ON THE RELATION BETWEEN VEGETATION AND SOIL-DEVELOPMENT IN DUNE-SHRUB VEGETATIONS

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SUMMARY

The relation between pattern and process is demonstrated with the dune-shrub communities of Voorne as an example. The landscape zonation and the underlying environmental gradients are described. Vegetational variation is reflected in a three-dimensional ordination model. The position of various shrub species in the model is discussed and the similarity between these positions and those in a local cross-section of the dunes is demonstrated.

An elaboration of the general aspects of pattern and process in dune vegetations as formulated in the preceding paper will be given with help of data on dune-shrub communities. This study is restricted to the dry and semi-dry shrub communities in the dune area of Voorne, the Netherlands.

The landscape shows a distinct zonation of rather low dune ridges and dune slacks, which are older in age and more complex in topography and vegetation at increasing distance from the sea.

The dune environment may be characterized as a gradient complex. We find a large-scale gradient across the zonation from the foreshore to the inner dunes, comprising i.a. a decrease in wind velocity and salt content of the air and resulting in an increase in vegetation development (VAN DER MAAREL 1966a, SLOET VAN OLDRUITENBORGH & HEERES 1969). Besides there are a number of micro-gradients such as gradients in height, level of the free-water table, concentration of organic and mineral matter, influence of man and animals. Of special importance are the numerous "gradients-in-time" caused by fluctuations of environmental components.

The large-scale pattern of the shrub vegetation is described as a differentiated and continuous series of communities from monotonous pioneer scrubs on the landward side of the coastal ridge, consisting of *Hippophaë rhamnoides* through numerous stages with mainly *Ligustrum vulgare*, *Salix repens*, *Rosa rubiginosa* as dominants to a tall shrub formation in the inner zone ($\pm$ 2 km inland) which is rich in species and structurally highly complex with *Crataegus monogyna* and *Rhamnus catharticus* as the most conspicuous shrubs of about twenty woody and climbing species. The dynamic character of the dune landscape (secondary dune movements) and the influence of man and animal enables pioneer communities to exist locally in the inner zone next to the climax vegetation.

The vegetation descriptions have been arranged by simple ordination within a three-dimensional spatial model (*fig. 1*).

The three axes of this model are constructed on the basis of floristic differences between 31 stands, comprising 133 species.

The index used for the expression of interstand dissimilarity is the information index of WILLIAMS, LAMBERT & LANCE (1965), as modified by VAN DER MAAREL (1966b).

Table 1 gives the 6 reference stands (number of species: 105 i.e. 79% of the total number of all 31 stands) to show the main types of the scrub complex.

The x-axis appears to represent the development from pioneer to climax communities: *Hippophaë* – scrub → *Crataegus-Rhamnus* – scrub.

It is remarkable that the extreme stand on the pioneer side (x-value: O) is not a *Hippophaë* scrub, situated on the landward side of the coastal ridge, but a stand situated in the inner (*Crataegus*) zone. Apparently the greatest variation in the vegetation occurs in one, notably the most differentiated zone.

The y-axis is perpendicular to the x-axis and represents the variation of certain components of the moisture complex. The reference stands are on the one hand a probably very stable, dry *Crataegus monogynus - Berberis vulgaris*-scrub and a wet *Ligustrum vulgare – Mentha aquatica* scrub on the other hand.

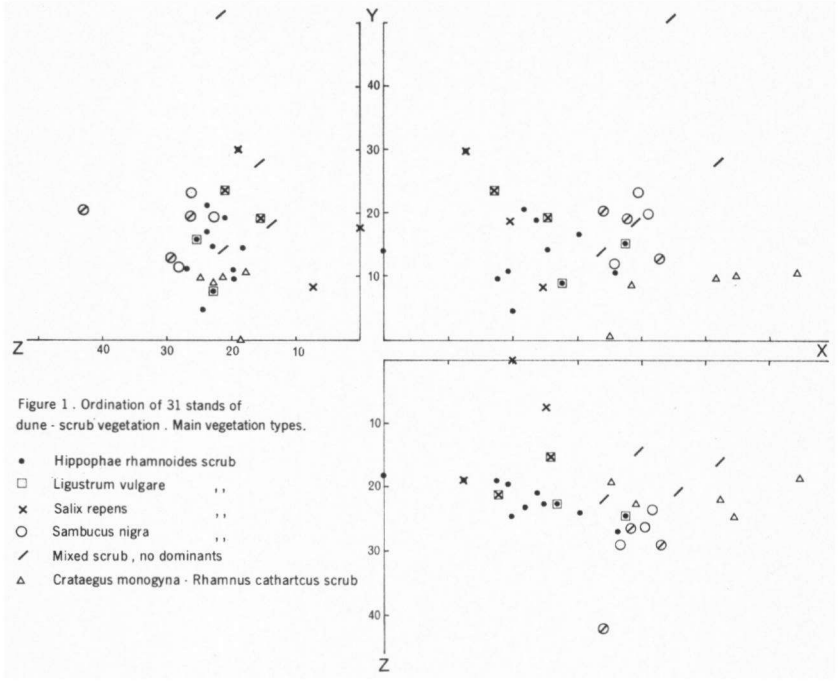

Figure 1. Ordination of 31 stands of dune - scrub vegetation. Main vegetation types.

- • Hippophae rhamnoides scrub
- □ Ligustrum vulgare ,,
- × Salix repens ,,
- ○ Sambucus nigra ,,
- / Mixed scrub, no dominants
- △ Crataegus monogyna - Rhamnus cathartcus scrub

The moisture complex however, needs further investigation. The position of the stands along the x-axis also indicates an increasing moisture content of the upper soil layer.

The z-axis is perpendicular to both x- and y-axis and represents the variation in humus break-down and humus formation, according to the fact that the reference stands of this axis are a *Salix repens – Epipactis helleborine* scrub and a *Sambucus nigra – Galium aparine* scrub respectively.

Salix repens communities are found in dry as well as in wet (dune slack) habitats, frequently accompanied by species like *Epipactis helleborine* and *Pyrola rotundifolia*. The common feature of these habitats is the supply of minerals in a relatively acid organic matter environment. This situation is found in dry dunes a.o. when raw humus is overblown by dune sand which is rich in minerals like carbonate or in dune slacks, where it is rinsed by fluctuating free water in which minerals are dissolved. The reverse process takes place in the *Sambucus nigra* environment where the organic matter reservoir is relatively mineralised.

In *fig. 2* some examples are given of the distribution of species in the ordination model characteristic for this antagonism.

For rank-correlation coefficients (according to SPEARMAN) between the axes see *table 2*.

One may say that the axes in the ordination model represent the variation of certain environmental components. Correlations between floristic gradients

Table 1. Main vegetation types represented by the six reference stands of the ordination model.

Number of stand	541	373	564	124	438	406
position on axis	x:0	z:0	z:42	y:0	y:52	x:65
height main shrub layer	0,6m	0,6m	1,5m	3m	1,5m	4m
coverage „ „ „	50%	70%	90%	100%	60%	100%
height „ herb „	0,1m	0,4m	1m	0,2m	0,2m	0,2m
coverage „ „ „	10%	40%	50%	10%	10%	90%
Species:						
Ammophila arenaria	1					
Erophila verna	x					
Erodium glutinosum	x					
Polygala vulgaris	2					
Luzula campestris	2					
Thymus pulegioides	1	x				
Viola tricolor, ssp. curtisii	x	x				
Viola canina		x–1				
Viola rupestris		x				
Epipactis helleborine		1				
Senecio jacobaea	x	x	x			
Galium verum		1		x		
Carex arenaria	2	1		x		
Arenaria serpyllifolia	x	1		x		
Crepis capillaris	1			x		
Sedum acre	1			x		
Leontodon nudicaulis	x	x			1	
Hypnum cupressiforme	4	2			1	
Cirsium vulgare	x	x			x	
Veronica arvensis	x					x
Cerastium holosteoides	x					x
Hippophaë rhamnoides	4		4		x	
Salix repens	x	4			2–3	
Rubus caesius	x	x	2	x–1	I	
Solanum dulcamare			x	2	x	x
Ligustrum vulgare	x	1	1	1	3–4	1
Bryonia dioica		x		1		x
Crataegus monogyna		x	x	5	1	4
Rhamnus catharticus		x	3	x	x–1	2
Rosa rubiginosa			x	x	2–3	
Berberis vulgaris				1		
Sambucus nigra			1			1
Lonicera periclymenum			x		1	x
Ribes sylvestre				2		x
Viburnum opulus					x	x
Calamagrostis epigeios	2	2	2		2	
Festuca rubra, var. arenaria	2	2–3		1	x	
Cynoglossum officinalis	1	x		1		x
Taraxacum spec.	x	1		x		x
Poa pratensis	1–2	x		1		
Cardamine hirsuta				1		x
Cirsium arvense		x	1		x	x
Polygonatum odoratum		x		x	1	x
Holcus lanatus	1		1			x

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coverage „ „ „	50%	70%	90%	100%	60%	100%
height „ herb „	0,1m	0,4	1m	0,2m	0,2m	0,2m
coverage „ „ „	10%	40%	50%	10%	10%	90%
Viola hirta	x	x			x	x
Asparagus officinalis			x	x		x–1
Urtica dioica	x		1	2	x	1
Brachythecium rutabulum		x	x	x	3	1
Moehringia trinervia			1	x	1	4
Eupatorium cannabinum		x	3		2	x
Glechoma hederacea	2					2
Dryopteris filix-mas			x		x	
Fragaria vesca			x			
Galium aparine			1			
Poa trivialis			1			
Stellaria media ssp. pallida				1		x
Geranium robertianum				2	2	2
Viola riviniana					x–1	x
Mnium undulatum					1–2	2
Lopholcolea bidentata					2	x
Amblystegium serpens					2	x
Ajuga reptans					x	x
Cirsium palustre					1	x
Galium uliginosum					x	x
Mentha aquatica					1	2
Valeriana officinalis					1	
Vicia cracca					x	
Prunella vulgaris					2	

Addenda:

541. Pastinaca sativa, x; Verbascum thapsiforme, 2; Rumex crispus, x; Rumex acetosella, x; Geranium pusillum, 1; Galium mollugo, 2; Hypochoeris radicata, x; Vicia sativa, ssp. angustifolia, x; Lotus corniculatus, 1; Festuca juncifolia, x;

373: Tortula ruraliformis, x; Brachythecium albicans, x; Satureja acinos x; Arrhenatherum elatius, x; Anthoxanthum odoratum, x; Cerastium arvense, 1–2;

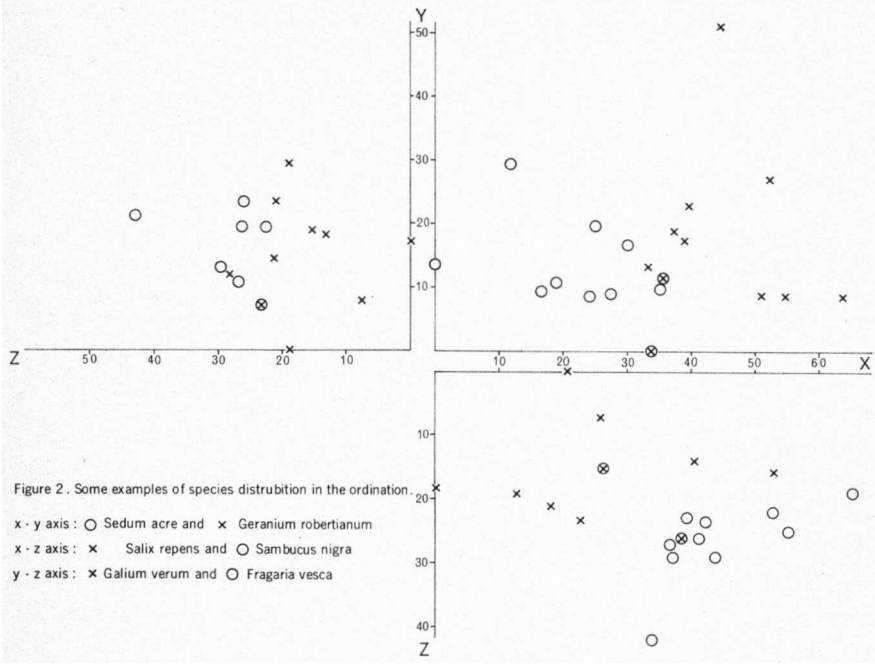
564. Rubus ulmifolius, x; Ribes nigrum, x; Ribes uva-crispa, x; Epilobium montanum, x; Publicaria dysenterica, x;

124. Melandrium rubrum, x;

438. Betula verrucosa, x; Agrostis stolonifera, x; Galium palustre, x; Polypodium vulgare, x; Pseudoscleropodium purum, x; Inula conyza, x; Listera ovata, x; Pulicaria dysenterica, x;

406. Veronica chamaedrys, 1; Achillea millefolium, x; Humulus lupulus, x; Myosotis arvensis, x; Arctium spec., x; Aira praecox, x; Mnium affine, x; Scutellaria galericulata, x; Anthriscus caucalis, X;

in the vegetation as found in the ordination model and some greatly variable soil factors (within the Voorne dune-shrub communities: $CaCO_3$ %: 0,1–9,4%; pH-value: 8,7–4,5; humus %: 0,3–27,2%; N_{total} %: 0,005–0,58%; actual water content: 0,3–28%;) are given in *table 2.*



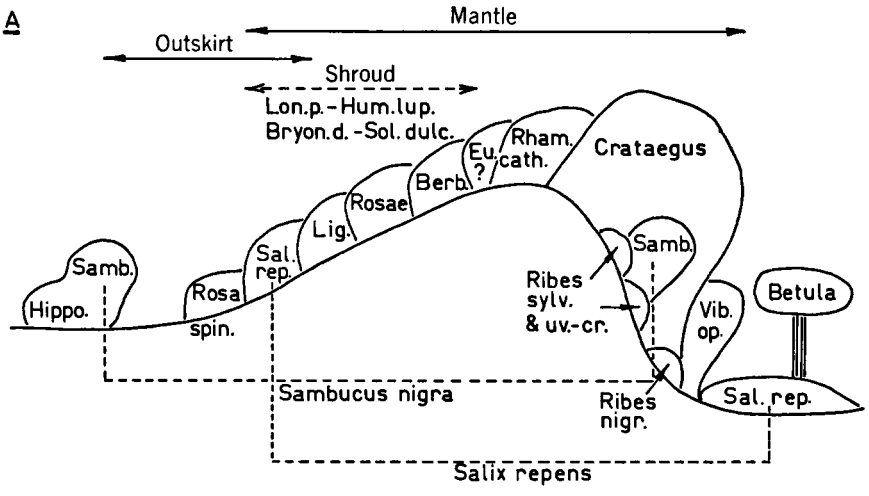
It follows from this table that the position along the x-axis is correlated with humus content and soil moisture and that along the y-axis with pH-value and soil moisture. No correlation could be found with the position of the stands along the z-axis.

Table 2. Rank-correlations between the axes of the ordination model mutually and with some estimated soil factors. On the right: figures of rR.100, on the left: level of significance.

	x-axis	y-axis	z-axis	$CaCo_3$%	Hu%	pH-value	N_{tot}%	H_2O%	100N/C
x-axis		+ 7°	+ 33°	— 27[1]	+ 45[1]	+ 12°	+ 34[2]	+ 75[3]	+ 3[2]
y-axis	–		– 1°	+ 12[1]	+ 7[1]	— 37°	+ 27[2]	+ 53[3]	
z-axis	–	–		+ 18[1]	+ 4[1]	— 9°	+ 12[2]	— 7[3]	+ 1[2]
$CaCo_3$%	–	–	–		— 68°	+ 20[1]	+ 6[2]	+ 13[3]	
Hu%	*	–	–	**		+ 23[1]	+ 54[2]	+ 10[3]	
PH-value	–	*	–	–	–		— 54[2]	+ 19[3]	
N_{tot}%	–	–	–	–	*	*		+ 20[4]	
H_2O%	**	**	–	–	–	–	–		

°n=31; [1]n=30; [2]n=17; [3]n=21; [4]n=12.
*: sign. for P = 0,05; **: sign. for P = 0,01.

An explanation of these results might be based on the assumption that the floristic composition of dune-scrubs is at least partly determined by the within-variation of certain environmental components. Therefore future research on



18 species of woody plants on 20 m^2

environmental factors in the highly complex dune-scrub communities should concentrate on range and variation of these factors in space and time, especially within each community.

Finally some remarks are made on the micro-pattern, in particular on the structure of the climax community in the inner zone of the dunes.

As mentioned above, locally pioneer stages of the scrub development can be found next to the tall *Crataegus-Rhammus* formation. The structure of the plant communities in these situations is mostly very complex and may show a continuous increase in height of the vegetation on a small area. No distinct boundaries between the different vegetation types are discernable and the number of woody and climbing species is relatively high.

Fig. 3 shows a (theoretical) cross-section of the scrub structure at one locality. The model is built up with help of observations on many fragments, scattered throughout the dune area. Some of these fragments, however, consisted of 80% of the number of species given in this picture. The sequence of the species appears to be essentially the same as that of the dominants on the x-axis of the ordination-model. The "macro gradient" seems to be repeated on a small scale in the structure of the climax vegetation.

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