VARIATION IN VEGETATION AND SPECIES DIVERSITY ALONG A LOCAL ENVIRONMENTAL GRADIENT

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SUMMARY

Quantitative data are presented of a study of a combined height-pH gradient in a primary dune slack at Schiermonnikoog. A transect of 10 × 4 m was floristically and ecologically analysed per sq m. Species number was taken as a measure of species diversity and was found to be related to range of pH and height: highest diversities occurred in the middle range of the gradient. This confirms a general rule described by Odum. Species-area relation in the transect fits into the Preston model, the slope index being slightly under the theoretical equilibrium value 0,27. Ordination and classification of quadrats on a basis of information index I showed continuous variation of vegetation, which was mainly governed by pH variation. The twofold differentiation of the interrelated height and pH is termed ecological amplification and discussed. The relation between floristic fall and gradient range and between floristic difference of vegetations and their distance along a gradient are discussed. The diversity pattern found is interpreted in terms of niche differentiation governed by spatial and temporal variation of the environment. The possible relation between niche differentiation and gradient structure of the environment is discussed.

1. INTRODUCTION

Both the study of gradient situations and vegetational variation and that of species diversity have made considerable progress in recent years (WHITTAKER 1956, 1960, 1965; CURTIS 1959; WILLIAMS 1964; PRESTON 1962; MARGALEF 1958, 1961). ODUM (1963) and WHITTAKER have paid attention to the relation between diversity and the gradient character of the environment, predominantly on a biogeographical scale. Odum has presented a sort of rule (loc. cit. p. 32): "... the greatest diversity occurs in the moderate or middle range of a physical gradient". He illustrates this rule with an example of mollusk species diversity in some Texas bays with different salinity levels and he states that this relation has been found in many other cases. However, to our knowledge only few quantitative data have been actually published.

Dutch workers have developed similar interests in gradient situations, mainly from the Relation Theory of VAN LEEUWEN (1965, 1966). One of the outcomes of this theory is the distinction between two types of boundary situations, the limes convergens and the limes divergens. The latter type represents the gradual transition from one environmental situation into another, e.g. salt – fresh, dry –wet, alkaline – acid, eutrophic – oligotrophic. Such a gradient can be considered as a complex boundary situation with a great number of micro-habitats (niches), each differing slightly from its surroundings. As VAN DER MAAREL (1964, 1966a) has pointed out, it is in accordance with the original descriptions of the terms ecotone and ecocline to identify these concepts with the limes convergens and limes divergens respectively.

Following the Relation Theory, VAN DER MAAREL (1966b) has postulated a relation between species diversity and ecocline character of the environment; he found that zones with high diversity values coincide with the middle range of both a topographical (moisture – humus) gradient and a treading intensity gradient within a dune grassland complex. It appeared afterwards that this statement was identical with that of Odum.

It seems opportune to collect more quantitative data on the local distribution of species diversity. The present paper deals with such a study. The field work involved was carried out mainly by the second author as part of a M.Sc. research project.

2. DESCRIPTION OF THE INVESTIGATED AREA

The study took place in the Drosera valley on the Dutch West-Frisian island Schiermonnikoog (53°29′ N, 6°12′ E; coordinates of the Dutch topographical map: 208,3 – 611,5). This primary dune slack is still irregularly flooded with water from the eastward salt marsh system. The occurrence of species like *Juncus maritimus* and *Plantago maritima* demonstrates this continuing influence. The valley as a whole is in a late phase of desalinisation. The speed of this process is very low and the effects of change are probably suppressed by extensive cattle grazing and mowing in the near past and by intensive rabbit grazing, which is still going on.

A considerable part of the valley bears a hygrophytic calcicole vegetation with *Schoenus nigricans* and associated species such as *Epipactis palustris.* On slight elevations we find a more mesophytic vegetation with species such as *Drosera rotundifolia* (after which the valley was named). The occurrence of this species suggested acid conditions on the elevations. A first determination of pH values showed an unexpected large range from 4 to over 7. Accordingly it was decided to analyse a small transect in detail.

3. DESCRIPTION OF THE TRANSECT ANALYSIS

A transect of 10 × 4 m was laid down in the transition between the *Schoenus nigricans* and the *Drosera rotundifolia* vegetations. In each sq m vascular plants, mosses, liverworths and lichens were recorded. Nomenclature of the first group is after HEUKELS–VAN OOSTSTROOM (1962), that of the following groups after MARGADANT (1960). Total height and cover and cover-abundance values of species according to the Braun-Blanquet scale were estimated per sq m.

pH (KCl) was determined September 1966 in each quadrat in a sample from the centre. In quadrats within which variation could be expected, additional measurements were made in the corners. To get a representative pH value for each quadrat, the value of the centre was corrected by taking the values of the surrounding quadrats into account. Analyses were repeated May 1967 in 15 quadrats laying in the transitional zone of the transect. At the same time the height of 4 points in each quadrat above the lowest point in the transect was determined.

Vegetational data were subjected to an ordination as well as a simple agglomerative classification, both based on the information parameter $I = a + b - 2c$, as an index of floristic difference between pairs of quadrats. (a and b are species numbers in two quadrats, c is the number of species common to both quadrats. Thus I equals the number of non-common species in sets of two quadrats). The ordination method of BRAY & CURTIS (1957) was used, with slight modifications in the selection of reference quadrats. The classification method was that of WILLIAMS c.s. (1966) with lowest group value of I as a fusion criterion. For a description and discussion of index and methods: see VAN DER MAAREL (1966b).

Species diversity was measured as total number of species per quadrat. As VAN DER MAAREL (1966b) has shown, the diversity index of C. B. WILLIAMS (1964) is correlated with total species number per unit area, at least within one vegetation formation, where the density of plant units doesn't vary considerably. This diversity index is indicated as $\alpha_v = G/\ln A$. (G is number of species, A is area). The unit area to be chosen depends on the α/N area as defined by HOPKINS (1955), i.e. the area determined by the striking point of α-line and absciss. In low herb vegetations with mainly grasses and mosses, this area turns out to be about 0,5 sq dm. Thus a species number of G/sq m in our transect corresponds with a value of $\alpha_v = G/\ln 200 = 0{,}19\ G$.

4. RESULTS

4.1. Species – area relationship

Fifty-nine species of vascular plants and 16 species of mosses, liverworths and lichens were recorded in the transect; average species numbers for 1 sq m were 25,4 and 3,9 respectively. The total number of 75 species on 40 sq m is rather high, though not exceptional for Dutch standards. Average and total number of vascular plants may have been still higher than has been actually recorded, since the heavy rabbit grazing may have resulted in a partial or complete disappearance from the above ground parts of a number of species.

Table 1 gives the species numbers for areas from 1 to 40 sq m, which were calculated as averages for combinations of adjacent sq m quadrats. A semi-log plotting of the data didn't give a satisfactory α-curve of Williams. However, a

Tabel 1. Species number and area in the Drosera valley transect

	A sq m					
	1	2	4	8	16	40
G total	29,3	35,9	45,5	52,6	59,3	75,0
G phanerogams	25,4	31,6	39,2	44,0	50,0	59,0

log-log plotting gave a fairly straight line according to Preston, with a slope index = 0,24. The species numbers for 1 and 2 sq m are slightly lower than may be expected from the log-log line. This may be due to the underestimation of vascular plants, already discussed above.

Alltogether the data fit reasonably into the model of PRESTON (1962) for species- area relations, with the following aequations:

$G = 27,5\ A^{0,24}$ for all groups of plants,

$G = 25,7\ A^{0,19}$ for vascular plants.

Thus the slope index for all species is only slightly below the theoretical value of 0,27. This means that the transect area as a whole is not far from acting as an ecological isolate in a state of equilibrium (PRESTON 1962).

4.2 Species diversity and environment

Species diversity, taken as total species number, varied from 17 to 43, with an average of 29,3; corresponding values of α_v are 3,2, 8,1 and 5,5 respectively. *Fig. 1* shows the relation between species diversity and pH class; *fig. 2* shows the diversity pattern within the transect. It is clear from these figures that diversity is highest on places with intermediate pH values, with a top between pH 5,1 and 5,7; these places are concentrated along intermediate height contours. The number of cryptogamic species is considerably higher on the acid parts.

The results suggest a relationships between pH and height, which was confirmed by Spearman's rank correlation test (see *table 2*).

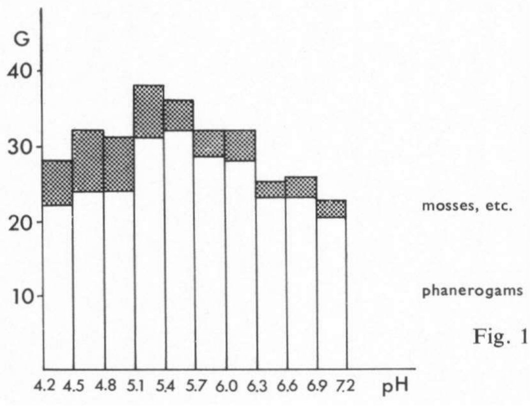

Fig. 1. **Relation between number of species G, and pH, in the Drosera valley transect.**

4.3 Ordination and classification of quadrats

The position of the 40 quadrats in a two-dimensional ordination model is shown in *fig. 3*. The results suggest a continuum-like variation in vegetation, as may be expected here. In *table 2* some rank correlation data are presented. X-axis and Y-axis appear to be significantly correlated. Both axes are correlated with pH and height; correlations with pH are slightly stronger, suggesting that the pH gradient is the principal source of vegetational variation.

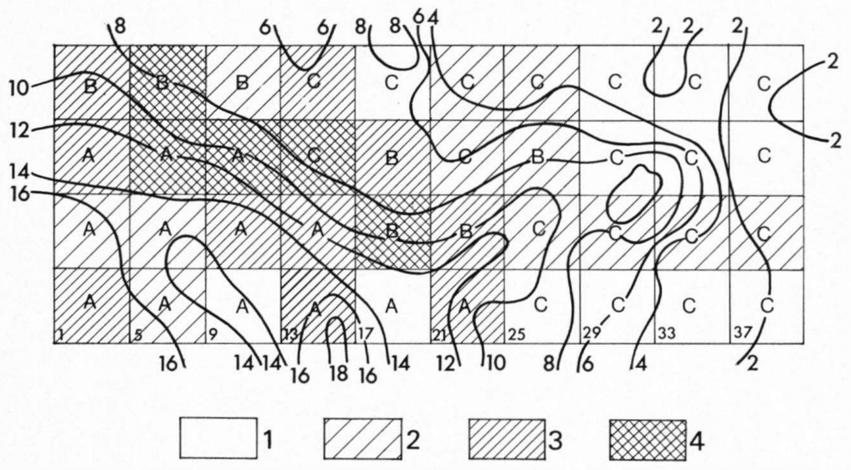

Fig. 2. Distribution of species-diversity, vegetation types and height in the Drosera valley transect. 2 cm contours are drawn in. Key to symbols: diversity class 1: 17–25 species /sq m; 2: 26–30 sp; 3: 31–35 sp; 4: 36–43 sp. Vegetation type A: Radiola linoides type; B: Linum catharticum type; C: Parnassia palustris type.

Table 2. Values of Spearman's rank correlation coefficient for correlation between ordination axes, pH and height. ** $P \leqslant 0{,}01$; *** $P \leqslant 0{,}001$

	X-axis	Y-axis	pH	height
X-axis		+0,65	+0,80	–0,73
Y-axis	***		+0,63	–0,48
pH	***	***		–0,92
height	***	***	**	

By means of the agglomerative classification the quadrats were roughly grouped into three classes, on a I-level of about 30, where the I value for the total set quadrats was 45. *Table 3* shows the species composition of the three vegetation types. Only species have been included with a frequency of over 20% in at least one type. The following species were found throughout the transect with a high frequency: *Calamagrostis epigejos, Calliergonella cuspidata, Carex flacca, Festuca rubra, Holcus lanatus, Juncus articulatus, Juncus gerardii, Mentha aquatica, Salix repens*, and *Taraxacum palustre* (minor species *hollandicum*). It follows from *table 3* that no single species is both frequent in and confined to one of the three vegetation types. Thus the types can be defined only roughly.

The following species groups may be used as indicators:

A. Radiola type: *Radiola linoides, Dicranum scoparium;*
B. Linum type: *Linum catharticum, Euphrasia borealis* ssp. *borealis;*
C. Parnassia type: *Parnassia palustris, Epipactis palustris;*

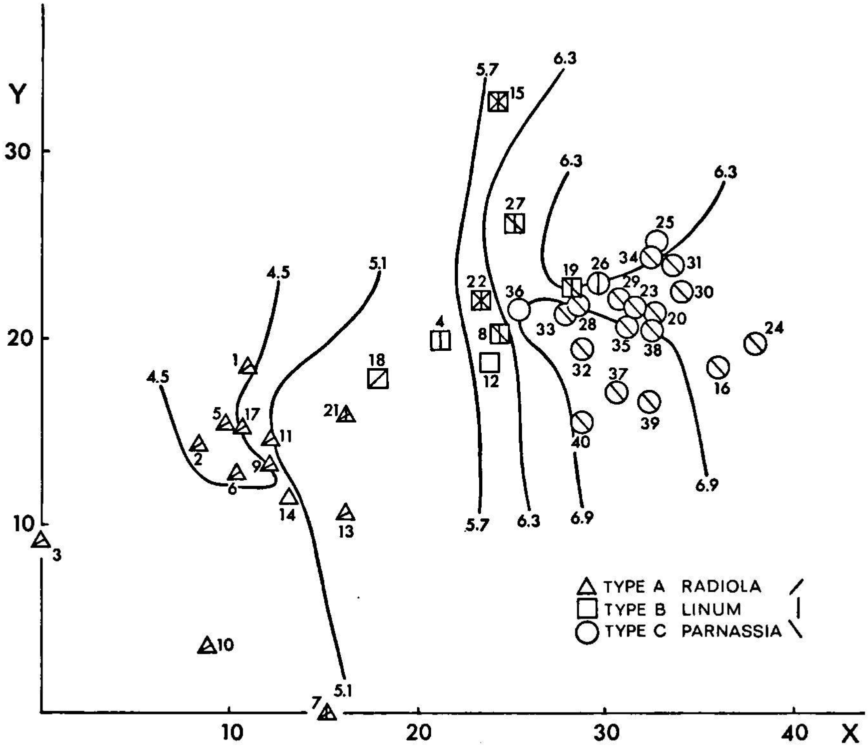

Fig. 3. Ordination of 40 quadrats of the Drosera valley transect with isonomes of pH.

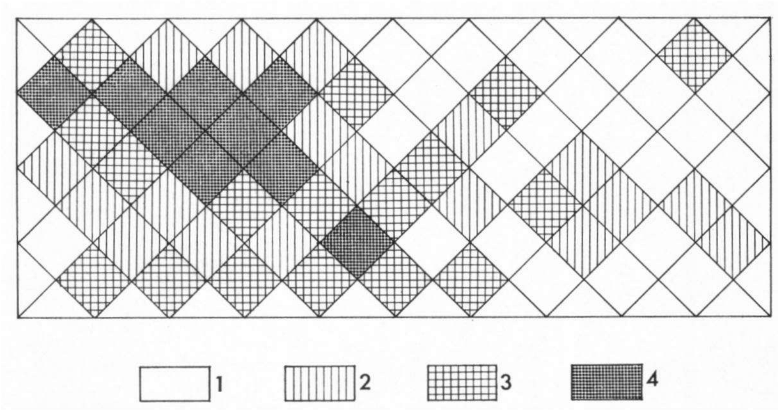

Fig. 4. Floristic fall in the Drosera valley transect, measured as I between adjacent quadrats. Key to symbols: floristic fall class 1: I >7; 2: I 7–13; 3: I 14–20; 4: I <20.

Table 3. Species composition of vegetation types in the Drosera valley transect

	A	B	C	pH range	height range cm
Dicranum scoparium	0			4.2–5.0	16–10
Calypogeia fissa	0			4.2–5.3	16–12
Eriophorum angustifolium	0			4.3–5.1	14– 8
Peltigera species	0			4.3–5.3	16–12
Festuca tenuifolia	0			4.3–6.2	16– 7
Pseudoscleropodium purum	0			4.6–5.3	16–12
Radiola linoides	+	0		4.2–6.0	16–10
Hypnum cupressiforme	+	0		4.2–6.0	16–10
Pellia epiphylla	+	0		4.3–6.0	16–10
Drosera rotundifolia	+	+		4.2–6.4	16–10
Potentilla erecta	+	+		4.2–6.7	16– 8
Prunella vulgaris	0	0		4.2–6.0	16–10
Luzula campestris	0	0		4.2–6.4	16–10
Carex arenaria	0	0		4.2–6.7	16–10
Carex serotina ssp. pulchella	0	0		4.2–7.0	14– 2
Carex panicea	0	+	0	4.2–6.1	16– 6
Cirsium palustre	+	+	0	4.2–6.4	16– 8
Sieglingia decumbens	+	+	0	4.2–6.8	16– 8
Rhytidiadelphus squarrosus	+	+	0	4.2–7.0	16– 2
Anthoxanthum odoratum	+	0	0	4.3–7.0	16– 4
Leontodon nudicaulis	+	0	0	4.3–7.0	16– 4
Linum catharticum	0	+		5.1–6.8	13– 8
Potentilla anserina	0	+	+	5.3–7.0	10– 2
Juncus maritimus	0	+	+	5.0–7.0	10– 2
Epipactis palustris	0	0	+	5.8–7.0	10– 6
Euphrasia borealis ssp. borealis		0		5.4–6.8	10– 8
Gentiana amarella ssp. uliginosa		0		5.3–6.2	10– 7
Poa pratensis		+	0	6.0–7.0	10– 6
Trifolium repens		+	0	5.5–6.8	10– 6
Festuca arundinacea		+	+	5.3–7.0	10– 2
Schoenus nigricans		+	+	5.4–7.0	10– 2
Cynosurus cristatus		0	0	5.3–6.8	10– 5
Carex nigra		0	0	6.1–7.0	8– 2
Parnassia palustris		0	+	5.5–7.0	10– 2
Campylium stellatum			0	6.1–6.8	9– 4
Eleocharis palustris ssp. palustris			0	6.9–7.0	5– 2
Galium palustre			0	6.9–7.0	5– 2
Samolus valerandi			0	6.9–7.0	5– 2

0 = frequency 21-80%   + = frequency 81-100%

A + B: *Drosera rotundifolia, Potentilla erecta;*
B + C: *Schoenus nigricans, Festuca arundinacea.*

The three leading species have been drawn in the ordination model to show their contiguous distributions.

The environmental data taken up in *figs. 2* and *3* show a distinct pattern and can be easily brought into connection with the vegetational variation: the Radiola type is bound to the relatively high zones, up from 10 cm above local zero, with pH values from 4.2 to 5.7; the Linum type is found in the intermediate zones between 6 and 10 cm, with pH boundaries 5.3 and 6.7; the Parnassia type occurs below 10 cm and above pH = 6.2.

In *fig. 4* the I-relations between adjacent quadrats are shown. Each rhombus represents an I-value between two quadrats. By drawing several I-classes we may obtain a picture of variation in "floristic fall" in the transect. It is clear from the figure that there is a zone with considerable floristic fall, which coincides with the zone of highest diversities.

5. DISCUSSION

The results show that the environmental gradient in the investigated transect is based on a simultaneous change in height and pH. Since the lower parts of the transect are regularly inundated, mainly from October until March, the variation in height will imply a variation in water conditions of the soil, especially lenght of inundation period and water saturation of the top layer. It may now be supposed that the variation in pH is, at least partly, caused by the variation in water conditions. This supposition can be derived from the relation between pH and soil water conditions throughout the year, which has often been found (*cf* LÖTSCHERT 1965). This relation may be a causal one, since it is known, that changes in the water content of the soil may lead to chemical changes, e.g. the oxydation of sulphides to sulphates in a drying phase, which may result in a change in pH from 7 to 4 (RUSSELL 1961). Detailed research on the seasonal changes in pH, water conditions and other soil characteristics will be necessary to elucidate this problem. This research is now in progress.

From a comparison of the pH values determined in September and May respectively we may conclude that changes occur, though not as great as to explain the spatial variation within the transect. – It should be noted that pH (KCl) values don't fluctuate as much as pH(H_2O) values do – An interesting difference could be noticed in that the May-values for the acid places tend to be higher than the September ones; the May-values for the neutral places tend to be lower, however, whilst the intermediate places showed only small changes. This phenomenon will be discussed later.

From the ordination model we may conclude that the vegetation of the Drosera valley transect varies continually. Thus the three vegetation types gradually merge into each other, forming together a syncline (VAN DER MAAREL 1960), or a coenocline (WHITTAKER 1960). Since it appeared that these two terms have identical meanings, we take over the latter term, since it has the advantage of not being liable to confusion with the geological term synclinal.

The main axis of the ordination model reflects the major environmental gradient. It is noteworthy, that a number of species situated at either side of the main axis are said to be acidophilous (acidofrequent), e.q. *Drosera rotundifolia*, or basiphilous, e.g. *Schoenus nigricans*, whilst they are not supposed to be sensitive to the small local difference in water conditions. On the other hand, species such as *Eleocharis palustris* ssp. *palustris* are considered as hygrophytes, species like *Festuca tenuifolia* as meso- to xerophytes, whilst both groups are known as pH-indifferent. This means that, although the combined height – pH gradient may have originated from only one source of environmental variation, its effect on vegetation is twofold, with pH as a slightly more differentiating factor. This effect may be termed ecological amplification (*cf* ASHBY 1964).

It follows from *fig. 3* that the correlation between X-axis position and pH value is not absolute: the extreme pH values are found towards, but not at the ends of the axis. This effect can be explained as follows: highest diversities appeared to occur in the middle range of the pH gradient. Thus highest values of I may be expected between vegetations in the middle range, since I as an information index immediately reflects total floristic difference. This implies that with growing distance along the gradient, after this maximum has been passed, floristic difference is gradually reduced, since species numbers decrease towards the ends of the gradient. The ultimate reduction is reached when at either end of the gradient no single species is able to exist. *Fig. 5* shows schematically the relation between floristic dissimilarity and distance between two points along a gradient, when situated at growing but equal distance from the centre of the gradient. The similarity line is drawn as well. The latter line is of the type WHITTAKER (1960) has described for an actual elevation gradient in mountainous areas – this gradient didn't cover, however, extreme situations as presented in the model here – One would conclude from *fig. 5* that a dissimilarity index such as I, is more meaningful in judging gradient situations.

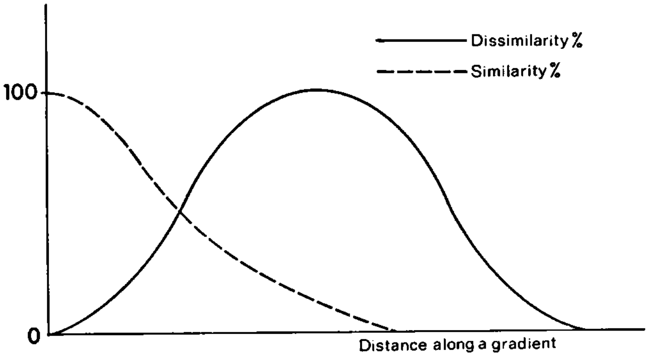

Fig. 5. Scheme of the relation between vegetational dissimilarity and similarity and distance along an environmental gradient.

The results presented here confirm the general rule mentioned in the introduction: highest diversities occur in the middle range of the local height -pH gradient. In our opinion the interpretation of this rule cannot be put simply in terms of unfavourableness of extreme environmental conditions versus favourableness of moderate conditions, although this view seems to find support in the regular shift in pH and height ranges of species, as shown in *table 3*. Biotic diversity should be primarly considered as an expression of environmental diversity, i.e. differentiation into microhabitats or niches. This view, is also held by HUTCHINSON (1959) and WHITTAKER (1965) and it is, as these authors have pointed out, in accordance with the well-known principle of Gause, that similar species do not occupy similar niches. With Van Leeuwen we might add environmental stability as a governing factor in niche differentiation. This means that fluctuations of relevant habitat factors have a definite bearing on niche structure and that niche differentiation is also determined by the spatial variation of environmental instability.

It will be necessary to study more local gradient situations, especially the occurring spatial variations and temporal variations of the supposed governing environmental factors. This research should be done in a very detailed manner, since it is becoming evident that variations and fluctuations may show very subtile patterns. This research may elucidate the relation between niche differentiation and the gradient character of nature.

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