DUTCH STUDIES ON COASTAL SAND DUNE VEGETATION, ESPECIALLY IN THE DELTA REGION

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ABSTRACT

A short history of Dutch dune vegetation research is presented as an introduction to the present research in the Delta region. Remarkably enough the main results of dune research were presented as dissertations. The classics F. HOLKEMA, L. VUYCK, J. JESWIET, J. BIJHOUWER and W. VAN DIEREN are mentioned.

The broadening basis is marked by the outstanding thesis of V. WESTHOFF, the first all-round phytosociological and ecological study of Dutch dunes. New ideas from this work are mentioned. The work of some pupils and collaborators of WESTHOFF is discussed.

The new approach consists of concentration of the research in the Delta region, development of new ideas and establishment of field stations in the dunes.

The scientific value of the Delta dunes is treated. Especially the Voorne dunes are considered as outstanding. Some future changes that threaten the area, are mentioned. The organisation of the Delta dune research is discussed, especially the work of a special Research Group, operating from the Biological Station "Weevers' Duin" at Voorne.

The current botanical problems are treated. It is stressed that they are placed in the framework of the ecological relation theory of C. G. VAN LEEUWEN, which is a new, highly stimulating, system-theoretical approach. This relation theory is introduced and commented.

Four environmental types are treated, the uniform, the variegated, the ecotone and the ecocline environment.

The dune environment is discussed as a system of gradients. The main gradients are mentioned: the zonation of dry dunes, zonation of slacks, gradient from sea dunes towards estuaries, the complex salt-fresh gradient, the complex wet-dry gradient, and the complex gradient in the human and animal factors.

The dune vegetation is treated as a continuum. 24 vegetational series are mentioned. A series consists of closely related communities, forming a continuum.

Some problems concerning selection and sampling are discussed. The controversy between Anglo-American and Zürich-Montpellier scholars is elucidated on some points. The Braun-Blanquet scale of combined estimation is advocated.

The study of pattern and instability in vegetation research is emphasized. Some methods in structure analysis are mentioned. Recent problems in vegetation systematics are discussed. The application of methods in the Delta research is consequently mentioned.

An extensive bibliography, covering important botanical work in Dutch dunes, ends the paper.

[1]) Own research mentioned in this paper, was carried out while the author was at the Botanical Museum and Herbarium, Utrecht.

1. Introduction

This paper aims at giving some information on recent studies in the Delta region. Since this work cannot be well understood without knowing the classical dune studies and since the latter ones are not well-known abroad, it may be useful to introduce our proper subject with some historical data.

The importance of the Delta dune research must be seen in the light of the outstanding scientific value as well as the coming changes of the area. Therefore some information on this context is added to the paper. In this research the study of vegetation has a central position. Since the author has been involved in some aspects of the vegetation study, he was asked to describe this part of current ecological work in the Netherlands.

2. History of dune research, a chain of theses

2.1. *The classics*

Extensive dune research started with the work of Franciscus Holkema, who wrote 1870 a thesis on the flora of the Dutch West-Frisian islands. He travelled all the islands, which was not a simple task in those days, and he composed a remarkable survey of both cryptogamic and phanerogamic species. He even presented quantitative data with a fourfold scale of local coverage and abundance, which is a precursor of the recent scale of Dansereau (1957). Unfortunately Holkema died when correcting the proofs and his supervisor, Professor H. C. van Hall had to publish the work.[2])

Nearly 30 years later Laurens Vuyck (1898) wrote his dissertation on the flora of the Dutch dunes. This work was similar to that of Holkema, but it was especially concerned with the mainland dunes and it had a special aim: to find out if there had occurred any changes in the dune flora as a result of the water catchment activities, which had started in the second half of the 19th century.

Reading the accurate and at the same time very poetic descriptions the Dutch classics in natural history, F. W. van Eeden and Jac. P. Thijsse of paradise-like dunes, dune marshes, lakes and brooklets, one can hardly imagine a serious devaluation as early as 1900. Indeed, one of Vuyck's conclusions was that the fear for deterioration amongst biologists of those days was unfounded. Nowadays the scenery has changed. The original freshwater supply in the dunes of Holland is going to be exhausted. In the mainland dunes the original flora and vegetation have strongly impoverished. To continue the drinking water supply, infiltration schemes have been developed and partly

[2]) It is a tradition in most Universities on the continent to publish in full the outcome of the research done for a doctor's degree, before one can be graduated.

carried out. This has restored the botanical richness to some extent. (see Boerboom, 1958, 1960a, b; Van der Maarel and Londo, 1960; Londo, 1964).

The proper investigations of Vuyck were performed very carefully and his results are still interesting.

He reviewed practically all historical work on dune floristics including Dodonaeus, David de Gorter and A.P. de Candolle. He also compiled contemporary knowledge on the dune flora as well as a lot of own inventories. Vuyck was one of the first Dutch botanists to include plant habitat and environment descriptions in his work.

Shortly after Vuyck Jeswiet (1913a) continued the remarkable tradition of presenting the main results of Dutch dune studies in the form of a thesis. Jeswiet definitely proved the existence of two main zones in the coastal dunes of North and South Holland. These are known as old dune landscape and young dune landscape; they were first recognised about 1850 by geologists. The floristic differences between the two landscapes were clearly shown by Jeswiet. The details of the origin and relations between the two zones are still a matter of investigation and discussion among geologists and ecologists.

In an additional paper (1913b) Jeswiet appeared to be an ecologist in the modern sense of the word. After he had given many data on dune soil and climate in his thesis he now published a fine study on growth form and life cycle of dune plants. He made a division into ecological groups, based on a lot of own observations, which was highly inspired by the work of the great Belgian dune ecologist Jean Massart (1908).

The next thesis in the series is that of Bijhouwer (1926) on the border area between the rich-in-lime southern dunes and the acid northern ones, near Bergen. His study is the first to apply phytosociological methods in Holland, e.g. the twin association concept of Hult, and the frequency method of Raunkiaer. The main value of his work is the detailed study of plant distribution in the proper border area. This study was partly repeated by Westhoff (Hoffmann and Westhoff, 1951).

Then followed the thesis of Van Steijn (1933) on dune afforestation. This study is again a valuable source of historical information and contains the results of nearly a century of practice in dune afforestation.

One of the outstanding theses in the series is that of Wouter van Dieren (1934), on organic dune development, one of the few that has got an international reputation. His study has shown remarkably clearly the relation between physical and biological processes in the formation of dune systems. In the description of vegetation types Scandinavian methods were followed. Van Dieren has died only one year after the completion of his masterpiece.

2.2. *The broadening basis*

The culminating thesis in this dune ecology series is that of Victor

WESTHOFF (1947) on the vegetation of dunes and salt marshes of the West-Frisian islands Terschelling, Vlieland and Texel.

Contrary to Dutch tradition and due to the post-war situation, this thesis has not been printed in full. Only an English summary has come into print, unfortunately in a very limited number of copies. Consequently the whole work is rather badly known, even in Holland.

Though Westhoff has received full appreciation as a leading European phytosociologist, in his own country as well as abroad, it remains a pity that his pioneer work is still rather obscure. It may be presumed, that much of the controversy between the Zürich-Montpellier school and the Anglo-American approaches as well as a good deal of the confusion about the various European approaches would have been elucidated already 20 years ago, had Westhoff's thesis been printed in full!

This study involved the first over-all description of dune vegetations in the Netherlands on an association basis.

– BRAUN-BLANQUET and DE LEEUW (1936) had then already published their study of the vegetation of Ameland, but this study is rather incomplete and not solid.

With help of the Braun-Blanquet method a minute analysis of dune and salt marsh associations and sociations was carried out.

It is largely due to this study that we have got in the Netherlands the first ideas of dynamic relationships between vegetational types and series as well as their environmental conditions. Moreover it contains many methodological and theoretical considerations, e.g. the application of Huxley's cline concept in phytosociology, the relation between vegetational environment and ecotypic variation in plants, the evolution of plant communities or synchronology, the geographical variation of associations and the association concept.

In the following years Westhoff has stayed to be active in doing and promoting dune vegetation research. Especially his former collaborators Boerboom and Doing have extended our knowledge of the subject. Westhoff himself made numerous excursions and special studies in many of our Dutch dune systems, and published a series of papers on various subjects. Major publications are HOFFMANN en WESTHOFF (1951) on the Bergen dunes, WESTHOFF (1952b) on scrub and forest communities of the inner dunes, WESTHOFF (1959) on dune pine forests and WESTHOFF, VAN LEEUWEN and ADRIANI (1961) on vegetation and soil of the Goeree dunes. Several minor papers are included in the reference list.

BOERBOOM concentrated his studies on the dunes near The Hague; he dedicated a number of papers to that area, among which is his thesis (1960a), a general description of the vegetation of those dunes. One of the main outcomes of his work is a better understanding of the historical determination of the present dune vegetation. Via study of historic sources in governmental archives he composed a scheme of dune development and human occupation up from the late Middle Ages.

Doing has emphasized the study and mapping of dune vegetations as landscape complexes, both for practical and theoretical purposes, i.e. to provide surveyable maps showing vegetation mosaics to find out the main lines of dune and dune vegetation development. He was able to discern some major vegetational zones in the dunes near Haarlem. He originally intended to present the results of this work as a thesis, but later on he turned to scrub and forest communities in the Netherlands. In his two papers on the latter subject, (DOING, 1962, 1963a) the first one being his thesis, a number of dune communities have been described. His proper dune studies are to be reported in a separate paper, which is now in preparation. Finally Doing's attempts towards a refinement of vegetation analysis must be mentioned here, since part of the underlying studies were carried out in the dunes. See DOING (1954) and BARKMAN, DOING and SEGAL (1964).

More or less independently V. DE VRIES has made interesting studies of vegetation- soil relationships in the dunes of Vlieland. He also wrote a thesis (1962) after he had already published (1950) a booklet on this work.

In many of the mentioned studies as well as some others (see reference list) vegetation maps were composed. Only a few have actually been published. Since this is often the case with maps, DOING and VAN DER WERF (1962) have listed all available manuscript maps, either printed later on or not, with notes on scale, methods, institute etc. The reader is referred to this list for further information on dune vegetation mapping.

2.3. *The new approach*

In recent years interest and rese arch concerning dune vegetations has steadily grown and new investigators and new approaches have come into being. There are three main points to be discussed:

1. The filling up of the geographical gaps in our knowledge;

2. The development of new methods and the application of new theories;

3. The establishment of biological field stations with full ecolcgica equipment.

The first point especially refers to the Delta region, and it will be treated separately. The second point can be easily discussed in this more detailed account on the Delta dunes.

The establishment of field stations in the dunes goes back to 1948. In that year some ecologists interested in dune ecology decided to establish a foundation for dune research, "STICHTING WETENSCHAPPELIJK DUINONDERZOEK", which will be referred to as SWD. The board of SWD have done valuable work, in the beginnings under hard circumstances, and they have succeeded in the major purpose, viz. to establish two field stations for dune research, one on the island of Terschelling, representing the northern dunes, the other on the island of Voorne, representing the southern dunes.

In 1948 the *Biological Station "Schellingerland"* was opened and in 1952 the *Biological Station "Weevers' Duin"*. This station was named after WEEVERS (1875–1952), formerly Professor of Plant Physiolgoy at the

University of Amsterdam, who was a very active plant ecologist and sociologist and the first chairman of SWD.

In the beginning these stations had a rather modest accommodation and they were predominantly intended to provide room for residence and simple research.

In the meanwhile ecology had received full appreciation from scientific authorities; there are now four university chairs in ecology, varying in age from one to fifteen years, one in animal ecology, one in conservation ecology, and two in plant ecology.

In 1954 the *Royal Dutch Academy of Sciences* established the *Institute for Ecological Research* and in 1957 the Biological Station "Weevers' Duin" was incorporated in this institute. This incorporation has resulted in a considerable improvement of the original equipment as well as the appointment of plant ecologists at "Weevers' Duin". At present they are Dr. Adriani, head, (plant-soil relationships), Dr. Stoutjesdijk (micrometeorology) and Mr. Freijsen (plant autecology).

Something similar happened to the Biological Station "Schellingerland"; it has become part of the *RIVON*, the *State Institute for Nature Conservation Research.* Again laboratory facilities has improved. Until now no scientists have been appointed here permanently.

A third field station was established by the *Biology Department* of the *State University* of *Groningen* on the West-Frisian island of Schiermonnikoog. The newly founded *Plant Ecology Laboratory* under Professor D. Bakker has started ecological studies on the dunes and salt marshes of this island.

Finally another field station on this island was established by the *Biology Section* of the *Free University of Amsterdam.*

Apart from being centres of field research, these stations have a very important task in providing facilities for undergraduate field courses from most University Biology Departments. Thus the number of students interested in dune research is steadily increasing.

3. The delta dunes, a chain of isolates

3.1. *The scientific value*

A vast area of coastal dunes remained unmentioned in this survey so far: the Delta dunes. See Fig. 1. Remarkably enough, prior to 1959 only incidental studies on the vegetation of these dunes can be reported – there is one exception, namely an extensive vegetation study by Weevers (1940) on the Goeree dunes.

The geographic isolation, the complicated and long travelling and the absence of suitable centres for field studies might be reasons for the curious isolation of these dunes. However, the same holds for the West-Frisian islands! Hence the main reason will be the comparatively small size of the Delta-dune systems as well as their less outstanding reputation. Still some parts of the area, in particular the Voorne dunes, are known as valuable for some tens of years and one of the most

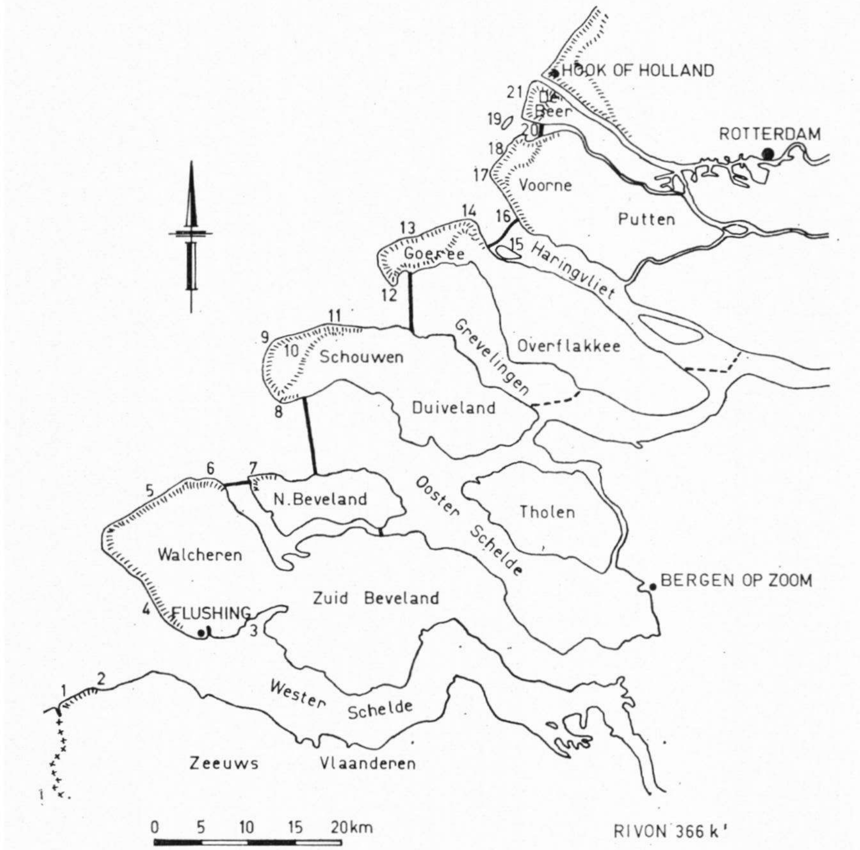

Fig. 1. Dune areas in the Delta region and their zonation[3]) (from VAN DER MAAREL, 1965b)

1. Zwin (A, B-C)
2. Verdronken Zwarte Polder (A, C–D)
3. Kaloot (B)
4. Walcheren, S.W. coast (C–D–F–G)
5. „ , N.W. coast (C–D–F)
6. „ , N. coast (C–B–D–F–G)
7. N. Beveland (B–C, C–D)
8. Schouwen, S.W.coast (C–D–F–G)
9. Westeren and Oosteren Ban (B–C–D–G)
10. Vronen of Renesse (G)
11. Schouwen, N. coast, incl. Zoute Haard (C–D–G)
12. Goeree, S.W. coast (B–C–D–F)
13. „ , N.W. coast (C–D–G)
14. Kwade Hoek (A–B–C–D–F)
15. Scheelhoek (A–B)
16. Voorne, S.W. coast, incl. Quackjeswater (B–C–D–F)
17. „ , W. Point (A–B–C–D–E–F–G)
18. „ , N.W. coast, incl. Breede Water and Heveringen (A–B–C–D–E–F–G)
19. Westplaat (B)
20. Brielse Gat, incl. Groene Strand and Kruiningergors (A–B–C–D, F)
21. De Beer (now extinct)

[3]) Explanation of zonation symbols A–G in § 4.3.

beautiful areas on this island, the Breede Water region, is one of the most favourite dune reserves in the country.

The Delta dunes have only recently been claimed as one of the outstanding Dutch natural landscapes, with a great international importance, both botanical and ornithological.

The following botanical arguments may favour our claim for the importance of the Delta dunes, especially those of Voorne and Goeree. See ADRIANI and VAN DER MAAREL (1962); VAN DER MAAREL (1962, 1965).

The dune systems of De Beer, Voorne, Goeree, Schouwen and Walcheren, which are the major ones, are rather similar as for history and present environmental conditions, but are distinguished from each other by numerous minor differences in origin, soil characteristics, zonation, human and animal influences etc. Consequently they form a very good series for comparative research. This holds especially for the herb and shrub communities of the xerosere.

A second general value lies in the existence throughout the area of large beach systems with salt-fresh gradient communities and fore dune vegetations, both with outposts of some mediterranean-atlantic species, such as *Catapodium marinum* and *Euphorbia paralias*.

The Voorne dunes have special values in the development of shrub communities, both wet and dry; in the presence of large dune slacks, both primary and secondary, with rare plant communities in all stages of their development, especially dwarf scrub of *Salix repens* (see for nomenclature VAN DER MAAREL and WESTHOFF, 1964). Furthermore these dunes have been built up periodically in an alteration of dune ridges and primary dune slacks, the latter being beach flats, cut off from sea and desalinated later on. This zonation is a very suitable object for vegetation and soil development studies. In Europe this type of dune development is rather rare. We only know it from Berck Plage and some other places in NW France and in the Ainsdale Dunes near Liverpool (VAN DER MAAREL and VAN DER MAAREL-VERSLUYS, 1963). A somewhat different situation can be found in the Studland dunes, Dorset, and in the Tentsmuir Sands (GIMINGHAM, 1964).

In Fig. 1 the principal dune regions on the Delta islands are indicated. The division given here is rather rough. A more detailed division as well as geomorphological descriptions would fall beyond the scope of this paper. For the latter information the reader is referred to VAN DER MAAREL (1965a, b) and following papers. In § 4.3 and § 4.4 some data on zonation and vegetation will be presented.

Within the large slacks two dune lakes are to be found on Voorne, viz. the Breede Water and the Quackjeswater. They are strikingly different in phytoplankton communities and they form one of the peculiarities of the Voorne dunes, see LEENTVAAR (1963).

We have made a very tentative estimation of the number of outstanding dune areas in NW Europe (VAN DER MAAREL, 1962) and have come to 15, including such systems as the Ainsdale dunes, Braunton Burrows, Berck Plage, Römö, Sylt. In a possible sequence of importance the Voorne dunes may be ranked rather high.

The dunes of Goeree are important mainly by the presence of the Kwade Hoek, a beach and marsh landscape bordering the Haringvliet. This is one of the most valuable areas as for size and diversity, especially in salt-fresh and wet-dry gradients. The relative importance of the area is increased by the extinction of the comparable "green beach" area of De Beer.

3.2. *The changing future*

Unfortunately scientific value often coincides with economic or touristic importance in many areas. So it does in the coastal landscape of the Delta region. Apart from a number of minor human influences that are to be found in each pseudo- or semi-natural landscape (terms from WESTHOFF, 1952a) in urbanized regions, such as local draining, levelling, cultivation, local afforestation, mowing and grazing, there are some giant projects in development, which will cause a total change in the area.

The so-called Delta plan covers the major part of these projects. It is the most ambitious Dutch plan in civil engineering that has ever come into reality and it will be one of the most fascinating water works in the world. The plan involves the closing of the estuaries, except one, viz. the Westerschelde, which forms the connection between Antwerp and the North Sea. It would go far beyond the scope of this chapter to mention all the consequences of this plan. (See VAN LEEUWEN and MÖRZER BRUYNS, 1954.) The biological aspects are being studied at the *Delta-department* of the *Hydrobiological Institute* at Yerseke.

Dune ecologists will meet the following changes in their working area, which will force them to speed up their studies and to prepare themselves on all kinds of abrupt ends.

1. The closing dams will cut off some eastward dunes from the sea, so that the latter will become secondary fresh water dunes. This is not necessarily a devaluation, except when man enters the area in considerable numbers, as may be expected after the dams will have been opened to the public traffic. We have followed one example so far, i.e. the Kruininger Gors along the Brielse Maas, the first estuary that was cut off, in 1950. More or less simultaneously, though in this case independently, the population of a neighbouring seaside holiday camp increased. The main changes in the dunes to be reported are a rapid scrub development together with an extension of trampled bare spots. Thus original diversity has been considerably diminished.

2. In some cases the building of a dam cannot be completed successfully without disturbing green beach areas along the estuaries. This threatens the Kwade Hoek in particular.

3. The dams will break the isolation of the islands and give way to thousands of holidaymakers, especially motorists and cyclists. This will

result in a tremendous recreational development involving new motorways, cyclepaths, beach accommodation, etc. Such a development can be disastrous for dune areas as a whole and in particular for gradient situations in wet and dry slack systems, unless local or conservational authorities will be able to canalize these new recreational streams. Some dune areas are fairly well preserved at the moment, either by private and governmental Nature Protection Bodies (Voorne, Schouwen), or by Water Catchment Companies (Goeree, Walcheren). One cannot be sure, however, that these areas will all remain closed for the great public.

4. The closing of the estuaries will cause a considerable change in water movement relations along the Delta coastline, and consequently in the pattern of sedimentation. Coastal engineering experts and geomorphologists are preparing models to predict future changes, but until now nothing certain is said in their predictions. Perhaps this change will turn to be the most dramatic of all. One has presumed that the coastline as a whole will be straightened which will result in the loss of valuable areas situated in the westward "points" of the islands (Fig. 1). Others have already dreamt of giant new lateral sand banks in front of the estuaries, enclosing enormous new lagoon and dune areas.

A more local event, partly connected with the Delta plan, is the expansion of the Rotterdam harbour and its industrial development. Some phases of the scheme have been passed already, e.g. the destruction of the dunes and beaches of De Beer, one of the largest green beach areas in our country. This area was especially famous for its breeding colony of the *Sandwich Tern* (*Sterna sandvicensis*). The botanical characteristics have been described by VAN LEEUWEN and WESTHOFF (1961) and summarized by ADRIANI and VAN DER MAAREL (1962). Van Leeuwen has done interesting research on the changes in vegetation following the closing of the Brielse Maas (not yet published). Recently two students from Utrecht University, SPEKMAN and GROTEN (1963), made a study of the *Sagina maritima* communities, while these were driven up by bulldozers and suckers.

The next phase will be the poldering of a part of the Maasvlakte, a shallow region in front of the coast of De Beer. These works will involve a dam from the Westplaat, a sandbank opposite to the Brielse Gat, to the coastline of Voorne. This will mean the loss, or at least a total change of the beach dune and salt marsh area, known as the Groene Strand (see Fig. 1).

The Voorne dunes, and its Northern part in particular, will be indirectly threatened by rural development, mass recreation and air pollution from petrochemical industry arising in the new harbour area of Rotterdam. The first signs of the latter seem to be found in the recent diminishing of some epiphytic mosses and lichens on *Sambucus nigra*, which were very common in the dunes near Oostvoorne (TOUW, pers. comm.).

3.3. *The organisation of research*

Systematic dune research in the Delta region dates from recent times, as was stated before. It will be appreciated that the need for intensive and coordinated studies in this area is rapidly growing. This was realised by SWD, especially by its members who were already active in dune research.

The establishment of the biological station "Weevers' Duin", and the appointment of full-time ecologists in particular may be considered as the first step in the organisation. The second step was the establishment of the RIVON in 1957, and the immediate interest of its staff in Delta dune ecology, both botany, hydrobiology and zoology.

The final step so far has been the establishment of a special *Research Group Coast of Voorne* under supervision of SWD and under chairmanship of Adriani. In this group all dune specialists with interest in the Delta dunes are co-operating in order to co-ordinate and speed up current research and to prepare new studies, with "Weevers' Duin" as a centre of research. The following disciplines are represented at the moment: plant ecology, phytosociology, animal ecology, entomology, ornithology, soil zoology, mycology, taxonomy, micrometeorology, geomorphology, hydrobiology, hydrology. The main partners in the group are "Weevers' Duin" and the RIVON. Besides scientists from various other institutes are member.

The Research Group has drawn up a detailed research programme. It consists of three groups of objects, viz. urgent, unique and fundamental objects, and it is mainly concerned with Voorne and the adjacent areas at the moment.

The urgent objects are related to areas that are threatened by destruction or by disastrous changes, such as De Beer and the Kwade Hoek on Goeree (see Fig. 1). The unique objects are concerned with areas or vegetation types that are considered as very remarkable and valuable in their biological features, e.g. the zonation and the dune lakes in the Voorne dunes, and the green beach area on the Kwade Hoek. As fundamental objects, i.e. basic studies from which other studies may gain, are to be mentioned methodology of soil analysis, cytotaxonomy and vitality studies.

The botanical studies involved in the programme have been initiated by Westhoff in 1947. The author has worked in the area incidentally since 1953 and regularly from 1958 onwards. It is emphasized that the RIVON contributes to the work by subsidizing temporary research, mainly done by students and that the Netherlands Organization for the Advancement of Pure Science is sympathizing with the project, which has already resulted in a grant for a long-term study.

In this way we may perhaps succeed in keeping ahead of the future changes in the area and in preparing in time a complete account on its ecology. Since the new situations may be "open" in many respects, it is of great importance for the ecologist to gain sufficient knowledge in order to help creating the new landscape as to provide compensation for the losses in ecological diversity as well as future objects of study.

4. Dune vegetation study, a chain of problems

4.1. *Problems and a general approach*

The Research Group has given relatively much attention to the fundamental studies on vegetation systematics and ecology, so far. This may be surprising, since dune vegetations are comparatively well-known in Holland, as was emphasized in § 2. Yet this situation may be easily explained by the rapid development of plant ecology as a science, especially objective description methods, pattern studies and ecosystem theory. Furthermore it must be realized, that the main strength of the Zürich-Montpellier school, among which most Dutch dune investigators may be reckoned, lies in the synthesis of vegetation on a rather broad scale, e.g. the surveying of plant communities of countries or vegetational districts, such as those by Tüxen (1955) and Oberdorfer (1957). The straightforwardness of the procedure is much less obvious when the entire local variation of vegetation, as on Voorne, is studied.

A series of theoretical and methodological problems have been encountered during the first years of the research. These problems are not only concerned with analysis and synthesis as such, but also with the nature of vegetation.

The relation theory of C. G. van Leeuwen (1963, 1964, 1965b), together with his considerations on borderline situations (1965a), have highly stimulated us to develop a general approach to the vegetation of the Delta dunes and to erect a system-theoretical framework within which the various problems may be adequately defined and tackled.

Our chain of problems may be taken up at the first stage in the description of vegetation, i.e. the selection of stands to be sampled. Sampling itself is the next stage and it bears a number of problems. The third group of problems is concerned with the analysis. Which characteristics of vegetation will be worth analysing and how is it to be done? The final stage in the proper description of vegetation is the synthesis of data in order to erect vegetational types and systems. When the vegetation has been described in some way, its ecology may become centre of interest. Which are the determining environmental factors, which are the relationships between a vegetation type and its environment, which are the relationships between vegetation types, whether functional or systematical, and finally, how do these relationships behave in time? These questions may be approached by descriptive and experimental studies. The Research Group will concentrate its studies on the description.

Treating these problems involves the comparison of different phytosociological schools that are active at the moment. In this paper will be discussed mainly the Zürich-Montpellier school, as expounded by Braun-Blanquet (1951), and the "Anglo-American" school, as represented by Cain and Castro (1959) and Greig-Smith (1964).

The new European approach, as surveyed by Van der Maarel, Westhoff and Van Leeuwen (1964), comprises a group of new trends that are developing but obviously deviating from the Z-M principles.

Our considerations start from a system-theoretical point-of-view as developed by Van Leeuwen, from basic ideas of ASHBY (1957) and MARGALEF (1958). They may be introduced in the following, before some of the actual problems will be outlined.

4.2. *Relation theory and environmental types*

4.2.1. The relation theory of Van Leeuwen

Since Van Leeuwen will publish an account on his theory in this issue, it is not necessary to introduce it here. Still it may be useful to mention some aspects which are especially relevant for the present study.

A first remark concerns the name of the theory. The basic considerations have been gathered under the name "*open-en-dicht theorie*" (VAN LEEUWEN, 1963). Ranwell has made a translation of this paper "The open-and-closed theory as a possible contribution to cybernetics", which has been added to a lecture at the 10th International Botanical Congress at Edinburgh (VAN DER MAAREL, WESTHOFF and VAN LEEUWEN, 1964).

Open and closed are terms of information-theoretical character. In the three basic relations as exposed by Van Leeuwen, open and closed indicate situations both in space and time. This has appeared not clear to all students of the theory. One source of confusion is that some cannot take open and closed as qualities of time; a second is that these terms are easily taken as absolute ones, in all situations.

A terminology based on the concept *change*, or *alteration*, symbol *a*, would avoid such confusions. Change then equals "*closed-in-space*", or *variety*, as well as "*closed-in-time*", or *instability*. Openness, meaning equality in space and stability in time, may be interpreted, in accordance with philosophy, as a particular situation of change, viz. *non-change*, symbol *ā*.

Since these are essentially relations of which characters are described and since the framework of the theory itself consists of three basic relations, the author prefers the neutral term relation theory for the theorems of Van Leeuwen. In a non-ecological context we may speak of ecological relation theory.

4.2.2. Environmental types

During a study of the plant communities of the alliance *Agropyro-Rumicion crispi*, Van Leeuwen came with help of the relation theory upon the distinction into two main types of borderline situations. In his recent papers (1965a, b) VAN LEEUWEN has elaborated his considerations and he has come to some very convincing statements, such as on the boundary-bound character of life in general, on the clear distinction between the limes divergens and the limes convergens type of boundary, and last not least on the antithesis between the old-fashioned agricultural pattern and the modern technical civilisation.

Referring to these papers and quoting VAN DER MAAREL, WESTHOFF and VAN LEEUWEN (1964) we mention the following four main types of environment. It is emphasized again, that these categories are possible extremes. Most ecological situations are intermediate.

1. **Uniform environment.** This is an environment with an aspect of homogeneity in the horizontal plane: open-in-space, or $\bar{a}$ (s). A uniform environment is instable, i.e. certain principal environmental factors, whether natural or human, considerably fluctuate in their effects: closed-in-time, or $a(t)$. The vegetation to be found in this environment tends to be very poor in species, the individuals of which are mostly very numerous, with few patterns and with erect growth forms as found in *Poaceae* and *Chenopodiaceae*. Examples in coastal regions are the *Salicornia* marsh, with the tidal movements as the main source of instability, and the seaward dunes with *Ammophiletum*, with the irregular sand movements as a factor of instability.

2. **Variegated environment.** This type is the opposite of type 1 in many respects. It is heterogeneous in space, $a(s)$ and rather stable, $\bar{a}$ (t). The stability is due to the absence of calamitous changes and to the regularity of minor changes, if present, such as rainfall. The vegetation correlated with this type of environment is very rich in species, with many different growth forms and a large amount of pattern. An example from the dunes is the *Ligustrum-Crataegus* scrub, alliance *Berberidion vulgaris*, with up to 80 species on areas of about 100 sq.m.

3. **Limes convergens environment.** This environment is characterized by sharp boundaries with rather different situations on either side of the boundary. The course of the boundaries is changing irregularly. Parallel to the boundary the environment is homogeneous and instable, $\bar{a}$ $(s) \leftrightarrow a$ (t); in the perpendicular direction the situation is heterogeneous and rather stable: $a(s) \leftrightarrow \bar{a}(t)$. The vegetation belonging to this type of environment is homogeneous, within coarse-grained patterns, rather poor in species, with few growth forms, especially rosettes and creepers. An example from the coast is the floodmark environment on spring tide level, where a sharp difference is found in the salinity. Here plant communities of the alliance *Agropyro-Rumicion crispi* and *Angelicion litoralis* occur (BEEFTINK, 1965).

As Van Leeuwen has clearly pointed out, the sharp boundaries may be fixed more or less by man. This stable limes convergens environment may be considered as a sub-type. It is often characterised by own species.

According to the original meaning of the term *ecotone*, described by Livingstone and Clements as a tension belt or a stress zone, VAN LEEUWEN (1965a) considers the limes convergens situation as more or less identical with the ecotone. Therefore i may be justified to use these terms as synonyms.

4. **Limes divergens environment.** This type is largely opposite to type 3. It is determined by an environmental gradient, i.e. a very gradual change in one or more environmental factors, with a high stability. As VAN LEEUWEN (1965a) has demonstrated, such an environment is built up by numerous minute boundaries. When looked upon as a whole, the divergent limit environment appears rather homogeneous. In fact it represents the ultimate state of heterogeneity. The corresponding symbols are $a(s) \leftrightarrow \bar{a}(t)$. The vegetation associated with this environment is very rich in species, most of which are poor in individuals. There is a great variety in growth forms. An example from the dunes is the dune grassland complex, with complex moisture and acidity gradients. On Voorne about 120 species are found on only 1000 sq.m.

It is obvious that the catena concept of soil scientists as well as the *ecocline* concept as used in taxonomy and vegetation systematics (VAN DER MAAREL and WESTHOFF, 1964) are related concepts. Consequently we may propose to use the term ecocline environment as a synonym.

Rather often some instability is superposed on the gradient, e.g. a fluctuating ground water table in a moisture gradient. VAN LEEUWEN (1965a) mentions some dune species which are characteristic for such an instable ecocline environment.

There is an obvious similarity between the environmental types 1 and 3 and 2 and 4 respectively. Just as we have called non-change a particular aspect of change, we may call a uniform environment a particular aspect of an ecotone environment, i.e. with no visible sharp boundaries and an instability on a relatively large area. In the same way a variegated environment may be considered as a special form of the ecocline environment, i.e. with a gradient on a relatively large scale.

Since the strong mutual bounds between vegetation and environment are in general very obvious and moreover, since the structure of vegetation seems to be correlated in some way to the type of environment, the environmental terminology may be extended to ecosystems. So far, this has not been done. It remains a very interesting task to elaborate the ecosystem typology in this sense and to gain more knowledge about the nature of the relation between type of vegetation and type of environment.

One of the principal problems is the development of parameters for environmental variety and stability, as well as for biotic diversity, structure and integration of vegetation. MARGALEF (1958, 1961, 1964) has made progress in the latter development; BRAY (1961) has made a start with the former one.

4.3. *The dune environment as a system of gradients*

In the following the dune environment will be treated as a system of gradients rather than as a system of factors. An outline of the principal factors is of value, but, as follows from the foregoing, the gradient character of these factors is of paramount importance for the interpretation of vegetation.

It will be clear, that the variety of an environment is generally determined by such conditions as the number of independently acting environmental factors or factor complexes, by the amplitudo of the variation of these factors, and by the continuity of these variations in the field. If these conditions are all met with, we may speak of gradients.

It is stated beforehand, that the dunes are very rich in gradient situations. The ecocline environment is the most common type, although it is mostly provided with minor instabilities. Therefore our data will be compiled in a description of gradients. The following main gradients are of importance in the dune systems of the Delta region.

1. **The zonation from the beach dunes via seaward ridge(s), seaward yellow dunes, middle yellow and grey dunes, towards landward dunes.** This is a *dry-dune gradient*, mainly based on the age of the dunes. Within this gradient there is a decrease in surfacial sand mobility, a decrease in $CaCO_3$ content, correlated with an increase in soil acidity, and finally an increase in humus development. This gradient resembles those in Australian dunes (BURGESS and DROVER, 1953), Lake Michigan dunes (OLSON, 1958), English dunes (SALISBURY, 1952) and Scottish dunes (GIMINGHAM, 1964).

Within the Delta dunes this gradient is best developed in the Voorne dunes. Here a regular discontinuous geomorphological zonation is found. The dating of this zonation, which is starting with dunes of about 2000 years old, is not yet satisfactory. Available data were summarized by VAN DER MAAREL and WESTHOFF (1964). The complicated interaction between historic development of the zonation, soil development and vegetational zonation, is subject to a detailed investigation (Adriani and Van der Maarel, in preparation). The main data on the vegetation development are already known; the local areas with the most pronounced zonation, viz. the Oostvoorne dunes and the dunes of the point of Voorne, have been carefully mapped by VAN DER MAAREL (1960) and SLOET VAN OLDRUITENBORGH (1965) respectively.

2. **A parallel,** but less obvious **zonation** is found in the **slacks.** In many cases each addition to the dune system of a new zone consists of a seaward ridge and a slack behind. Here and there secondary sand movements have changed the original pattern. Under equal ground water conditions a similar soil development as in the dry dunes is found in the slacks.

The zonation may be summarized as follows:

A. **Green beaches,** i.e. elevated beaches, mostly situated along the estuaries, where the tide comes in from the estuarian side. These beaches are partly sandy, partly silty and generally covered with vegetation.

B. **Fore dunes,** situated on the higher parts of the beach in front of the dunes

C. **Present coastal ridge,** which is on many stretches partly or wholly built up with human help and consequently rather sharply distinct from the dunes on either side.

D. **Seaward yellow dunes,** comprising the mobile dunes, directly behind the coastal ridge.

E. **Outer slacks,** being the large primary dune slacks, cut off recently from the sea, and thus being formerly beach flats. Small ridges in between the slacks are reckoned to this zone as well.

F. **Middle dunes,** comprising the yellow, semi-fixed, relatively high dunes behind zones C and D, being of medium ages, i.e. 100-300 years old. Small secondary (blown out) slacks occur in this zone.

G. **Old landward dunes** ("binnenduinen"), comprising the relatively low, old dunes at the landward side of the dune systems, which have been used for grazing for centuries. These dunes are directly comparable with the Scottish machair.

The distribution of these zones is presented in Fig. 1, § 3.1.

3. **A gradient from sea-exposed dunes in the "points" of the islands towards dunes situated along the estuaries.** In terms of plant geography this is a gradient from the proper *Dune District* to the *Fluviatile District,* as described by VAN SOEST (1929); see HEUKELS–VAN OOSTSTROOM (1962) and BARKMAN (1958) for a general division of the Netherlands into floristic provinces.

The Dune District is characterized by some species groups, i.a. continental and southern species, such as *Erodium glutinosum, Rosa* *spinosissima*, *Viola rupestris* and *Phleum arenarium*. (All are strictly or predominantly dune species in the Netherlands).

The Fluviatile District comprises species groups from continental origin, e.g. *Carduus nutans*, *Sedum boloniense* and *Eryngium campestre*. (In the Netherlands they are mainly restricted to the region of the great rivers Rhine and Meuse.)

A considerable number of species occur equally common in both Districts, e.g. *Silene nutans*, *Knautia arvensis*, *Cynoglossum officinale*, *Silene conica* and *Berberis vulgaris*. Some other species from the one District have allies in the other one, e.g. *Koeleria albescens – cristata* and *Thalictrum minus ssp. dunense – ssp jaquinianum*. It is very remarkable that many species of the latter group show a rather strong preference within the Delta for the estuarian parts of the dunes. Examples are *Eryngium campestre*, *Thalictrum minus ssp. dunense*, *Koeleria albescens* and *Berberis vulgaris*. Fig. 2 shows the distribution of some of these species throughout the Voorne dunes.[4])

This gradient will be at least partly determined by the decrease of salt spray influence. Presumably it has a soil-ecological basis as well; this has not been demonstrated so far. A considerable part of the dunes has been formed upon clay. Now it may be expected that the physical and chemical properties of the clay may depend on the way and the place they have been deposited. Fig. 2 also shows the course of early medieval tributaries of the Haringvliet estuary. The correlation between the present distribution of dominant Berberis vulgaris and the former bed of the river Goote is obvious.

The distribution of the fore dune species *Elymus arenarius* is another demonstration of the estuarian effect. It follows from data by BAKKER (1965) and the author, that this species comes to dominance exclusively on fore dunes situated along the estuaries, most of which are situated to the North (especially on the North coast of N. Beveland, Walcheren and Voorne). Little is known about the causes of this distribution. In Britain this boreo-atlantic species is more common and more dominant on the east coast (PERRING and WALTERS, 1963; SALISBURY, 1952) as well as on dune systems elsewhere in Britain, on eastward coastlines, such as in Dawlish Warren and Studland dunes (VAN DER MAAREL and VAN DER MAAREL-VERSLUYS, 1963). Salisbury's hypothesis on the salt sensitivity of *Elymus* is not contradicted by our data.

4. **The gradient from sandy places within the daily salt water inundation influence towards completely fresh water dunes.** This gradient extends only over a small distance in the green beach areas, where the tide comes in via the estuary. On many places this gradient is most pronounced in small scale zonations on slopes of little dunes on these beaches. The *Saginion maritimae* communities are

[4]) These floristical data have been taken from a minute analysis of the flora of the Voorne dunes, carried out by W. F. Dortmond and the author. The first results of this investigation, which is going on, will be published in VAN DER MAAREL (1965a).

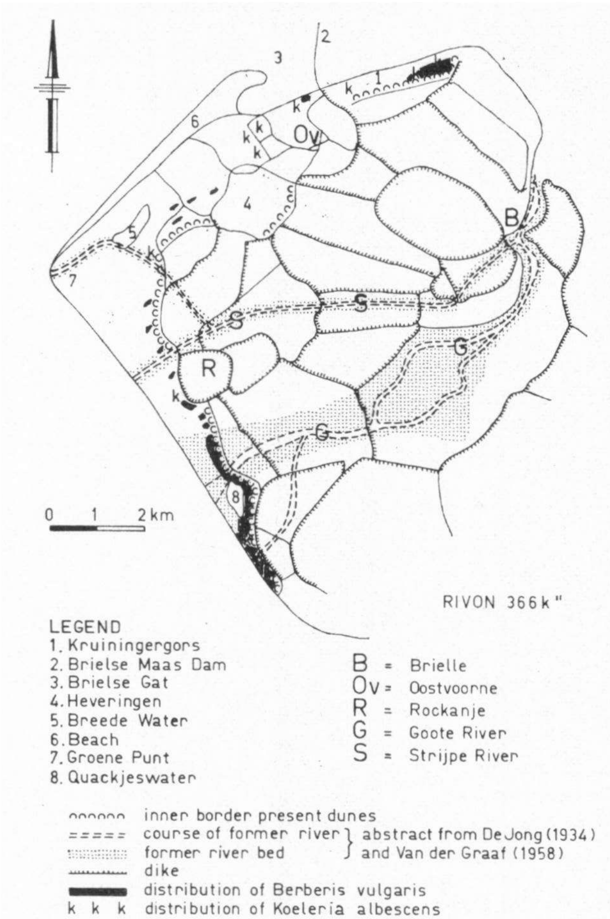

Fig. 2. Distribution of Berberis vulgaris and Koeleria albescens in the dunes of Voorne.

very characteristic for this gradient, with rare species such as *Sagina maritima*, *Catapodium marinum* and *Pottia heimii* and besides *Juncus maritimus* and *Scirpus rufus*, the latter two species being especially characteristic for the Kwade Hoek.

A related phenomenon is found in the Zoute Haard along the North coast of Schouwen, where salt water spring occurs behind the dike. Again *Juncus maritimus* is a characteristic species.

Finally there is a salt gradient in some of the outer slacks in the Voorne dunes, namely those where the closing dunes are still weak and salt water comes in very irregularly.

5. **The gradient from wet to dry.** This gradient occurs in all forms and sizes, from completely xerosere, via dry slack and wet slack,

to permanent inundation conditions. The large primary slacks in the Voorne dunes all are wet slacks in the sense of RANWELL (1959), where the summer free water table does not fall below 1 m from the surface. The annual range of the water table in the outer slacks on Voorne is well comparable with that in Newborough Warren. Within these slacks large depressions occur, in which the surface is permanently under water, except in extremely dry summers. These are the famous dune lakes Breede Water and Quackjeswater.

In general the slacks have a very gentle slope from the seaward side up to the landward side, with height differences of only some dm over some tens of m. In this we recognize the slope of the former beach flat, which is, of course, maintained after the flat has been cut off from sea.

Within these slacks many little dunes occur. They are the result of secondary blow-in's from the main ridge. Here we find small and relatively steep gradients.

Vegetational variety in wet slacks seems to be mainly determined by the occurrence of a slow gradient in the height of the summer free water table in the range from 1 m below surface to surface level and it is this part of the gradient that is present in so many of the large outer slacks. The combination of this gradient with the seasonal variations in the ground water table leads to the subtype instable limes divergens environment of Van Leeuwen. A number of well-known slack species such as *Parnassia palustris*, *Gentiana amarella* and *Equisetum variegatum*, are characteristic for this type.

6. **The complex gradient in the influence of animals and man.** Within this complex the principal factors are mowing, manuring, (now practically extinct), grazing, especially by cattle, horses and rabbits, soil hardening and local devastating. As Van Leeuwen has pointed out, many of these influences show a certain gradient in intensity.

In general the vegetational variety that is determined by a basic environmental gradient, is enlarged by superpositional influences from this category. It is very difficult to detect all the variety in physical and chemical factors. One simple and still appropriate estimation may be found in the flora: species richness is a measure of the amount of gradients. Two famous areas on Voorne are relatively rich in species as well as rich in gradients, which occur moreover in different combinations.

The first example is the Vliegveld slack, with the wet-dry transition as the basic gradient and manuring, mowing, former grazing by horses, present grazing by rabbits, and trodding as the common minor gradient-factors. On an area of 8 ha 200 species occur, among which are rare species such as *Scirpus planifolius*, *Anagallis tenella*, *Equisetum variegatum*, *Eleocharis pauciflora*, *Orchis incarnata* and *Liparis loeselii*. An adjacent slack of 10 ha, where the ground water table is some dm higher (a drainage mill runs superfluous water from the Vliegveld slack to this one), the moisture gradient is less pronounced; the area partly misses the critical part of the gradient. Superpositional anthropogenic gradients are absent. Here only 120 species have been noticed!

The other example is the dune grassland of the Heveringen, where a moisture gradient connects dry and relatively warm situations on bare southern slopes with moist and relatively cool situations on northern and eastern slopes, and wet situations in the hollows, just under influence of the free water table (dry slack situation). A second gradient connects alkaline secondary $CaCO_3$ rich sand with fairly acid conditions, with a pH range from 4–8. The third gradient connects heavily trodden places with scarcely effected ones. The latter influence is now mainly coming from man (especially the investigators!); formerly the area was grazed by horses and goats and afterwards it served as a golf-links. The number of phanerogamic species found on only 1 ha of these dunes, about 220, is a maximum within the Delta dunes and it may be exceeded only by a few landscapes elsewhere in temperate regions. (An ordinary grassland of that size will contain only some tens of species.)

Again the large number of species coincides with the occurrence of rare species, such as *Potentilla tabernaemontani*, *Gentiana campestris ssp. baltica*, *Eleocharis pauciflora* and *Scirpus planifolius*. On Goeree, in a comparable grassland complex the very rare species *Trifolium micranthum* and *Spiranthes spiralis* are found.

In conclusion we may state that the amount of gradients within an area determines the vegetational variety as well as the floristic richness of that area. We are in need of parameters for these varieties; the number of species may serve as a first overall measure.

4.4. *The dune vegetation as a continuum*

Dune vegetations are known for long to be rich in species and varied in composition, as may be learnt from the authors mentioned in § 2. Although these and other investigators must have been aware of the continuum character of dune vegetation in general, they have hardly pointed this out. Still the manifold transitions between vegetation types are so obvious, that the investigator can hardly escape from special adaptations in his approach to vegetation.

The vegetation research in the Delta dunes has started from the idea that a non-dogmatical, realistic approach will be most promising. The problems involved in this approach are the object of the final part of the paper. The following outline of the main vegetational series throughout the dunes is meant as a basic information on these problems. Each series comprises a number of vegetation types that are directly connected with each other by transitions. The term series has no definite meaning; it is used here merely for convenience. The description of series will follow the rough zonation, given in § 4.3.

It is stressed that the continuum point-of-view does not exclude the use of vegetation types in the description. In many cases we will even use Braun-Blanquet synsystematical units for the indication of series.

A. **Green beaches**

1. **Elytrigia juncea series.** This series comprises communities poor in species from the Agropyretum boreo-atlanticum and the alliance Ammophilion, on the highest parts of the beaches and on low dunes. In the Delta region the occurrence of *Eryngium maritimum* and *Euphorbia paralias* in this series is remarkable (BAKKER, 1965). The variety within this series, which is characterized by *Elytrigia juncea*, is presumably determined by the amount of shell particles in the sand and of tidal drift deposits.

2. **Saginion maritimae series.** This series connects the *Juncetum gerardii* and the *Junceto-Caricetum extensae* on relatively low lying, silty places, where tidal inundation occurs only with spring tide, with the communities of the *Koelerion albescentis* on dry and fresh water dunes above tidal influence. The series is determined by an instable gradient from dry-and-fresh to wet-and-salty (WESTHOFF *et al.*, 1961; TÜXEN and WESTHOFF, 1963; SPEKMAN and GROTEN, 1963; BEEFTINK, 1965). It is questionable whether this series is to be described by one association only, viz. the *Saginetum maritimae*, since the participating species such as *Sagina maritima*, *Catapodium marinum*, *Plantago coronopus* and *Parapholis strigosa* have distinct (though overlapping) ranges.

3. **Salsolo-Honckenyon series.** This series comprises communities on shifting sand upon tidal drift and it occurs along the foot of small dunes on the beach. Important species are *Honckenya peploides*, *Cakile maritima* and *Salsola kali*. Transitions occur with series 1, 2 and 4. Detailed descriptions of this series and series 4 were given by BEEFTINK (1965) and DE JONG (1964).

4. **Elytrigia pungens series.** This is again a tidal drift series, consisting of communities with *Elytrigia pungens*, *Atriplex hastata*, *Cirsium arvense*, occurring on decayed drift material, often in died-off *Hippophae* vegetations. DE JONG (1964) has clearly shown the continuum character of tidal drift communities.

5. **Carex distans series.** This series comprises communities of the wetter parts of the green beaches and it is correlated with a salinity gradient. WESTHOFF *et al.* (1961) have described a catena of *Scirpus planifolius* and *Carex distans*, which they have situated into the alliance *Agropyro-Rumicion crispi*, on the Kwade Hoek. Their description partly refers to other green beach areas. Important species are *Agrostis stolonifera*, *Leontodon autumnalis*, *Trifolium repens*, *Trifolium fragiferum* and species of the alliance *Armerion maritimae*.—Of course halosere communities occur as well in these areas; this paper is restricted, however, to dune studies in a strict sense.—

B. **Fore dunes**

Only series 1 is found here in about the same composition.

C. **Coastal ridge.**

6. **Ammophila arenaria series.** This is the series starting with *Elytrigia juncea* at the foot of the ridge and ending in an open *Hippophaë rhamnoides* vegetation, directly behind the ridge. It is found in most coastal dunes in the Delta, especially along the North Sea coastline. The series is determined by the decreasing sand mobility from the exposed beach to the sheltered dunes behind the seaward ridge. BAKKER (1965) has made a detailed study of the composition of communities in this series, together with series 1 and 4.

7. **Elymus arenarius series.** This series is to be placed into the alliance *Ammophilion*, as are the series 1 and 3. It also starts with *Elytrigia juncea* and it is characterized by two other species of this genus: pungens and repens. On the whole the series shows a nitrophilous tendency. It may be seen as the counterpart of series 6 along the estuaries.

D. **Seaward dunes**

8. **Hippophaetum series.** Behind the seaward ridge *Hippophaë rhamnoides* is a dominant species almost everywhere in the Delta dunes. Transitions occur from

series 6 and 7 to this series, as well as to series 9 and 11. Dependent on the stability of the surface the understory varies from annuals such as *Cerastium semidecandrum*, to graminoids such as *Calamagrostis epigeios* and *Carex arenaria* and lianic species such as *Rubus caesius* and *Solanum dulcamara*. *Cynoglossum officinale* is a characteristic species from the transition between dense *Hippophae rhamnoides* vegetation and open pioneer communities. This series is also found on exposed and rejuvenating places in the middle dunes. There more species of the alliance *Berberidion vulgaris* take part in the series, e.g. *Ligustrum vulgare* and *Asparagus officinalis*.

9. **Tortuleto-Phleetum series.** This series occurs in a mosaic with *Hippophaetum vegetations*. Transitions are found to more stabilized communities, where the dominating moss *Tortula ruralis* is replaced by *Brachythecium albicans*. Also transitions occur to pioneer communities within the influence of the free water table. *Centaurium vulgare* and *Gnaphalium luteo-album* mark the transition. Local variation depends on exposition, sand mobility and rabbit influences and has been described by SLOET VAN OLDRUITENBORGH (1965).

E. Outer slacks

10. **Centaurium vulgare series.** *Centaurium vulgare* is one of the pioneer species in young primary slacks, on not too wet places (FREIJSEN, 1964). It is one of the conspicuous species of the association *Centaurieto-Saginetum*, which is in fact a series, as the *Saginetum maritimae*. It shades off into series 9 on the dryer borders of the slacks and into *Glaux maritima-Centaurium pulchellum* communities in the wetter parts. The rare atlantic-mediterranean species *Blackstonia perfoliata* occurs in the series.

11. **Salix repens series.** Salix repens is by far the dominating species in the large primary slacks. Its height and dominance are mainly determined by the free water table and the combined effect of mowing and rabbit grazing. It mostly occurs in a mosaic with grassy patches, with *Carex trinervis*, *Juncus gerardii*, *Festuca rubra* and *Agrostis stolonifera*. Variation within the series is further determined by the depth of the underlying humus layer. Characteristic species are manifold. Some of them have already been mentioned, viz. at the description of the wet-dry gradient.

12. **Salix cinerea series.** In the older and wetter places tall growing *Salix* species replace *Salix repens*. Especially *Salix cinerae* and *purpurea* form large patches. with species such as *Hydrocotyle vulgaris* and *Eupatorium cannabinum* in the understory,

13. **Betula verrucosa series.** This series may be considered as the terminal phase in the dryer parts of the primary slacks. Humus formation in the *Betula* woodlands varies and accordingly variations in the vegetation are found. *Pyrola rotundifolia* is characteristic for them of some. In other types *Berberidion vulgaris* species such as *Ligustrum vulgare* and *Rhamnus catharticus* are found in the woodland. This series is presumably subject to a cyclic succession, which is in accordance with the general behaviour of the genus *Betula*, as described by DOING (1963b). The series 11 and 12 are probably involved in this cyclus.

14. **Alnion glutinosae series.** This series is presumed to be the ultimate phase in vegetational development of the older slacks. At present only a small area of *Alnus glutinosa* woodland is known, namely in the Quackjeswater region. Fragments of this series are found more commonly. Characteristic species are *Iris pseudacorus*, *Eupatorium cannabinum*, *Phragmites communis*, *Lysimachia vulgaris*. These herb species often occur in separata patches in between patches of woodland or scrub.

F. Middle dunes

15. **Hippophaeto-Ligustretum series.** In the fixed dunes, outside the immediate influence of the sea winds, this association, belonging to the alliance *Berberidion vulgaris*, comes to full development—the outpost have been mentioned already—. It is a very varied series, determined by the dominance of *Hippophae rhamnoides*, *Ligustrum vulgaris*, *Salix repens* and *Sambucus nigra*. The variety partly depends on the exposition. The main environments of this series are an open, dry habitat with species such as *Asparagus officinalis*, a moist habitat with hygrophilous species such as *Eupato-*

rium cannabinum, and a habitat probably relatively rich in nitrates, especially in the *Sambucus nigra* phase, with *Anthriscus vulgaris*. *Cynoglossum officinale* and *Polygonatum odoratum* occur throughout the series on open places. The variety has been described in detail by VAN DER MAAREL and WESTHOFF (1964).

16. **Crataegus monogyna series.** This is the optimal phase in dune scrub development, occurring at the landward side of the middle dunes. Along the estuaries it may be found nearer to the sea. *Crataegus monogyna* is a dominating species. Along the estuaries (Fig. 2) *Berberis* may replace *Crataegus*. The series belongs to the alliance *Berberidion vulgaris*. It is connected with series 15 and 17.

17. **Alno-Ulmion series.** This alliance comprises, as for the dunes, woodlands with dominance of *Betula verrucosa*, *Populus tremula*, *Populus nigra*, *Ulmus campestris* coll. and *Quercus robur*. (DOING, 1962, 1963a, b). The communiites belonging to this series are still rich in *Berberidion* species, such as *Lithospermum officinale* and *Ligustrum vulgare* and in common understory species such as *Geum urbanum*, *Aegopodium podagraria*, *Geranium robertianum*, *Moehringia trinervia*. Also some more characteristic species occur: *Listera ovata*, *Dactylorchis fuchsii ssp. fuchsii* and *Scrophularia vernalis*. The series is connected with series 13, 14, 15 and 16.

18. **Cladonia series.** This series comprises communities, consisting mainly of lichens and mosses and growing in older parts of the middle dunes, which were mobile until recently. Dominating species are *Cladonia rangiformis*, *Cladonia foliacea var. alcicornis*, *Hypnum cupressiforme* and *Dicranum scoparium*. DOING (1963a) has erected a special alliance *Dicrano-Cladinion* to place these communities in. Transitions occur with series 9, 19 and those of the landward dunes (see below).

19. **Corynephorus canescens- Koeleria albescens series.** These two bunch forming grasses have a rather similar range in the Delta dunes, although they are placed into quite different alliances or even orders. They build up communities with a large group of common species, among which is *Silene conica* (VON KOENIGSWALD en DE ZWAAN, 1965). The systematic place of these communities is not yet clear.

20. **Rubus caesius - Galium verum series.** This series comprises herb vegetations and dwarf shrub communities in a mosaic. It is floristically intermediate between the *Tortuleto-Phleetum* — and the *Festuceto-Galietum* series. It is especially well developed on sheltered, north and east exposed places and it often occurs in a mosaic with the *Hippophaeto-Ligustretum* series as well. Some species of the association *Anthyllideto-Silenetum* (see BOERBOOM, 1957) are found in this series, mainly on Walcheren and Voorne. Examples are *Silene nutans*, *Anthyllis vulneraria* and *Thalictrum minus ssp. dunense*. The underlying gradients are probably found in the amount of humus formation and the exposition.

G. Old, landward dunes

21. **Festuceto-Galietum series.** This very complex series, which is hardly to indicate with the association only, covers a major part of the old, low, decalcified dunes that have been or are still being grazed. Some of the tens of characteristic species are *Festuca tenuifolia*, *Galium verum*, *Lotus corniculatus*, *Plantago lanceolata* and *Agrostis tenuis*. The series is connected with the following ones.

22. **Aireto-Caricetum arenariae series.** This series comprises communities of the same habitats as series 21 is found in. It is not yet clear which environmental factors determine the difference between the two series. This series is named after a newly described association (WESTHOFF *et al.*, 1961) and it is characterized by *Aira praecox*, *Rumex acetosella*, *Carex arenaria*, *Dicranum scoparium* and by the absence of species such as *Festuca tenuifolia* and *Plantago lanceolata*.

23. **Calluna series.** In the most acid parts of the old, landward dunes heath may develop. On the drier spots *Calluna vulgaris* may establish, on the moister areas *Erica tetralix* is also present. The series was of importance on Goeree (WEEVERS, 1940), but it is now almost extinct, as a result of cultivation.

24. **Carex panicea-Hydrocotyle vulgaris series.** This series is as complex as series 21, and may be considered as its counterpart in hollows within the dune grassland complex. It contains a mixture of grassland species from the *Festuceto-Galietum* and the alliance *Arrhenaterion*, e.g. *Cerastium holosteoides, Trifolium pratense, Cynosurus cristatus,* as well as species from dune slacks such as *Carex panicea, Hydrocotyle vulgaris, Carex nigra, Potentilla erecta.* The composition of the series 21-24 is determined by the gradients that have already been mentioned before.

4.5. *Selection and sampling*

4.5.1. On a confusion

As was stated before, the selection of stands of vegetation for sampling may be considered as the first step in vegetation study. Thus our chain of problems may be taken up at this link. A first problem concerns a certain confusion about selection of stands and selection of sample plots. This confusion may be explained by the insufficient mutual appreciation of Anglo-American multiple plot workers and European single plot students. Advocates of the multiple plot or plotless sampling methods, sometimes think that the Zürich-Montpellier students locate their single plots more or less haphazard within a stand. In fact in many cases the selection of the stand has taken place so as to make it opportune to analyse the entire stand as a single plot. In other words, the Z-M student considers only a very limited area sufficiently uniform for sampling and in those cases it is easy to defend the single plot method. Thus a good deal of criticism of the single plot method is in fact criticism of stand selection.

On the other hand some single plot workers are in confusion about the randomness of the choice of multiple plots within a stand, which they appear to interpret rather as a random choice of stands. Thus their criticism of the supposed irreality of a random choice of stands in a relatively large area which they suppose to be heterogeneous, is in fact only a criticism of the multiple plot method. This confusion is, no doubt, fostered by the differences in opinion as to the delineation of stands on grounds of homogeneity and representiveness. In general the A-A workers take larger areas for sampling, which are often relatively heterogeneous in the opinion of European students. Most classical Z-M studies are concerned with much smaller areas, but according to the recent considerations on gradients and other patterns many of those stands are as heterogeneous as the A-A ones.

The solution of this problem may be found in a careful consideration of the scale of homogeneity one requires for a certain study of certain vegetations. This may determine the average size of the stands one wishes to analyse, as well as the most appropriate method of analysis.

In this way one may consider, to give one example, a dune grassland complex as a landscape unit that can be compared with other units, such as scrubs and woodlands, and with other grasslands. The order of size of stand will then be 1 ha, and a multiple plot analysis will be appropriate. The same dune grassland may be seen as a complex of minor communities, determined by local structure and species composition. The order of size of stand may then not exceed 1 sq.m. and an analysis of the entire stand is obvious. During a clarifying discussion in the field with Professor D. M. de Vries and Ir. J. G. P. Dirven, it appeared that these experienced grassland workers tend to take stands of intermediate size, viz. order of size 100 sq.m., as representative and comparable with inland grassland situations.

It is, in conclusion, necessary to keep in mind the close connection between stand interpretation and the purpose of study, and to inform the reader clearly on this point.

4.5.2. The selection procedure

As far we have learnt from literature and practical experience in the field, there is but little attention focussed on the question how to select stands. Most investigators start the discussion at the next stage, viz. the selection of a chosen stand for homogeneity.

First reconnaissance will give a survey of major vegetation types, which will be physiognomically determined in most cases. The question then reduces to how to select stands of a certain vegetation type.

A choice at random, if ever justifiable, over a large area, e.g. the dunes of Voorne, is of course practically impossible. The common procedure, i.e. a more or less haphazard location of stands, as ascribed to the average Z-M worker by EGLER (1954) and, mutatis mutandis, to the average A-A worker by ASHBY (1948) is rejectable as well. Such an opportunistic selection may easily lead to irrepresentative descriptions of a vegetation type. We have found this to be true for most dune associations, e.g. *Hippophaeto-Ligustretum*, *Acrocladieto-Salicetum* and *Festuceto-Galietum*.

One of the most effective improvements in the selection procedure seems to be the cruising of the area under investigation at regular intervals across the main zonation, if present, and to choose stands along these cruising lines. This a is kind of large transect method, which is not unfamiliar to the Z-M student, since he uses transects of a smaller size for definite ecological purposes. Surprisingly enough the transect method is hardly in use for synsystematical purposes. In the description of most associations there is a serious discrepancy between the number and location of stands and the suggested distribution of the association.

In the Delta dune research systematic stand selection is now in progress. All stands that have been described, are plotted on physiognomic survey maps, so that we know where each vegetation type is still inadequately sampled. Transect sampling will be consequently used in the extensional phase. In this way SLOET VAN OLDRUITENBORGH (1965) described the entire vegetation complex of a local area; BAKKER (1965), DE JONG (1964) and SPEKMAN and GROTEN (1963) made regional studies of one vegetation type.

On places where the local zonation is very pronounced, it will be appropriate to study a local transect via a series of stands, each representing an element of the pattern. It will be clear, that this is a very common practice everywhere, but again we may remark that this method is commonly not followed when the typology of vegetation is the primary purpose.

In the dune grassland complex this transect method appeared not satisfactory enough. In this area the transects laid down, were mapped on a scale 1: 200; each part of the transect that was considered structurally uniform, was investigated separately (VAN DER MAAREL, 1963). Afterwards each stand delineated in this way, was analysed. The transects were laid down on places where the vegetational variety was apparently maximal, which is almost contrary to the common practice! This method was applied in a part of the Heveringen dunes near Oostvoorne, that was already mentioned as a species-rich complex. Later the method was extended to other parts of the Heveringen and to dune grasslands on Goeree (NOORMAN and GARTEN, 1965).

4.5.3. The sampling procedure

It follows from the foregoing that in detailed vegetation studies as described above, the stands chosen for analysis are rather small and they may be easily analysed as a whole. Therefore no reason became apparent to deviate from the normal Z-M procedure and consequently practically all analyses were made on the single plot basis.

The problem whether the Braun-Blanquet scale of combined estimation must be changed or even abandoned, has received much attention during the preparation of the work. Finally it was decided to use the scale in its original form, despite the heavy criticism that has been published against it, both in Anglo-American and Zürich-Montpellier circles (see GREIG–SMITH, 1964 and BARKMAN, DOING and SEGAL, 1964, respectively). We fully agree with the theoretical objections, pointed out by these and other authors, such as the independence of abundance and cover, the irregularity of the intervals of the scale, and the inadequate estimation of pattern.

Our considerations in favour of the Braun-Blanquet scale are:

1. Each visual estimation is subject to serious errors and fluctuations, bound to the investigator. The more detailed a scale of estimation is, the greater will be the relative inaccurateness. This was clearly demonstrated during a test among 15 Dutch phytosociologists. Braun-Blanquet scale estimations made by each worker were compared with detailed cover % estimations. Variation appeared to be rather great, but most ranges of one estimation remained within the limits of a certain Braun-Blanquet interval. (Complete information will be published; see VAN DER MAAREL, 1964a, for some remarks.)

2. Since it is impossible to use only one scale, i.e. either abundance or coverage, because of their independence, it is very difficult to use one single parameter for the occurrence of a species. Thus each attempt

towards refinement of the analysis by using more than one parameter will hamper the synthesis of data. Recent developments in the synthesis (see GREIG-SMITH, 1964) suggest that the association between species is the most appropriate tool. Mathematically trained workers such as DAGNELIE (1960) advice to use only presence-absence data for calculations. Hence a simple estimation of presence is sufficient. Species with low presences may be omitted in the calculation; Braun-Blanquet values to omit, may vary from + to + and 1, and +, 1 and 2, dependent on the maximum coverage a species may reach.

3. The recent considerations on vegetational variety force us to enlarge the numbers of the analyses rather than to refine the analysis. The proposals by BARKMAN *et al.* (1964) are excellent as such; however, following them would mean that one relevé takes far more time than a simple Braun-Blanquet one does.

4. Refined estimation scales should be restricted to detailed ecological investigations, such as permanent plot studies. For such studies the Braun-Blanquet scale and directly comparable ones, such as the Domin scale are less appropriate. (DOING, 1954, originally intended to refine the estimation scale particularly for permanent plot studies.) But again the question may be raised whether detailed estimations are sufficiently accurate to detect small gradual changes in the performance of species. It is probably more satisfactory in some cases to count individuals, flowering stalks, etc. With help of simple parameters, it is possible to give fairly accurate estimations of species and vegetational biomass and seed production, since it appeared that characters such as plant height and rosette diameter are correlated with them. (VAN DER MAAREL, 1964; VAN DER MAAREL and FRESCO, 1965).

4.6. *The analysis of variation in space and time*

4.6.1. Pattern

The description of vegetation is hampered by both variation in space, pattern, and variation in time, instability. The "ideal" descriptional circumstances are, on the contrary, homogeneity and stability. However, according to the theory of Van Leeuwen these two situations do exclude each other! Most vegetations are both more or less heterogeneous and more or less instable. Hence the description of vegetation is determined by the amount of pattern and the scale of pattern occurring in it.

As was said in the foregoing (the delineation of the stand), the degree of uniformity "required" for a description of vegetation largely depends on the scale on which the vegetation is studied. The decription of formations and that of micro-communities of mosses are, of course, different things. In most cases our vegetation types are of an integration level in between these two extremes and thus we cannot avoid considering the existing patterns.

The large-scale patterns, as to be found in the ecotone environment, do not give difficulties; most investigators tend to take the border of the pattern of prominent species as the border of the stand. In this way associations such as *Ammophiletum*, *Salicornietum* and *Puccinellietum* are described and typified.

The very small-scale patterns, as to be found in the ecocline environment do not give problems either, since these patterns are generally not recognised. The vegetation of those environments is easily considered as uniform. This is, of course, another kind of uniformity than that existing within a large-scale pattern of the limes convergens environment. The latter uniformity may be called internal, the divergent uniformity may be called external.

In this type of vegetation the pattern is not the problem for the delineation, but still there is a problem; when contiguous stands of medium size, e.g. along a line across the underlying gradient, are compared with each other, they appear to form a direct continuum. In these cases the delineation of the stand is largely decisive for the typification. The delineation is mostly based on optimal occurrence of rare, but locally conspicuous species, with which the investigator may already have a certain pre-occupation. Consequently there is much confusion and discussion about the synsystematics of vegetations from such gradient situations, e.g. the *Trifolio-Geranietea* borderline communities.

In the remaining vegetation types medium-size patterns occur. It is rather difficult to decide whether a vegetation type should comprise only one pattern in the prominent layer or a mosaic of patterns. This may explain the rather obvious heterogeneity in tables of many sociological units as for size of the relevé, number of species and number of growths forms.

It is to be hoped that the stimulating Anglo-American studies of pattern (see KERSHAW, 1964) will present results that can be directly used in vegetation typology. It seems necessary that the European vegetationists develop their knowledge of large-size patterns, so that the two approaches may be linked in future.

In the dune research we are still in the phase of vegetation description. The study of patterns is therefore mainly applied to typification. The medium-size patterns as occurring in grasslands scrubs and pioneer communities are detected by means of detailed analysis of structure (see § 4.7.) The delineation of stands is then based on the difference between external and internal structural uniformity, i.e. when a spot of vegetation shows structural differences with surrounding spots that are greater than the differences within that spot, the spot is considered a stand.

In cases of marked mosaics or zonations, such as in the already mentioned variegated slacks and dune grasslands, the surrounding spots, delineated in the same way, are described as well and afterwards the floristic similarity between the stands is determined in order to judge whether certain contiguous stands should be combined after all. This method has been tried out in a dune grassland complex (VAN DER MAAREL, 1965c).

4.6.2. Instability

The changes in time of vegetation are also a serious problem in the description. Until now nearly all descriptions of vegetation types are based on relevé's at one time. Apart from the risk of missing certain species when analysing only once a season, there is a fairly good chance that not all aspects of structure and floristic composition are encountered by taking only one year into account.

Again we may distinguish between two extreme situations that cause relatively few difficulties: in very instable environments the occurring communities are poor in species and relatively constant in composition, although the actual places where the community develops, may change from year to year. The other extreme is the very stable environment with communities rich in species and again rather constant in species composition.

Most vegetation types are more or less intermediate in stability. Hence it is necessary to study changes, whether they are successional or cyclic. The classic considerations of WATT (1947) may be mentioned here with emphasis as a starting-point.

The dune research has concentrated the study of changes on Voorne. About 100 permanent plots are being investigated, some of them from 1955 onwards. Recently a start has been made with the study of permanent transects, that are places with a pronounced zonation or a mosaic, where the pattern is mapped yearly and the structure and floristic composition is followed. In this way the spatial movements of species can be followed as well.

4.7. *The analysis of structure*

The study of structure, i.e. the spatial arrangement of the components of vegetation, has been part of the investigation since long. It is rather remarkable that the methods used have not much improved, as compared with the development of floristic analyses. European descriptions generally do no contain more than a rough indication of height of vegetation and pronounced stratification. In tables with relevé's these data are often omitted and the synthesis of types seems hardly to take into account structural characters. The same holds, mutatis mutandis, for Anglo-American descriptions.

Since structure is a very convenient tool in the rapid recognition of types, since it is a most important character of the largest vegetational units, the formations, and since it is probably a very sensitive indicator of dynamic relationships between vegetation and environment (as follows from the theory of Van Leeuwen), it is worth while concentrating our vegetation study rather on the structural aspects. Moreover structure is of paramount importance for animal ecology. LENSINK (1963) has given examples of the relation between dune vegetation structure and the behaviour of grasshoppers. It is emphasized that each attempt towards refinement of structure analysis should start from the work of DANSEREAU (1957 a.o.).

In our dune research refinements in the description of structure are twofold: a large number of height classes is distinguished and a number of growth forms is studies separately, such as rosettes, creepers, cushion plants, bunch grasses (VAN DER MAAREL, 1963, 1965c).

In addition a method of estimating the amount of discontinuity in horizontal and vertical direction is being developed. The latter development may be of importance, since we have found (VAN DER MAAREL, 1965c) that a relation exists between those structural characters and the floristic minimal area of a community.

4.8. *On vegetation systematics*

In accordance with European tradition the attention for systematics in dune research is comparatively great. Of course the striving for the erection of systems is not only determined by the need for classification. Contrary to wide-spread supposition, a classification is not a goal for the average Zürich-Montpellier worker. It is a means for the better understanding of vegetation, and a great help for practical vegetation study.

When classification is taken broadly, when it means the general study of vegetational systems, and the study of ecosystems, i.e. the interaction complexes between vegetation and environment, it may be called a goal indeed. As we have recently stated, the Braun-Blanquet system of plant communities is one of the possible approaches in vegetation systematics. Since it tries to deal with more aspects of vegetation than other systematical approaches, it may be called the most advanced system. The physiognomic-structural system is probably the most important counterpart. It should be useful to continue the attempts by DOING (1957, 1962) and others to bridge the gap existing between these two systems.

In the description and mapping of dune vegetations, we have developed a new approach by creating a system of local formations. These formations may be arranged into the physiognomic-structural system, thus into formation classes and such units, as well as in the Braun-Blanquet system. The latter procedure did not give serious difficulties (VAN DER MAAREL and WESTHOFF, 1964; SLOET VAN OLDRUITENBORGH, 1965).

A different trend is recognizable in the Braun-Blanquet school itself, especially among West-German and Dutch workers: the structure of vegetation is considered of equal or even more importance than the floristic composition in the delineation of higher rank units of the system, such as classes and orders. An example are the scrub vegetations from the *Berberidion vulgaris*. This alliance was situated into a woodland order, but it is now a special order *Prunetalia spinosae* (Tüxen) or even a special class (Doing).

The accepting of the Braun-Blanquet system does not exclude necessarily any criticism. Some objections were already made under selection and sampling, some other concerning synthesis may be added: It is weakness of the procedure that much of the material present is not statistically treated, or that the material even does not allow any objective treatment.

The number of successful attempts towards objectivation of methods, both in Anglo-American and Zürich-Montpellier circles (see GOODALL, 1953–1961; GREIG–SMITH, 1964; DAGNELIE, 1960; DE VRIES, 1954; LOOMAN and CAMPBELL, 1960; WILLIAMS and LAMBERT, 1961–1964) is too large as to ignore the possibilities of mathematical improvement of the Braun-Blanquet method in this respect. Both the evaluation of affinity, i.e. similarity of relevé's and species-association, as well as tentative tests of significance should find a place in Z-M studies.

Finally some remarks on ordination are made. As was pointed out by VAN DER MAAREL, WESTHOFF and VAN LEEUWEN (1964), ordination, in the sense of Bray and Curtis, and classification, are not only principally co-existent approaches (as was categorically denied some years ago by various workers), but even directly supplementary techniques (GOODALL, 1963, seems to be still intermediate in his point-of-view). Both are systematic trends that try to establish types and relations within a system.

Classification, whether it is natural or an arbitrary one, emphasizes the convergency of the existing systematical relations, and ordination emphasizes the divergency of these relations.

As the theory of Van Leeuwen has learnt us, each vegetation has aspects of convergency as well as aspects of divergency, dependent on the variety and stability of the environment. Thus classification tends to be the most useful approach in vegetations that are of a convergent character, while ordination is most suitable in vegetations of a divergent character.

Since most vegetations consist of types intermediate between the two mentioned extremes, thus having both convergent and divergent aspects, most vegetations should be approached by both systematical techniques, classification and ordination.

This statement is illustrated in Fig. 3, that shows graphically the relation between the two procedures. We have added the common dune vegetations to the original graph (presented at the Edinburgh lecture) as to make it more comprehensible in this context. We are still in need of a balanced combined approach, based on the two techniques.

This brings us to an end of this survey of problems that are actual in the study of the Delta dune vegetations. Some problems have been solved, others have hardly been defined. As may be read from the many recent references, the work is in progress. So this paper has slightly favoured the past as well as the future above the present. This may be, perhaps, excused by the special character of this issue!

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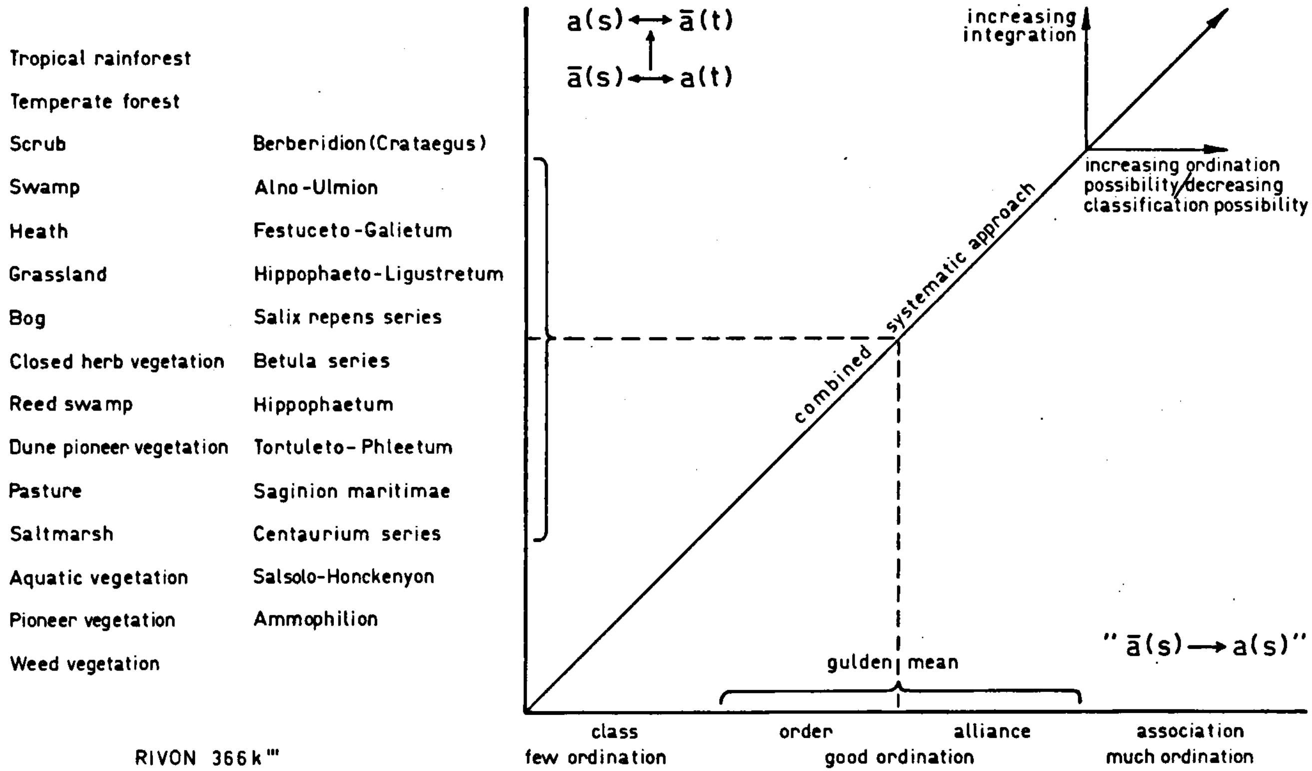

Fig. 3. Relation between integration of vegetation and the systematic approach after Van der Maarel, Westhoff and Van Leeuwen (1964)

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