN (1965): *Vergelijkend-oecologische studie van Corynephorus canescens en Koeleria albescens*. Doct. Versl. Inst. syst. Plk. Utrecht.

LEEUWEN, C. G. VAN (1960): Micropatronen in pioniervegetaties. *Jb. Kon. Ned. bot. Ver.* **1960**: 38–39.

— (1963): Iets over de betekenis van onze Waddeneilanden voor de veldbotanie. *De Levende Natuur* **66**: 135–139.

— (1965): Het verband tussen natuurlijke en anthropogene landschapsvormen, bezien vanuit de betrekkingen in grensmilieu's. *Gorteria* **2**: 93–105.

— (1966): Het botanisch beheer van natuurreservaten op structuur-oecologische grondslag. *Gorteria* **3**: 16–28.

— (1966): A relation theoretical approach to pattern and process in vegetation. *Wentia* **15**: 25–46.

— (1967): *Patroon en Proces* (Plantkunde III). Rapport RIVON Zeist, 30 pp.

MAAREL, E. VAN DER (1961): De zonering in landschap en plantengroei van de duinen bij Oostvoorne. *De Levende Natuur* **64**: 223–234.

— (1966): Dutch studies on coastal sand dune vegetation, especially in the Delta region. *Wentia* **15**: 47–82.

— (1966): *Over vegetatiestructuren, -relaties en -systemen, in het bijzonder in de duingraslanden van Voorne*. Thesis Utrecht, 170 pp.

— & C. G. VAN LEEUWEN (1967): *Beziehungen zwischen Struktur und Dynamik in Ökosystemen*. Vortr. Int. Symp. Syndynamik Rinteln.

— & V. WESTHOFF (1964): The vegetation of the dunes near Oostvoorne, the Netherlands. (with one vegetation map). *Wentia* **12**: 1–61.

RANWELL, D. S. (1960): Newborough Warren, Anglesey III. Changes in the vegetation on parts of the dune system after the loss of rabbits by myxomatosis. *J. Ecol.* **48**: 385–395.

WATT, A. S. (1947): Pattern and process in the plant community. *J. Ecol.* **35**: 1–22.