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SMALL-SCALE ANALYSIS OF A MARSH VEGETATION FED BY SEEPAGE[1]

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Abstract. Stowe-Wade methods to detect small-scale vegetation patterns were, as far as we could determine, very rarely applied. Here, they are used with data of a hummock-pool marsh fed by calcium rich canal water, to relate the three-dimensional vegetation structure to the dynamics of surface water and some management effects. Of the two methods, the species-region technique seemed to be the most appropriate one.

Introduction

Pattern in vegetation can be studied at different levels. The large at scale pattern concerns the geographical distribution of species over the surface of the earth. Small scale patterns exist on the level of plant communities or species combinations (Greig-Smith 1983). The present contribution is concerned with patterns of very small scale, involving the distributions of individual species or plant individual assemblages.

Focussing on the study of medium- and small-scale patterns, different techniques have already been described. Greig-Smith (1952) collected abundance data from grids and used a blocked quadrat variance technique which seemed suitable for the detection of patterns at a scale of decimeters. A few years later, this technique was applied on line transects by Kershaw (1957). Many of the shortcomings were eliminated later (Usher 1969, Hill 1973, Goodall 1974, Ludwig and Goodall 1978, Galiano 1982), followed by an expansion from one- to multi-species analyses (Galiano 1983). Sometimes, species sequences were studied using such Markovian approach (Pielou 1962, 1967) and spectral analysis (*e.g.*, Ripley 1978, Kenkel 1988).

In 1979, Stowe and Wade described two alternative techniques, both examining transect data, sampled by equidistant points. The first technique, species juxtaposition, derives from Pielou's (1967) method which tests departure from random expectation in the sequence of species along a transect through a vegetation mosaic. The second method divides the transect into "species regions". These methods have some interesting advantages. Firstly, they are plotless and need no quantitative estimates which often imply a less objective sampling. Secondly, both techniques are appropriate for detecting patterns at a scale of a few centimeters, for which quadrat methods have failed. They measure small-scale positive or negative associations between species (by means of species association indices), and not two concrete dimensions the clumps.

In general, association between species can be interpreted as a result of the response of different species to one or more predominant environmental factors. This will often be the case on large-scale levels. Lower scale intraspecific and interspecific associations are more complex and likely caused by the interaction of low-scale environmental conditions and the existing plant individuals. The occurrence of a plant individual can be a reason for another individual to exist in its direct vicinity, or to avoid the locality. On this level, phenomena such as plant-plant interactions (competition, coexistence, allelopathy) are important (Stowe 1979). At this scale, the separation of "pattern" and "association" is arbitrary (Kershaw 1973). Therefore, the small-scale association method, described by Stowe and Wade (1979) is, in view of small-scale environmental differences and individual growth morphologies, an analysis of pattern. Because this method puts the emphasis on species interactions more than on the patches, the formulation "*small-scale structure analysis*" is appropriate. We believe that because of the above properties, the Stowe and Wade (1979) method is adequate to describe and to explain the formation of hummocks and the mosaic structure in marsh vegetation.

Study area

The Nature Reserve Het Buitengoor (Mol/Belgium, 51°13' N, 05°11' E) is characterized by mineral poor, acid and sandy soils, strongly influenced by above ground seepage, and is situated in the phytogeographical district of the Campine. The morphology pattern of the seepage area consists of a mosaic of pools and hummocks, as a result of the constant ground water supply. Before the construction of irrigation systems in the beginning of this Century, this marsh area was charac-

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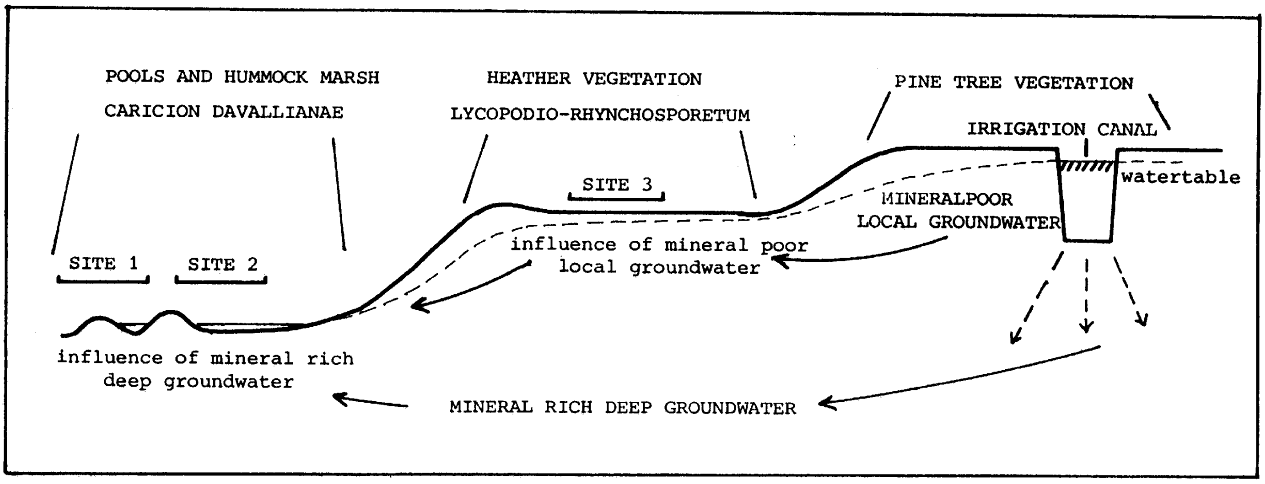


Fig. 1. Plot locations on the cross-section of the marsh area.

terized by oligotrophic to mesotrophic seepage. Afterwards, the quantitative and qualitative influence of the irrigation systems, feeding the marsh with mineral rich canal water, resulted in a large-scale horizontal gradient from calcium rich to oligotrophic and acid conditions (Lembrechts and Van Straaten 1982). These large-scale patterns were described using multivarate techniques (Van Straaten and Lembrechts 1982).

The complex vegetation structure of the marsh area reflects two major conditions:

- position along the horizontal mineral gradient (more or less influence of canal water)

- hummock formation, which is strongly influenced by surface water flow (seepage), as a result of the topography of the marsh area (Fig. 1).

Hypothetically, the development of micro-scale pattern and structure can be postulated in different phases:

1. Initial colonization of the bare peat (or shallow pools); this is strongly influenced by the prevailing abiotic conditions such as the chemical composition of the peat and water level fluctuations.

2. Initial hummock formation by aggregation of turf-forming individuals *(Carex demissa, C. dioica, Eriophorum latifolium)*. The local accumulation of organic material and concentration of new germinating individuals reinforce further development of hummocks. Running surface water may suppress this process. Bryophytes play an important role in the process, but they are not included in the data set.

3. Arrival of species with an "aggressive" growth morphology *(e.g., Molinia caerulea)*, which reinforces real hummock formation.

4. On the side of the Molinia tussocks, seeds of other species such as *Carex dioica* and *Carex demissa* germinate. The growth of the "aggressive" species determines the large-scale patterns in the marsh.

Three sites were chosen in the pool hummock marsh (Fig. 1). Some ecological characteristics and the species

Table 1. Ecological characteristics of the sample sites. Sapropelium consists of fine organic material, a more decomposed form of peat.

Site number	1 and 2	3
General aspect	small scale pools and hummocks structure	humid heath vegetation cleared by cutting sods
Phytosociological place	Caricion davallianae	Lycopodio-Rhynchosporetum albo-fuscae
Soil	15 cm sapropelium (gradually intermingled with underlying sandy soil)	5 cm peat
Hydrology .water level fluctuation	20 cm	30 cm
.inundation period	2/3rd of the year	rare
.inundation level	0 - 15 cm	---

Table 2. Species frequencies within sample sites. Nomenclature follows De Langhe e.a. (1983). The first column gives the 6-character codes as used in the text and figures.

Site number		1	2	3
Number of points		976	1275	1240
Species composition		% frequencies		
BLANCO	open peat surface	30.6	9.7	23.4
CALVUL	Calluna vulgaris			2.9
CARDEM	Carex demissa	16.8	20.2	.3
CARDIO	Carex dioica	28.5	30.1	
CARPAN	Carex panicea			5.9
CARROS	Carex rostrata	2.6	.2	
CARSCA	Carex scandinavica			27.1
ELEQUI	Eleocharis quinqueflora	7.8	4.7	
EQUPAL	Equisetum palustre	.6	.2	.7
ERIANG	Eriophorum angustifolium	1.5	.7	
ERILAT	Eriophorum latifolium	1.6	.4	
ERITET	Erica tetralix	.2	.1	17.6
JUNALP	Juncus alpinoarticulatus	.7	2.8	
JUNART	Juncus articulatus	.6		2.0
JUNBUL	Juncus bulbosus	1.6	2.4	2.8
MOLCAE	Molinia caerulea	5.0	21.0	14.0
MYRGAL	Myrica gale	.2	.9	1.1
POTERE	Potentilla erecta			1.8
POTPOL	Potamogeton polygonifolius		6.4	
RHYALB	Rhynchospora alba			.5
TRIPAL	Triglochin palustre	1.4	.2	

composition are displayed in Tables 1 and 2. These sites are strongly influenced by the mineral-rich canal water (due to their position close to the irrigation canal). As a consequençe, the local groundwater (site 3) and surface water (sites 1 and 2) are neutral (pH ±6.5), rich in calcium (±40 ppm), magnesium (±5.0 ppm), sodium (±30 ppm) and chlorides (±45 ppm), and have relatively high conductivity (±400 μS/m) (at least for what might be expected in humid heath in the northern Belgium).

The vegetation of sites 1 and 2 belongs to the Caricion davallianae according to Westhoff and Den Held (1975) and shows a typical pool character (Table 1), expressed by the occurrence of some calcicolous pool species, such as *Eleocharis quinqueflora* and *Juncus alpinoarticulatus*. In comparison with site 2, site 1 shows much uncovered sapropelium, probably owing to the intensity of the superficial waterflow. Hydrologically, site 1 is situated in a drainage zone, consisting of a complex of small ditches, draining the surface water westwards. The permanent waterflow prevents seed germination, and consequently, the development of a vegetation cover. Because site 2 is not located in a drainage zone, it has a much lower superficial water flow intensity. Site 2 is characterized by a closed vegetation cover, dominated by small *Molinia caerulea* tussocks, and aggregates of *Carex demissa*. The pool vegetation is typically composed of *Potamogeton polygonifolius* and *Eleocharis quinqueflora*.

The vegetation of site 3 belongs to the *Lycopodio-Rhynchosporetum albo-fuscae* (according to Westhoff and Den Held 1975), which is typical for sod cutting places in humid heathlands. Because of this recent activity, site 3 shows largely bare soil; it is colonized by seedlings of *Erica tetralix* and *Carex scandinavica*. The occurrence of this last species underlines the influence of the mineral rich ground water.

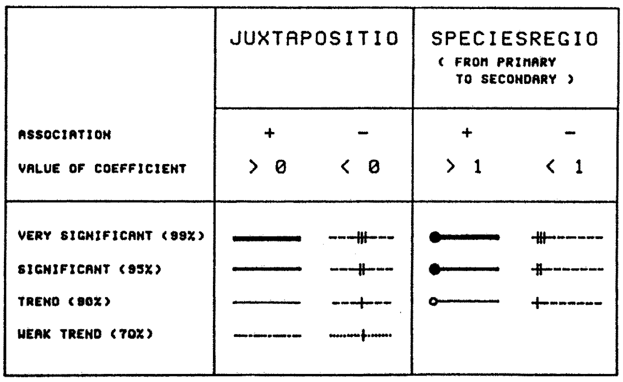
Materials and methods

At each site, several parallel transects, composed of equidistant points, were laid on the ground; for each point, and within a radius of 2 cm, the species rooting nearest to that point was recorded. To make the "sample circles" contiguous, the interpoint distance was 4 cm. The radius value of 2 cm was retained after several trials at each site with radii of 1, 2, 4, 6 and 8 cm. Although this choice gives a rather high percentage of bare peat surface for sites 1 and 3 (Table 2), the percentage for site 2 is only 10% (Stowe and Wade 1979).

In order to cover a representative portion of the sites, the line transects were laid in a back-and-forth pattern, with the parallel transect segments at a distance of 8 cm apart and 1 sample point in between at each turn. For the analysis, we considered the whole back-and-forth sequence as one continuous chain, as it is were one-dimensional on a transect. We used both methods of analysis as mentioned above: the species-juxtaposition method (**"JuxtaPosition"**) and the species-region method (**"SpeciesRegio"**).

In **JuxtaPositio**, the collapsed chain is compared with the Markow chain generated for a random sequence of species. "Collapsing" means that the runs of species are replaced by single occurrences. So, we can test if a species occurs immediately adjacent to another species significantly more often or less often than its random expectation. The probability of observing a given value of positive or negative association can be determined (Table 3), because, as we assumed, the calculated index of association is normally distributed.

Table 3. Symbols and significance levels for association coefficients.



	JUXTAPOSITIO		SPECIESREGIO (FROM PRIMARY TO SECONDARY)	
ASSOCIATION	+	−	+	−
VALUE OF COEFFICIENT	> 0	< 0	> 1	< 1
VERY SIGNIFICANT (99%)	━━━━	---⧺---	●━━━━	⧺------
SIGNIFICANT (95%)	────	---‖---	●────	‖------
TREND (90%)	────	---+---	○────	+------
WEAK TREND (70%)	--------	……+……		

In **SpeciesRegio**, each species is chosen as the "primary" and another as the "secondary" species; other species are considered as "tertiary". The transect is divided into regions surrounding the primary species; the occurrences of the secondary and tertiary species inside and outside those regions are counted. A 2×2 con-

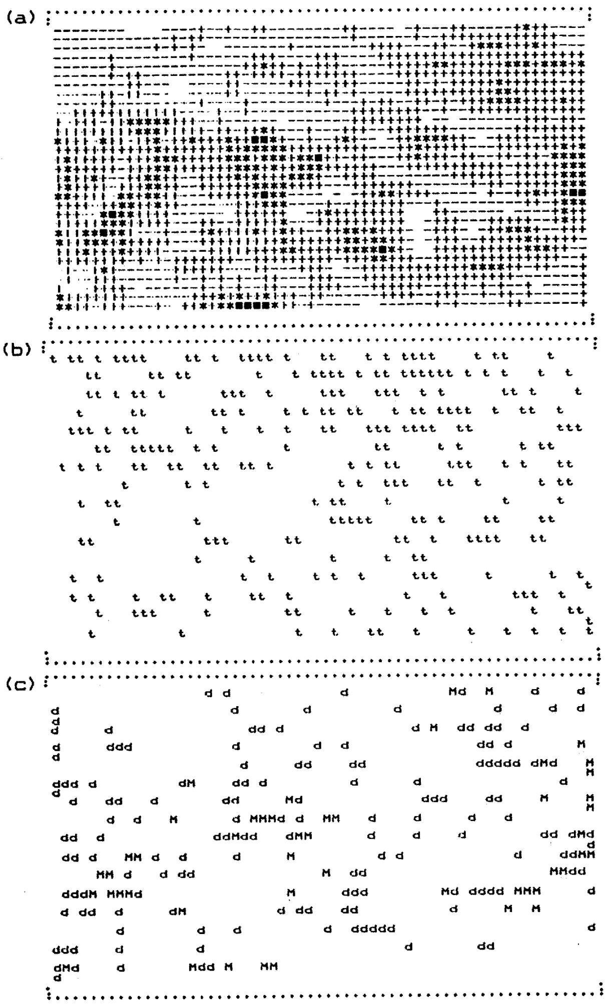


Fig. 2. Topography and species distribution, site 1.
(a) Height (h) classes (cm) distribution: ■ = $10.5 \geq h > 8.5$; * = $8.5 \geq h > 6.5$; + = $6.5 \geq h > 4.0$; — = $4.0 \geq h > 2.0$; [blank] = $2.0 \geq h$.
(b) Distribution of *Carex dioica* (t).
(c) joint distribution of *Carex demissa* (d) and *Molinia caerulea* (M).

tingency table, constructed from these frequencies, can be used to test if an individual's likelihood of being a particular species is significantly dependent on whether or not it occurs in the regions of the primary species. An index of association is calculated (Table 3). In fact, there are two contingency tables and two indices of association for each species pair. When **SpeciesRegio** is conducted based upon the collapsed chain, the regions are "circles" around individuals of the primary species, including only those individuals which are immediately adjacent to the primary species. For the analysis of the uncollapsed chain, the regions can be considered as annuli: individuals upon and outside the annulus are recorded, those at closer distances are ignored; larger and larger annuli may be constructed, and the distance at which associations change may be determined. We only considered radius multiplication factors 1, 2 and 3 ($r = 1$, $r = 2$, $r = 3$), this means annuli radii of 2 cm, 4 cm and 6 cm.

JuxtaPositio and **SpeciesRegio** were implemented in a (VAX/VMS) FORTRAN computer program. From the obtained coefficients, species constellation diagrams were constructed. These are only meant to help the reader visualize the results. The relative distances between the species are not directly related to the actual association values. From here on, the 6-character codes of the species (Table 2) will be used in the text.

Numerical analysis: results

Site 1

The relatively fast, running surface water is typical during more than 9 months of the year, resulting in an open character of the vegetation (high frequency of open peat surface). In comparison with site 2, there are not many "real" MOLCAE tussocks, and they are not growing vigorously. This can be deduced from two observations: MOLCAE has no *long runs* (Table 4) and the maximum height of the tussocks is 10.5 cm (Fig. 2a). A possible explanation is the restraining influence of the dynamics of the running surface water upon the aggressive growth of MOLCAE. Nevertheless, the global chi squared test of **JuxtaPositio** indicates a tendency towards association (**i.e.**, pattern formation, probability = 0.89).

In the diagram of **SpeciesRegio** based upon the uncollapsed chain ($r = 1$) we can distinguish two distinct groups (Fig. 3c):

(1) CARROS + BLANCO + CARDEM + MOLCAE
(2) JUNBUL + CARDIO + ELEQUI + ERIANG

Species Regio based upon the collapsed chain shows only one important difference compared to the analysis based upon the uncollapsed chain: the two groups are connected by positive associations between BLANCO and CARDIO (Fig. 3b). **JuxtaPositio** (Fig. 3a) only shows trends of positive and some significant negative associations.

Site 2

Here, the velocity of the surface water is lower than at site 1. Site 2 appears as a somewhat isolated pool, having no real drainage function. The vegetation is more closed (less BLANCO) and hummock formation is further developed than in site 1. The hummocks are higher and larger (Fig. 4a). This is reflected by the length of the runs of MOLCAE (longer than at sites 1 and 3, Table 4).

SpeciesRegio (collapsed chain, and uncollapsed chain, $r = 1$) now shows an association of CARDIO with CARDEM and MOLCAE (Figs. 5b and 5c) **JuxtaPositio** and **SpeciesRegio** (uncollapsed chain, $r = 1$) indica-

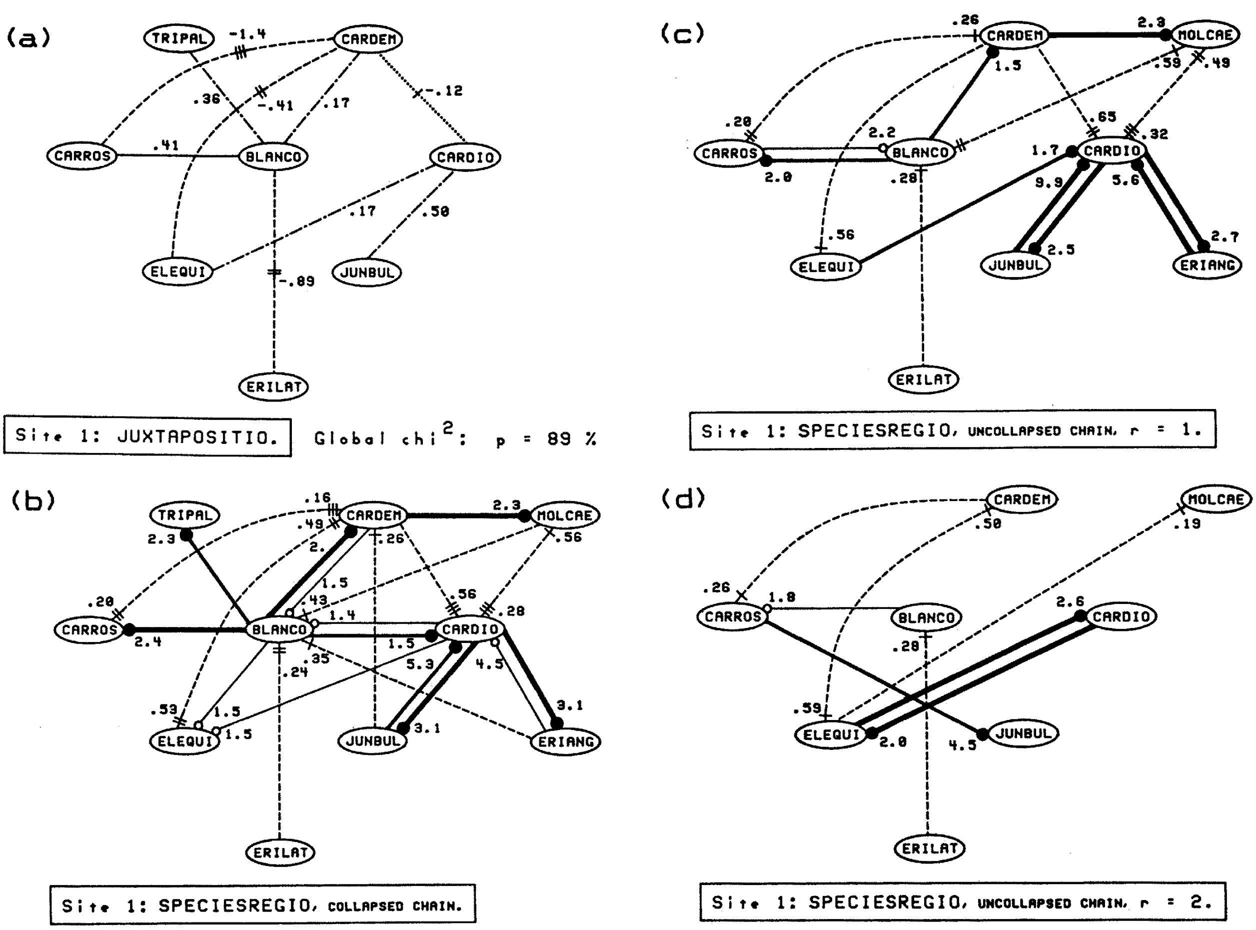


Fig. 3. Association diagrams, site 1. Figures refer to association values, line-types to significance levels (see Table 3).

te an association between ELEQUI, JUNBUL and BLANCO (Figs. 5a and 5c). Compared with site 1, BLANCO and CARDIO are interchanged to some degree in the **SpeciesRegio**-associations. Again, **JuxtaPositio** shows positive trends, and some very significant negative associations. The global chi squared test shows a very high probability, 99%.

Table 4. Run lengths and run frequencies of species within sample sites. Run lengths are measured in points; the distance between two points is 4 cm.

site	1						2							3							
run length	1	2	3	4	5	6	1	2	3	4	5	6	7	1	2	3	4	5	6	7	8
BLANCO	106	44	20	6	3	1	93	14	1					118	37	11	7	2	2	1	1
CALVUL														24	4		1				
CARDEM	74	27	6	2	2		128	44	8	3	1			4							
CARDIO	104	47	12	7	2	1	155	69	15	5	4	1									
CARPAN														43	7	4	1				
CARROS	23	1					3														
CARSCA														99	38	24	9	3	5		1
ELEQUI	55	4	3	1			36	9	2												
EQUPAL	6						2							8							
ERIANG	13	1					9														
ERILAT	7	3	1				5														
ERITET	2						1							126	33	5	1			1	
JUNALP	7						22	5	1												
JUNART	6													15	5						
JUNBUL	16						24	3						21	7						
MOLCAE	22	9	3				82	36	13	8	3		4	95	20	10	2				
MYRGAL	2						10	1						12	1						
POTERE														22							
POTPOL							40	13	4	1											
RHYALB														6							
TRIPAL	14						2														

Site 3

The site is characterized by the absence of small-scale patterns in vegetation structure, typical for poorly developed pioneer vegetation. The global chi squared value is not significant ($p = 0.06$), which suggests a global random mingling of the different species, but not necessarily a random ground distribution of the individuals of the species. **JuxtaPositio** discovers a very strong negative association (MOLCAE-POTERE), and some positive trends (Fig. 7a). In any case, two distinct groups appear with a positive association in **SpeciesRegio** (collapsed chain and uncollapsed chain, r = 1; Figs. 7b and 7c):

1. CALVUL + JUNBUL + BLANCO + JUNART
2. CARSCA + ERITET + MOLCAE + CARPAN

ERITET shows some significant negative associations with the species of the other group. CARPAN and MOLCAE have a distinct asymmetric positive association (**SpeciesRegio**, all radii).

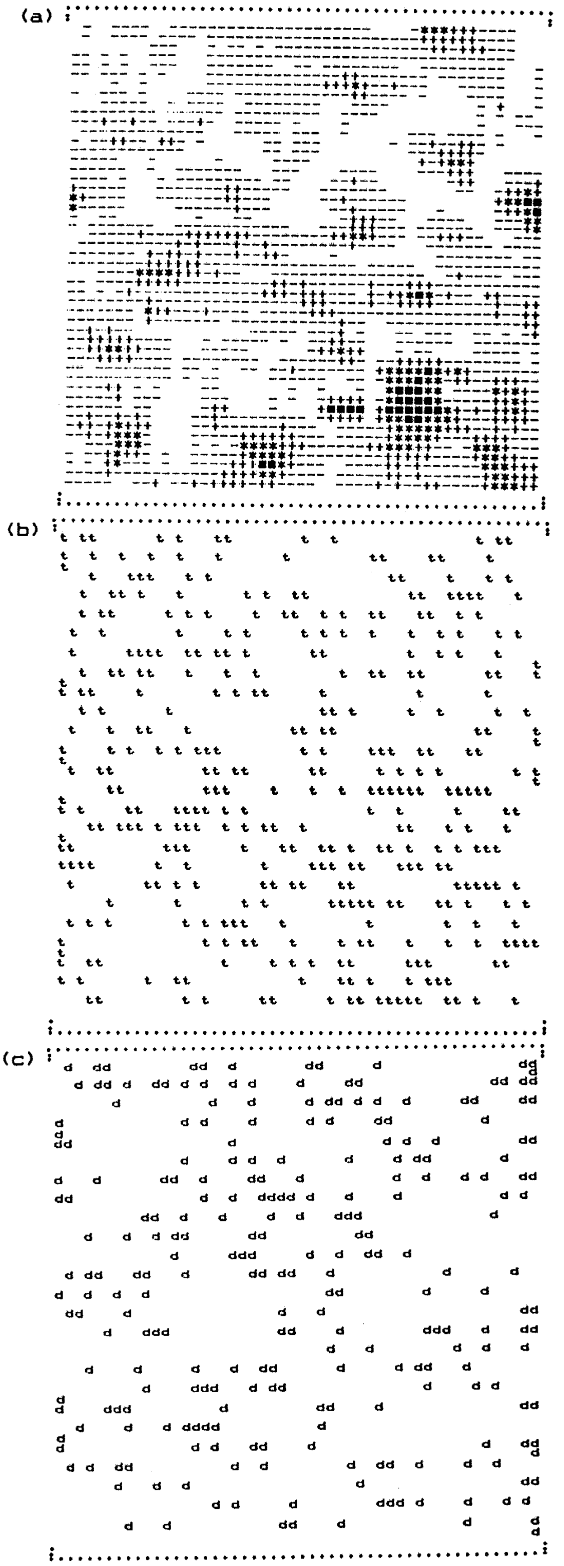


Fig. 4. Topography and species distribution, site 2.
(a) Height (h) classes (cm) distribution: ■ = 18.5 ≥ h > 15.0; * = 15.0 ≥ h > 11.0; + = 11.0 ≥ h > 7.5; — = 7.5 ≥ h > 3.5; [blank] = 3.5 ≥ h.
(b) Distribution of *Carex dioica* (t).
(c) Distribution of *Carex demissa* (d).

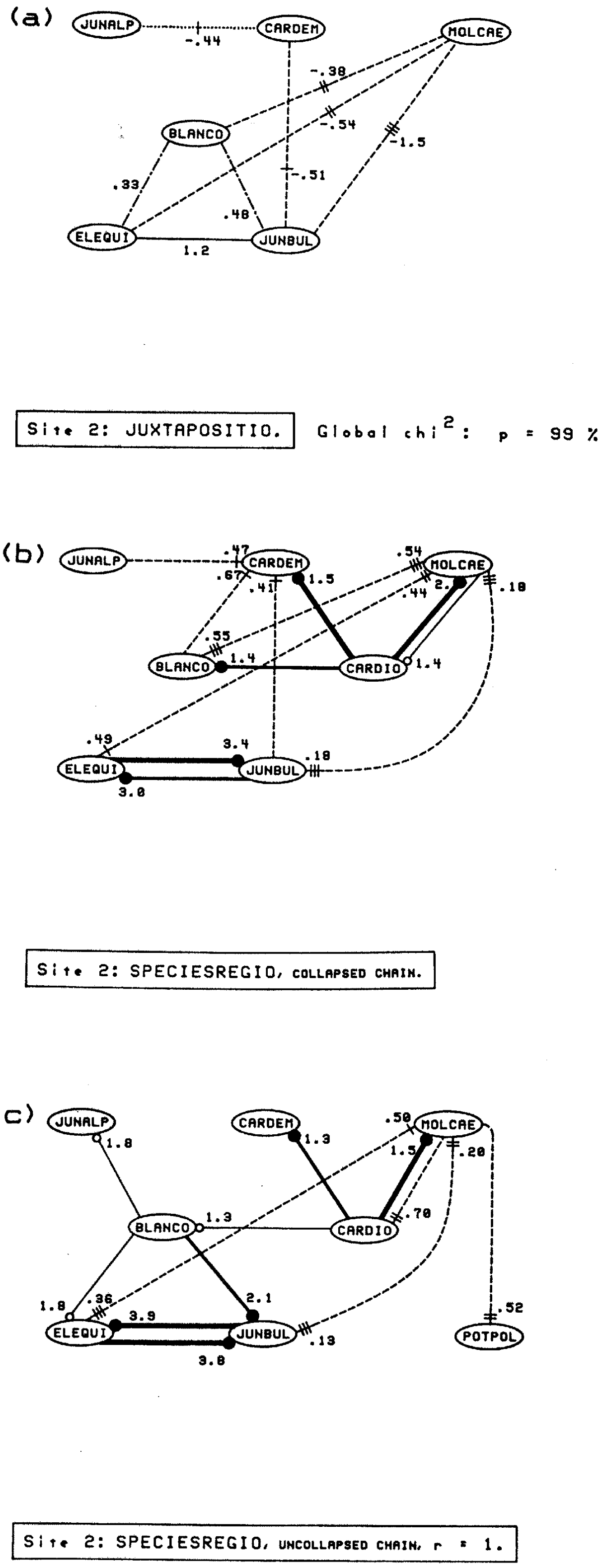


Fig. 5. Association diagrams, site 2. Figures refer to association values, line-types to significance levels (see Table 3).

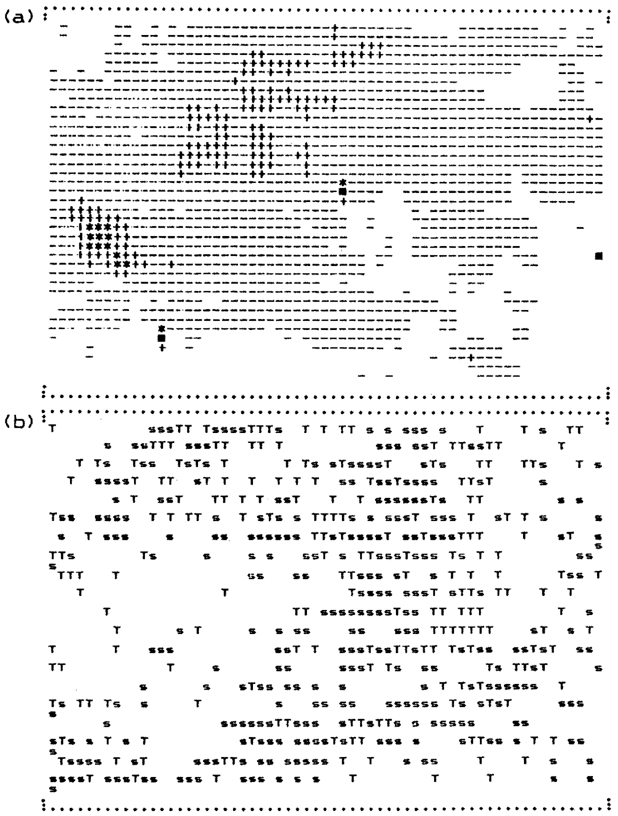


Fig. 6. Topography and species distribution, site 3.
(a) Height (h) classes (in cm) distribution: ■ = $17.5 \geq h > 14.0$; * = $14.0 \geq h > 10.5$; + = $10.5 \geq h > 7.0$; — = $7.0 \geq h > 3.6$; [blank] = $3.5 \geq h$.
(b) Joint distribution of *Carex scandinavica* (s) and *Erica tetralix* (T).

Discussion

Site 1

Within the postulated hummock formation process, the association MOLCAE + CARDEM can be interpreted as follows:

- aggregates of CARDEM-individuals initiate hummock-forming, reinforced by the eventual MOLCAE-tussocks (Fig. 2c);
- CARDIO also forms aggregates, but it is not really forming turf; its distribution is restricted to the somewhat lower parts of the site (Figs. 2a and 2b), which explains the positive associations with the "real" pool species like ERIANG and JUNBUL, and negative associations with MOLCAE and CARDEM.

That CARDEM and MOLCAE together are tussock forming excluding other species, is confirmed by the negative associations of both with the other species.

Interesting to note about **SpeciesRegio** is the possibility to perform tests symmetrically: the asymmetric or "one-way" positive correlation MOLCAE-CARDEM-BLANCO (Figs. 3b and 3c) suggests that CARDEM takes an "intermediate" place between BLANCO and MOLCAE, and shows some commensalism towards MOLCAE. These observations give the opportunity to refine the "hummock-forming" hypothesis (Fig. 8).

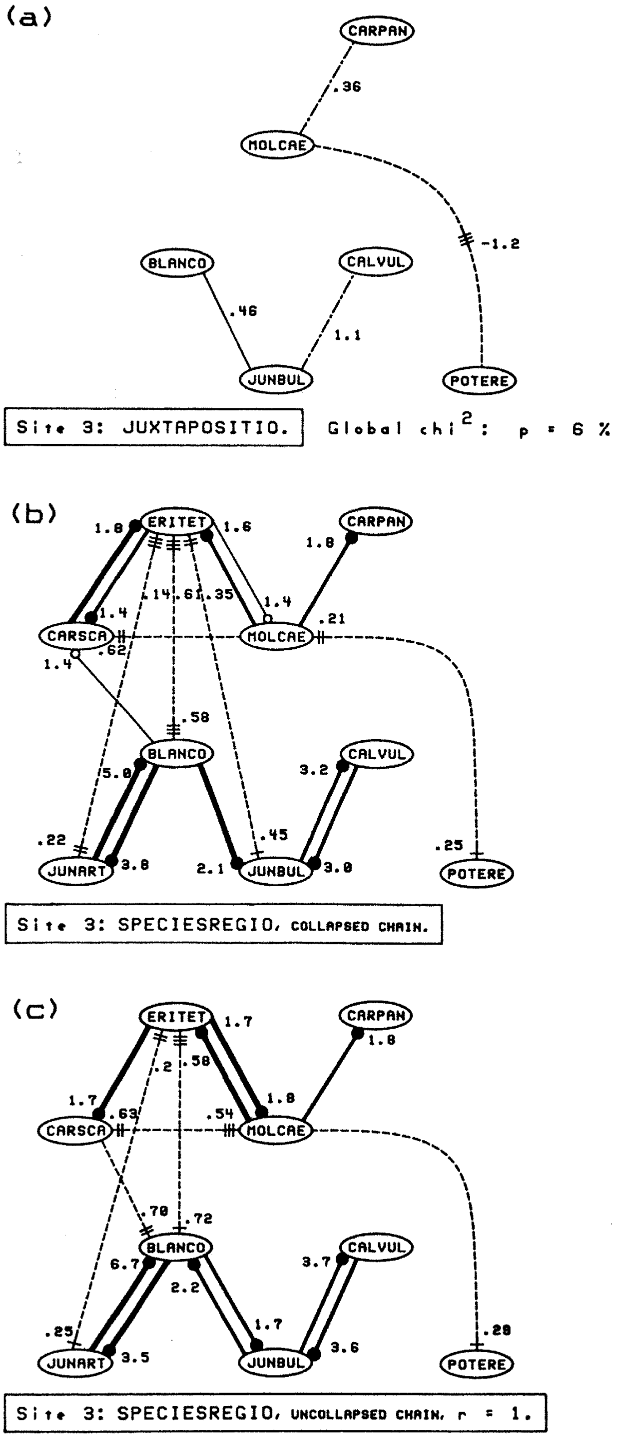


Fig. 7. Association diagrams, site 3. Figures refer to association values, line-types to significance levels (see Table 3).

In the analysis of the uncollapsed chain (Figs. 3c and 3d), the positive correlation CARDIO + ERIANG disappears at annulus radius 2 (4 cm). Although CARDIO and ERIANG are typical pool species, they are already forming a locally closed vegetation (at a scale of centimeters); the frequency of ERIANG is much less than that of CARDIO (Tab. 2), so ERIANG has a lower probabili-

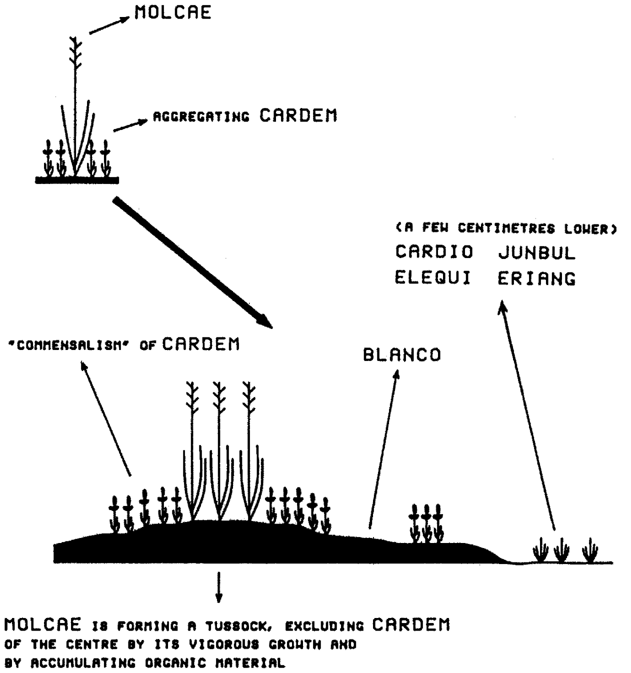


Fig. 8. Schematic diagram of initial hummock formation in site 1.

ty to grow at the edge of such a patch and has less direct contact with BLANCO (and thus relatively more with CARDIO). The positive association CARDIO+ELEQUI becomes stronger. We note that ELEQUI is a typical pool species but has a higher frequency than ERIANG.

Site 2

The analyses of the collapsed chain as well as of the uncollapsed chain (Figs. 5b and 5c) reveal simple, clearly defined structures and few associations. An important difference compared to site 1 is the absence of the association MOLCAE+CARDEM. MOLCAE is now the hummock former, but this species builds up isolated tussocks, which accounts for negative associations, up to annulus radius 2, in the analysis of the uncollapsed chain.

Some associations are asymmetric: CARDEM-CARDIO mirrors a trend of aggregation of CARDIO plants around CARDEM, whereas BLANCO-CARDIO outlines that CARDIO seems to surround the hummocks; visual inspection of the topography and the species distribution in Figs. 4a, 4b and 4c bears this out. The latter is confirmed by the association MOLCAE+CARDIO int he collapsed as well as in the uncollapsed chain, despite the frequent long runs (Tab. 4) of both species. On the first right contradictory negative association of CARDIO with MOLCAE (**SpeciesRegio** upon uncollapsed chain, r=1, Fig. 5c) is, in fact, a confirmation that starting from a MOLCAE tussock one frist has to cross a belt of CARDIO to reach BLANCO, while CARDIO itself is not exclusively associated with MOLCAE.

In general, globally the result indicates a clear "separation" of pool species and hummock species. Moreover, not only the negative associations support the pool-hummocks complex hypothesis, but also the comparison of histograms, giving the distribution of each species over topography height classes (Fig. 9). Exami-

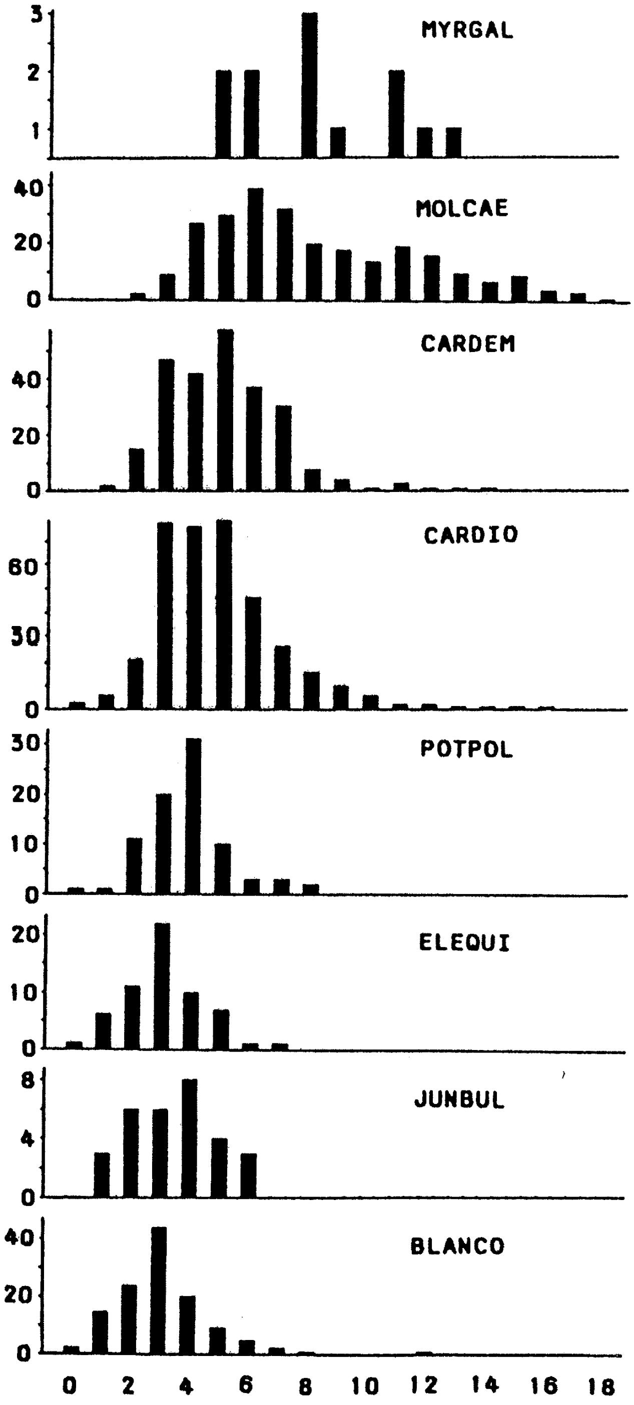


Fig. 9. Histograms of eight marsh species in site 2. Ordinate = frequency, abscissa = vegetation height in cm.

ning the latter, a real species sequence, reflecting the hummock-pool gradient, can be detected:

MYRGAL MOLCAE CARDEM CARDIO POTPOL ELEQUI JUNBUL BLANCO.

Site 3

Here, the associations cannot be explained by assuming small-scale aggregation of different plant species, forming a microtopographic hummock, because at this site the microtopography is generated by the recent sod-cutting activities, so it is rather the cause than the result of aggregation. Very probably, the associations are created by species having similar demands for a germination environment, for example seedlings of ERITET, MOLCAE and CARSCA on the one hand, and those of CALVUL and JUNBUL on the other. The seedlings are growing in mass, without distinct vegetation structure. The dominance relationships only develop after further succession.

The plot is slightly sloping (Fig. 6a) which has serious consequences on the distribution of certain species. CARPAN occurs in the lowest zones with fluctuating water, JUNBUL prefers the transition zone, while the older plants of CALVUL are predominant on an unmown MOLCAE tussock and its seedlings prefer the transition zone. The association of JUNART and JUNBUL with BLANCO is interesting. These two *Juncus* species are the first pioneer species after recent sod-cutting (Figs. 7b and 7c).

The negative correlations can be explained by the fact that the most frequent species also have, some relatively long "runs" (BLANCO, ERITET, MOLCAE, CARSCA, Tab. 4). CARSCA and ERITET seedlings often occur in relatively high frequencies one after the other (Fig. 6b), which generates a positive association. These species occur in long composite runs, forming a closed vegetation. Typical is the disappearance of the positive association (MOLCAE + ERITET) at radius 3 (= 6 cm): most of the runs of both species have length 2 (= 4 cm), so at a radius of 6 cm there is a greater chance of "jumping over".

SpeciesRegio shows one distinct positive asymmetric association: CARPAN-MOLCAE (collapsed chain, and uncollapsed chain, all radii). MOLCAE reacts rather indifferently and grows at random everywhere in the plot (most of the time as a seedling). CARPAN prefers to grow in the lower regions, and only there does a non-zero correlation exist.

Conclusions

Structure in the vegetation of site 1 has been revealed by the presence of several associations. CARDEM plays a constant role on the borderline of the hummocks. Site 2 is a typical example of a closed vegetation; in this case, the morphological pattern is determined by the formation of large MOLCAE tussocks. Between the tussocks, mainly CARDEM and CARDIO occur. The association of these 3 species is evident in the **SpeciesRegio** analysis of both chain types. Typical pool species, like JUNBUL, ELEQUI and POTPOL, are associated with the lowest, bare grounds. The microtopography of site 3 is generated by the past activity of sod-cutting (shallow or deep, while at the other sites, the topographic differences are merely a consequence of the aggregation of plant individuals and the growth morphology of certain species, such as MOLCAE. Consequently, at site 3 we find a typical wet heath vegetation, deprived of a sod cover by cutting. The characteristic species include JUNBUL, MOLCAE, CARPAN and ERITET. Because of the relatively high calcium content of the groundwater (and of the peat) some calcicole species also occur in mass (*e.g.* CARSCA).

Considering the data, **JuxtaPositio** seems to be more conservative than **SpeciesRegio**, which is expected, in testing based upon a coefficient which is normally distributed. However, Stowe and Wade (1979) did not have this problem, probably because their chains were much longer (4000 points) than ours (about 1000 points). With chains shorter than 500 points, **JuxtaPositio** should not be calculated.

The methods described by Stowe and Wade (1979), although very useful, give no clear-cut answer to the question: "Which pattern exists in this vegetation?" We believe there is no method capable of giving an answer to this question. In fact, it is up to the investigator, to perceive, describe, and explain patterns. The methods give hints and they stimulate further thought why a positive or negative association, aided by other methods which produce species distribution maps, topography printouts, and histograms for simple visual comparison.

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