VARIATION IN SOME SALTMARSH AND DUNE VEGETATIONS IN THE NETHERLANDS WITH SPECIAL REFERENCE TO GRADIENT SITUATIONS

D. C. P. THALEN[1]

Laboratorium voor Plantenoecologie van de Rijksuniversiteit, Groningen

SUMMARY

Variation in vegetation as related to variation in some environmental factors was analysed in five quadrats, four of 32 sq. m and one of 64 sq.m, laid out in different coastal saltmarsh and dune vegetations including two distinct gradient situations. Vegetational variation was measured with five methods, viz. species diversity (number of species/area, α Williams, formulas of Margalef and Shannon applied to frequency data) and floristic fall between adjacent subquadrats ($I = A + B - 2C$). Environmental factors examined included detailed height measurements and analysis of soil samples for six factors, viz. moisture, pH, N, $CaCO_3$, humus and e.c., taken in July and October-November. The results show how environmental variation is reflected in the vegetation, the total number of phanerogams in the quadrats ranging from 2 to 61. Highest species diversity was observed in the middle part of local environmental gradients, and frequency and distribution data revealed how four different types of species contribute to this high diversity, the most interesting being those species that are confined to the gradient. In one case a very high number of species (45 per sq. m.) was found in the gradient. The methods applied for measurement of vegetational variation are briefly discussed.

1. INTRODUCTION

Coastal saltmarsh and sanddune vegetations in the Netherlands have been extensively studied (BEEFTINK 1965, VAN DER MAAREL 1966a) but not much work has been reported on quantitative analysis, on a small scale, of the variation in the different vegetation types. The present study aimed at making such an analysis, relating vegetational variation to variation in environmental factors and at the same time analysing changes in composition of the vegetation along local transition zones.

Variation in the vegetation usually reflects variation in environmental factors. Severe or specialized physico-chemical factors tend to reduce the number of species in a community although the number of individuals may increase (ODUM 1959, WILLIAMS 1964). This may prove to be of great value for research on the effect of those types of pollution where man introduces such factors. The relation between number of species and number of individuals or, as more generally used in botanical investigations, between number of species and area, can be expressed in an index of species diversity. Determination of species diversity is one method to quantify variation in the vegetation, measurement of heterogeneity

[1] Present address: Institute for Applied Research on Natural Resources c/o U.N.D.P., P.O.Box 2048, Alwiyah, Baghdad, Iraq.

is another. Different methods have been proposed in this respect, e.g. by WILLIAMS (1964), and MARGALEF (1958) and discussions on interrelations and aspects of application have been given (DAHL 1960, PIELOU 1966, VAN DER MAAREL 1966b, THALEN 1968). VAN DER MAAREL (1966b) applied some of the techniques mentioned to dune grasslands and confirmed the principle that highest diversity occurs in the moderate or middle range of a physical gradient. During the last years more studies have been carried out, especially in gradient situations (VAN DER MAAREL and LEERTOUWER 1967) also with a view to illustrate the general relation between variation and stability as expressed by VAN LEEUWEN (1965, 1966), and of general value for a theoretical background for the management of nature reserves on a sound scientific basis.

2. INVESTIGATED AREAS

Fieldwork for the present study was carried out during the summer of 1967 in the coastal vegetations of the Dutch West Frisian island Schiermonnikoog (53°29′N, 6°12′E) and included a detailed analysis of four areas of 32 sq.m. and one area of 64 sq.m. The areas represent some of the vegetation types encountered when going from the low-water mark through a saltmarsh to a dune area. A brief description of the plots is given below. Nomenclature is after HEUKELS and VAN OOSTSTROOM (1962).

Quadrat I: Area (4 × 8) sq.m. Lower saltmarsh, below tide-line, flat, with a vegetation of scattered single plants of *Salicornia europaea* and *Spartina townsendii*;

Quadrat II: Area (4 × 8) sq.m. Saltmarsh, below tide-line, almost flat, with a dense cover, mainly consisting of *Salicornia europaea*, *Suaeda maritima*, *Puccinellia maritima*, and *Spartina townsendii*;

Quadrat III: Area (4 × 16) sq.m. Higher saltmarsh, irregularly flooded. Local differences in height up to 20 cm. Vegetation in the lower part as in quadrat II, higher parts bearing a vegetation with *Festuca rubra* and *Glaux maritima*;

Quadrat IV: Area (4 × 8) sq.m. Transition zone of saltmarsh to dune area, during wintertime partially flooded. Gradient in height of about 40 cm. Vegetation of the lower part is dominated by *Juncus gerardii*, *Glaux maritima* and *Plantago maritima*, whereas in the higher part *Lotus corniculatus*, and *Trifolium repens* are the most common species;

Quadrat V: Area (4 × 8) sq.m. Dune slack, a few times per year partially flooded during wintertime. Gradient in height of about 20 cm. Vegetation very rich in species with *Salix repens*, *Carex panicea*, *Potentilla erecta*, and *Drosera rotundifolia*.

3. METHODS

3.1. Vegetation sampling

Quadrats I, II, III and IV were sampled in the following way. Each quadrat was examined per square metre, using a wooden frame of one sq.m., subdivided into smaller areas by stretching strings over it, and placed at adjustable height above the vegetation. Per square metre were noted a species list of phanerogams, the local – rooted – frequency (using a subdivision of 16 subquadrats) and layering, height and estimated cover percentage. Data for species-area relations were sampled by counting in each sq.m the number of phanerogams in nested quadrats from the centre in areas of 1/256, 1/128, ... 1/1 sq.m successively. The outcome of the countings of all areas of equal size was averaged per quadrat and plotted against plot size in order to obtain the species-area curve for the vegetation types of the analysed quadrats. Quadrat V was analysed in more detail, being taken into account earlier work in part of this area by VAN DER MAAREL and LEERTOUWER. A species list was prepared for each 1/16 sq.m in the total area of 32 sq.m. Layering, height and estimated percentage cover were noted per sq.m. Some supplementary countings were done to obtain data for the species-area curve.

3.2. Analysis of vegetation data

Variation in the vegetation was determined by calculating the mean of an index of floristic difference for all adjacent square metres ($I = A+B-2C$, where A and B are numbers of species in each of two adjacent square metres and C is the number of species these square meters have in common) and by determining a number of species diversity indices, as follows. Number of species per unit area was calculated on a 1/16, 1/4 and 1/1 sq.m. basis. The species-area curve provided data for obtaining the values for the diversity index (α_w) proposed by WILLIAMS (1964).

MARGALEF (1958) developed a diversity index on an information-theoretical basis, using the number of indidivuals counted per species in a sample:

$$I_g = \frac{1}{N}\,{}^2\log\frac{N!}{n_1!\,n_2!\,\ldots\,n_n!}$$

where N = total number of individuals and $n_1, n_2 \ldots n_n$ – number of individuals of species 1, 2 ... n, respectively. This formula was applied to vegetation data, sampled per sq.m for the five quadrats, using the presence in the 16 subquadrats as "individuals number" for the sq.m.

MARGALEF's index is based on a general information formula given by SHANNON and WEAVER (1964) which was, in a slightly modified form, also applied to the data, viz.

$$I_{sh} = \sum_{i=1}^{n} \left(\frac{Ai}{N}\,{}^2\log\frac{Ai}{N}\right)$$

where n = total number of species

N = total number of individuals
Ai = number of individuals of species i (or, modified, number of subquadrats where species was found present).

Computation of I_g, as well as I_{sh}, for the five quadrats was carried out with the help of a Telefunken TR4 computer.

3.3 Environmental factors

Detailed relative height measurements were taken in all five quadrats. The number of measure points was dependent on the height differences observed with the unaided eye: 2, 4, 9, 13 and 13 measure points in each square meter for the quadrats I–V respectively resulted in detailed contour maps.

Soil was collected from 4, 8, 10, 10 and 8 square metres for the quadrats I–V respectively, the sampled square metres being systematically spaced over the quadrats. Within each sq.m. sampled the soil (0–5 cm) of nine points equally spaced over the sq.m. was mixed to give a single pooled sample for analysis. Samples were taken in the beginning of July after a warm, dry period and at the end of October, beginning of November during a wet period. The following factors were determined in the samples after transportation to the laboratory: percentage moisture, pH (H_2O and KCl), percentage total nitrogen, percentage $CaCO_3$, percentage humus (corrected) and electro-conductivity. Depth of ground water table was determined at two points near quadrat V and recordings were kept during the period September–November 1967.

4. RESULTS

4.1. Comparison of the five quadrats

A total number of 82 phanerogams was found in the five analysed quadrats, ranging from a total of two species in quadrats I to 61 in quadrat V. In *table 1* the species are listed with frequency numbers of occurrence in each quadrat.

Table 2 presents a characteristic of the environment on the basis of the analysed factors of the soil samples. Quadrats I, II, and III show a relatively low degree of variation in environmental factors, especially if compared to quadrats IV and V. Quadrat IV shows for all computed factors a very high value for the coefficient of variation (CV). This is apparently due to the height gradient, as this gradient resulted, as was observed, in differences of flooding with brackish water (a mixture of rainwater and seawater) during wintertime for the different parts of the quadrat. This is supported by the high CV-values for the electro-conductivity: 102.4 and 132.9 in July and November, respectively, and the high CV-values for moisture. Results of analyses in quadrat IV are discussed in more detail under 4.3.

Quadrat V shows a trend similar to quadrat IV, but with less variation in environmental data which could be expected as the gradient situation in V is less pronounced.

The e.c.-data of the five quadrats for July and October-November reflect the effect of flooding in summer and winter. Quadrats I and II do not differ marked-

Table 1. Local – rooted – frequency of the species found in the five quadrats.

quadrat number	I	II	III	IV	V
area in sq.m	32	32	64	32	32
number of subquadrats	512	512	1024	512	512
Agrostis stolonifera	–	–	–	84.4	23.8
Anthoxanthum odoratum	–	–	–	–	34.0
Armeria maritima	–	–	1.3	66.6	–
Artemisia maritima	–	–	16.3	1.4	–
Aster tripolium	–	0.4	27.5	–	–
Betula verrucosa	–	–	–	–	5.7
Calamagrostis epigejos	–	–	–	–	92.1
Cardamine pratensis	–	–	–	–	0.2
Carex arenaria	–	–	–	–	5.7
Carex distans	–	–	–	15.2	–
Carex flacca	–	–	–	–	67.4
Carex nigra	–	–	–	–	57.0
Carex panicea	–	–	–	–	35.1
Carex serotina	–	–	–	3.7	8.8
Centaurium littorale	–	–	–	0.4	–
Centaurium pulchellum	–	–	–	8.8	0.4
Cerastium holosteoides	–	–	–	–	0.8
Cirsium palustre	–	–	–	–	32.4
Cochlearia anglica	–	–	5.8	–	–
Cynosurus cristatus	–	–	–	–	2.7
Drosera rotundifolia	–	–	–	–	28.5
Eleocharis palustris	–	–	–	–	10.4
Eleocharis quinqueflora	–	–	–	–	1.0
Elytrigia pungens	–	–	–	13.3	–
Elytrigia repens	–	–	–	–	55.7
Epilobium palustre	–	–	–	–	1.2
Epipactis palustris	–	–	–	–	22.9
Eriophorum angustifolium	–	–	–	–	12.1
Euphrasia odontites	–	–	–	37.9	–
Euphrasia officinalis	–	–	–	–	5.9
Festuca ovina	–	–	–	–	15.4
Festuca rubra	–	–	13.5	67.7	66.4
Galium palustre	–	–	–	–	2.3
Gentiana amarella	–	–	–	–	2.9
Glaux maritima	–	0.2	19.5	42.4	0.2
Halimione portulacoides	–	–	6.9	–	–
Hippophaë rhamnoides	–	–	–	1.0	–
Holcus lanatus	–	–	–	–	81.4
Hydrocotyle vulgaris	–	–	–	–	90.8
Hypochaeris radicata	–	–	–	–	1.8
Juncus alpinus	–	–	–	0.6	4.5
Juncus articulatus	–	–	–	–	31.8
Juncus conglomeratus	–	–	–	–	6.4
Juncus gerardii	–	–	–	47.5	71.7
Juncus maritimus	–	–	–	1.4	18.0
Leontodon autumnalis	–	–	–	–	35.9
Leontodon nudicaulis	–	–	–	–	39.6
Limonium vulgare	–	2.1	5.3	27.5	–
Linum catharticum	–	–	–	–	14.6

(continued)

Lotus corniculatus	–	–	–	45.3	10.9
Luzula campestris	–	–	–	–	15.0
Lychnis flos-cuculi	–	–	–	–	2.5
Mentha aquatica	–	–	–	–	43.9
Parapholis strigosa	–	–	–	1.4	–
Parnassia palustris	–	–	–	–	10.2
Phragmites communis	–	–	–	–	25.2
Plantago coronopus	–	–	–	4.5	–
Plantago lanceolata	–	–	–	–	0.2
Plantago major	–	–	–	–	0.2
Plantago maritima	–	–	20.3	47.1	22.5
Poa pratensis	–	–	–	1.6	18.6
Polygala vulgaris	–	–	–	–	7.6
Potentilla anserina	–	–	–	–	44.7
Potentilla erecta	–	–	–	–	78.5
Prunella vulgaris	–	–	–	–	36.7
Puccinellia maritima	–	46.9	92.8	–	–
Radiola linoides	–	–	–	–	42.0
Ranunculus flammula	–	–	–	–	0.8
Sagina maritima	–	–	–	0.4	–
Sagina nodosa	–	–	–	7.2	7.8
Sagina procumbens	–	–	–	–	26.0
Salicornia europaea	24.6	100.0	95.6	0.4	–
Salix repens	–	–	–	–	95.5
Schoenus nigricans	–	–	–	14.6	22.5
Sieglingia decumbens	–	–	–	–	85.7
Spartina townsendii	1.4	31.4	26.3	–	–
Spergularia marginata	–	8.4	26.5	–	–
Suaeda maritima	–	21.9	85.6	0.2	–
Trifolium fragiferum	–	–	–	0.2	–
Trifolium pratense	–	–	–	–	2.9
Trifolium repens	–	–	–	55.3	28.7
Triglochin maritima	–	0.6	1.7	6.1	–

ly in this respect, both being regularly flooded in summer as well as in winter. Quadrat III is in summer occasionally partially flooded, in winter more often and totally, and this results in a lower e.c. in summer and a higher one in winter. However, a high CV for this factor obtains in summer as compared with that for wintertime. Quadrat IV is between July and November at least a few times almost totally flooded and this gives rise to a more than twofold increase in e.c. Quadrat V was apparently not flooded by seawater during this period. Rainwater, however, had here a strong influence and very likely reduced e.c. This is supported by the very high moisture content in the October-November samples.

Table 3 summarizes the computed vegetation characteristics for the five analysed quadrats. It can be seen that the five quadrats together form a range from a very low to a very high number of species found in comparable areas and thus provide a good opportunity to compare different methods for the measurement of species diversity. This will be given under 5. All methods, however, show an

Table 2. Descriptive statistics of some environmental factors, analysed in the soil samples of the five quadrats: mean ($\bar{x}$), standard deviation (s) and coëfficient of variation (CV).

		July samples					Oct.-Nov. samples				
		I	II	III	IV	V	I	II	III	IV	V
	$\bar{x}$	13.8	23.8	32.0	20.6	35.6	20.8	30.3	41.5	34.4	42.4
%	s	0.8	1.2	1.6	17.5	8.0	0.1	2.0	2.5	11.2	6.2
moisture	CV	5.4	4.9	4.8	85.0	22.5	1.9	6.5	6.1	32.6	14.6
	$\bar{x}$	1.51	4.82	6.43	2.87	4.23	1.22	3.53	7.19	4.40	4.69
%	s	0.46	2.21	1.99	1.98	0.71	0.16	0.20	0.33	3.77	1.38
humus	CV	30.5	45.85	30.95	68.99	16.78	13.11	5.67	4.58	85.7	29.42
	$\bar{x}$	1692	3059	2897	745	222	1996	2991	4440	1705	125
e.c.	s	256	685	796	763	117	114	281	741	2266	75
	CV	15.1	22.4	27.5	102.4	52.7	5.7	9.4	16.7	132.9	60.0
	$\bar{x}$	0.04	0.10	0.20	0.12	0.16	0.03	0.11	0.21	0.12	0.16
%	s	0.015	0.024	0.028	0.100	0.085	0.008	0.005	0.017	0.101	0.104
N-total	CV	37.5	24.0	14.0	83.3	5.3	26.6	4.5	8.1	84.2	6.5
	$\bar{x}$	1.33	3.32	6.06	0.28	–	1.50	4.24	6.16	0.13	–
%	s	0.10	0.47	0.58	0.14	–	0.18	0.60	0.32	0.10	–
$CaCo_3$	CV	7.5	14.2	9.6	50.0	–	12.0	14.2	5.2	76.9	–

increase in computed values going from quadrat I to V and a strong correlation can be observed at first glance. Comparison of tables 2 and 3 gives a rough idea of the relation between species diversity and variation in environmental factors as these were computed in the five cases. The general idea that variation in environmental factors is reflected by a variation in the vegetation is clearly seen, but closer examination of the gradient situations is necessary as these data can provide the knowledge of changes in species composition and number of species if the environment varies to a greater or lesser extent.

Table 3. Some computed quantitative vegetation characteristics for the five analysed quadrats.

	I	II	III	IV	V
total area in sq.m.	32	32	64	32	32
maximum no. of species/sq.m.	2	8	14	19	45
minimum no. of species/sq.m.	0	2	3	6	21
no. of species 1/256 sq.m.	0.00	1.16	2.72	3.88	5.37
no. of species 1/16 sq.m.	0.28	2.34	4.06	6.63	16.07
no. of species 1/4 sq.m.	0.75	3.59	5.31	8.88	24.64
no. of species 1 sq.m.	1.06	4.72	7.16	11.81	32.88
no. of species 4 sq.m.	1.38	6.13	10.88	15.75	45.63
no. of species 16 sq.m.	2.00	8.00	13.50	25.00	57.50
no. of species 32 sq.m.	2.00	9.00	15.00	29.00	61.00
I = A+B–2C	0.36	1.42	3.21	4.36	11.58
α Williams (1–32 sq.m.)	0.27	1.23	2.26	4.95	8.12
I Margalef (frequency)	0.0703	1.4885	2.2155	2.8310	4.3275
I Shannon (frequency)	0.1092	1.7172	2.4409	3.1084	4.6428

4.2. Height and species composition in quadrat III

Figure 1A shows a contour map of quadrat III and the number of species found in each sq.m as related to height. The greater part of the area is flat, but locally small hillocks occur, as seen in the middle and eastern part of the quadrat. The low lying part bears a vegetation composed of only a few species, viz. *Salicornia europaea*, *Puccinellia maritima*, and *Suaeda maritima* and less frequently *Plantago maritima*, *Spartina townsendii*, *Spergularia marginata*, and *Aster tripolium*. In the higher parts, in addition species such as *Glaux maritima*, *Cochlearia anglica*, *Limonium vulgare*, *Halimione portulacoides*, and *Festuca rubra* were found. A general increase in the number of species with height was expected, and for the 64 sq.m analysed the mean height was calculated from the nine measured points in each sq.m and plotted against the number of species. The result is shown in figure 2. For the first 10 cm or so of relative height increase an increase in number of species is also seen. From about 10 to 20 cm a similar trend is observed but it is less pronounced. The interesting point is, however, that the highest sq.m viz. 55, 56 and 60, bear a relatively lower number of species and that the sq.m 26, 50, 51, and 58 bear the highest number of species whereas their average height is in the middle range. Closer observation of *fig. 1A* reveals that the last mentioned group consists of four sq.m all situated in a height gradient. This leads to the conclusion that the transition zones of quadrat III are richer in species than the lower and the higher situated parts.

4.3. Species diversity and species composition along a distinct gradient

The gradient in height in quadrat IV is clearly shown in *fig. 1B*. It appeared from the soil analysis that this transition entailed a gradient in almost all analysed environmental (soil) factors. This can be seen from *table 4* where results of analyses

Table 4. Values of some environmental factors at eight regularly spaced places along the gradient of quadrat IV.

		1	2	3	4	5	6	7	8
moisture %	July	47.4	38.7	18.5	21.2	10.2	6.6	5.2	5.6
	Oct.	52.9	41.4	35.7	29.3	30.6	27.6	23.8	24.8
humus %	July	–	7.2	2.4	3.6	3.5	1.3	2.1	1.4
	Oct.	11.0	5.9	3.0	2.7	3.1	2.3	1.6	1.7
pH (KCl)	July	6.3	7.1	7.0	6.9	6.9	6.3	7.0	6.8
	Oct.	5.7	6.9	7.0	7.1	7.1	7.6	7.4	7.1
e.c.	July	1852	1028	410	420	–	190	118	87
	Oct.	4987	3154	1694	918	372	247	339	175
N tot. %	July	0.37	0.21	0.05	0.09	0.10	0.06	0.08	0.08
	Oct.	0.30	0.11	0.09	0.07	0.08	0.07	0.05	0.04
$CaCO_3$ %	July	–	0.30	0.50	0.20	0.30	0.10	–	0.25
	Oct.	0.36	0.17	0.17	0.14	0.09	0.02	0.14	0.04
relative height		0 cm ———							——— 40 cm

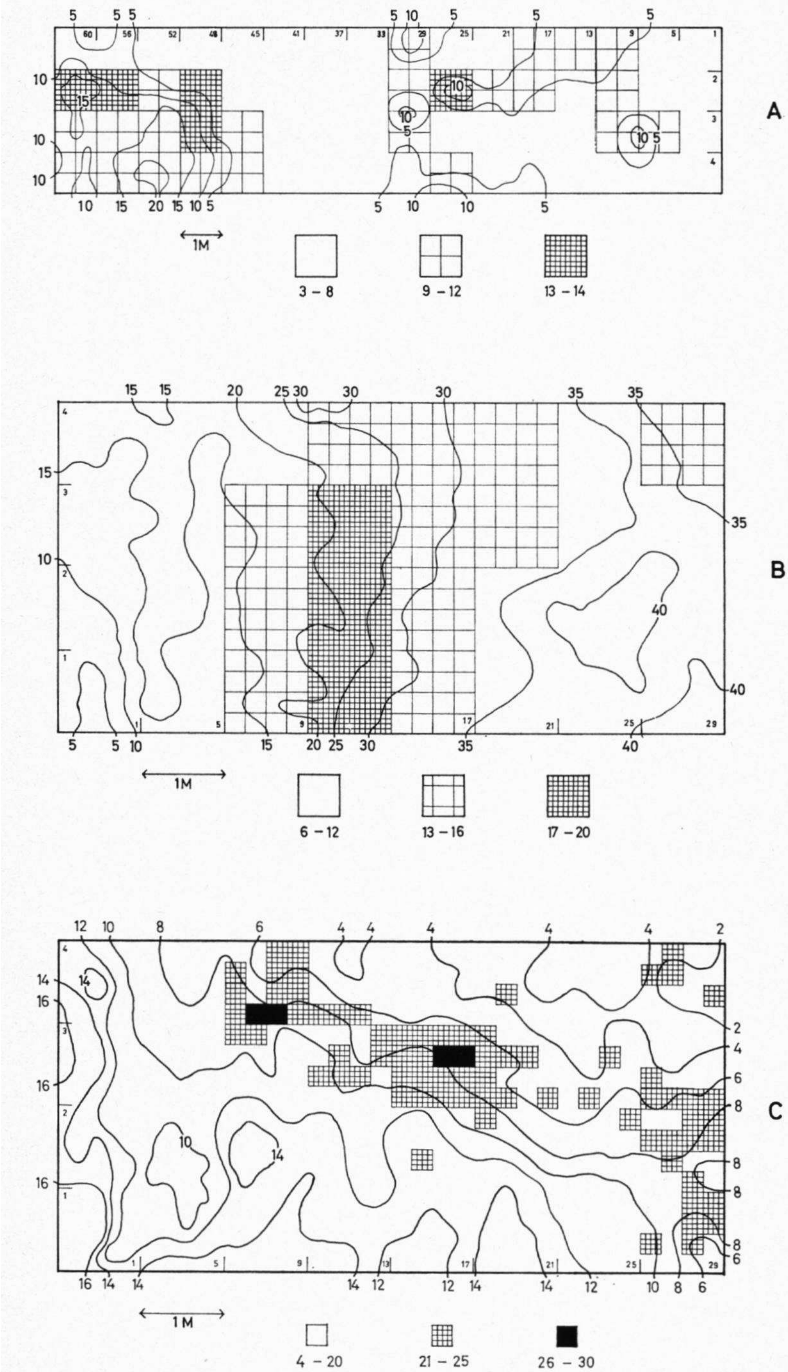

Fig. 1. Distribution of species diversity (measured as number of species/unit area) and contour lines (height in cm) in quadrats III (A), IV (B) and V (C). Smaller written numbers indicate numbering of square metres in each quadrat.

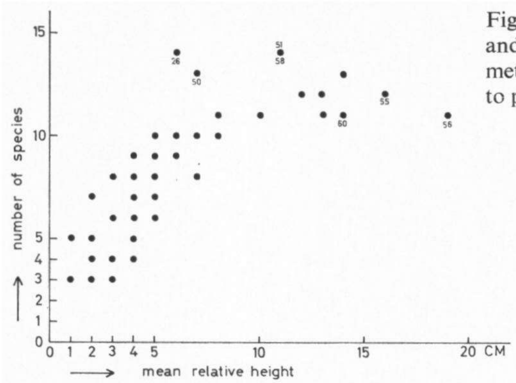

Fig. 2. Relation between number of species and mean relative height of the square metres in quadrat III. Numbered dots refer to particular square metres (see text).

are given of eight sq.m along the gradient. All analysed factors except pH clearly decrease when going from the lower to the higher part along the transition zone. A few times during the winter half year part of the quadrat is flooded by water from the Waddenzee and only under extreme weather and tidal conditions the higher part may also be inundated for a short period. The observed differences in the measured environmental factors are apparently due to a great extent to this difference in duration of inundation, possibly combined with an effect of leaching by rainwater. It may be seen from *table 4* that moisture content of the soil fluctuates much more in the higher part of the gradient and e.c. more in the lower part, this indicating that the middle part of the gradient presents the smallest changes. The striking differences in environmental factors along the gradient are reflected in the species composition of the vegetation, varying from halophytic species (*Salicornia europaea, Suaeda maritima*) to psammophytes (*Hippophaë rhamnoides, Elytrigia pungens*).

An overall analysis of the vegetation along the transition zone showed the highest variation in the middle part of the gradient. Simply measured as number of species per unit area (sq.m), it is shown in *fig. 1B*. The result of determination of the Margalef index for species diversity per sq.m if based on the local frequency recordings, is shown in *fig. 3B*. Vegetational variation, measured as differences in species composition between adjacent square metres (I = A+B−2C) is given in *fig. 3A*.

Table 5 allows closer examination of variation in terms of frequency and species composition. From this table it can be seen that high variation in the middle part of the gradient in terms of species diversity is based on

- species occurring in the middle part and in the lower and higher part as well, e.g. *Armeria maritima* and *Agrostis stolonifera*,
- species occurring in the middle part and in the lower part, e.g. *Glaux maritima* and *Limonium vulgare*,
- species occurring in the middle part and in the higher part, e.g. *Sagina nodosa* and *Lotus corniculatus*,

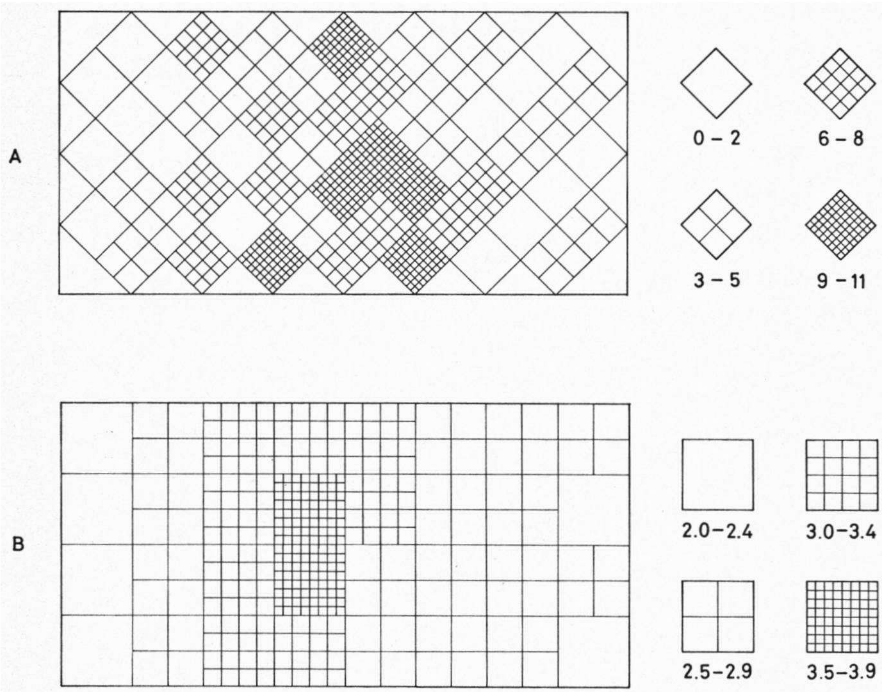

Fig. 3. Variation in the vegetation of quadrat IV measured as (A) floristic fall between adjacent subquadrats and (B) Margalefs index calculated per square metre with frequency data as individuals numbers.

- species confined to the middle part of the gradient, e.g. *Carex serotina* and *Juncus maritimus.*

To illustrate the relation and also the differences between the middle part of the gradient and the lower and higher part a classification was carried out for the 32 sq.m. on the basis of recorded frequencies of the species in each sq.m., using the method of nearest neighbour sorting. The result is shown in the dendrogram of *fig. 4.* Two vegetation types can be distinguished between the levels 230 and 430. They might be called the saltmarsh type and the dune type. The intermediate position of the sq.m. 12–16 in the middle part of the transition of these two vegetation types can clearly be seen between the levels 150 and 200.

4.4. Detailed vegetation analysis of a combined height-pH gradient

Part of quadrat V was analysed earlier by VAN DER MAAREL and LEERTOUWER (1967). They showed a marked pH-fall in the height gradient of less than 10 cm and a highest species diversity in the middle of the gradient. Contourmapping, soil analysis and very detailed vegetation analysis in about the same area confirmed this picture and provided additional information. *Fig. 1C* shows the distribution of species diversity, recorded as the no. of species per 1/16 sq.m, in re-

Table 5. Local frequency of species in the lower, middle and higher parts of the gradient in quadrat IV.

	lower part sq.m 1–8 128 subquadrats	middle part sq.m 9–20 192 subquadrats	higher part sq.m 21–32 192 subquadrats
Salicornia europaea	1.6	–	–
Suaeda maritima	0.8	–	–
Glaux maritima	100.0	46.4	–
Limonium vulgare	71.1	25.5	0.5
Juncus gerardii	100.0	52.0	7.8
Plantago maritima	79.7	51.6	20.8
Triglochin maritima	10.2	7.8	1.6
Euphrasia odontites	19.5	70.8	17.2
Carex serotina	–	9.9	–
Artemisia maritima	–	3.6	–
Juncus maritimus	–	3.6	–
Juncus alpinus	–	1.6	–
Centaurium littorale	–	1.0	–
Sagina maritima	–	1.0	–
Trifolium fragiferum	–	0.5	–
Armeria maritima	46.1	82.8	64.1
Carex distans	0.8	28.1	12.0
Agrostis stolonifera	68.0	89.1	91.7
Festuca rubra	3.1	78.1	100.0
Trifolium repens	0.8	68.2	78.6
Centaurium pulchellum	–	22.4	1.0
Plantago coronopus	–	10.4	1.6
Schoenus nigricans	–	32.8	6.3
Sagina nodosa	–	14.6	4.7
Parapholis strigosa	–	2.6	1.0
Poa pratensis	–	0.5	3.6
Lotus corniculatus	–	35.4	85.4
Hippophaë rhamnoides	–	–	2.6
Elytrigia pungens	–	–	35.4
total no. of species	13	25	19

lation to the contour map. An extremely high number of species along the transition belt can be seen. More than 26 species of phanerogams in a small area of 1/16 sq.m clearly illustrate the value of gradient and dune slack vegetations from the point of view of species diversity.

The sampling method adopted permitted composition of a distribution map for each species within quadrat V. Four different distribution types could be distinguished. An example of each type is given in *fig. 5*. Most of the species were found in the transition zone and in the lower or higher part of the quadrat, e.g., *Mentha aquatica* (*fig. 5A*) and *Potentilla erecta* (*fig. 5B*). Few species were recorded all over the quadrat, apparently independent of the transition zone, e.g., *Salix repens* (*fig. 5C*). Most interesting, however, were a few species that were clearly confined to the gradient. *Linum catharticum* (*fig. 5D*) provided the clearest example.

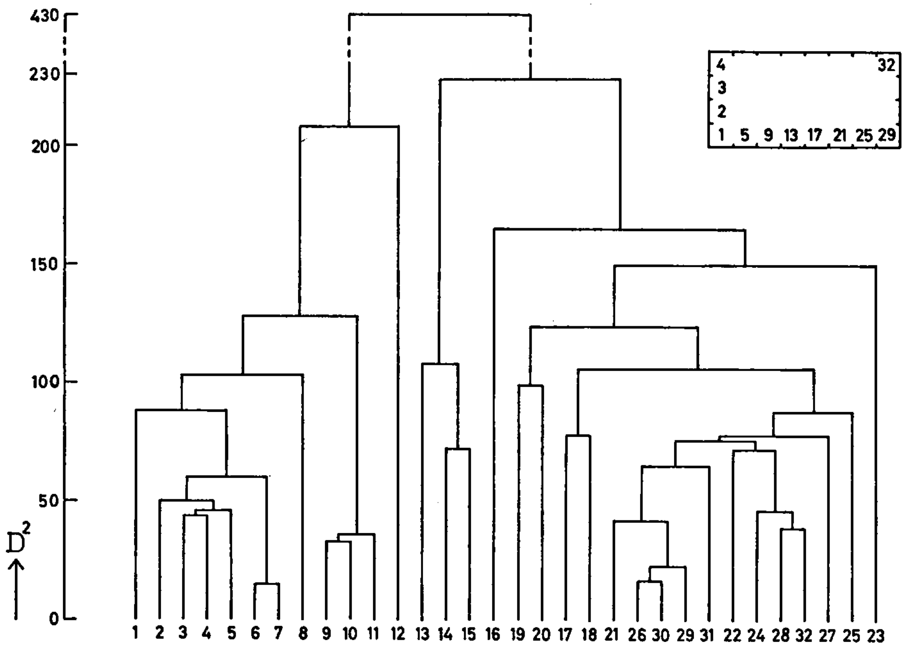

Fig. 4. Classification model of the 32 subquadrats of one square metre in quadrat IV, based on local frequency data from each subquadrat and using euclidean distances and nearest neighbour sorting. Inset shows numbering of subquadrats.

5. DISCUSSION

The results presented show how variation in environmental factors is reflected in the vegetation and how vegetational variation can be quantified. The different methods for measurement of variation in the vegetation, as they were applied to the same areas, allow a comparison. Correlations in *table 6* are computed from the data given in *table 3*. The high correlation between the results from Margalef's formula and Shannon's formula might be expected as they go back to the same information theoretical principle. A close correlation between the index devised by Williams, number of species per unit area, and variation measured as floristic difference between adjacent sq.m can also be seen (*table 6*). These results

Table 6. Correlation coefficient for some methods for quantifying variation in the vegetation, calculated on the basis of data obtained from five widely differing vegetation types.

	species/m²	I = A+B–2C	α Williams	I Margalef
I Shannon	0.908	0.923	0.951	0.999
I Margalef	0.916	0.931	0.956	
α Williams	0.962	0.966		
I = A+B–2C	0.997			

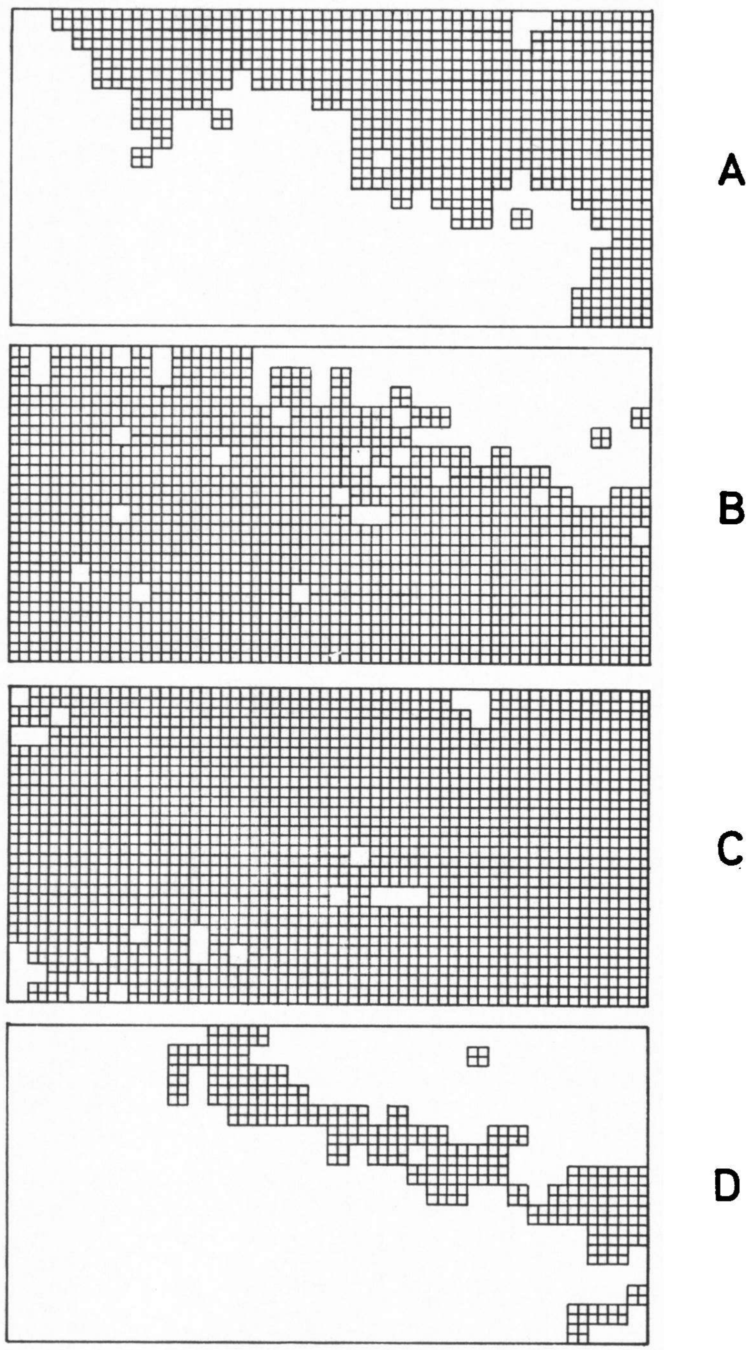

Fig. 5. Distribution of four species in quadrat V: (A) *Mentha aquatica*, (B) *Potentilla erecta*, (C) *Salix repens* and (D) *Linum catharticum*.

indicate that a comparison of variation in the vegetation, or more specifically between species diversity in different vegetations, can satisfactorily be made by either of the methods here applied. Each method, however, will have its preference for a particular situation. Work carried out for this study revealed that the least time consuming ones, viz. the number of species per unit area and α Williams, are generally preferable. The first method seems most suitable – at least for vegetation types comparable to the ones discussed here, as distinct from, for instance, tree or lichen vegetations – for smaller areas up to a few sq.m. The second one cannot be applied for characterizing too small areas, but easily to areas in the range from about 10 to 100 sq.m. Floristic difference measured for adjacent quadrats provides a possibility to quantify differences in vegetations, if values are calculated along a transect and can therefore indicate boundaries in the vegetation which may be useful for vegetation mapping in smaller areas. Margalef's and Shannon's formulas seem to have their highest value if applied to data where the number of individuals is known for each species and thus scope for zoological work seems better than for vegetation studies.

The results further show the high species diversity that may be found in the middle part of local gradient situations and the four different types of species that can be distinguished as contributing to this high value. Van der Maarel and Leertouwer (1967) have already mentioned that this biotic diversity should be considered as an expression of differentiation into microhabitats or niches. It would be useful to study further which environmental factors actually define the differences in species composition, especially with respect to those species that are confined to the gradient. Among the factors analysed in quadrat IV, electro-conductivity and moisture-content show such differences that for certain species they may be the determining factors. In quadrat V the pH and moisture content could play a similar role for certain species. Ranwell (1959), while studying the duneslack habitat (duneslacks as defined by Tansley 1949) of the Newborough Warren, emphasized the important role of groundwater level that reaches or approaches the surface of the sand. This was the case in quadrat V, where the groundwater level during the winter halfyear reaches the surface, as was read from a few groundwater observations during that time. Ranwell mentions that this... "has big effects on several important habitat factors affecting plant growth: soil aeration is much reduced, the rate of humus decomposition lowered and the carbon to nitrogen ratio increased". He also found the pH fall in the neighbourhood of the watertable; a sudden increase by as much as 3 pH units with an increase in depth of only 5 cm was observed. This general picture fits well into that found in quadrat V at Schiermonnikoog. An idea about the extremely high values for diversity found along the gradient in quadrat V may be obtained from a comparison with values of 244 species/area relations presented by Williams (1964) in a figure in his book (page 94), values being obtained from different environments from all over the world. The numbers 26 and 45 of species of phanerogams, found on 1/16 sq.m and 1 sq.m, respectively, are higher than any presented there. Results of this study provide therefore reasons for protecting transition zones as very rich communities in relatively small areas.

ACKNOWLEDGEMENTS

Thanks are due to Dr. E. van der Maarel for suggestions, support and discussions, to Prof. Dr. D. Bakker for his interest in the investigations and help in publishing the results, to Mr. L. F. M. Fresco for processing the data through the computer, and to Mr. D. Bottrill for correcting the English text.

REFERENCES

Beeftink, W. G. (1965): "De zoutvegetatie van ZW-Nederland beschouwd in Europees verband". *Meded. Hydrobiol. Inst. afd. Delta-Onderzoek*, Ierseke, 30.

Dahl, E. (1960): Some measures of uniformity in vegetation analysis. *Ecol.* **41**: 805–808.

Heukels, H. & S. J. van Ooststroom (1962): *Flora van Nederland*. Noordhoff, Groningen.

Leeuwen, C. G. van (1965): Het verband tussen natuurlijke en anthropogene landschapsvormen, bezien vanuit de betrekkingen in grensmilieus. *Gorteria* **2**: 93–105.

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

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

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

— & J. Leertouwer (1967): Variation in vegetation and species diversity along a local environmental gradient. *Acta Bot. Neerl.* **16**: 211–221.

Margalef, R. (1958): Information theory in ecology. *Gen. Syst.* **3**: 36–71.

Odum, E. P. (1959): *Fundamentals of Ecology*. W. B. Saunders Company. Philadelphia and London.

Pielou, E. C. (1966): The measurement of diversity in different types of biological collections. *J. Theoret. Biol.* **13**: 131–144.

Ranwell, D. (1959): Newborough Warren, Anglesey. I. The dune system and dune slack habitat. *J. Ecol.* **47**: 571–601.

Shannon, C. E. & W. Weaver (1964): *The mathematical theory of communication*. Urbana: University of Illinois Press.

Tansley, A. G. (1949): *The British Islands and their Vegetation*. Cambridge.

Thalen, D. C. P. (1968): *Soortsdiversiteit en variatie in enkele duin- en kweldervegetaties op Schiermonnikoog in relatie tot variatie in het milieu*. Report to Laboratorium voor Plantenoecologie, Haren (Gr.).

Williams, C. B. (1964): *Patterns in the balance of nature and related problems in quantitative ecology*. Academic Press, London–New York.