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The Horizontal Structure of Reed Stands (*Phragmites communis*) and Its Relation to Productivity

Horizontální struktura porostů rákosu (*Phragmites communis*) a její vztah k produktivitě

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Abstract — Measurements along a transect through littoral stands of *Phragmites communis* show that productivity and density are positively correlated. The density in these stands decreases from the shore. This gradient can be attributed to the accumulation of old plant parts, producing more organic material in some regions of the stand. The spacing of individuals is contagious: the dimensions of the pattern are examined by block size analysis. The clumping is most pronounced in the most productive plots.

Introduction

Although there are many interesting features of horizontal structure and spacing of plants in crop stands, only those directly related to dry matter production are here considered. When assessing the amount of production in different plant stands from pot or field experiments, as is usually done, effects of variation in horizontal spacing are usually dominated by appropriate experimental design or selection of field site. In many natural stands, however, the effects of density must be taken into account.

Changing density will affect many environmental factors: soil composition, light and temperature, specific conditions of tillering, competition, etc. These variations will affect the statistical significance of mean production values obtained from random samples throughout the stand. Not only overall density but pattern must be taken into account, since the scale of pattern and its nature will affect the size of sample required. Three main types of pattern may be distinguished: random, regular and contagious. If the distribution is contagious, sample sizes must exceed those of clusters, since the variance of samples of the same size as clusters is very large.

Density measurements

Density, its distribution and influence on productivity were studied in two stands of *Phragmites communis* in different ecotopes growing near each other and experiencing the same macroclimate. The first (site V) is a typical littoral ecotope of the South Bohemian region, forming an almost pure monospecific community along the shore of Opatovický pond, a band about 25—30 m wide. The flooding level varies from 25—90 cm above soil surface, being shallowest on the shoreward side. The second limosal ecotope (site S) is never actually flooded, although the water table comes very close to the surface. Since this stand is not subject to wave erosion much more detritus accumulates on the bottom than in site V.

Tab. 1. — The mean density (n = average number of shoots per 1 m²) and coefficient of variation (V) determined by the transect and by the nearest distance methods at sites V and S

		V-site	S-site
Transect	$\bar{n}$	52	81
	V (%)	24.8	31.5
nearest distance method	$\bar{n}$	65	73

The mean density was determined by counting when harvesting a transect of contiguous quadrats at right angles to the shore. Site V shows a clear gradient of density and productivity along this transect, but for site S no such gradient was detected. Table 1 shows the mean values of density and their coefficients of variation, together with values obtained by the distance method of COTTAM and CURTIS (1956), based on the measurement of distances of the four plants closest to a random point. This last method proved the most reliable and was therefore adopted. (Methods depending on measurement of a single distance only, as suggested by CLARK and EVANS (1954) or MORISITA (1954) give a biased estimate due to clumping.)

Tab. 2. — Correlation coefficients (r) for testing the mutual dependence of production (W), average height of plants (h), the density (n) and number of flowering plants (n_f) per 1 m². The values of r marked with the asterisk indicate that the correlation is significant at 1% level

r	W—n	W—h	n—h	n—n_f
V-site	0.50**	0.30*	—0.01	—0.74**
S-site	0.82**	0.22	—0.81**	0.03

Production is largely correlated with density as shown by correlation analysis in table 2. For comparison, correlations with other parameters, average plant height and number of flowering plants per square metre are also given. The dependence of production on density is significantly greater than on height. Density is extremely variable, as the coefficients of variation in table 1 show, so determining production figures reliably will require many samples. This is discussed in more detail in ONDOK (1969).

To account for the density gradient we determined the thickness of the detritus layer and its weight per square metre as well as density and production. The gradient of thickness and weight of detritus follows that of density, suggesting that production depends on the amount of organic material from detritus in the soil. This would also explain in part the higher average production at site S, where the detritus layer is thicker than at site V. The thickest layer of detritus was found in the first third of the transect at the open water end, where highest production was also found. (Fig. 1.) Accumulation of detritus in these regions is presumably due to trapping of material by the *Phragmites* stems as it is driven shoreward by the waves.

Pattern analysis

The production is also affected by pattern in density distribution. Hence pattern analysis can help account for differences in production between stands. The pattern analysis is based on departure from randomness, as measured by a Poisson-type distribution. A simple criterion of non-randomness is the χ^2 test, which can also be used to test the fit of alternative distributions such as Thomas, Neyman, negative binomial and other so called contagious distribution curves.

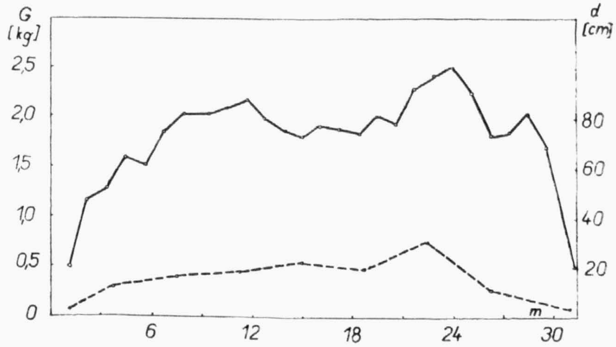

Fig. 1. — The production (G) in kg of fresh weight per (———) 1 m^2 and the height of detritus layer in cm (- - - - -) along the transect on V-site in the direction from the shore to the open water.

Clark and Evans (1954), Hopkins (1954) and others suggested using the mean nearest neighbour distance as a test for non-randomness. The variance-mean ratio is also convenient. For a Poisson distribution it is 1, for contagious distributions greater than 1, and the significance can be obtained from a t test. This treatment, together with examination of effects of quadrat size in a contiguous grid of quadrats was used to examine pattern. Further details can be found in the reviews of Greig—Smith (1952, 1964), Kershaw (1964) and Vasilevič (1969).

Tab. 3. — Number of pattern occurring in 8 replicates of measurement by the method of contiguous grid of squares at sites V- and S
The values of squares are given in cm

	10×10	10×20	20×20	20×40	40×40	40×80	80×80	80×160
V-site	2	1	4	5	2	2	1	
S-site	2	2	4	4	3	1	3	

Instead of using the common mean square test, which only gives partly quantitative terms, we chose another method for dimensional analysis. Within blocks of size 2, 4, 8, 16, 32, 64, 128 and 258 unite quadrats 10×10 cm (with a 160×160 cm grid), the total variance of the density was partitioned between blocks and the mean square/mean score ratio calculated. This has a χ^2 distribution, which is used to test the significance of departures from random in the blocks and thus the dimension of clusters in the plant distribution. Values above the upper confidence limits indicate overdispersion, those below the lower limits underdispersion (regular distribution). Combining this method with a transect method using a t-test, we obtained the results in table 3 for the two sites. No great differences in clumping at the two sites were found. The pattern dimension mostly lies in the range 20×20 to 40×40 cm, but marked differences for individual plots along the transect

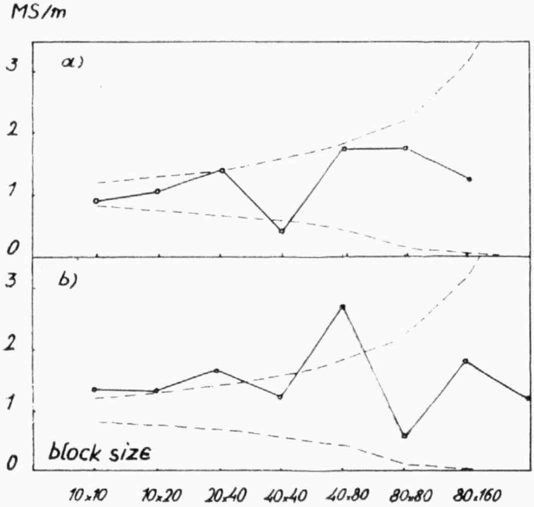

Fig. 2. — Dimension analysis of pattern in V-site. — a) — the plot with a small layer of detritus; b) — the plot with a large layer of detritus. — Dashed line marks the confidence bands (P = 0.05)

Tab. 4. — Dimension analysis for two plots in site V. I. plot — little layer of detritus, II. plot — large layer of detritus

SS — sum of squares, MS — mean square, m — mean score of density per 1 quadrat 10×10 cm. Asterisk marks the values above level of significance (P = 0,05)

Plot		I			II		
within block of	degrees of freedom	SS	MS	MS/m	SS	MS	MS/m
2	128	122	0.94	0.94	146	1.14	1.36*
4	64	70	1.09	1.09	73	1.14	1.36*
8	32	44	1.37	1.37	45	1.41	1.67*
16	16	7	0.43	0.43	10	0.62	0.75
32	8	14	1.75	1.75	18	2.25	2.68*
64	4	7	1.75	1.75	2	0.5	0.6
128	2	2	1.0	1.0	3	1.5	1.8
256	1	1	1	1	1	1	1.2
			m = 1.0			m = 0.84	

were found. Clumping was most pronounced in plots with heavy layers of detritus. The pattern is presumably affected by external factors as well as the internal morphogenetic ones, such as sprouting of new shoots from the base of the culms. An assessment of pattern for two plots at site V, one with a thin, the other with a thick layer of detritus is given in table 4, and plotted in fig. 2. Regular distribution of underdispersion was found in only two plots.

Comparison with results from other methods show some discrepancies. The transect method is suspect when mean density varies continuously along a gradient. This was particularly the case at site V. Another disadvantage of the transect method is that it only gives linear scales for pattern, whereas the contiguous grid of quadrats enables us to assess the area dimension of the pattern. On the other hand, estimates of dispersion from the variance/mean ratio agreed well with our estimates.

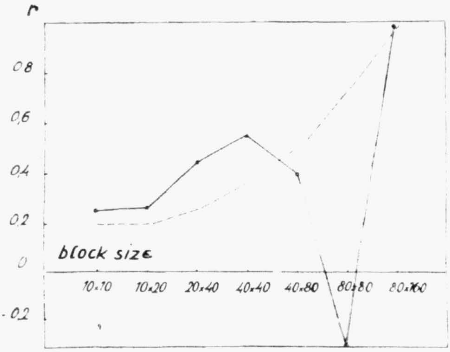

Fig 3. Correlation between new and old stems as dependent on block size. — r — correlation coefficient, dashed line: confidence bands (P = 0.05)

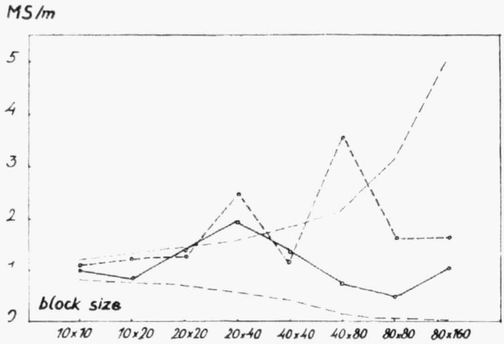

Fig. 4. — Dimension analysis for pattern of new and old stems in V-site. ——— new stems, — — — — old stems. — Thin dashed line: confidence band (P = 0.05)

To distinguish in more detail external from internal pattern we have assumed that there is a correlation between the numbers of old culms from the previous year and new culms in the present growth season. This correlation at different sample scales, should show the radius of spreading of plants around a parent. Not only lateral sprouting but also the appearance of new tillers from rhizomes was taken into account, which should show changes in density or clustering from season to season. As before, the same block of contiguous quadrats was used to examine density of old and new culms in the individual quadrats. The correlation coefficient plotted against block size in fig. 3 shows the interdependence between number of old and new culms. The variation between 4 replicates was, however, considerable. Nevertheless the correlation between old and new culms is significant for block sizes from 10×10 cm to 20×40 cm. At larger block size the coefficient is generally negative. This means that the number of new culms in blocks larger than 40×40 cm is generally greatest in blocks with the least number of culms in previous seasons.

Otherwise few comments on the radius of spread of shoots in relation to culm density can be made. The significant positive correlation for block sizes 10×10—20×40 cm must be due to lateral tillering of new shoots, as shown in fig. 3. The significant value of r for block size 40×80 cm was found in only one of 4 replicates.

Pattern scale can change with time on the same plot as fig. 4 shows, where the patterns in new and previous years are plotted, but this may not be a general phenomenon. Among the measurements are some cases in which density in old and new shoots is identical. Further measurement is needed to settle this problem.

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Souhrn

Měřením podél transektu v litorálních porostech rákosu (*Phragmites communis*) bylo zjištěno, že produkce nadzemní biomasy je positivně korelována s hustotou porostu. Hustota v těchto porostech má výrazný gradient ve směru kolmém na břeh. Tento gradient souvisí s množstvím detritu v půdě a jeho průběh lze vysvětlit ze způsobu, jakým sedimentují na dně porostu odumřelé části rostlin. Distribuce hustoty je kontagiosního typu a vytváří shluky, jejichž rozměry byly zjišťovány metodami kvantitativní ekologie, vypracovanými převážně anglosaskými autory. Shlukování je výraznější na místech s větším množstvím detritu a ovlivňuje velikost produkce.

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