ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. XLVII, nr 1—2
1978

# Some remarks on the methods of assessing the population density of higher plants in cases of aggregated spatial structure

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(Received: November 25, 1977)

Abstract

This paper presents a comparative analysis of the methods used for assessing the density of higher plants. The analysis was carried out on natural population (*Vaccinium myrtillus* L.) characterized by aggregated spatial structure. Attention has been paid to the surface methods with high (0.25 $m^2$) and low (0.01 $m^2$) basal unit, as also to the non-surface methods: the closest individual, the nearest neighbour, and the wandering quarter. Studies have shown that these methods do not give comparable results. The discussion points out which methods can be used for the assessment of the density of aggregated populations, and what conditions must be fulfilled in order to obtain reliable results.

## INTRODUCTION

A review of the literature on the methods of assessing the population density of higher plants (Kwiatkowska, Symonides, 1978) leads into two basic conclusions:

1. in view of a large number of various methods there is a general lack of comparative studies, undertaken for the same object in natural conditions, aimed at testing the reliability of data obtained with these methods;

2. many methods of assessing the density do not take into account the effect of spatial structure of the object under study upon the results of measurements. This remark refers especially to non-surface methods. The fact that these methods give convergent results in model systems with random spatial distribution of individuals (Cottam and Curtis, 1956) does not mean that they are equally effective for natural aggregated populations. However, the general opinion that all non-surface

methods are equally valuable and useful was strengthened by the results of Cottam and Curtis (1956). Consequently, the only criteria adopted so far in selecting the method of studies are the practical aspects: speed and facility of the measurements.

In view of the above it seemed advisable to undertake comparative analysis of the methods used for assessing the density in natural conditions, on a natural model object characterized by aggregated spatial structure. Additionally an attempt was made to determine the range of applicability of various methods to aggregated spatial structure of the populations.

*Vaccinium myrtillus* L. was selected as the model object, suitable for our studies mainly due to the way of reproduction. In case of vegetative reproduction of this species it can be safely accepted that the distribution of individuals in space is close to the aggregated type, at least on a microscale.

Studies were carried out in the Białowieża Forests, in a physiognomically homogenous patch of mixed pine-oak forest, with high share of fenberry in the undergrowth.

## METHODS

In our studies attention was paid to the surface methods, and to the most frequently used and most differentiated non-surface methods: of the closest individual, nearest neighbour, and wandering quarter (see Kwiatkowska and Symonides, 1978). All methods were based on a systematic sampling plan due to the necessity of obtaining detail informations on the spatial distribution of the object under study.

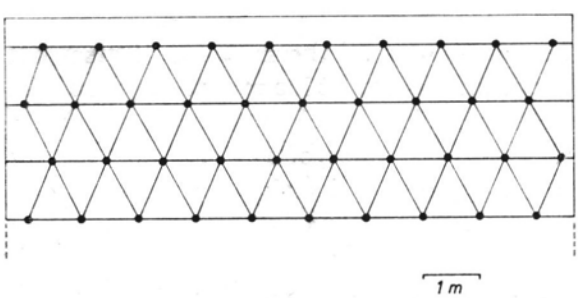



Fig. 1. Sampling scheme in the surface method (circular basal unit of 0.25 $m^2$)

Sampling area consisted of a square $10 \times 10$ m, localized in the centre of the biochore of selected phytocenosis. 10 transects were selected upon its area, in 1 m intervals, parallel to one side. Sampling places on the transects depended on the method used for assessing the density:

a) in the surface method sampling points (circular, of the area 0.25 $m^2$) were selected on the basis of a grid of triangles (Fig. 1); total size of the sample being 100;

b) in the closest individual and nearest neighbour methods samples were taken from 30 points, selected at equal intervals along each transect. In this case total size of the sample amounted to 300 measurements;

c) in the wandering quarter method initial points and direction of sampling were randomly selected. Measurements were taken in several series so as to reach the total sample size of 300.

Data taken for the analysis of the microstructure and population density originated from seven 1 m chequered squares (the basic units being rather small, of 0.01 $m^2$), randomly distributed upon the area under study. Each chequered square was divided into 100 equal (also squared) basic fields.

Data obtained from non-surface methods were analysed and presented in a graphic form: as the continous interpolation map (data from the area of 0.25 $m^2$), and as a cartogram (data from the area of 0.01 $m^2$).

Preliminary statistical analysis of the results consisted of constructing several frequency distributions for the given feature under study (number of individuals per unit of area or the values of the distance), and calculating some basic characteristics: the arithmetic mean ($\bar{x}$), the standard deviation (s), and the coefficient of variability $\left(V = \frac{s}{\bar{x}}\right)$.

Verification of the null hypothesis to the empirical distribution with respect to the proper, random theoretical distribution, was based on the chi-squared test of concordance (G r e ń, 1974). Due to the fact that the aim of our studies necessitated a detailed knowledge on the spatial structure of the object under study, the type of spatial distribution was additionally analysed taking advantage of the median modification of the runs test (K w i a t k o w s k a, 1972). On the basis of the interval estimation average values of the densities per 1 $m^2$ were compared. All conclusions about the differences between average values were based upon confidence intervals. As regards the surface method (0.25 $m^2$), and the closest individual method, it was also necessary to make additional verification of the results taking advantage of the "u test" for the differences in average values (O k t a b a, 1966). The level of error risk in all statistical analyses amounted to 0.05.

In the non-surface methods the surface area per 1 individual, as also the density per 1 $m^2$, are given by proper equations (C o t t a m and C u r t i s, 1956; K w i a t k o w s k a and S y m o n i d e s, 1978). In the nearest neighbour method, due to systematic sampling (similar to the method of random pairs), the value of the coefficient used in calculations was taken as equal to 0.64.

Independently of the method used, one individual was defined (according to R a b o t n o v 1950) as each above-ground shoot of the fenberry.

## RESULTS

The interpolation map of the density (Fig. 2), and the cartograms (Fig. 3) point to the fact that *Vaccinium myrtillus* forms, both on a macro-and microscale, a visible mosaic of overdensed and underdensed areas, the first occuring on significantly smaller area than the latter. It also appeared that macro-aggregations are not evenly distributed upon the

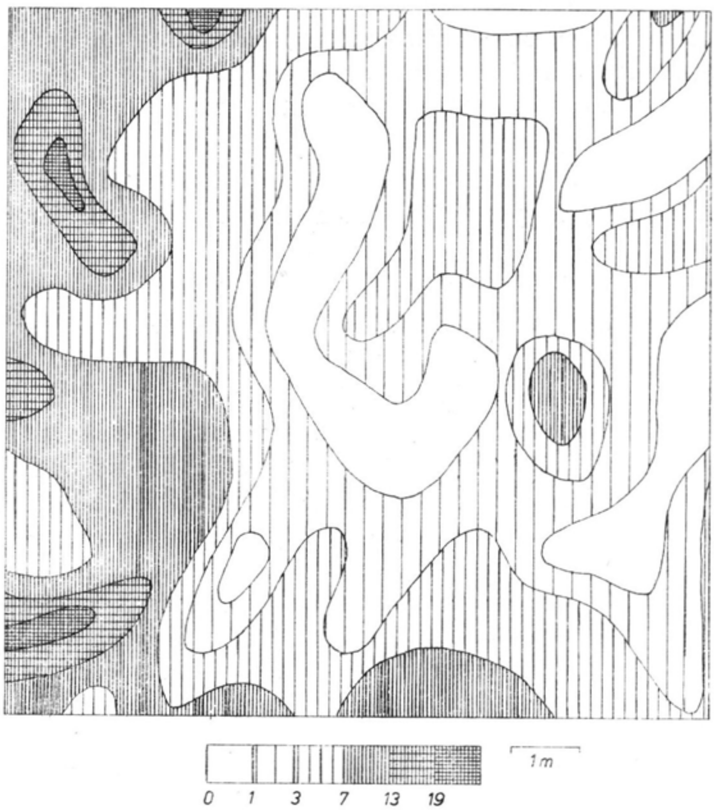
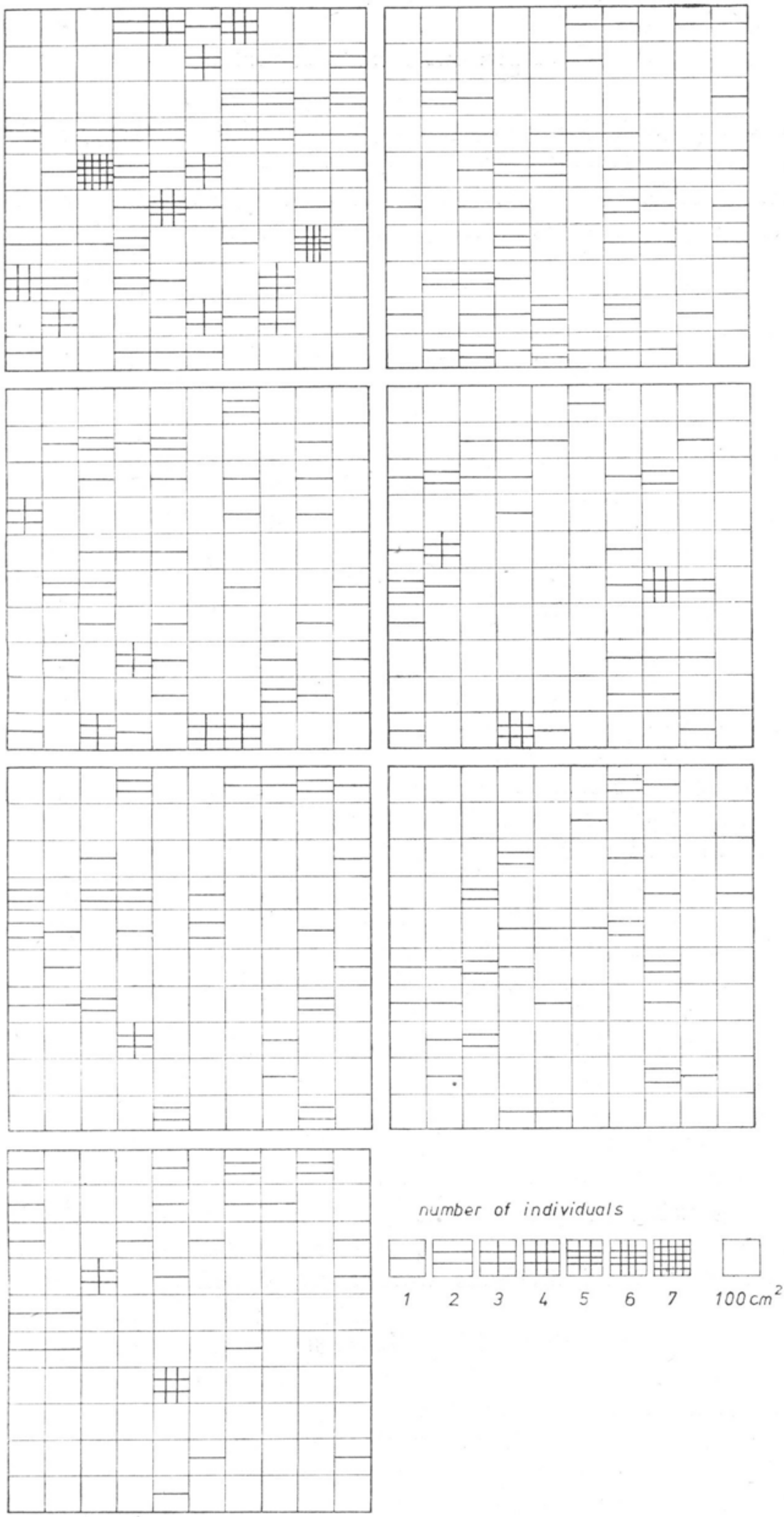



Fig. 2. Variability of *Vaccinium myrtillus* density upon the area under study (data from the area of 0.25 m²)

Fig. 3. Spatial microstructure of *Vaccinium myrtillus* (data from squares)


number of individuals
1
2
3
4
5
6
7
100 cm²

area, and occur only in certain points. This type of spatial organization of the individuals results in the fact that the probability of finding high and low (in relation to $\bar{x}$) values of the density is not similar (Fig. 4), being also different for different parts of the surface area (see Fig. 2).

Table 1

Average density per 1 m² ($\bar{x}$), confidence semi-intervals (L), standard error of the mean (e), and coefficient of variability (V) for particular methods

| Metod | $\bar{x}$ | L | e | V |
|---|---|---|---|---|
| Surface 0.25 m² | 20.24 | 0.92 | 0.47 | 0.92 |
| Surface 0.01 m² | 51.57 | 0.06 | 0.03 | 1.67 |
| Closest individual | 18.39 | 0.86 | 0.44 | 0.66 |
| Nearest neighbour | 33.28 | 0.87 | 0.39 | 0.66 |
| Wandering quarter | 13.29 | 1.18 | 0.60 | 0.76 |

Empirical distribution of the number of individuals per one unit of area differs significantly from the Poisson distribution (Fig. 4, Tab. 1). According to the common view this is a good proof of the aggregated type of the population spatial distribution (for instance, Svedberg after Vasilevič, 1969; Dice, 1952; Cottam, Curtis, and Halle, 1953; Kershaw, 1964; Odum, 1977; and others). Also empirical distribution of the distance values significantly differs from the theoretical normal distribution (Fig. 5 *A-C*, Tab. 1), being of a positive skewness. According to Dice (1952) this is an illustration of the aggregated spatial distribution of individuals.

Nevertheless, in our opinion the concordance of empirical distribution with the model of random distribution does not univocally point to this type of spatial distribution of the population. Consequently, statistical analysis of the spatial distribution was additionally enlarged by the non-parametrical run test for the values higher (+) and lower (—) than the average value of the distance ($\bar{x}$), obtained on the basis of the wandering quarter method. Results of this test univocally proved that on a macroscale the individuals were characterized by an aggregated spatial distribution.

Summing up, population of *Vaccinium myrtillus* is characterized by the aggregated spatial distribution of the density, both — as regards the probability structure for respective values (Fig. 4 and 5 *A-C*), and with respect to the type of the organization of these values in the space (Fig. 2 and 3). Aggregated spatial structure of the object under study is also visibly hierarchic: large aggregations (macrostructures) posses their own, internal aggregated structure (microstructure).

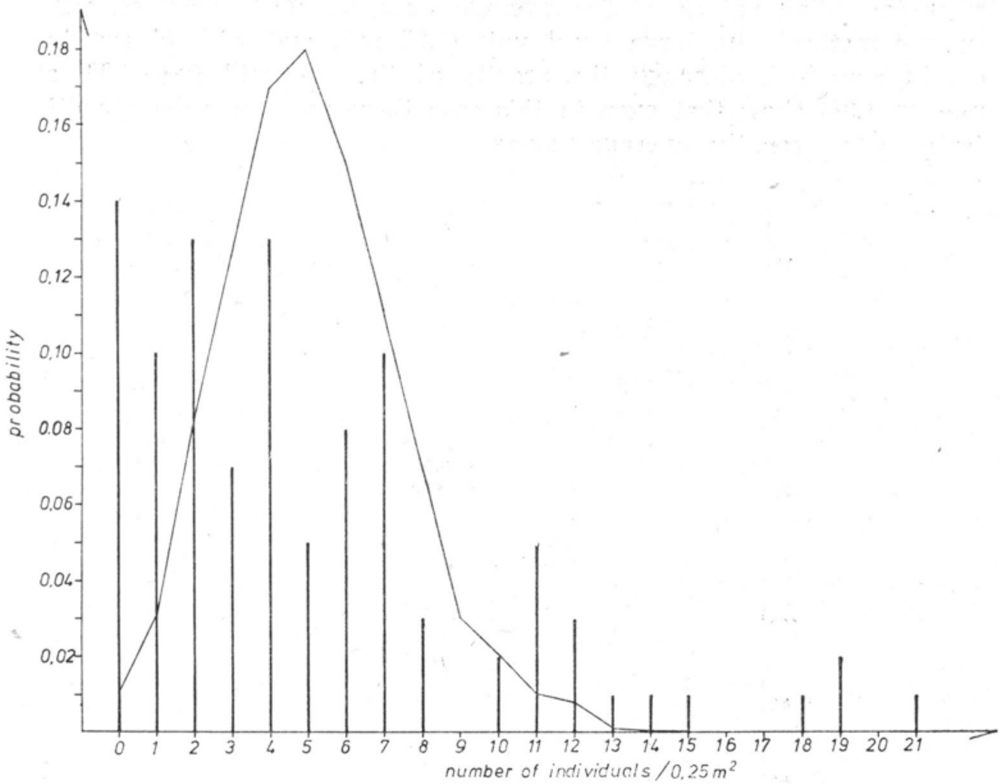



Fig. 4. Comparison of the distribution of individuals upon 0.25 m² with the Poisson's distribution

Table 2

Comparison of empirical distributions with random distribution, test and limit chi² values

| Metod | Test chi² value | Limit chi² value |
|---|---|---|
| Surface 0.25 m² | 220.70 | 16.91 |
| Closest individual | 26.97 | 11.07 |
| Nearest neighbour | 30.96 | 9.49 |
| Wandering quarter | 23.72 | 14.07 |

Measurements of the density based on different methods gave visibly differentiated results (Tab. 2, Fig. 6). The most significant differences were noted in comparing the average densities in the surface method (with small basal unit of 0.01 m²) with the average densities in the wandering quarter method. In the latter method the average number of individuals per 1 m² is almost four times lower. Less significant, but well visible differences, were noted in comparing all other results. The most coinciding values of the average densities were obtained with surface method with large basal unit (0.25 m²), and with closest individual method, although the results of the "u test" ($u = 2.88$, at $u_{0.05} = 1.96$) show that even in this case there were considerable differences between the average values.

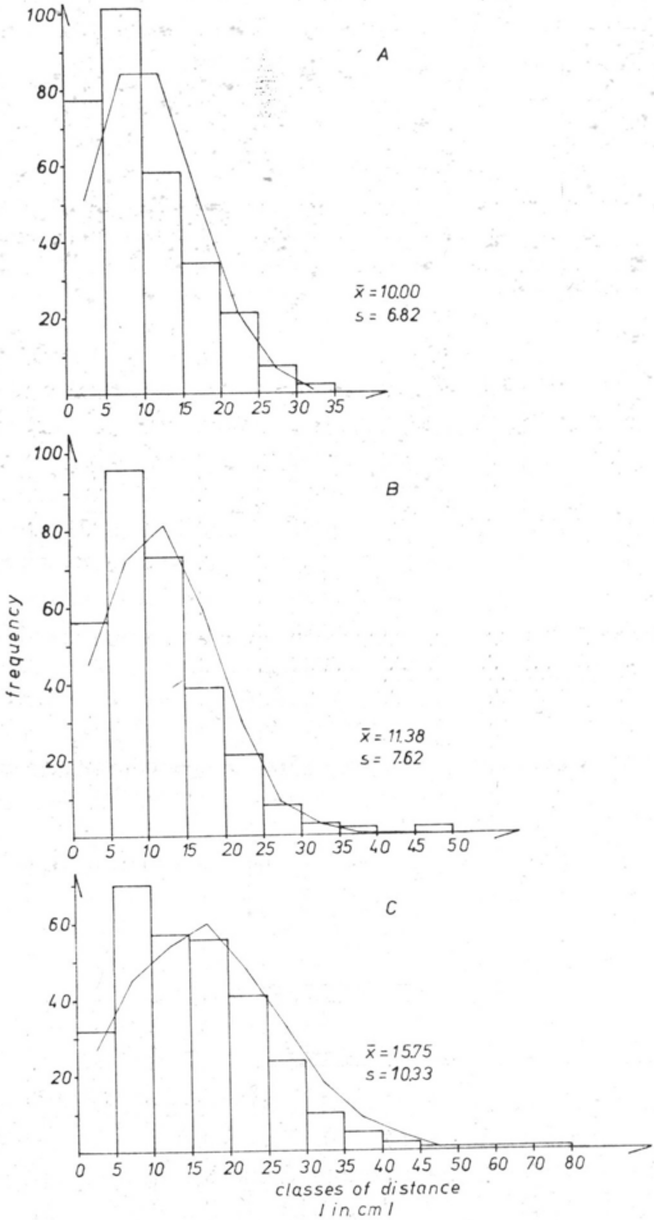



Fig. 5. Comparison of the distribution of individuals with normal distribution in the methods of: *A* — nearest neighbour, *B* — closest individual, *C* — wandering quarter

Surface methods with large basal units gave lower values of the average density than the methods with small basal units. The same refers also to the value of the coefficient of variability.

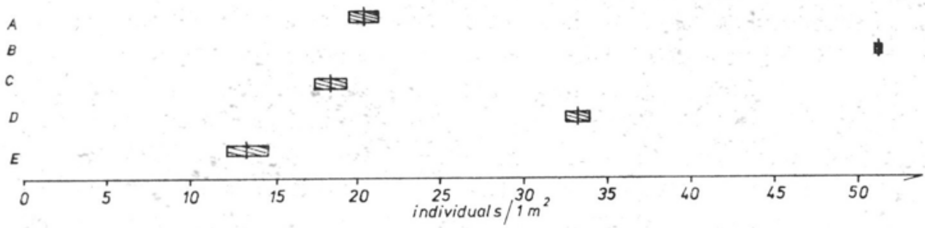



Fig. 6. Confidence intervals for the average density per 1 m² in the methods of: *A* — wandering quarter, *B* — nearest neighbour, *C* — closest individual, *D* — surface (basal unit of 0.01 m²), *E* — surface (basal unit of 0.25 m²). In the methods *A-C* 300 repetitions were made, in the *D* — 700, and in *E* — 100

Non-surface methods gave different results not only with respect to the average densities, but also as regards the empirical distribution of the distance values (Fig. 5 *A-C*). Although each distribution is asymetric, with positive skewness, the range value is different in each method, and the probability of obtaining similar values of the distance between individuals varies according to the method. And thus, in the nearest neighbour method empirical distribution is characterized by the most pronounced "shifting" of the probabilities toward low values, and by the lowest range value (Fig. 5 *A*). In the closest individual method the positive skewness is less pronounced: probability of obtaining higher values of the distance, as also higher range values, is much higher than in the method of the nearest neighbour (Fig. 5 *B*). The empirical distribution in the method of wandering quarter is characterized by the least deviation from normal distribution; the probability of assessing the average and high values of the distance is here the highest. Large range results also in higher value of the coefficient of variability compared to other methods under study (Fig. 5 *C*).

## DISCUSSION

The results of our studies support the necessity of undertaking comparative analyses of the methods used for assessing the density. They also confirmed our hypothesis that different methods are not equally valid as regards the aggregated spatial structure of the population. In discussing the causes of differences noted in the assessment of the density with various methods it must be underlined that every method fulfilled the condition of statistical representativeness, as proved by low (not exceeding 10%) value of the standard error of means

(Tab. 2). Hence, each method gave statistically reliable estimates of the density. In view of the above it might be possible that the differences in the assessment of the density were caused by the lack of homogeneity in the reference set.

Theoretically, the reference set in our studies consisted of all *Vaccinium myrtillus* individuals present within the biochore of the mixed forest. Practically it consisted only of individuals present within the area under study. As regards the number of individuals per one unit of area — it was not a homogenous set. It was possible to distinguish — on a macroscale — at least two subsets: with higher (aggregations) and lower (dispersions) values of the average density. In view of this lack of the homogeneity the following problems should be discussed: 1. whether all methods fulfilled the condition of structural representativeness of the sample, 2. whether the sample in each method represents the same set, or different sets. In the latter case it is significant to know what sets are represented by various methods; and 3. to what an extent particular methods refer to the reference set as such, i.e. to the set of *Vaccinium myrtillus* individuals upon the area under study.

We have assumed that our scheme of sampling reflected — independently of the method used — in the same degree the spatial relations between aggregations and dispersions upon the area under study. The only exception was the scheme used in the surface method with small basal units (0.01 $m^2$). Due to the fact that the arrangement of samples in the checkered square was of a block character, sample area had a summaric value (7 $m^2$), and the squares were randomly distributed, it is undoubtful that in this case the sample does not reflect spatial relations on the macroscale. Consequently, it is not structurally representative for the whole area, especially if the size of aggregations and dispersions extends beyond the area of the checkered square.

Discussing the value of the surface method with small basal unit it can be generally stated that, as a result of random sampling of the dependent sample, and low number of squares, the estimated density of aggregated population would be highly accidental, depending on whether the sampling squares are close to each other, or dispersed. Consequently, the results of measurements will either refer to the set of aggregations or to dispersions. If the biochore is predominated by the dispersions and the aggregations are randomly distributed, the result representing the dispersions will most probably be underestimated with respect to the average for the reference set. On the other hand, if the biochore is predominated by the aggregations, and the dispersions are randomly distributed, the result representative for the aggregations will most probably be overestimated with respect to the average for the reference set. However, if the aggregations are not randomly distributed within the biochore, there is no possibility of predicting neither the direction of the deviation from the average, nor the range of the structural representativeness of the data.

In our studies analysis was made of only seven "points" in relation to the area of the biochore. Consequently, in assessing the value of the average density for the whole population it would be necessary to estimate the average value for the sample of 7 (and not 700). As a result, value of the confidence intervals would fall within a broad range of from 29.9 to 73.2, and the error for the average would also become much higher.

In the surface method with large basal unit (0.25 $m^2$), sample consisting of 100 points systematically distributed upon the biochore area, equally represents each part of the biochore. Hence, it also fulfilled the condition of structural representativeness for the analysed area, as well as of representativeness for the total reference set. The method has also an advantage of relatively large area of the total sample, covering $^1/_4$ of the total area under study.

Large differences noted between the densities estimated with surface methods with large and small basal unit resulted from: 1. the fact that data from the area of 0.01 $m^2$ were treated as independent samples, and 2. the basal units were of different size. In assessing the density of the population with aggregated spatial structure, the size of the basal unit significantly affects the result (Kwiatkowska, Symonides, 1978).

Summarizing the discussion on surface methods it should be underlined that:

1. At low number of small squares the obtained results are not representative for the whole population due to the fact that the condition of structural representativeness of the sample is not fulfilled for the whole biochore.

2. Small basal unit in the systematic cluster sample (squares) gives representative results for the internal structure of the population (microscale), hence they characterize the values which the random variable ascribes to the reference subsets, corresponding to aggregations and dispersions.

3. In the surface method with small basal units the sampling points should equally represent all parts of the biochore, and the numerosity of the sample should be as high as possible.

4. Ratio between the summaric area of the sample and the size of the biochore cannot be too low. It is, however, more economic (in view of the labour requirements) to use larger sampling area at lower numerosity, instead of smaller sampling area at correspondingly higher numerosity of the sample.

Contrary to surface methods, in non-surface methods the density is calculated indirectly: from the measurements of the distances and coefficients obtained from a model. Hence, it might have been expected that the results would differ, but the value of the density should at least be of the same order. Nevertheless, our studies showed that in comparing any two methods some differences were always noted, independently of the fact whether the methods belonged to the same, or to different categories.

Within non-surface methods, i.e. the closest individual method and the nearest neighbour method, the results are of the same order (several individuals per 1 m$^2$). On the other hand, value of the density assessed with the nearest neighbour method shows a significant deviation.

The closest individual method gives the results most close to those obtained with surface method with large basal unit. This fact is totally understable considering that the sampling scheme was identical in both cases, and the condition of structural representativeness was also fulfilled. Most probably differences between the two methods resulted from the fact that in one the density is assessed directly, whereas in the other — indirectly. Although there was no possibility of comparing our reults with an objective model, i.e. with the number of *Vaccinium myrtillus* individuals per 100 m$^2$, we are of the opinion that direct measurements (at structural representativeness of the sample), i.e. the value $\bar{x}$ for samples from 0.25 m$^2$, are most close to the real value of the average.

The results obtained with the wandering quarter method differ slightly from the results obtained with both, the surface and the closest individual method. Compared to other non-surface methods, measurements carried out with the wandering quarter method refer to the largest range of values that the random variable can represent, and the possibility of embracing high values of the distance between individuals is most probable. The method in itself implies that the sampling scheme cannot be restricted to any regular geometric net since each sampling place is determined by the distribution of particular individuals, and this cannot be planned in advance. Net of points, i.e. of sampling places, is empirically determined during the measurements. Consequently, it must differ from any other sampling schemes. Due to this, particular parts of the biochore may not be represented in the same degree although the measurements are carried out in large number of series. The value of the average density must thus be more or less different than the results obtained with methods based on other sampling schemes.

The advantage of the wandering quarter method consists of the fact that the real spatial succession of the distance between the individuals is totally preserved. The measurements automatically give the size of the sections of aggregations and dispersions, as well as the value of the distance between individuals within the aggregations and dispersions. This method is also highly informational. It allows not only for assessing the average density for the whole population, but also its value separately for aggregations and dispersions. Furthermore, it allows for testing the type of spatial distribution of the population (with the method of non-parametric median modification of runs test).

High value of average density, very high probability of embracing low distance values, and the lowest range value suggest that the method of the nearest neighbour, compared to other non-surface methods, takes into account most of all these values which the random variable ascribes to the reference belonging to the aggregated areas. This results from the method in itself, as the measurements are taken only between the nearest neighbours. Selection of the individuals from which the measurements are being taken is less important. Independently of the fact whether the individual will be randomly selected (as in the method of the nearest neighbour), or defined by the point (as in the method of random pairs), the measurement will refer to the distance between the individual and its nearest neighbour.

Selectivity of the measurement results in the fact that in both methods assessment of the density, in relation to the overall average, will be the more overestimated the largest area is occupied by the aggregations, and their distribution the more close to the random, as the probability of taking the measurement within the aggregation will increase.

In case of *Vaccinium myrtillus* population, high value of the average density, obtained with the method of the nearest neighbour, is additionally increased by aggregated distribution of individuals on a microscale, caused by vegetative reproduction of the plant. Spatial aggregation of individuals from vegetative reproduction results in the fact that the nearest neighbour is always close to the given individual (on a microscale), independently of the fact whether the measurements are taken within an aggregation or a dispersion (on a macroscale).

In case of the method of the nearest neighbour it is very difficult to state to what general community refer the results. It is always necessary to take into account selective selection of higher values from all values that the random variable ascribed to the references. On the other hand, the result refers to the set of values corresponding to the area of the reference microaggregation. Selectivity of the method of the nearest neighbour is thus of a double character: it refers both, to the value set and to the reference subset.

Summarizing, it can be stated that from among non-surface methods, results representative for the whole population are obtained with the wandering quarter method and the closest individual methods (at proper sampling scheme). The wandering quarter method is most advisable due to substantial (high information) and practical (quick and easy measurements) reasons. The methods of the nearest neighbour and of random pairs do not give representative results; their application should be restricted only to specific, selected problems.

Our studies showed also that the values of the coefficient of variability should not be always considered as the best criterium of the utility of the method. This results from the fact that tendentious decreasing of the variability, as is the case with the nearest neighbour method, constitutes a significant shortcoming. Contrary, the wandering quarter method can register even rare events, and thus may give values of the coefficient of variability, but this fact does not diminish its utility and substantial correctness.

## CONCLUSIONS

The results of our studies suggest the following conclusions:

1. In case of natural communities of aggregated spatial structure the methods under study do not give comparable results.

2. The basic reason of the differences in the results of the assessment of the density with various methods is the fact that not all the methods fulfill the condition of structural representativeness of the sample.

3. Two methods do not fulfill the condition of structural representativeness, i.e. the methods of the nearest neighbour and of random pairs. These methods should not be used for assessing the density of aggregated populations.

4. Apart from the methods of the nearest neighbour and of random pairs, all the other methods fulfill the condition of structural representativeness if the sampling scheme is properly arranged, taking into account all parts of the biochore equally.

5. In the surface methods sampling points should represent all parts of the biochore in the same degree, and the ratio between total area of the sample and total biochore should not be too low.

6. Assessment of the density corresponds to different scales of the spatial structure, depending on the size of the basal unit, numerousity of the sample, and the sampling scheme.

7. Small basal units in the scheme of systematic cluster sample (squares) give reliable estimates of the density only on a microscale.

8. Within non-surface methods the most realistic results are obtained in case of the closest individual method (at proper sampling scheme), and of the wandering quarter method. The latter is especially advisable due to its high information content, and quick and easy methods of measurements.

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## *Studium metodyczne oceny zagęszczenia populacji roślin wyższych w przypadku skupiskowej struktury przestrzennej*

### Streszczenie

Praca poświęcona jest porównawczej analizie metod pomiaru zagęszczenia, wykonanej dla modelowej populacji naturalnej (*Vaccinium myrtillus* L.) o skupiskowej strukturze przestrzennej. Celem jej była próba określenia zakresu stosowalności poszczególnych metod w przypadku — najczęściej spotykanych w warunkach naturalnych — skupiskowych typów rozkładu osobników.

Badania przeprowadzono w fitocenozie boru mieszanego w Puszczy Białowieskiej. Uwzględniono w nich metodę powierzchniową (przy jednostce podstawowej 0.25 m² oraz 0.01 m²) a także najczęściej stosowane i równocześnie najbardziej różniące się między sobą metody bezpowierzchniowe: punktową, najbliższego sąsiada i ruchomego kąta. Ze względu na konieczność zachowania możliwie dokładnej informacji o strukturze przestrzennej obiektu analizy, we wszystkich metodach zastosowano systematyczny schemat pobierania próby, przy czym szczegółowy sposób postępowania uzależniony był od metody pomiaru.

Wszystkie wyniki opracowano statystycznie; we wnioskowaniu statystycznym przyjęto poziom ryzyka błędu 0.05.

Wykazano, że populacja *Vaccinium myrtillus* ma skupiskowy typ rozkładu przestrzennego wartości zagęszczeń (w mikro- i makroskali), zarówno pod względem organizacji tych wartości w przestrzeni (ryc. 2 i 3), jak też pod względem struktury prawdopodobieństw, odpowiadającym poszczególnym wartościom (ryc. 4 i 5 *A-C*).

Ważniejsze wyniki naszych badań ująć można następująco:

1. Dla obiektu naturalnego o skupiskowej strukturze przestrzennej analizowane metody nie dają porównywalnych wyników (tab. 1 i 2, ryc. 6), mimo że dla każdej metody zachowany był warunek reprezentatywności statystycznej próby.

2. Podstawowa przyczyna rozbieżności tkwi w tym, że nie wszystkie metody, z założenia, mogą spełnić warunek reprezentatywności strukturalnej próby. Warunku tego nie spełniają metody: najbliższego sąsiada i par losowych, których wobec tego nie powinno się stosować do oceny zagęszczenia populacji skupiskowych. W pozostałych metodach warunek reprezentatywności strukturalnej próby można zachować poprzez odpowiedni schemat pobierania prób, uwzględniający w jednakowym stopniu wszystkie części biochory.

3. W kategorii metod powierzchniowych zależnie od wielkości powierzchni podstawowej, liczebności i schematu pobierania próby ocena zagęszczenia odpowiada różnym skalom struktury przestrzennej. Stosowanie małych powierzchni podstawowych w układzie próby gronowej (kraty) daje wiarygodne wyniki zagęszczenia jedynie w mikroskali.

4. W kategorii metod bezpowierzchniowych najbliższe rzeczywistości wyniki pozwalają uzyskać metody: punktowa (przy odpowiednim schemacie pobierania próby) oraz ruchomego kąta, szczególnie godna zalecenia z uwagi na jej nadinformatywność oraz szybkość i łatwość wykonania pomiarów.