Acta. Bot. Neerl. 37(1), March 1988, p. 95–109

Relationship analyses of the flora of the Dutch, German and Danish Wadden Islands

J. H. IETSWAART*, R. BOSCH* and E. J. WEEDA†

**Biologisch Laboratorium, Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam and*
†Rijksherbarium, Postbus 9514, 2300 RA Leiden, The Netherlands

SUMMARY

Flora and vegetation of the Dutch, German and Danish Wadden Islands were compared with the aid of similarity computer programs. The Wadden District, often described as an exclusively Dutch phytogeographical entity, was found to cover the whole area. From a comparison with the floras of the neighbouring Dune and Haff District and the more distant Kempen District, it was concluded that the Wadden District forms a distinct unity by its relatively large internal cohesion. Within the Wadden District three groups of islands could be discerned: a western group including the Dutch islands and Borkum, a central group of German islands and a northern group of partly German, partly Danish islands. Nordstrand, Pellworm and Skallingen usually showed only slight similarities with the last group. Texel was clustered sometimes with the northern group. Ecological differentiation chiefly determines the presence or absence of species in the islands, and thus the degree of (dis)similarity of their floras and vegetation types. Surface, position, soil structure and man mainly contribute to this ecological differentiation. Local climate plays a minor role.

Key-words: flora, relationship analyses, vegetation, Wadden Islands.

INTRODUCTION

Van Soest (1924, 1925, 1929) introduced a phytogeographical division of The Netherlands, that holds eleven districts: Wadden, Dune, Haff, Drenthe, Gelderland, Flanders, Subcentral European, Loess, Chalk, Kempen and Fluviatile District. Although he considered this division to be provisional, it has not been basically altered since. Only recently, Weeda (1983) proposed some slight alterations to the district boundaries. More details on the history of the phytogeographical division of The Netherlands can be found in Mennema (1978). Because more data have become available since 1929, it is possible now to study the geographical division according to van Soest (1929) in detail.

Most versions of this phytogeographical division, e.g. those in the two Dutch phanerogamic floras (Heimans *et al.* 1965, van der Meijden *et al.* 1983b), contain a Wadden District, the eastern limit of which is not exactly indicated.

The present study tries to answer the following questions. (1) To what extent do the Wadden Islands differ floristically from other Dutch phytogeographical districts? (2) Are

there differences in flora and vegetation between the Dutch and the German, and/or the Danish Wadden Islands? (3) How can possible differences be explained?

Questions two and three have also been dealt with by Weeda & Mennema (1983), but our procedure differs by using computer programs to analyse the relationships.

METHODS

Only Dutch, German and Danish Wadden Islands larger than 10 km^2 were selected (18 in number), which were each assumed to be a phytogeographical unity. The topography of the islands is given in Fig. 1, and in Table 1 a number of their primary data are shown. Skallingen became a peninsula early in the twentieth century. The area between Den Helder and Bergen, also belonging to the Wadden District, is omitted from this study, because there are no detailed floristic data available on the area. In order to compare the flora of the Wadden Islands with that of the two neighbouring districts, namely Haff and Dune District, two areas were chosen: one southwest of Leeuwarden (Haff District) and another west of Haarlem, known as "Amsterdamse Waterleiding Duinen" (Dune District). Moreover, a comparison was made with the flora of an area south of Breda in the Kempen District which is not adjacent to the Wadden District (see Fig. 1 and Table 1). These areas were especially chosen because their surface is comparable to that of the islands and their floras are very well known.

The aforementioned areas were only compared with the Wadden Islands on a floristic basis, while comparison within the Wadden Islands encompassed ecological, phytogeographical and vegetational as well as floristic differentiation. The floristic comparison was not only related to vascular plants, but also to lichens, because the distribution of the latter group is less influenced by man (putting aside the negative influence via air pollution). Similarity coefficients were calculated for the floristic and ecological data using Sörensen's program (Odum 1971) in the FORTRAN IV translation made by Hillebrand & Klapwijk (1976). A similar program made by Bray & Curtis (1957) was used for the vegetational data. Dendrograms were composed with the aid of the single and average linkage cluster analysis.

The data on the vascular plant floras of the Wadden Islands were based on the list given by Mennema & Weeda (1983). The data on the lichen floras were taken from Brand & Ketner-Oostra (1983). Data on the vascular plants of the selected area in the Haff District (squares 10·17, 10·18, 10·27 and 10·28 of the IVON grid) came from van der Ploeg (1977); those of the selected Dune District area from Boerman (1975) and those of the selected Kempen District area (squares 50·13, 50·14, 50·23 and 50·24) from Cools & Cools (1981). Obviously introduced and unnaturalized species were omitted from the calculations.

The vascular plants of the Wadden Islands were divided into the nine ecological groups as described by van der Meijden *et al.* (1983a).

The area of the vegetation types and other features, given by Dijkema (1983) in the appendix maps, were estimated as follows: each area was cut out and weighed, and each weight was put in a percentage of the maximum value for that vegetation type or other feature. By uniting some minor types, calculations were carried out with 25 vegetation types, instead of the 29 original ones.

For the sake of the geographical approach, the phytogeographical classification of Europe, as found in the Flora Europaea (Tutin *et al.* 1964–1980), was combined with that

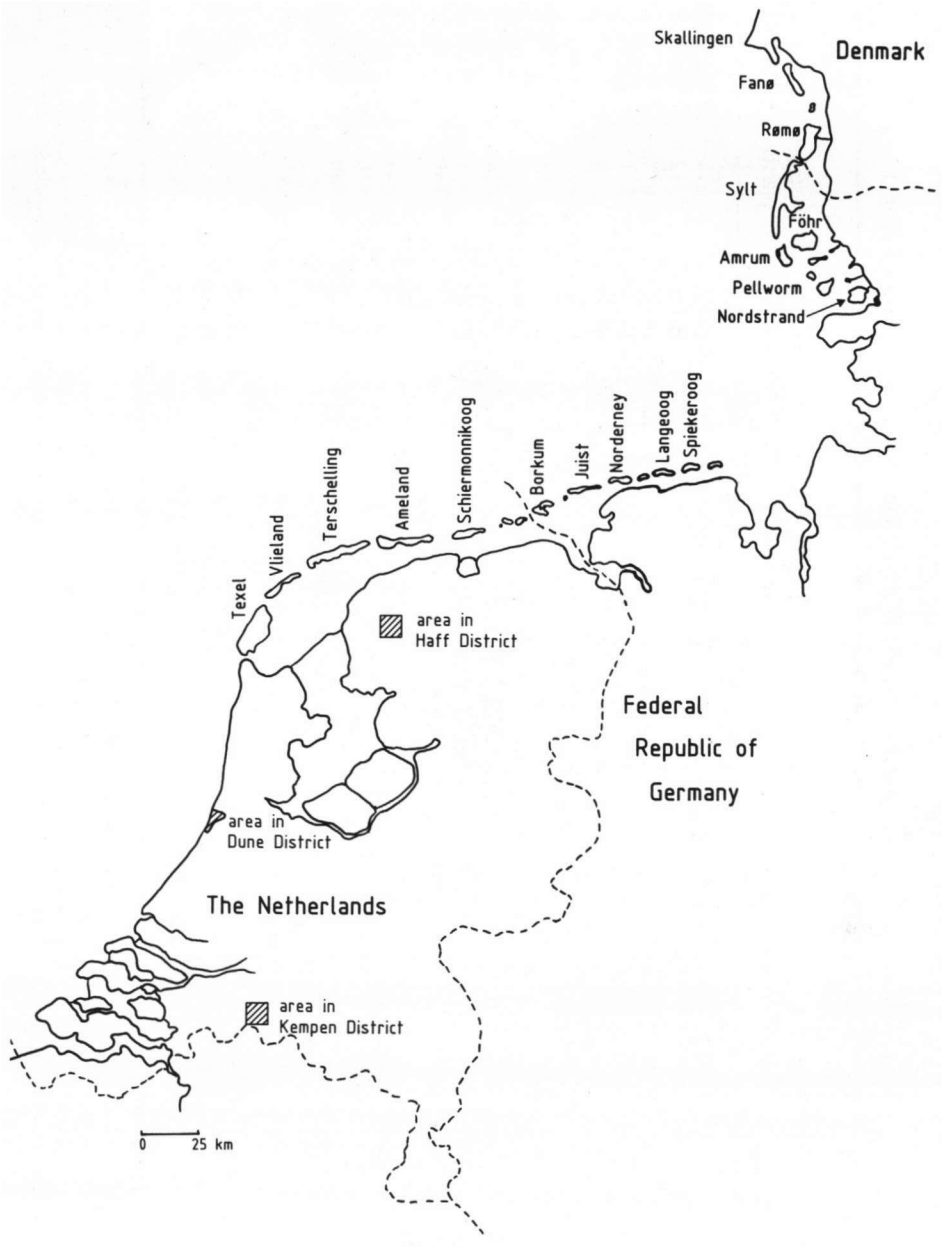

Fig. 1. Position of the eighteen Wadden Islands and the three other areas in The Netherlands of which flora and vegetation were compared.

given by Walter & Straka (1970) (see Fig. 2). In this way five categories were obtained: North-European elements (e.g. *Salix pentandra* and *Juncus balticus*), West-European elements (e.g. *Erica tetralix* and *Carex trinervis*), Central-European elements (e.g. *Liparis loeselii* and *Corynephorus canescens*), Subsouth-European elements (e.g. *Carlina acaulis* and *Silene conica*) and South-European elements (e.g. *Tuberaria guttata*). A sixth category

Table 1. Primary data concerning the eighteen Wadden Islands and the three other areas of which flora and vegetation were compared

	Short	Size (km^2)	Island type	Soil types	$CaCO_3$ content in soil (%)	Vascular plants	Lichens
Texel	TEX	183	1(+3)	(+pleistocene loam)	(1–)5–10	674	150
Vlieland	VLI	33	2		1–5(–10)	512	137
Terschelling	TER	107	2		1–5(–10)	650	159
Ameland	AME	63	2		1–5(–10)	581	124
Schiermonnikoog	SCH	46	2		(1–)5–10	558	114
Borkum	BOR	28	3+3		1–5(–10)	627	142
Juist	JUI	11	2		(1–)5–10	515	120
Norderney	NOR	25	2	holocene sand,	1–5(–10)	526	151
Langeoog	LAN	15	2	marine clay,	1–5(–10)	428	107
Spiekeroog	SPI	17	2	(peat)	1–5(–10)	372	91
Nordstrand	NRD	47	3		<1	261	103
Pellworm	PEL	38	3		<1	318	57
Amrum	AMR	22	1		<1	459	86
Föhr	FOH	84	1		<1	578	137
Sylt	SYL	101	1	(+pleistocene loam)	<1	608	219
Römö	ROM	90	1		<1	522	167
Fanö	FAN	52	1		<1	582	138
Skallingen	SKA	24	1		<1	275	25
Area in Haff District	HAF	100	—	marine clay, peat	—	643	—
Area in Dune District	DUI	34	—	holocene sand	(10–)30–100	293	—
Area in Kempen District	KEM	100	—	pleistocene sand and loam	±0	516	—

Abbreviations as used in figures and tables; size, according to Joenje & Westhoff (1976); island type as defined by Doing (1983a), (1) larger island with Pleistocene nucleus and therefore not moving, (2) larger island moving slowly in northwest–southeast-direction and (3) smaller island with a more or less roundish shape (as distinct from 1 and 2 which possess a longitudinal shape); approximate amount of calcium carbonate in the dune sand according to Doing (1983a,b); number of native and naturalized vascular plant species, as conceived in this paper; number of lichen species according to Brand & Ketner-Oostra (1983). Dash means data not relevant or not considered.

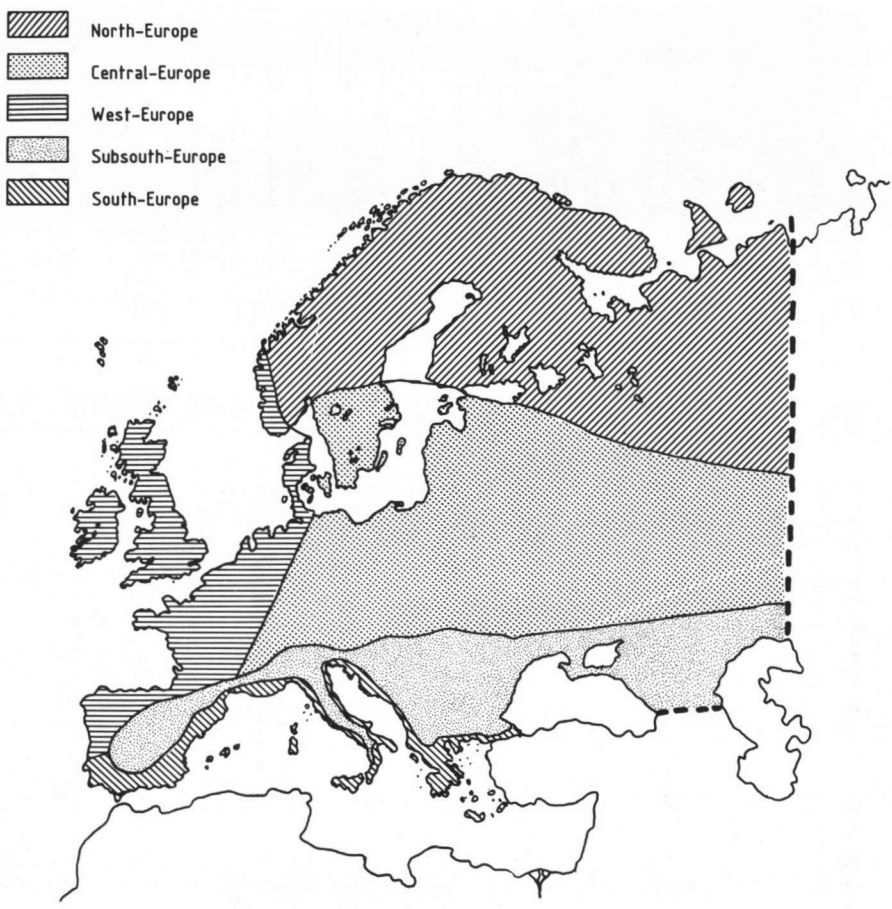

Fig. 2. Rough phytogeographical division of Europe with which the percentages of the phytogeographical elements of the eighteen Wadden Islands were calculated.

was also discerned: All-European elements, that occur in (nearly) all parts of Europe (e.g. *Plantago major* and *Anthyllis vulneraria)*. With the aid of the *Flora Europaea* (Tutin *et al.* 1964–1980) each vascular plant species present on the Wadden Island was placed in one or more categories. In this manner scores were calculated for each category per island.

From the premises it will be clear that this phytogeographical study is a comparatively small scale one, in the border between floristics and ecology.

RESULTS

Comparison of floras

Comparison of vascular plant floras for eight islands and three other districts. The results of a comparison of the vascular plant floras of eight selected islands, namely Texel, Terschelling, Schiermonnikoog, Borkum, Norderney, Föhr, Sylt and Römö, with those of the selected areas from the Dune, Haff and Kempen District are presented in the dendrogram of Fig. 3. The Wadden Islands clearly show more relationship between one another

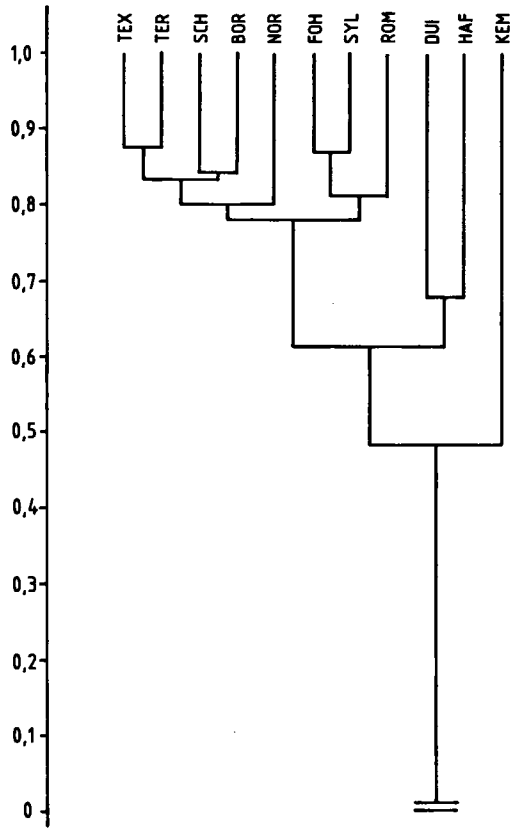

Fig. 3. Dendrogram obtained by average linkage cluster analysis of the vascular plant floras of eight selected Wadden Islands and the areas chosen from three other phytogeographical districts in The Netherlands.

than with other areas. The areas from Dune and Haff District, however, are clustered with the islands at the comparatively high level of 0·61.

Comparison of vascular plant floras for eighteen islands. The dendrogram of Fig. 4 shows the clustering of the islands, comparing the vascular plants. In this dendrogram four groups may be discerned, the first three of which cluster above the 0·7 level. The first cluster comprises Texel, Terschelling, Ameland, Schiermonnikoog, Vlieland and Borkum. The second cluster consists of Juist, Norderney and Langeoog, while the third cluster is composed of Föhr, Sylt, Römö, Fanö and Amrum. The remaining group contains Spiekeroog, Skallingen, Nordstrand and Pellworm.

Comparison of lichen floras for eighteen islands. The dendrogram in Fig. 5. represents the clustering of the islands after comparison of lichen floras. Four groups can be discerned here too, the first three of which cluster above the 0·6 level. The first cluster contains: Juist, Norderney, Langeoog, Spiekeroog and Nordstrand. The second cluster covers Vlieland, Terschelling, Schiermonnikoog and Ameland, and again includes Borkum. In the third cluster Texel accompanies Römö, Fanö and Skallingen. The remaining group is composed of Föhr, Sylt, Pellworm and Amrum.

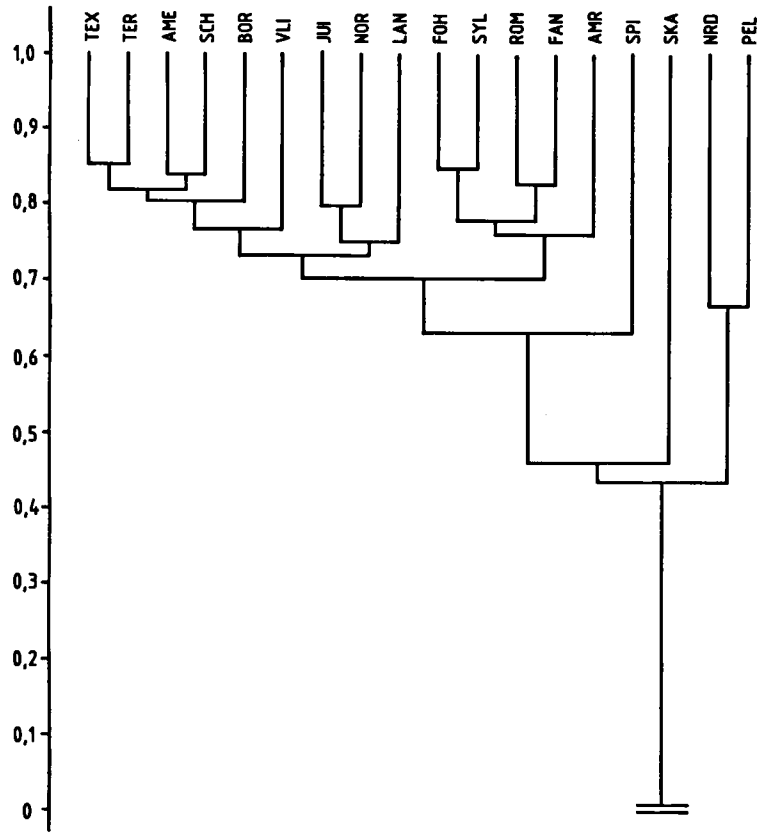

Fig. 4. Dendrogram obtained by average linkage cluster analysis of the vascular plant floras of the eighteen Wadden Islands.

Comparison of ecological groups for eighteen islands

The percentages of the species in each of the nine ecological groups are given in Table 2. Differences between the islands are apparent, but show no geographical tendencies. The similarity coefficients and dendrograms obtained for each ecological group are not presented in full, but the essentials are summarized in Table 3. For most ecological groups the mean similarity coefficients for the islands lie at or above 0·6. Lower means were found for the ecological group of woods (category 9, mean 0·56) and for that of fresh water marshes (category 7, mean 0·59). The highest mean (0·73) was found in the ecological group of salt marshes etc. (category 3). Nordstrand, Pellworm and Skallingen frequently cluster at a low level, and show different numbers for some ecological groups (Table 2).

Comparison of vegetation types for eighteen islands

The dendrogram in Fig. 6. illustrates the similarity between the islands, comparing vegetation types. In this dendrogram three groups may be discerned. One cluster is formed by Terschelling, Schiermonnikoog, Ameland, Borkum and Norderney, and a second one by Texel, Sylt, Römö and Fanö. The remaining group is very large, containing no less than nine islands which join singly or in pairs. The levels of similarity in this

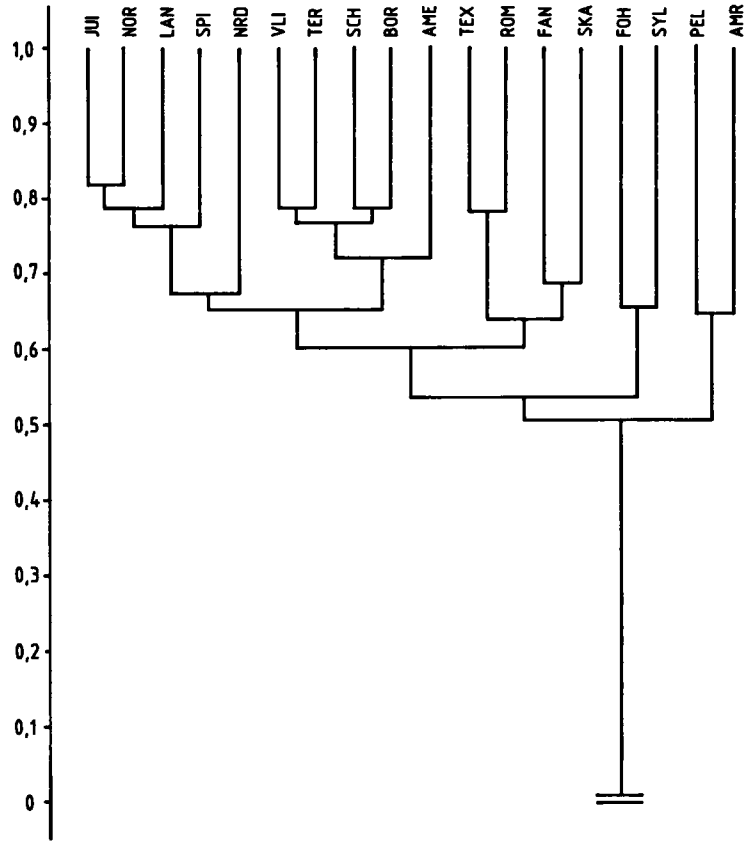

Fig. 5. Dendrogram obtained by average linkage cluster analysis of the lichen floras of the eighteen Wadden Islands.

dendrogram are mainly very low compared with those in other dendrograms (cf. Figs 4 and 5).

Comparison of phytogeographical origin of vascular plants for eighteen islands

Table 4 gives a survey of the percentages of species in each geographical category for the islands. The following trends may be observed from this table. The numbers of South- and Subsouth-European elements decrease slightly in the area from southwest to northeast, while the number of North-European elements increases towards the north. In the south-eastern corner of the area the number of West-European elements is slightly lower than in the other parts of the range. The other two categories (All-European and Central-European elements) show more or less the same values over the whole range, with the exception of Nordstrand and Pellworm.

DISCUSSION

The data presented in this study justify the conclusion that the Wadden Islands belong to one phytogeographical entity, which may be called the Wadden District (Figs 4 and 5, Tables 2 and 3). It seems logical to exclude Skallingen and, particularly, the

Table 2. Proportional share of the nine ecological groups (conform van der Meijden *et al.* (1983a), in the floras of the eighteen Wadden Islands.

	Plants of cultivated and dry waste places (1)	Plants of disturbed or open, damp to wet soils, poor in humus (2)	Plants of sea dunes, salt water and salt marshes (3)	Plants of fresh water and neighbouring shores (4)	Plants of fertilized grasslands on rich, moist to wet soils (5)	Plants of dry grasslands and walls (6)	Plants of moors, peatbogs, unfertilized grasslands and calcareous marshes (7)	Plants of fellfields, woodland margins and scrubs (8)	Plants of woods (9)
TEX	18·5	11·2	8·8	13·4	8·6	10·4	12·0	8·2	8·9
VLI	18·0	13·1	11·8	10·6	8·6	9·7	11·6	6·9	9·7
TER	18·5	11·8	8·9	13·9	8·6	10·0	12·1	6·8	9·4
AME	19·6	12·5	8·9	13·6	8·8	9·9	11·1	7·7	7·9
SCH	19·7	13·0	10·0	11·8	9·8	8·9	10·4	8·2	8·2
BOR	20·3	11·6	8·4	12·2	9·1	9·5	12·3	8·6	8·0
JUI	20·7	10·5	9·4	10·3	9·2	10·9	9·9	8·2	10·9
NOR	21·1	12·6	9·1	10·7	9·1	10·0	11·7	7·6	8·1
LAN	20·8	11·7	11·0	10·3	9·8	10·3	11·2	7·6	7·3
SPI	18·6	13·6	12·8	6·5	9·1	11·5	11·2	7·0	9·7
NRD	29·1	13·2	12·1	14·7	14·3	3·4	1·9	7·9	3·4
PEL	28·1	14·3	10·9	13·4	11·2	7·5	1·6	8·7	4·3
AMR	21·6	10·0	11·3	9·7	9·5	12·6	13·4	5·8	6·1
FOH	20·6	11·2	8·8	13·8	9·1	10·3	11·4	7·6	7·2
SYL	19·8	10·6	8·6	10·6	8·3	12·1	11·9	8·8	9·3
ROM	18·8	12·0	9·2	12·2	9·0	11·7	14·3	5·8	7·0
FAN	18·9	9·5	8·8	13·1	9·4	10·7	13·6	6·5	9·5
SKA	12·6	13·3	16·5	11·9	11·2	14·7	14·4	1·4	4·0

Table 3. Essentials of the similarity coefficient calculations etc. with the data from the nine ecological groups for the eighteen Wadden Islands

	Ecological category (for definition see Table 2)								
	1	2	3	4	5	6	7	8	9
Mean similarity coefficient for all islands	0·66 ± 0·19	0·70 ± 0·13	0·73 ± 0·19	0·62 ± 0·12	0·67 ± 0·14	0·64 ± 0·22	0·59 ± 0·29	0·60 ± 0·21	0·56 ± 0·21
Islands with a low similarity coefficient	Langeoog Spiekeroog Skallingen	Nordstrand Pellworm Skallingen	Nordstrand Pellworm	Spiekeroog Skallingen	Skallingen	Nordstrand Pellworm	Nordstrand Pellworm	Skallingen	Skallingen Nordstrand Pellworm
Number of species found in all the islands (%)	17	14	37	2	22	8	3	3	1

Table 4. Proportional share of the six phytogeographical elements in the floras of the eighteen Wadden Islands

	All-European element	North-European element	Central-European element	West-European element	Subsouth-European element	South-European element
TEX	18·0	10·3	17·7	20·7	24·8	8·5
VLI	19·9	10·7	17·0	20·2	24·1	8·2
TER	18·4	10·7	17·7	20·4	24·3	8·5
AME	19·9	10·7	17·6	18·6	24·9	8·3
SCH	20·8	10·4	17·1	19·7	24·2	7·8
BOR	19·3	10·8	17·8	19·2	25·1	7·8
JUI	20·2	10·5	17·7	18·9	24·9	7·8
NOR	20·8	10·7	17·5	18·7	24·2	8·1
LAN	22·2	10·8	16·7	18·8	24·3	7·2
SPI	23·1	10·7	16·5	18·6	23·6	7·5
NRD	30·7	9·4	14·0	16·0	21·9	8·0
PEL	30·2	9·4	14·4	15·9	22·4	7·7
AMR	20·9	11·6	17·9	20·5	21·8	7·3
FOH	19·5	11·5	18·1	20·0	23·9	7·0
SYL	20·2	11·1	17·7	19·5	24·3	7·2
ROM	20·4	12·8	18·2	20·0	22·6	6·0
FAN	19·2	12·7	18·5	20·1	23·0	6·5
SKA	22·8	13·1	17·1	20·1	20·4	6·5

'polder-islands' Nordstrand and Pellworm from this district due to their low similarity levels in the dendrograms. Within this Wadden District some clustering tendencies are found. A western, a central and a northern group of islands can be discerned, which are, respectively, Dutch, German and mixed German/Danish. The German island Borkum often clusters with the western group, the Dutch island Texel sometimes with the northern group.

The Wadden District seems to be distinct from other Dutch phytogeographical districts, although it clusters with the neighbouring Dune and Haff District at the comparatively high level of 0·61. Furthermore, it is remarkable that the Dune District first clusters at the fairly high level of 0·68, with the Haff District and not with the Wadden District (Fig. 3). The absence of salt vegetation in this Dune District area will partly account for this. Furthermore it should be noted that in the area chosen from the Dune District man has recently dug many canals, where several "Haff species" have been found (Boerman 1975).

It can be concluded from Table 4 that climate plays a minor role in the differences in flora and vegetation between the islands. Heykena (1965), who studied flora and vegetation of the whole German and Danish North Sea coast, drew the same conclusion. The relatively high number of West-European elements on most of the northern islands and of Subsouth-European elements on some of them is in agreement with a pronounced type of Atlantic climate in that area (Piontkowski 1970).

The differences between the islands in flora and vegetation are mainly determined by the degree of ecological differentiation. For instance, the islands that often show low similarity coefficients, namely Nordstrand, Pellworm and Skallingen (e.g. Fig. 4) also have the lowest species numbers (Table 1). The main cause for this is that some ecological groups are poorly represented in these islands (Table 2), i.e. that some biotypes are not fully developed (e.g. dunes). To this ecological differentiation contribute the size of the islands, their position with respect to the mainland, their orientation, and their soil types, but most of all man's influence. These different factors will be discussed shortly.

The larger islands often have more vascular plant species than the smaller ones. For this reason the smaller islands usually show low similarity coefficients, and not because they possess many other species than the larger islands. The islands Texel, Amrum, Sylt, Römö and Fanö, and the peninsula Skallingen, possess a Pleistocene nucleus, and are north–south oriented. Furthermore, they have been inhabited by man for a longer period and more continuously. The west–east oriented islands, particularly the larger ones, can "build-up" environmental differentiation by land expansion in the eastern part, while the decrease in the west is greatly reduced by man today. Edaphic factors play a role in the ecological differentiation, e.g. the presence of lime. We were not able, however, to correlate between the percentage of lime in the dune sand or the area covered by peat, on the one hand, and the number of calcicole or calcifuge species on the other. Detailed studies, as carried out by Rozema *et al.* (1985) on the calcium contents of the dunes of Schiermonnikoog, would be very useful for the other islands too.

A general problem should be pointed out here: a sole specimen observed only once counts, in a floristical sense, just as heavily as a large population growing for years in the same place, but in an ecological and phytogeographical sense these two are totally different.

That man influences ecological differentiation is evident. Some examples have already been given. Others are: connecting neighbouring islands (parts of what are now Texel and

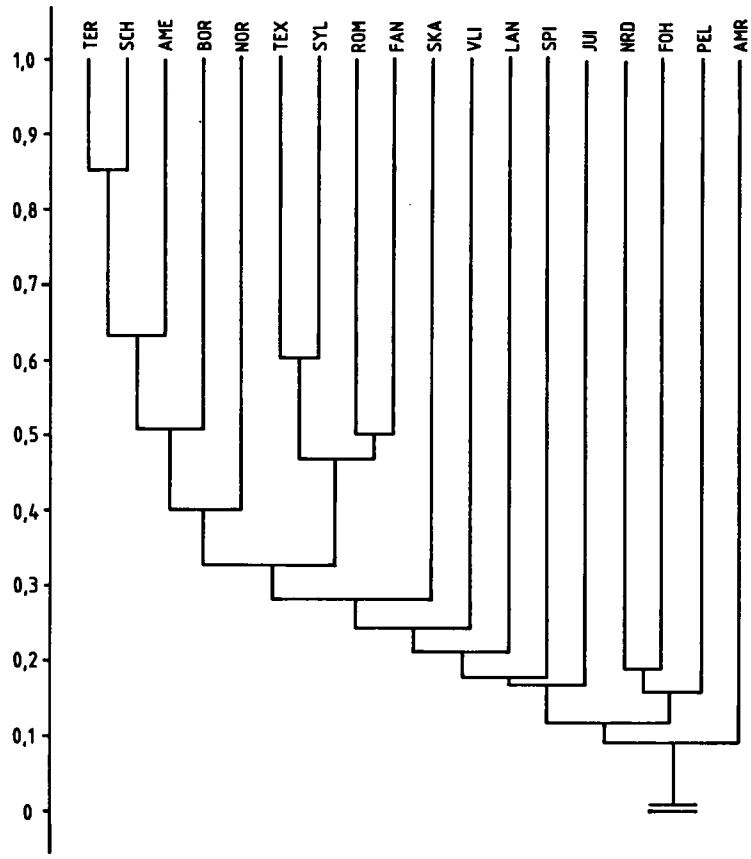

Fig. 6. Dendrogram obtained by average linkage cluster analysis of the 25 vegetation types which were discerned for the eighteen Wadden Islands.

Borkum), constructing dikes around polders and as connections between islands and the mainland (Nordstrand, Skallingen), digging ponds and constructing duck decoys, planting trees and introducing other species, which often naturalize. In the light of these facts the low similarity coefficients we found when comparing vegetation types (see Fig. 6) are not surprising. More examples on this subject can be found in Abrahamse *et al.* (1976) and Dijkema & Wolff (1983). Because man influences the vascular plant flora and vegetation so drastically, more information on the phytogeographical relationships between the islands may probably be obtained by comparing their lichen and moss floras, particularly if these become known in more detail. The clustering presented in Fig. 5 has already given a good impression of possible relationships between the islands, but it might also partly reflect the way in which inventories and identifications of lichens in the Wadden Islands have been carried out in the past.

Weeda & Mennema (1983: 231) have found a number of relative limits in the area with the aid of numbers of species that reach distribution boundaries. These relative limits generally do not coincide with our cluster limits at all. For instance, in their study, 24 species reached their distribution limit between Schiermonnikoog and Borkum, while we found that Borkum clusters with the group including Schiermonnikoog at the very high level of 0·81 (Fig. 4). For the Sylt/Römö situation these values are, respectively, 25 species

and a clustering level of 0·78. In our methods the similarities in the rich floras of the islands overwhelm the comparatively slight differences between them.

ACKNOWLEDGEMENTS

We thank Dr H. Hillebrand for his continuous help in the use of the computer methods. Thanks are also due to Professor Dr M. Vroman and Professor Dr W.H.O. Ernst for their constructive comments, and to Dr T.A. Dueck for correction of the English. Mrs M.J. Brockhoff-van Wissen is gratefully acknowledged for drawing the figures, and Mrs S. Richter for typing the manuscript.

REFERENCES

Abrahamse, J., Joenje, W. & Leeuwen-Seelt, N. van (1976, eds): *Waddenzee, natuurgebied van Nederland, Duitsland en Denemarken.* Landelijke Vereniging tot Behoud van de Waddenzee, Harlingen & Vereniging tot Behoud van Natuurmonumenten in Nederland, 's-Gravenland.

Boerman, M.O. (1975): *10 jaar botanische inventarisatie in de Amsterdamse Waterleidingduinen.* Gemeentewaterleiding, Amsterdam.

Brand, A.M. & Ketner-Oostra, R. (1983): Flora, lichens. In: Dijkema, K.S. & Wolff, W.J. (eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas:* 73–84. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

Bray, J.R. & Curtis, J.T. (1957): An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monographs* **27:** 325–349.

Cools, J. & Cools, T. (1981): *De flora van Midden-Brabant en omstreken, 1970–1980.* Staatsbosbeheer, Tilburg.

Doing, H. (1983a): Geomorphology and soil of dunes. In: Dijkema, K.S. & Wolff, W.J. (eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas:* 12–26. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

— (1983b): Landscape and islands types. In: Dijkema, K.S. & Wolff, W.J. (eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas:* 242–264. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

Dijkema, K.S. (1983): Landscape and vegetation: In: Dijkema, K.S. & Wolff, W.J. (eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas:* 85–133. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

— & Wolff, W.J. (1983, eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas.* Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

Heimans, E., Heinsius, H.W. & Thijsse, J.P. (1965): *Geïllustreerde Flora van Nederland.* Versluys, Amsterdam-Antwerpen.

Heykena, A. (1965): *Vegetationstypen der Küstendünen an der östlichen und südlichen Nordsee.* Mitt. Arbeitsgem. Floristik Schleswig-Holstein Hamburg, Heft **13.**

Hillebrand, H. & Klapwijk, S.P. (1976): Distribution of multicellular benthic algae in an eutrophic ditch. *Hydrobiol. Bull.* **10:** 48–58.

Joenje, W. & Westhoff, V. (1976): Plantengroei. In: Abrahamse, J., Joenje, W. & Leeuwen-Seelt, N. van (eds): *Waddenzee, natuurgebied van Nederland, Duitsland en Denemarken:* 177–195. Landelijke Vereniging tot Behoud van de Waddenzee, Harlingen & Vereniging tot Behoud van Natuurmonumenten in Nederland, 's-Gravenland.

Mennema, J. (1978): Floristisch onderzoek naar van Soest's plantengeografische districten van Nederland. *Gorteria* **9:** 142–154.

— & Weeda, E.J. (1983): Flora, Vascular plants. In: Dijkema, K.S. & Wolff, W.J. (eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas:* 38–61. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

Meijden, R. van der, Arnolds, E.J.M., Adema, F.A.C.B., Weeda, E.J. & Plate, C.L. (1983a): *Standaardlijst van de Nederlandse Flora.* Rijksherbarium, Leiden.

—, Weeda, E.J., Adema, F.A.C.B. & Joncheere, G.J. de (1983b): *Heukels' Flora van Nederland.* Wolters-Noordhoff, Groningen.

Odum, E.P. (1971): *Fundamentals of Ecology.* W.B Saunders, Philadelphia.

Piontkowski, H.-U. (1970): *Untersuchungen zum Problem des Atlantischen Klimakeils.* Mitt. Arbeitsgem. Floristik Schleswig-Holstein Hamburg, Heft **18.**

Ploeg, D.T.E. van der (1977): *Atlas fan de Floara fan Fryslan.* Fryske Akademy, Leeuwarden.

Rozema, J., Laan, P., Broekman, R., Ernst, W.H.O. & Appelo, A.J. (1985): On the lime transition and decalcification in the coastal dunes of the province North Holland and the island of Schiermonnikoog. *Acta Bot. Neerl.* **34:** 393–411.

Soest, J.L. van (1924): Flora van Arnhem II. *Ned. Kruidk. Archief* **1923:** 68–115.

— (1925): Flora van Arnhem III. *Ned. Kruidk. Archief* **1924:** 89–133.

— (1929): Plantengeografische districten in Nederland. *Levende Natuur* **33:** 311–318.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.A., Walters, S.M. & Webb, D.A. (1964–1980): *Flora Europaea* **1–5**. Cambridge University Press, Cambridge.

Walter, H. & Straka, H. (1970): *Grundlagen der Pflanzenverbreitung*. **2.** *Arealkunde (Einführung in die Phytologie* **3**). Ulmer, Stuttgart.

Weeda, E.J. (1983): Over de plantengeografische indeling van Nederland. *Natura* **80:** 324–329.

— & Mennema, J. (1983): Phytogeographical aspects. In: Dijkema, K.S. & Wolff, W.J. (eds): *Flora and Vegetation of the Wadden Sea Islands and Coastal Areas:* 221–242. Stichting Veth tot Steun aan Waddenonderzoek, Leiden.