

SPACE RELATIONSHIPS WITHIN POPULATIONS OF ONE OR MORE SPECIES

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De Wit & Ennik (1958) studied competition between plant species which influence each other in a relatively simple way in order to arrive at some useful characteristic for denoting 'competitive power'. An analogy between competition phenomena and the theories underlying exchange processes was noted and on the basis of this analogy a theory was developed which enables many competition phenomena to be described quantitatively. This approach is in many ways connected with other theories which have been more or less independently developed in the field of animal ecology, plant ecology, population genetics, enzyme kinetics and competitive uptake of ions by plants.

An outline of this approach is given in this paper. For full details on the interpretation in relation to plant and animal competition, much more experimental data, and a more comprehensive review of literature the reader is referred to de Wit (1960).

CROWDING FOR THE SAME SPACE AT ONE SPACING

The present theory is mainly based on many results of experiments on competition between barley and oats. The number of barley kernels and oat kernels per unit surface area in a sown mixture are Z_b and Z_o and the total seed number sown is kept constant. Let it be supposed now that the 'spaces' of the field which are occupied by barley (A_b) and by oats (A_o) (at the time O_b and O_o are measured) are in the proportion of

$$A_b : A_o = b_b Z_b : b_o Z_o = k_{bo} Z_b : Z_o,$$

so that the sum of these two spaces is constant and arbitrarily chosen to be one.

The fraction of the total space occupied by barley is now

$$A_b = k_{bo} Z_b (k_{bo} Z_b + Z_o)^{-1}$$

and by oats

$$A_o = Z_o (k_{bo} Z_b + Z_o)^{-1}.$$

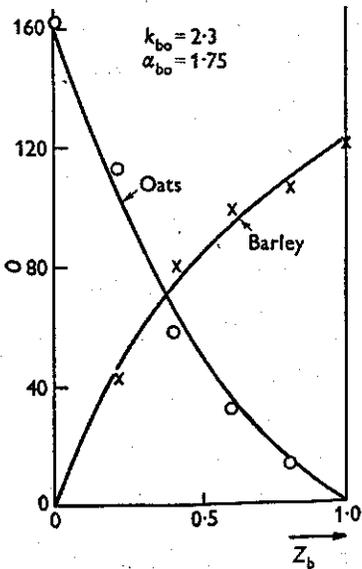
The number k_{bo} ($= b_b b_o^{-1}$) is called the relative crowding coefficient of barley with respect to oats and is supposed to be independent of the relative seed frequency.

These equations define mathematically the term 'crowding for the same space'. The physiological background of this term can only be worked out by studying the results of experiments. Let it be assumed that the number of harvested kernels of a plant species in the mixture is proportional to the relative space occupied, so the number of harvested seeds of the mixture are equal to:

$$\left. \begin{aligned} O_b &= k_{bo}Z_b(k_{bo}Z_b + Z_o)^{-1}M_b, \\ O_o &= Z_o(k_{bo}Z_b + Z_o)^{-1}M_o, \end{aligned} \right\} \quad (1)$$

in which M_b and M_o are the yields in number of kernels of pure stands of barley and oats, respectively.

10⁶ kernels/ha. (a)



(b)

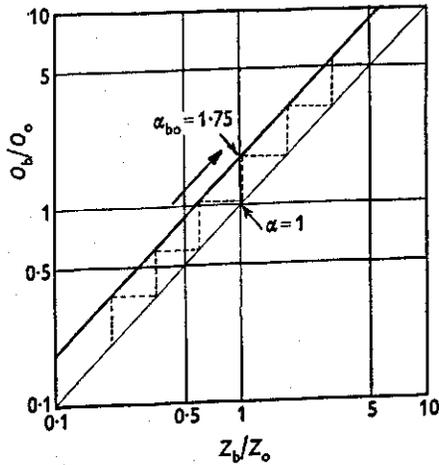


Fig. 1. (Exp. IBS 246—1959.) (a) Crowding for space between barley and oats at a normal seed rate of 3.2×10^6 kernels/ha. ($= 31 \text{ cm.}^2/\text{kernel}$) $x_b = Z_b/(Z_b + Z_o)^{-1}$. (b) The ratio-diagram for this data. The results at a seed rate of 0.32×10^6 kernels/ha. ($310 \text{ cm.}^2/\text{kernel}$) are $M_o = 102 \times 10^6$ and $M_b = 85 \times 10^6$ kernels/ha., $k_{bo} = 1.2$ and $\alpha_{bo} = 1.02$.

Although here $(Z_b + Z_o)$ is kept constant, similar equations hold if, in a replacement series, $(c_b Z_b + c_o Z_o)$ is kept constant, i.e. if the experiment is carried out in such a way that c_o^{-1} kernels of oats are replaced by c_b^{-1} kernels of barley. The multiplication factors c can be eliminated from all equations by replacing the seed and harvest rates by $Z'_b = c_b Z_b$, $O'_b = c_b O_b$, $M'_b = c_b M_b$, and so on.

The reproductive rate of a species is equal to the number of seeds harvested divided by the number of seeds sown, whereas the relative reproductive rate is equal to the ratio of both and, from equation (1), equals

$$\alpha_{bo} = (O_b/Z_b)(O_o/Z_o)^{-1} = k_{bo}M_bM_o^{-1}. \quad (2)$$

The relative reproductive rate is independent of the composition of the seed mixture.

The results of one of thirty-four experiments are given in Fig. 1. The relative frequencies of barley $z_b [= Z_b(Z_b + Z_o)^{-1}]$ and oats are given along the horizontal axis and the yields of each are shown on the vertical axis of Fig. 1*a*. The curves satisfy equation (1), the value of k_{bo} being 2.3 and of M_b and M_o being 123×10^6 and 162×10^6 kernels/ha., respectively. The relative reproductive rate of barley with respect to oats is, according to equation (2), $[2.3 \times 123/162 =]1.75$. Thus, although the yield of barley in monoculture is lower than the yield of oats, the proportion of barley in a mixture increases because the barley has an advantage as far as crowding for space is concerned (the *Montgomery* effect; cf. Gustafsson, 1951.) The advantage, however, is of small value in pure stands. The curvature of the yield curves is governed by the value of k .

If k equals one, straight lines are obtained. This special case of the model is often used in population genetics. Unless (plant) densities are small, this special case appears to be of small practical value.

From equation (2) it follows that

$$\log O_b O_o^{-1} = \log \alpha_{bo} + \log Z_b Z_o^{-1},$$

so that, the relative reproductive rate being constant, the observations plotted on double logarithmic paper with $Z_b Z_o^{-1}$ and $O_b O_o^{-1}$ along the axes are on a straight line parallel to the diagonal. The value of α_{bo} is then read at the intercept of the line and the vertical at $Z_b Z_o^{-1} = 1$. Such a plot is called the ratio-diagram and the data of Fig. 1*a* is so given in Fig. 1*b*. The number of steps of the broken line in this figure corresponds to the number of generations necessary for a given shift in the composition of the mixture.

The equations (1) may be formally extended to cases where n species compete with each other, the yield of the j th species being given by:

$$\left. \begin{aligned} O_j &= b_j Z_j \left(\sum_{k=1}^n b_k Z_k \right)^{-1} M_j, \\ \sum_{k=1}^n Z_k &= \text{constant}, \end{aligned} \right\} \quad (3)$$

in which the n coefficients b , of which $(n-1)$ are independent, are used instead of the relative crowding coefficients $k_{jk} = b_j b_k^{-1}$ for reasons of symmetry.

THE INTERPRETATION OF EXPERIMENTS
ON SPACING

The equations (1) may be applied also to the situation where diseased plants crowd for space with healthy plants. Very diseased seeds do not germinate at all so that under such conditions competition experiments between healthy and diseased plants degenerate into a spacing experiment of healthy plants only. For reasons of continuity it is to be expected that the result of a spacing experiment can be described also by means of one of the equations (1), which needs some rearrangement before application.

In equation (1) barley (b) is supposed to be the 'growing species', and oats (o) the 'non-growing' species. The second equation vanishes and the first may be written as follows:

$$O_b = k_{b0}Z_b(k_{b0}Z_b + Z_o)^{-1}M_b = k_{b0}Z_b[k_{b0}Z_b + (m^{-1} - Z_b)]^{-1}M_b,$$

because $Z_b + Z_o = \text{constant} = m^{-1}$,

i.e.
$$O_b = [m(k_{b0} - 1) + m][m(k_{b0} - 1) + 1/Z_b]^{-1}M_b.$$

By putting $1/Z_b = s$ or the surface allotted to one seed, $O_b = M_s$ or the yield at a spacing s , $m(k_{b0} - 1) = \beta$ (which is independent of m) and $M_b = M_m$ or the yield at a spacing m . It is found that

$$M_s = \frac{\beta + m}{\beta + s} M_m = \frac{\beta}{\beta + s} \Omega. \quad (4)$$

The constant Ω is the extrapolated yield at an infinite seed density. The extrapolated yield of one seed growing wide apart from other seeds is equal to

$$(M_s)_{s \rightarrow \infty} = \beta \Omega, \quad (5)$$

and β is a constant which is numerically equal to the spacing at which the yield is the half of Ω .

According to equation (4) the following relation holds:

$$\beta + s = \beta \Omega M_s^{-1}. \quad (6)$$

Hence, if the inverse of the yield of a spacing experiment is plotted against the space per seed (or the inverse of the seed rate) a straight line is obtained.

A spacing experiment with oats and with peas was carried out with seed rates ranging from 0.125 to 10 times the normal spacing which was 31 cm.²/kernel for oats and 139 cm.²/kernel for peas. The seed and harvest rates of peas are expressed in pea-units, one kernel of peas being equal to $[139/31 =] 4.5$ pea-units, to simplify comparison of the relations.

In Fig. 2 the inverse of the harvest rate expressed in cm.² per oat-kernel or pea-unit is plotted against the inverse of the seed rate expressed in

similar units. The observations indeed lie on a straight line up to a spacing of 0.5 times the normal spacing. The normal spacings, the yields of which are determined on a larger number of plots, are represented by large symbols. The value of Ω is the inverse of the intercept of the straight line with the vertical axis and appears to be 1.35 oat-kernel/cm.² and 1.32 pea-units/cm.² The values of β are read at the intercept with the horizontal axis and are 580 cm.²/oat-kernel and 100 cm.²/pea-unit. The yield of one

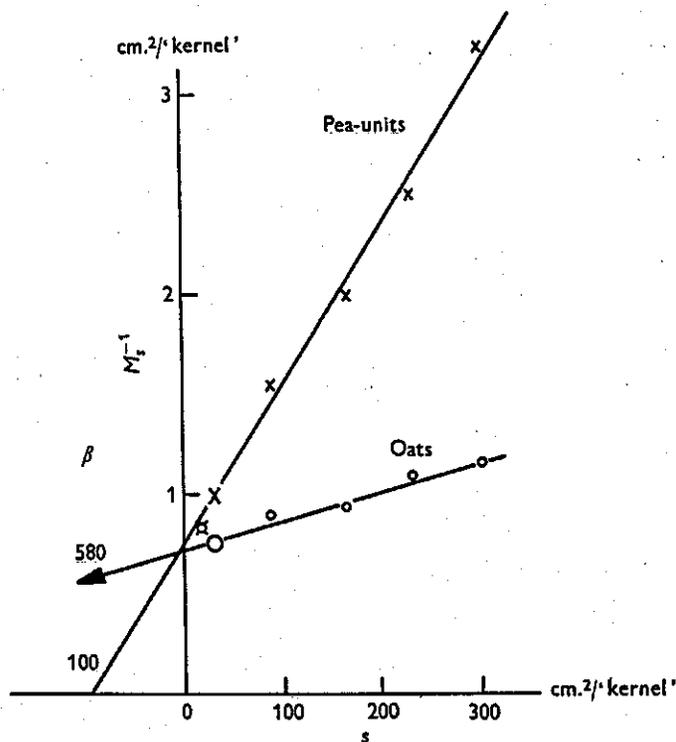


Fig. 2. (Exp. IBS 245—1959.) The results of a spacing experiment with peas (1 pea-kernel \equiv 4.5 pea-units) and oats. The lines satisfy the equations. $M = 580(580 + s)^{-1}/1.35$ oat-kernels/cm.² and $M = 100(100 + s)^{-1}/1.32$ pea-units/cm.²

oat-kernel or one pea-unit planted wide apart from other seeds is equal to the product $\beta\Omega$ or, apart from different units along the axis, the cotangents of the slopes of the lines, that is 780 oat-kernels and 132 pea-units.

Seed rates higher than two times normal are not plotted because these deviate from the line, there being always a threshold density beyond which the plants leave each other such a small space that normal development is not possible and yield depressions occur. By plotting the data in the normal way, the reader may satisfy himself that the normal type of 'saturation curve' is obtained.

LOGISTIC GROWTH

Let it be supposed that the harvest in one year is re-sown quantitatively the next year under the same conditions, so that the spacing formula (4) is valid.

The relation between the yield in the $(t+1)$ th year (M_{t+1}) and the t th year (M_t) is then given by

$$M_{t+1} = \beta(\beta + M_t^{-1})^{-1}\Omega. \tag{7}$$

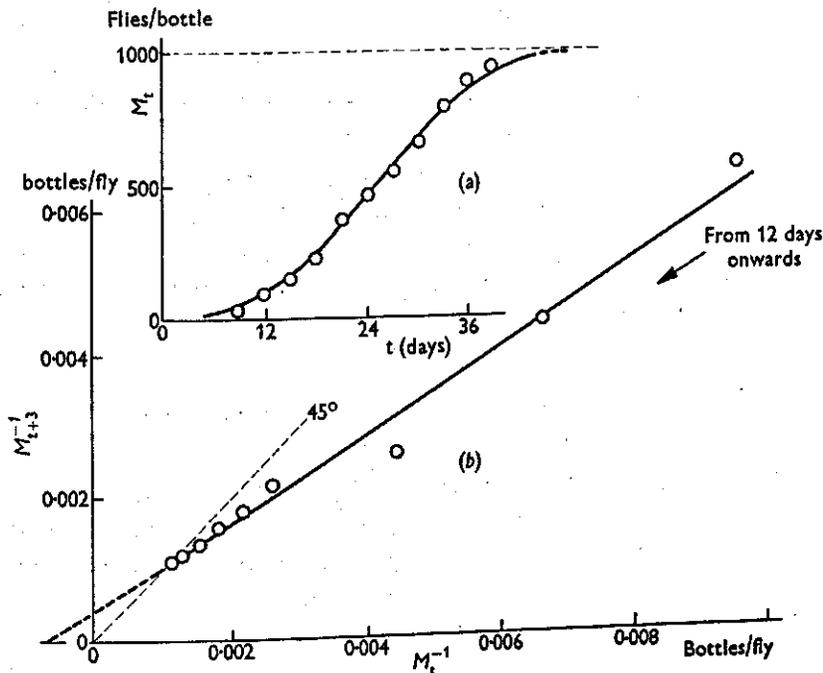


Fig. 3. The growth of a *Drosophila* population, plotted (a) as a growth curve, and (b) treated as a spacing experiment (data of Pearl, 1930).

The differential equation of logistic population growth is

$$dM_t/dt = rM_t(K - M_t)K^{-1}, \tag{8}$$

in which r is the coefficient of increase if ample space is available, K the maximum or equilibrium yield and M_t the yield at time t . Solving this differential equation and substituting

$$\left. \begin{aligned} \Omega &= K e^{r\Delta t} (e^{r\Delta t} - 1)^{-1}, \\ \beta &= (e^{r\Delta t} - 1) K^{-1}, \end{aligned} \right\} \tag{9}$$

the following relation is obtained:

$$M_{t+\Delta t} = \beta(\beta + M_t^{-1})^{-1}\Omega, \tag{10}$$

in which $M_{t+\Delta t}$ and M_t are yields at times in interval Δt apart. This relation is identical with equation (7), so that the present spacing formula is a solution of the differential equation of logistic growth.

The result of one of the well-known experiments of Pearl (1930) on growth of *Drosophila* populations is given in Fig. 3a. The inverse of the number of flies on the t th day is plotted against the inverse of the number of flies on the $(t+3)$ th day in Fig. 3b. The observations are indeed on a straight line. The equilibrium density K is given by the inverse of the value read at the intercept of the experimental line and the diagonal (broken line in Fig. 3b). It follows from the formulae that

$$K = \Omega - \beta^{-1} \quad \text{and} \quad \beta\Omega = e^{r\Delta t}. \quad (11)$$

It is well known that the logistic model is only applicable in animal ecology if the conditions are rigidly simplified. In contrast, it appears that an analogous model is of far greater value in plant ecology. The main reason for this difference is that in spacing experiments the experimental conditions are far less complicated. It may be worth while to carry out spacing experiments with animals which are of a similar design as spacing experiments with plants.

CROWDING FOR THE SAME SPACE AT DIFFERENT SPACINGS

Equation (3) describes the result of crowding for the same space between species at constant spacing. It may be supposed here again that one of the n species in equation (3) does not germinate to obtain an equation which should describe the result of crowding for the same space over a range of spacings. The following relation is then obtained:

$$\left. \begin{aligned} O_j &= \beta_j Z_j \left(1 + \sum_{k=1}^n \beta_k Z_k \right)^{-1} \Omega_j, \\ j &= 1, 2, \dots, n, \end{aligned} \right\} \quad (12)$$

in which Ω and β are the same constants as in equation (4), and β and Z are expressed in such units that their product is without dimension.

The relative reproductive rate of the k th species with respect to the j th species is

$$\alpha_{kj} = (\beta_k \Omega_k) (\beta_j \Omega_j)^{-1}, \quad (13)$$

which is independent of the seed rate of any species. It is recalled that the product $\beta\Omega$ is equal to the yield of one seed when planted alone.

The relative crowding coefficient of equation (1) is equal to

$$k_{jk} = \left(1 + \beta_j \sum_{l=1}^n Z_l \right) \left(1 + \beta_k \sum_{l=1}^n Z_l \right)^{-1}, \quad (14)$$

and approaches therefore to one with decreasing seed rate. The most extreme value ($\beta_j \beta_k^{-1}$) would be reached at an infinite seed rate but for the fact that the whole relation breaks down at very high seed rates.

The present formulae contain only constants calculated from seed rate and final harvest data. If it is found, for instance, by means of spacing experiments that the product $\beta\Omega$ is the same for two plant species, it may be concluded from equation (12) that the relative reproductive rate is one and independent of the seed rate of the mixture. It is, however, perfectly possible that one of the species is earlier in its development than the other and occupies already a large part of the available space at the time that the other begins its grand period of growth. As a consequence the relative reproductive rate of the earlier species is larger than that calculated from the spacing experiments, and this is more so at closer spacings. Equation (13) can hold, therefore, only if the ratio $(\beta_k \Omega_k)(\beta_j \Omega_j)^{-1}$, as measured by periodic harvests of spacing experiments, remains practically constant during the whole period of growth; that is, if the growth curves are practically synchronous and similar.

At first sight this seems a necessary condition for two species affecting each other only by crowding for the same space. This appears to be, however, not the case. Two species may crowd for the same space if their growth curves are synchronous but not similar. Equation (13) is under these conditions not valid, but equations (1) and (4) still hold, because the period during which the space is actually claimed may be assumed practically independent of the relative seed frequency as long as the total seed rate is kept constant. These two situations are best illustrated by examples.

On the same field as the spacing experiments of Fig. 2 were carried out, peas (1 pea kernel = 4.5 pea-units) and oats were grown in competition at different relative frequencies, but at the same spacing of 31 cm.²/oat kernel or pea-unit. Because both plants are annuals and the nitrogen level of the field was high, any complication due to a possible advantageous effect of the nitrogen which may be fixed in the nodules of the pea roots on the growth of oats was absent.

The results (Fig. 4) were mathematically treated according to equation (1). The fit is such that it must be concluded that oats and peas affect each other only by crowding for the same space. The relative reproductive rate of oats with respect to pea-units (α_{po}) is here equal to 0.16. This value, α_{po} , can be calculated independently from the results of the spacing experiments presented in Fig. 2, by taking the ratio of the products $\beta\Omega$ (equation 13). This ratio was 0.17. Since the values of α_{po} calculated in both ways were similar, it may be concluded that equations (12) validly represent competition between oats and peas in this experiment.

EBS XV

Barley and oats affect each other also only by crowding for the same space, as is to be concluded from the data presented in Fig. 1. However, the relative reproductive rate of barley with respect to oats (α_{bo}) appears to be 1.75 at a spacing of 31 cm.²/kernel and 1.02 at a spacing of 310 cm.²/kernel, whereas α_{bo} as calculated from spacing experiments with these crops on the same field is 1.04. (These latter data are not reported in full.) The value of α_{bo} at the wide spacing is equal to the value calculated from the

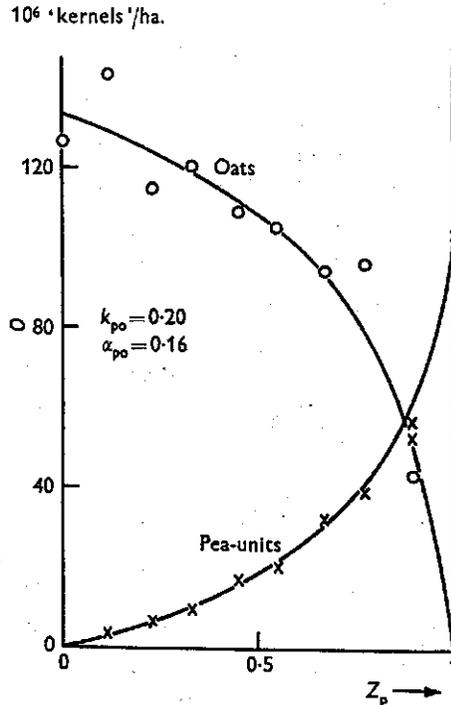


Fig. 4. (Exp. IBS 245—1959.) Crowding for space between oats and peas (1 pea-kernel \equiv 4.5 pea-units) at a spacing of 31 cm.²/oat-kernel or pea-unit.

spacing experiment, but at the narrow spacing considerably higher. The reason for this difference is that, although barley and oats crowd for the same space, their growth curves are not similar. Barley develops earlier in the season and is, therefore, at an advantage at closer spacings.

THE LOTKA-VOLTERRA EQUATIONS OF COMPETITIVE GROWTH

By combining equations (11) and (13) it is found that the relative reproductive rate of two species in the time interval Δt is equal to:

$$\alpha_{12} = (O_1^{(t+\Delta t)}/O_1^{(t)})(O_2^{(t+\Delta t)}/O_2^{(t)})^{-1} = e^{(r_1-r_2)\Delta t} \quad (15)$$

in which r is the coefficient of increase, and $O^{(t)}$ and $O^{(t+\Delta t)}$ the yields at the times t and $t+\Delta t$.

Volterra (1928) supposed that the growth of two populations growing on the same food may be governed by

$$\left. \begin{aligned} dO_1^{(t)}/dt &= [r_1 - \gamma_1(h_1 O_1^{(t)} + h_2 O_2^{(t)})] O_1^{(t)}, \\ dO_2^{(t)}/dt &= [r_2 - \gamma_2(h_1 O_1^{(t)} + h_2 O_2^{(t)})] O_2^{(t)}, \end{aligned} \right\} \quad (16)$$

in which r is the coefficient of increase and $r(\gamma h)^{-1}$ the maximum or equilibrium density of the species under the conditions of growth. A partial solution of this set of differential equations is

$$O_2^\gamma O_1^{-\gamma_2} = e^{(r_1 \gamma_1 - r_2 \gamma_2)t} \text{ constant}, \quad (17)$$

which after introducing an arbitrary time interval Δt may be rewritten as follows:

$$(O_1^{(t+\Delta t)} / O_1^{(t)})^{\gamma_1} (O_2^{(t+\Delta t)} / O_2^{(t)})^{-\gamma_2} = e^{(r_1 \gamma_1 - r_2 \gamma_2) \Delta t}. \quad (18)$$

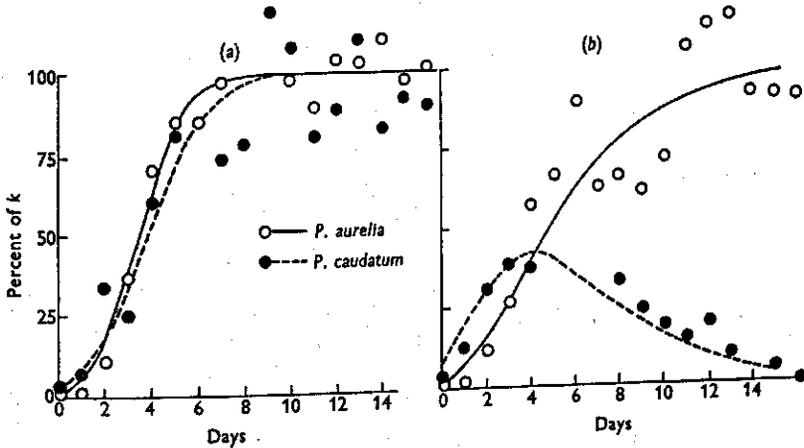


Fig. 5. The growth of *Paramecium aurelia* and *P. caudatum* (a) alone, and (b) in competition (data of Gause, 1934).

Equations (15) and (17) are the same, if it is supposed that Volterra's constants γ_1 and γ_2 are both equal to one. Equations (12) are therefore solutions of simplified ($\gamma = 1$) Lotka-Volterra differential equations if yields at the times t and $t+\Delta t$ are substituted for Z and O , respectively.

The well-known growth curves of *Paramecium caudatum* and *P. aurelia* as determined by Gause (1934) under constant conditions are given in Fig. 5(a) on a percentage basis. The coefficients of increase (r) and equilibrium yield (K) as calculated by Gause (1934) under the supposition of logistic growth are 1.124 day^{-1} and $245 \text{ individuals}/0.5 \text{ cm}^3$ for *P. aurelia* and 0.704 day^{-1} and $64 \text{ individuals}/0.5 \text{ cm}^3$ for *P. caudatum*.

The values of β and Ω for the two species for periods of two days can be calculated by substituting the above values in equations (9). By

substituting these values of β and Ω in equation (12) the following relations between the number of individuals at time t and $t + 2$ as a percentage of the equilibrium density are obtained:

$$\left. \begin{aligned} O_a^{(t+2)} &= 0.085 O_a^{(t)} (0.085 O_a^{(t)} + 0.039 O_e^{(t)} + 1)^{-1} 112 \quad (\text{for } P. \textit{aurelia}), \\ O_e^{(t+2)} &= 0.039 O_e^{(t)} (0.085 O_a^{(t)} + 0.039 O_e^{(t)} + 1)^{-1} 126 \quad (\text{for } P. \textit{caudatum}). \end{aligned} \right\} (19)$$

Gause cultivated the same species in competition under the same conditions. These results are, again on a percentage basis, given in Fig. 5*b*. It is seen that at the fifth day the yield of *P. aurelia* is about 52% and of *P. caudatum* about 40% of the maximum. These values are substituted in equation (19) to calculate the yields at $(5+2)$ and $(5-2)$ days, and these yields are again used to calculate the yields at $(5+4)$ and $(5-4)$ days and so on. The resulting calculated growth curves for the two species are given in Fig. 5*b*. As far as the observations go, the agreement between the observations and the calculated growth curves is reasonable.

THE RELATIVE REPRODUCTIVE RATE OF PERENNIAL GRASSLAND SPECIES

The relative reproductive rate of two seed-producing species as barley and oats can be calculated from the composition of a sample of the seed mixture in two subsequent winters. Likewise the relative reproductive rate of two perennial species can be calculated from observations during the winter rest period. The yield during the growing period gives in principle no information because the harvested parts of the plant are lost.

It appeared that the number of tillers of grass per unit surface is a reasonable measure of the amount of grass present in winter and the length of the stolons per surface unit a good measure of the amount of clover present in winter.

The relative reproductive rate of one grass species with respect to another, or a grass species with respect to clover, is thus obtained by plotting in a ratio diagram (as in Fig. 1*b*) the ratio of the number of tillers of both species in the first winter against this ratio in the second winter or by doing the same for the ratio between the length of the stolons of clover and the number of tillers of grass. Ennik (1960) and van den Bergh & de Wit (1960) carried out some experiments on this basis in a phytotron where mixtures were grown in containers and winter treatments of one month and summer treatments of two months were given.

The result of an experiment with *Anthoxanthum odoratum* and *Phleum pratense* is given in Fig. 6. The relative reproductive rate differs slightly from one in this case and is independent of the ratio between the two

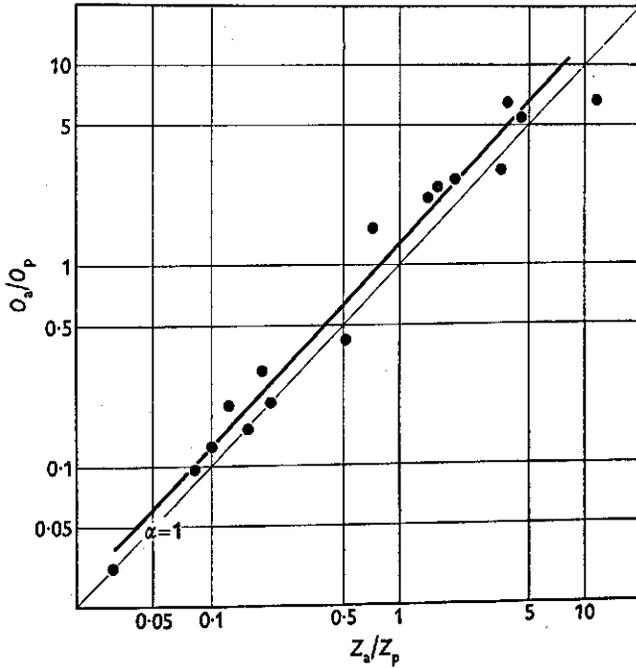


Fig. 6. The ratio-diagram of *Anthoxanthum odoratum* and *Phleum pratense*, grown in containers in a phytotron. $Z_a Z_p^{-1}$ and $O_a O_p^{-1}$ are the ratios of the number of tillers of *A. odoratum* and *P. pratense* at the end of the first and the second winter treatment, respectively (data of van den Bergh & de Wit, 1960).

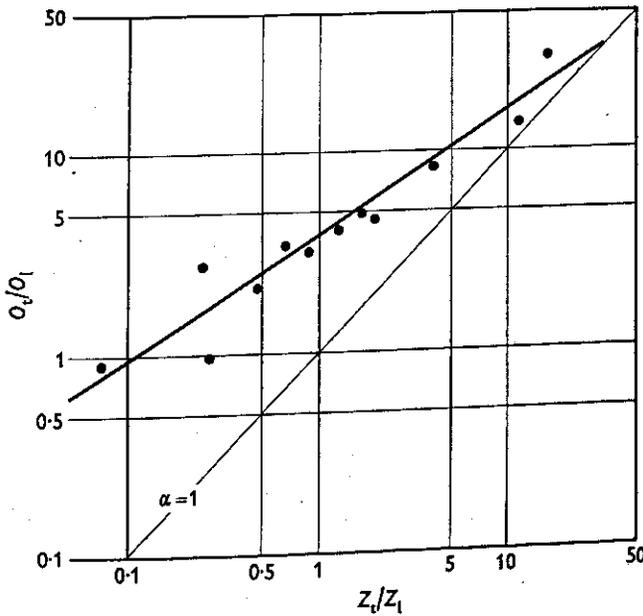


Fig. 7. The ratio-diagram of *Lolium perenne* and *Trifolium repens*, grown in containers in a phytotron. $Z_t Z_l^{-1}$ and $O_t O_l^{-1}$ are the ratios of the length of stolons of *T. repens* and the number of tillers of *L. perenne* at the end of the first and second winter treatment, respectively (data of Ennik, 1960).

species. Hence it must be concluded that these two species affect each other only by crowding for the same space.

The result of Ennik's experiment with *Trifolium repens* and *Lolium perenne* is given in Fig. 7. It appears that the observations are arranged around a line with a slope less than 45° so that the relative reproductive rate depends on the composition of the mixture. The two species affect each other, therefore, in some other way besides crowding for the same

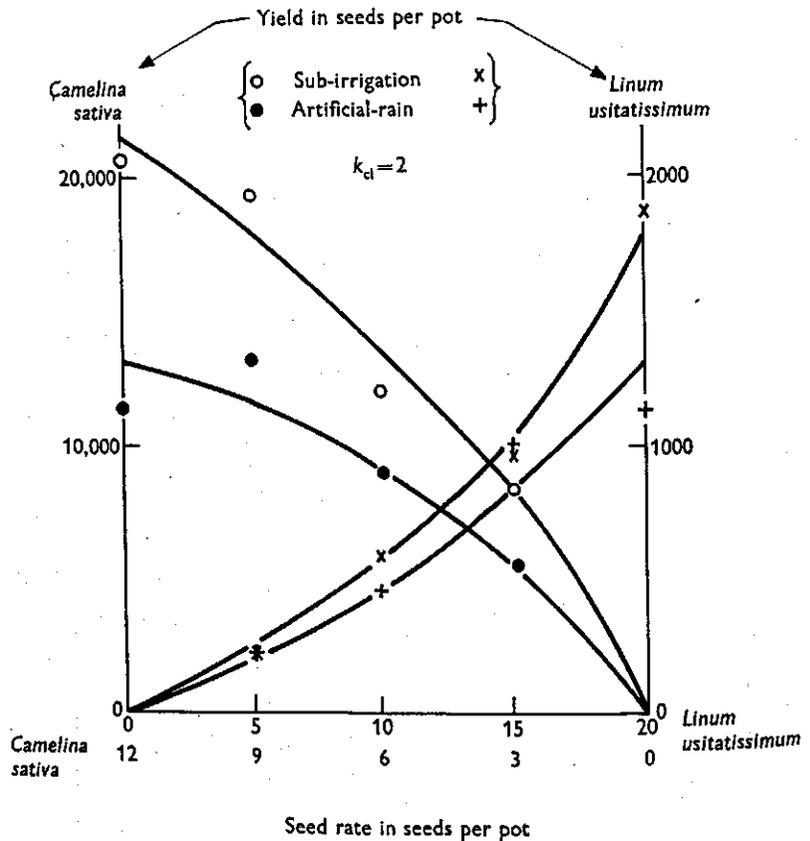


Fig. 8. Crowding for space between *Linum usitatissimum* and *Camelina sativa* grown in containers in a greenhouse and watered by sub-irrigation and by artificial rain.

space. This is here due to the ability of clover to obtain nitrogen from the air and, because the soil nitrogen was low, the clover thereby having a much better nitrogen supply than the grass. It is easily seen that these two species tend to an equilibrium given by the value at the intercept of this line with the diagonal.

The observations are also arranged around a line with a slope less than 45° if the two species affect each other only by crowding for space which is not completely the same for both species. This is, for instance, the case

if one grass species develops mainly early in the season and the other late in the season; part of the space is then used at two different times. It was found, for instance, that the species *Anthoxanthum odoratum* with early growth and *Phleum pratense* (with late growth) tend to an equilibrium under field conditions, whereas this was not so in the phytotron.

Lines with a slope greater than 45° can only be found if the two species hamper each other not only by crowding for space but also by some 'active' process such as producing a toxic substance which restricts the

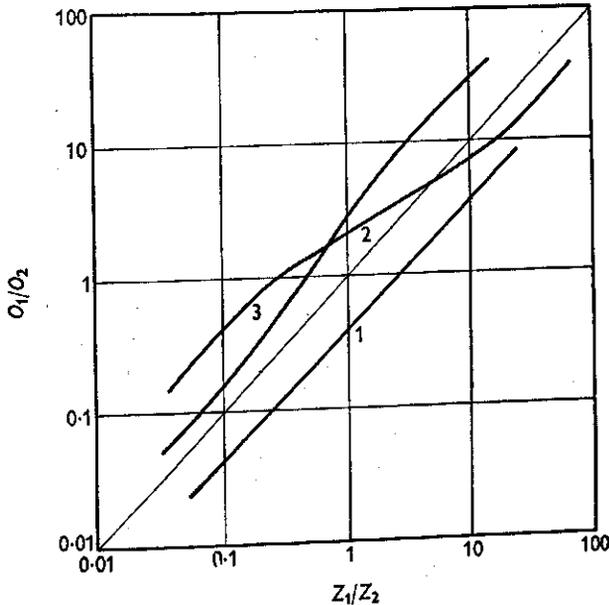


Fig. 9. Examples of types of curves found in a ratio-diagram. $Z_1 Z_2^{-1}$ and $O_1 O_2^{-1}$ are the ratios of the number of plant units of the first and second species after a first and second rest period, respectively (for explanation, see text).

growth of the other species. According to Grümmer (1958; p. 226 of this volume), the yield of flax (*Linum usitatissimum*) is adversely affected by some toxic substance produced by false flax (*Camelina sativa*),* especially under conditions where the mixtures of both plants are subjected to rain. We have carried out experiments where both crops were grown in Mitscherlich containers in a greenhouse at different proportions, one series being watered by sprinkling and the other by sub-irrigation. The result of this experiment is given in Fig. 8. The curves in the figure satisfy equation (1), the observations do not show any systematic deviations from these curves, and the relative crowding coefficients were the same for both treatments. Hence, the toxic effect, if any, was too small to be shown in this way.

* Grümmer maintains that *Camelina alyssum* is far more toxic to flax than is *C. sativa*—
Editor.

In both water treatments, the relative crowding coefficient of false flax with respect to flax is 2, in spite of the fact that the seed rates are chosen such that five seeds of flax are replaced by only three seeds of false flax. False flax is, therefore, a very serious weed apart from any toxic effect it may have. The yields of both crops were lower where the plants were subjected to artificial rain, but this does of course not prove the existence of toxic substances.

It is shown (de Wit, 1960) that the observations from associations where species affect each other not only by crowding for the same space are arranged around the S-shaped curve, with its ends parallel to the diagonals. Some examples are given in Fig. 9. For a full mathematical treatment of the data in these, the reader is referred to Ennik (1960), van den Bergh & de Wit (1960) and de Wit (1960).

SUMMARY

A mathematical treatment of crowding for the same space within populations of one or more species is given and illustrated by means of experimental results mainly with species of plants. A preliminary analysis can be based on the ratio-diagram, in which the ratio of the number of two species at the beginning of a suitable time interval is plotted against this ratio at the end of this time interval on double logarithmic paper.

The models of the systems which have been studied may be classified as follows:

Model I

This simplest model of competition occurs if the (absolute) reproductive rate of each individual of each species is independent of the relative frequency of the species and the density. The relative crowding coefficient is then at any seed density equal to one. Unless seed densities are very small, this model is of little practical importance, although many calculations in population genetics are based thereon.

Model II

The observations in the ratio-diagram are, independent of the seed density, on the same straight line parallel to the diagonal (Fig. 9, curve 1). The species influence each other only by crowding for the same space; they grow synchronously and have similar growth curves (e.g. oats and peas).

Model III

The observations in the ratio diagram are at constant density on the same line parallel to the diagonal, the position of this line depending on the

seed density. The species influence each other only by crowding for the same space; they grow synchronously but do not have similar growth curves (e.g. barley and oats).

Model IV

The observations in the ratio-diagram are on a line with a slope smaller than 45° , even at the same seed density (Fig. 9, curve 2). A stable equilibrium may result if this line intercepts the diagonal. This model occurs if: (a) one species profits from the presence of the other (e.g. grass and clover); (b) the species affect each other only by crowding for space, this space being not completely the same for both species. This is always so if the growth curves are not synchronous (e.g. *Anthoxanthum* and *Phleum* under field conditions).

Model V

The observations in the ratio-diagram are on a line with a slope greater than 45° , even at the same seed density (Fig. 9, curve 3). An unstable equilibrium results if this line intercepts the diagonal. This model may occur if one species hampers the growth of others, not only by crowding for space but also by some 'active' process such as producing a toxic substance. Examples are not known.

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