

DETERMINATION OF THE DEGREE OF INTRASPECIFIC COMPETITION IN MONOCULTURES

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Abstract

The maximal distance of interference between individuals of plant populations of the same age can be determined by measuring the dry mass of the plant individuals and the distance between the surrounding individuals. The degree of competition is proportional to the number of the neighbouring individuals and the square of their distance. In lack of competition the maximal mass of the plant individuals of given age can be calculated from the reckoned degree of the competition as well as from the measured dry masses. That distance grade approaches the maximal distance of the competitive effect, where the maximal dry mass is of the highest value.

Key words: density dependence, distance of interference, neighbourhood model, *Plantago indica*, *Scabiosa ochroleuca*.

Introduction

In the various plant populations the organic matter production of the average plant individual is in regular relationship with the density of the neighbouring individuals in the environs.

The average dry mass of individuals of populations grown in monoculture gives a horizontal and a sloping straight line, respectively, in the function of the density of the individuals illustrated on logarithmic scale. The intersection of these lines is found at that critical density where the individuals of given age are already in competitive interaction (KIRA et al., 1953). The difficulty of the method is that two linear regressions have to be applied at the same time. SHINOZAKI et al. (1956) established linear connection between the reciprocal of mean plant weight and the density ("reciprocal yield law"). Apart from density, the distance of the neighbouring individuals can also be used for expressing the competitive effect (MACK and HARPER, 1977; WEINER, 1982). WEINER (1982) suggested the neighbourhood model for determining the degree of interactions, where he counted the number of the neighbouring individuals around the test individual in concentric rings and the degree of competition was proportionated to the square of the median distance of the rings (neighbourhoods).

In this paper the aim was to seek for a suitable method, setting out from the previous model, which could be used in the case of a small number of samples for determining the distance where the individuals start to influence each others growth in a population of given age.

THE MODEL

Such function is suitable for the description of the result of density-dependent competition, which has maximal values if there is no competition, and asymptotically nears to zero with the increase in density. One of the simplest functions of this kind is the hyperbola, which was applied by KIRA et al. (1953) for the production of evenly distributed population in the reciprocal yield law. The mathematic description of this is as follows:

$$\frac{1}{V} = a + bN \quad (1)$$

where V = average plant production

N = density of the population.

This model was elaborated by WEINER (1982) in his neighbourhood-model as follows:

$$\frac{1}{V} = \frac{1 + W}{V_{\max}} \quad (2)$$

where W = the degree of competition, furthermore

$$W = \sum_{i=1}^n \frac{1}{d_i^2} \sum_j C_j N_{ij} \quad (3)$$

where d_i = the average distance of the i th neighbourhood,

N_{ij} = the individual count of the j th species in the i th neighbourhood,

C_j = average competitive effect of an individual from the j th species.

The farthest neighbourhood ($i=n$) is regarded where the individuals are still in interaction with the test individual.

When studying the monoculture of a species the (2) formula could be set down in the following form:

$$\frac{1}{V} = \frac{1 + C \sum \frac{N_i}{d_i^2}}{V_{\max}} \quad (4)$$

The neighbourhood-model composed of concentric rings could rather be applied to populations of nonuniform distribution (WEINER, 1982). In uniformly distributed population the median distance of the concentric rings could be substituted for the concrete distance of the neighbouring individuals, in such way the under- or overestimation of the degree of competition becomes exterminable which occurs in the case of the inequality of the two distances.

In this paper the slightly modified variant of the model described above was used for determining the degree of competition and the distance of interaction regarding plant individuals of uniformly distributed *Plantago indica* and *Scabiosa ochroleuca* populations, grown in laboratory.

The concrete distance of each individual was used instead of the median distance of the concentric rings. In the case of hexagonal regular pattern the neighbouring

individuals are arranged along the concentric rings (which is analogous to the median distance of the "neighbourhood").

The relative distance and the individual count of the neighbouring individuals in the populations of hexagonal arrangement are demonstrated in Tables 1 and 3. The measured distance of the neighbouring individuals in the population of various density is also shown in these Tables.

Materials and Methods

The annual xerophyten *Plantago indica* L. and the perennial *Scabiosa ochroleuca* L. are the members of the secondary succession of the experimental grasslands at Bugacpuszta. Knowledge on the inter- and intraspecific interactions complements the population dynamic survey carried out at the area.

The studied populations of the two plant species were grown in light chambers under controlled conditions at 20–25 °C temperature besides 8000 Lux light intensity, in 10/14 hr light-dark cycle. Seeds collected from the experimental area at Bugacpuszta were used for sowing and the sandy soil of the experimental area was used as substrate. (For characteristic parameters of soil see: KÖRMÖCZI, 1983).

The sowing was prepared in 30×30×10 cm sized plastic boxes in 4 different densities in regular hexagonal arrangement. The average densities and the average distance of the neighbouring individuals were: 10.4, 18.5, 25.2, 37.3 individual/dm² and 3.3, 2.5, 2.1, and 1.8 cm resp., in the case of *Plantago indica*, and 5.7, 9.4, 18.5, 51.3 individual/dm² and 4.5, 3.5, 2.5, and 1.5 cm, resp., in the case of *Scabiosa ochroleuca*.

The plants were watered with distilled water by spraying from the top.

The *Plantago* crop was processed at the age of 3 months. From every stand the part above the soil was cut off in the case of 20–20 individuals and the dry mass and leaf count was calculated.

The *Scabiosa* crop was harvested with the same method at the age of 2.5 months, but in this case the above parameters were measured on 30–50 individuals.

Results

By evaluating the experimental data the aim was to determine the distance (d_{max}) within which interference may occur between the individuals of the studied population. Hence, when calculating the degree of competition (W) the presumed maximal distance of the competition was gradually increased by 0.5 cm. The resulted W -values are demonstrated in Tables 2 and 4, in respect to both dry matter and leaf count.

Table 1. Data regarding the distance of the *Plantago* individuals

| ith neighbour | N_i | m_{rel} | measured distances at the various densities (cm) | | | |
|---------------|-------|-----------|--|------|------|------|
| | | | 10.4 | 18.5 | 25.2 | 37.3 |
| 1 | 6 | 1.00 | 3.3 | 2.5 | 2.1 | 1.8 |
| 2 | 6 | 1.73 | 5.8 | 4.3 | 3.7 | 3.1 |
| 3 | 6 | 2.00 | 6.7 | 5.0 | 4.3 | 3.5 |
| 4 | 12 | 2.66 | 8.8 | 6.6 | 5.7 | 4.7 |
| 5 | 6 | 3.00 | 10.0 | 7.5 | 6.4 | 5.3 |
| 6 | 6 | 3.46 | | 8.7 | 7.4 | 6.1 |

N_i = individual number of the i th neighbour

m_{rel} = relative distance of the i th neighbour, if $m_1=1$.

Following this, regression analysis was performed per d_{\max} -grade for determining the V_{\max} and C values. In the case of both studied variables the measured values corresponded best to that expected if the presumed maximal distance was 4.5 cm in the case of *Plantago indica* population. The best correlation coefficient was 0.96 for the dry matter and 0.98 for the leaf count. The W-values as well as the V_{\max} -values of the studied parameters were also the highest at 4.5 cm distance (Tables 1, 2; Figs. 1, 2).

Table 2. W values in the *Plantago* crops calculated on the basis of individual density and dry matter relatedness.

| Nr | d_{\max} | W | | | | r | C | V_{\max} |
|----|------------|------|------|------|------|------|------|------------|
| | | 10.4 | 18.5 | 25.2 | 37.3 | | | |
| 1 | 3.0 | 0.00 | 1.08 | 1.47 | 2.18 | 0.90 | 1.13 | 88.46 |
| 2 | 3.5 | 0.67 | 1.19 | 1.62 | 3.20 | 0.89 | 1.24 | 108.16 |
| 3 | 4.0 | 0.55 | 0.98 | 1.77 | 3.12 | 0.94 | 1.02 | 105.55 |
| 4 | 4.5 | 0.74 | 1.75 | 2.83 | 4.19 | 0.96 | 1.37 | 139.92 |
| 5 | 5.0 | 0.48 | 1.36 | 1.85 | 3.23 | 0.91 | 0.89 | 110.61 |
| 6 | 5.5 | 0.41 | 1.15 | 1.57 | 2.90 | 0.90 | 0.76 | 101.61 |
| 7 | 6.0 | 0.62 | 1.31 | 1.77 | 3.31 | 0.90 | 0.86 | 111.57 |

W values in *Plantago* crops calculated on the basis of individual density and leaf number relatedness.

| Nr | d_{\max} | W | | | | r | C | V_{\max} |
|----|------------|------|------|------|------|------|------|------------|
| | | 10.4 | 18.5 | 25.2 | 37.3 | | | |
| 1 | 3.0 | 0.00 | 0.23 | 0.31 | 0.46 | 0.92 | 0.24 | 23.42 |
| 2 | 3.5 | 0.13 | 0.23 | 0.31 | 0.61 | 0.93 | 0.24 | 24.63 |
| 3 | 4.0 | 0.10 | 0.18 | 0.34 | 0.59 | 0.97 | 0.19 | 24.38 |
| 4 | 4.5 | 0.11 | 0.27 | 0.43 | 0.63 | 0.98 | 0.21 | 25.44 |
| 5 | 5.0 | 0.09 | 0.25 | 0.34 | 0.59 | 0.95 | 0.16 | 24.62 |
| 6 | 5.5 | 0.08 | 0.23 | 0.31 | 0.57 | 0.94 | 0.15 | 24.26 |
| 7 | 6.0 | 0.11 | 0.24 | 0.33 | 0.61 | 0.94 | 0.16 | 24.73 |

In the case of *Scabiosa ochroleuca* the correlation of the regression line in the case of both studied variables (dry mass and leaf number) showed maximum at $d_{\max}=2.5$ cm value (0.98 and 0.90), however, the highest values of V_{\max} were obtained in the case when $d_{\max}=5.0$ cm (67.6 and 12.2), and even the rise of the regression line was the slightest at this value (Tables 3 and 4; Figs. 3, 4).

Table 3. Data of distances for *Scabiosa ochroleuca* individuals

| ith neighbour | N _i | m _{rel} | measured distances at the various densities (cm) | | | |
|---------------|----------------|------------------|--|------|------|------|
| | | | 5.7 | 9.4 | 18.5 | 51.3 |
| 1 | 6 | 1.00 | 4.5 | 3.5 | 2.5 | 1.5 |
| 2 | 6 | 1.73 | 7.8 | 6.1 | 4.3 | 2.6 |
| 3 | 6 | 2.00 | 9.0 | 7.0 | 5.0 | 3.0 |
| 4 | 12 | 2.66 | 12.0 | 9.3 | 6.7 | 4.0 |
| 5 | 6 | 3.00 | 13.5 | 10.5 | 7.5 | 4.5 |
| 6 | 6 | 3.46 | 15.6 | 12.1 | 8.6 | 5.2 |
| 7 | 12 | 3.61 | 16.3 | 12.6 | 9.0 | 5.4 |

Table 4. W values in *Scabiosa* crops calculated on the basis of individual density and dry matter relatedness

| Nr | d _{max} | W | | | | r | C | V _{max} |
|----|------------------|------|------|------|------|------|------|------------------|
| | | 5.7 | 9.4 | 18.5 | 51.3 | | | |
| 1 | 2.5 | 0.00 | 0.00 | 0.88 | 2.44 | 0.98 | 0.92 | 62.31 |
| 2 | 3.0 | 0.00 | 0.00 | 0.48 | 2.10 | 0.95 | 0.50 | 56.03 |
| 3 | 3.5 | 0.00 | 0.27 | 0.53 | 2.33 | 0.92 | 0.55 | 60.66 |
| 4 | 4.0 | 0.00 | 0.21 | 0.42 | 2.17 | 0.91 | 0.44 | 57.92 |
| 5 | 4.5 | 0.14 | 0.24 | 0.62 | 2.53 | 0.93 | 0.46 | 64.07 |
| 6 | 5.0 | 0.15 | 0.25 | 0.79 | 2.74 | 0.95 | 0.52 | 67.61 |
| 7 | 5.5 | 0.13 | 0.21 | 0.66 | 2.55 | 0.94 | 0.43 | 64.26 |

W values in *Scabiosa* crops calculated on the basis of individual density and leaf number relatedness

| Nr | d _{max} | W | | | | r | C | V _{max} |
|----|------------------|------|------|------|------|------|------|------------------|
| | | 5.7 | 9.4 | 18.5 | 51.3 | | | |
| 1 | 2.5 | 0.00 | 0.00 | 0.10 | 0.29 | 0.90 | 0.11 | 12.15 |
| 2 | 3.0 | 0.00 | 0.00 | 0.06 | 0.26 | 0.83 | 0.06 | 11.95 |
| 3 | 3.5 | 0.00 | 0.03 | 0.06 | 0.27 | 0.81 | 0.06 | 12.06 |
| 4 | 4.0 | 0.00 | 0.03 | 0.05 | 0.26 | 0.79 | 0.05 | 11.98 |
| 5 | 4.5 | 0.02 | 0.03 | 0.07 | 0.28 | 0.81 | 0.05 | 12.13 |
| 6 | 5.0 | 0.02 | 0.03 | 0.08 | 0.29 | 0.84 | 0.06 | 12.22 |
| 7 | 5.5 | 0.01 | 0.02 | 0.07 | 0.28 | 0.82 | 0.05 | 12.14 |

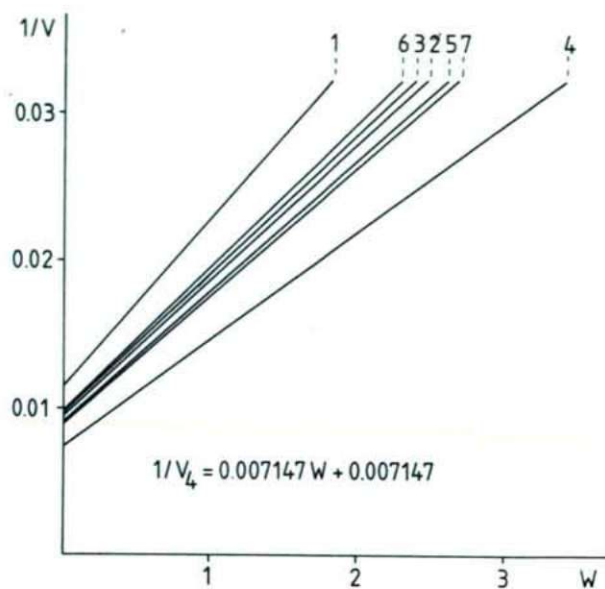


Fig. 1. Regression curves on the basis of the dry masses of *Plantago indica*.

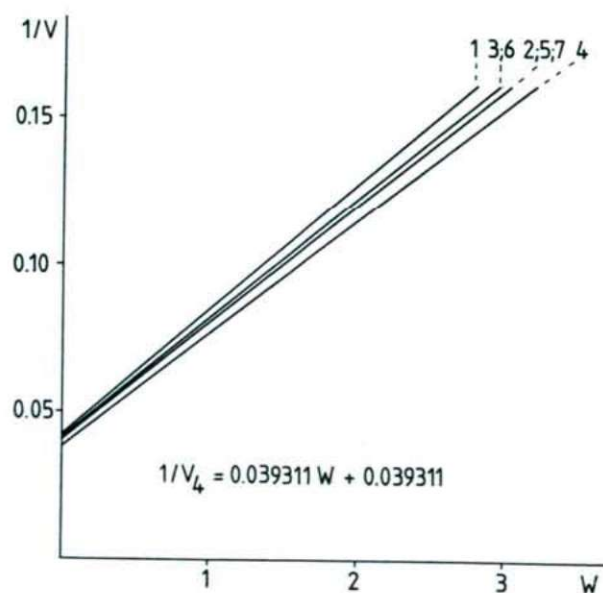


Fig. 2. Regression curves on the basis of the leaf numbers of *Plantago indica*.

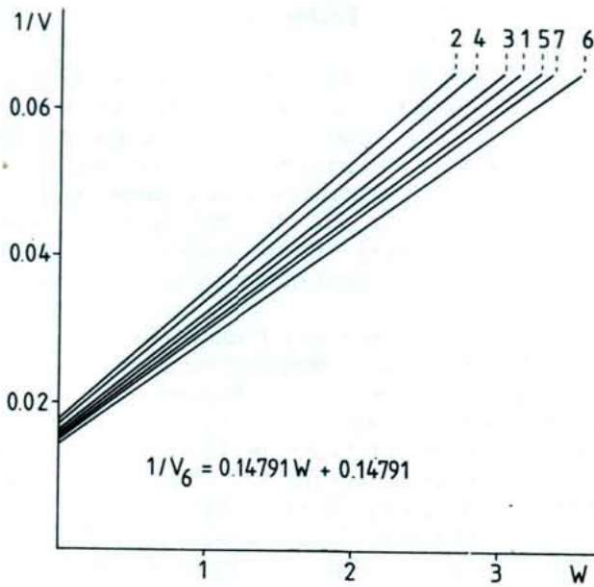


Fig. 3. Regression curves on the basis of the dry masses of *Scabiosa ochroleuca*

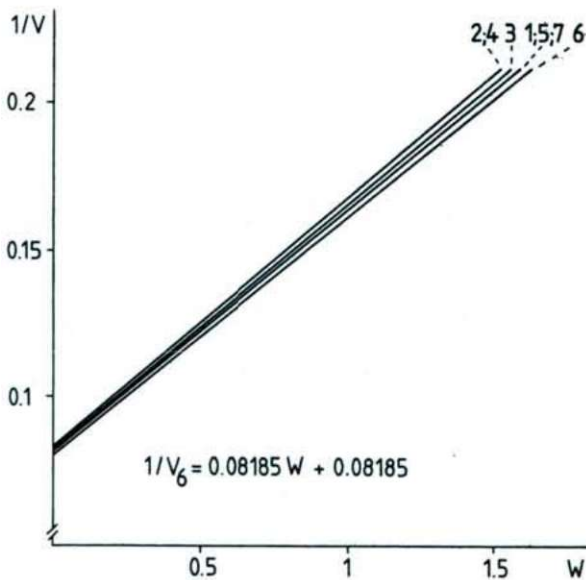


Fig. 4. Regression curves on the basis of the leaf numbers of *Scabiosa ochroleuca*.

Evaluation

The log/log transformation of the plant individuals' dry mass-plant density function is suitable for determining the maximal distance of the interaction of plant species. However, this estimation requiring two regression analyses demands several (8—10) crops of various density, furthermore, it is also necessary for the distance of the plant individuals to be greater than the distance of the interaction in the case of at least two most thinly sown crops. In case when these terms — mainly the latter one — are not fulfilled, the analysis cannot be accomplished since one of the two intersecting straight lines will be lost and thus the sought point of intersection will not be obtained.

The neighbourhood-model is suitable for approaching the maximal distance of competition from few samples. The reciprocal of the average individual weights was illustrated in the function of the W -values calculated on the basis of this model. According to the performed experiments, it can be determined that it was that d_{\max} distance grade which approximated the competitive distance the best, in which the correlation of the regression curve was the best. However, the question can firstly be decided by where the V_{\max} value is the highest.

In the case of *Scabiosa ochroleuca* the correlation coefficient was the greatest at $d_{\max}=2.5$ cm, but not the V_{\max} -value. The log/log transformation also supports the $d_{\max}=5.0$ cm approach.

In the case of *Plantago indica* the maximum of both values coincided, and the approached distance was 4.5 cm.

The distance at which the individuals of a plant population of given age start to show interaction can also be approached from small number of samples. In such case that distance grade should be determined where the dry mass — or other density-dependent parameter — of the average plant individual assumes maximal value. In such manner the analysis can be performed in the case of populations of various distribution type, nevertheless the individuals of the population are required to be of the same age.

The behaviour of the two species having various phenological rhythm was rather similar in the first two phenophases. During the time of the experiment self-thinning was not experienced at either of the populations, the competitive interaction manifested in the volume of the average dry mass and the average leaf count of the individuals of crops of various density.

Their reproductive allocation would presumably also similarly reflect the density dependence of the interaction, using monoculture furtheron.

Nevertheless, under natural circumstances the members of the plant communities at the sandy grasslands regulate each others density by comprehensive interactions, the effect of which could be measured best in the ratio of the reproductive organs. Further studies are necessary, however, to be able to answer these questions.

References

- HARPER, J. L. (1977): Population biology of plants — Academic Press, London, 151—235.
KIRA, T., OGAWA, H. and SHINOZAKI, K. (1953): Intraspecific competition among higher plants. I. Competition-density-yield inter-relationship in regularly dispersed populations. — J. Inst. Polytech. Osaka Cy. Univ. D. 4, 1—16.

- KÖRMÖCZI, L. (1983): Correlations between the zonation of sandy grasslands and the physico-chemical condition of their soil in Bugac — *Acta Biol. Szeged.* 29, 117—127.
- MACK, R. N. and HARPER, J. L. (1977): Interference in dune annuals: spatial pattern and neighbourhood effects — *J. Ecol.* 65, 345—363.
- SHINOZAKI, K. and KIRA, T. (1956): Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. — *J. Inst. Polytech. Osaka Cy. Univ.* 7, 35—72.
- WEINER, J. (1982): A neighborhood model of annual-plant interference — *Ecology* 63, 1237—1241.

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