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COMPETITION AND NON-PERSISTENCY AS FACTORS AFFECTING THE COMPOSITION OF MIXED CROPS AND SWARDS

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Summary. An outline of a theory on competition between plants within mixed crops and swards is given. Five models of competition are distinguished and situations which lead to non-persistency of plants are discussed. Experiments on competition between barley and oats, two grass species, grass and clover, and crop and weeds are discussed as examples of some models of competition.

Résumé. On expose les grandes lignes de la théorie sur la rivalité entre les plantes dans les récoltes mélangées et l'herbe. On choisit cinq modèles de rivalité et on discute les circonstances différentes, causes du manque de persistance des plantes.
Des expériences sur la rivalité entre l'orge et l'avoine, deux espèces d'herbe, l'herbe et le trèfle, et entre la bonne herbe et la mauvaise sont discutées, comme exemples de quelques modèles de rivalité.

Zusammenfassung. Die Theorie des Wettbewerbs zwischen den Pflanzen eines gemischten Standes oder Rasens wird in grossen Umrissen aufgezeichnet. Es sind fünf verschiedene Formen des Wettbewerbs gefunden worden und es werden die Bedingungen besprochen, die zu der mangelnden Lebensfähigkeit der Pflanzen führen.
Versuche über Wettbewerb zwischen Gerste und Hafer, zwei Grasarten, Gras und Klee, Nutzpflanzen und Unkraut werden als Beispiele gewisser Wettbewerbsformen besprochen.

Introduction

At this Institute competition phenomena have been successfully approached from a theoretical view-point in recent years (De Wit and Ennik, 7; De Wit, 5; Reestman and De Wit, 4; De Wit, 6; Van den Bergh and De Wit, 1; Ennik, 2).

Some basic aspects of these studies are presented in this paper. Experiments were carried out either in the field or in containers in the glasshouse or climate chambers. The technique of studying different plant combinations side by side in one period has been used, rather than following the history of one mixture in course of time.

Competition between barley and oats

The present theory is based on many results of experiments on competition between barley and oats.

If the numbers of barley kernels and oat kernels in a sown mixture are Z_b and Z_o, and the total seed number sown is (Z_b+Z_o) and is kept constant, then the relative frequencies of barley and oats in the sown mixture are $z_b = \frac{Z_b}{Z_b+Z_o}$ and $z_o = \frac{Z_o}{Z_b+Z_o}$, respectively. Suppose a barley plant surrounded by oat plants occupies a space which is k_{bo} times the space of a barley plant surrounded by barley plants. The proportion of the total space that is occupied by barley will be $A_b = \frac{k_{bo}z_b}{k_{bo}z_b+z_o}$, while the oat plants of the same mixture will occupy $A_o = \frac{z_o}{k_{bo}z_b+z_o}$. The number k_{bo} is called the relative crowding coefficient of barley with respect to oats.

These equations are mathematical expressions of the statement that the 2 species affect each other only by crowding for the same space. For space may be read growth factors which are homogeneously distributed over, and in, the field where the mixture grows.

If the number of harvested kernels of one plant species of the mixture is proportional to the relative space occupied, then the number of harvested seeds of the mixture will be:

$$O_b = A_b M_b = \frac{k_{bo}z_b}{k_{bo}z_b+z_o} M_b \text{ (barley)}$$
$$O_o = A_o M_o = \frac{z_o}{k_{bo}z_b+z_o} M_o \text{ (oats)} \quad [1]$$

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

The reproductive rate of a species is equal to the number of seeds harvested divided by the number of seeds sown. The relative reproductive rate of barley with respect to oats is equal to the ratio of the reproductive rate of barley and oats, and, according to equation [1], equal to

$$\alpha_{bo} = \frac{O_b/Z_b}{O_o/Z_o} = k_{bo}\frac{M_b}{M_o} \quad [2]$$

which is independent of the relative frequency. In fact, the relative reproductive rate is found in experiments to be independent of the relative seed frequency, in spite of the fact that the reproductive rates vary with the relative seed frequency. If the mixture that is harvested is used for seed in subsequent years, the relative frequency of barley increases in course of time if α_{bo} is greater than 1 and decreases if α_{bo} is smaller than 1.

It may happen that the relative reproductive rate of barley is greater than 1, so that the proportion of barley increases, in spite of the fact that the yield of the pure stand of barley is lower than of oats (the Montgomery effect).

The ratio diagram

The constancy of the relative reproductive rate can be shown in a simple way by means of a ratio diagram (Figure 1a) where the ratio Z_b/Z_o (or Z_1/Z_2) of the sown mixture is plotted against the ratio O_b/O_o (or O_1/O_2) of the harvested mixture.

It follows from equation [2] that

$$\log \frac{O_1}{O_2} = \log \alpha_{1\cdot 2} + \log \frac{Z_1}{Z_2} \quad [3]$$

so that, the relative reproductive rate being constant, the observations in the ratio diagram are arranged around a straight line parallel to the diagonal. The number of steps of the 'staircase' drawn in the figure corresponds to the number of generations necessary for a given shift of the composition of the mixture.

For perennial plants like grasses or clovers the reproductive rate may be defined as the ratio of the numbers of tillers, of the amounts of soluble carbohydrates or of the lengths of the stolons, at corresponding stages of 2 consecutive growing cycles or vegetation periods. This has been shown in experiments described below.

Models of competition

MODEL I

The simplest form of competition occurs if 2 species compete for the same space and the relative crowding coefficient at any spacing is equal to 1. In this case the relative reproductive rate is equal to the ratio of the yields of the pure stands, this ratio being independent of the spacing. Examples of this model have not been found although many calculations in population genetics are based thereon.

MODEL II

This model occurs if 2 species affect each other only by crowding for the same space, finish their growth in the same length of time and have similar growth curves.

It appears that under these conditions the relative reproductive rate is independent of the botanical composition of the mixture and the spacing of the 2 species, in spite of the fact that the reproductive rates themselves depend on these factors and both the yields of

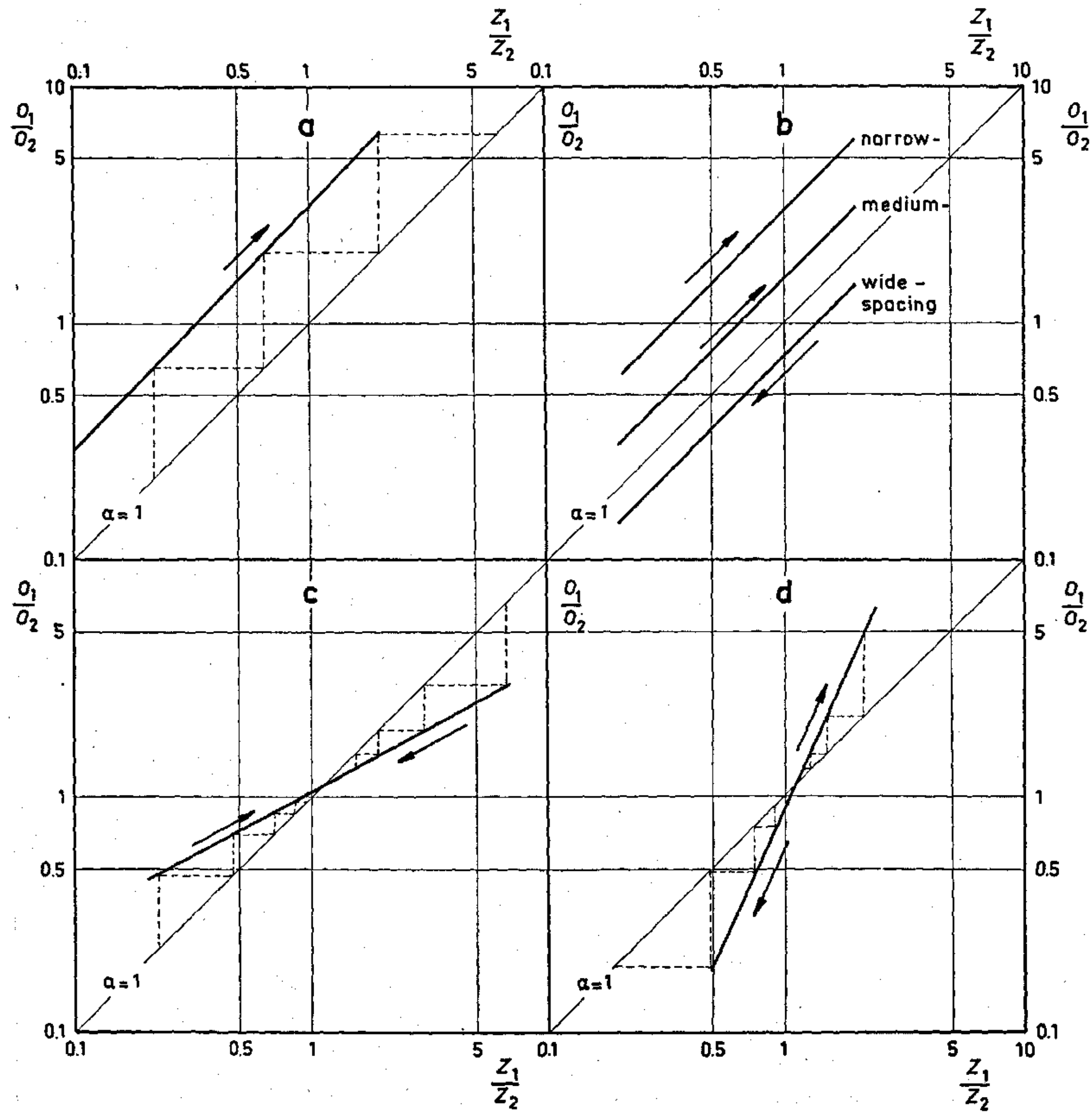

Fig. 1. Ratio diagram showing the ratio of two species sown (Z_1/Z_2) and their ratio in the harvested mixture (O_1/O_2).

the pure stands and the relative crowding coefficient depend on the spacing.

It can be shown that this model occurs if observations at any spacing and composition are found on a line with a slope of 45° in the ratio diagram (Figure 1a). The location of the line in the figure and likewise the value of the relative reproductive rate depend on the growing conditions and the plant species. Examples of this model have been found where 2 strains of the same species compete with each other.

Model III

This more complex model occurs if 2 species having the same growing period crowd for the same space, but have dissimilar growth curves. Under these conditions the relative reproductive rate and the relative crowding coefficient depend on the spacing but are independent of the composition of the mixture.

The relative reproductive rate and the relative crowding coefficient of the earlier-growing species with respect to the later-growing are greater with closer spacings.

The observations for different compositions of the mixture at constant spacing are still found on lines parallel to the diagonal of the ratio diagram, but the lines shift with changing spacings (Figure 1b). The competition between barley and oats can be described with this model. The equations [1] and [2] hold for models I, II and III.

MODEL IV

A very complicated pattern of competition is found if 2 species crowd for space which is not exactly the same for both species. This may occur if some requisite obtained from the soil limits growth and one species can explore the soil to a greater depth than the other. The same applies if one species has a more prolonged growing period. The reproductive rate of a species with such an advantage clearly increases with decreasing relative frequency in the mixture, as does also the relative reproductive rate.

The observations in the ratio diagram are then found on a line or curve with a slope $<45°$. The level of this line or curve may depend again on the spacing, and the line or curve may intersect the diagonal. This point of intersection represents a stable equilibrium (Figure 1c).

Such a stable equilibrium may also be found if one of 2 species, crowding for space, benefits from the presence of the other. This occurs when, say, one species fixes nitrogen or liberates minerals from the soil which can be used by the other or helps to support the other, and so on. Competition between grass and clover is an example of this model.

MODEL V

This model may be expected to occur if one of the species hampers the growth of the other, not only by crowding for space, but also by some process such as the production of toxic substances harmful to the other. The observations in the ratio diagram are then arranged around a line or curve with a slope $>45°$, so that an unstable equilibrium may result (Figure 1d). Examples are not known to us as far as plant species are concerned.

Non-persistency

A species is called non-persistent if it disappears in course of time when planted in a pure stand. This complex phenomenon cannot be treated from one point of view because:

1. The reproductive rate of single growing plants may be less than one.
2. A species may be subject to a decrease of the reproductive rate of single seeds or tillers in succeeding growth cycles. This may be an autonomous ageing process, but it may also be due to accumulation of diseases (virus, etc.) in the successive growth cycles.
3. The reproductive rate may decrease in course of time owing to deterioration of growing conditions (accumulation of diseases in the soil included), if the species is grown for several years on the same field.

To avoid complications due to non-persistency, competition phenomena can be studied by cultivating different compositions of the mixture in one year rather than following the composition of one mixture over a period of time. Another advantage of this technique is that it shortens the duration of the experiment and that difficulties due to year-to-year differences (weather, etc.) are avoided.

Ageing or accumulation of diseases in or on the plant occurs if the relative reproductive rate of seeds or tillers from one generation or growth cycle with respect to seeds or tillers of a subsequent generation or growth cycle is greater than one, even when cultivated on a fresh medium.

Examples of competition

BARLEY/OATS (COMPETITION MODEL III)

The results of 1 of a series of 33 experiments are given in Figure 2. The relative frequency of barley and oats in the sown mixture is given along the horizontal axis and the yields of both are given along the vertical axis. The curves in the figure satisfy equation [1], the value of k_{bo} being 2 and of M_b and M_o being 72×10^6 and 83×10^6 kernels per ha, respectively.

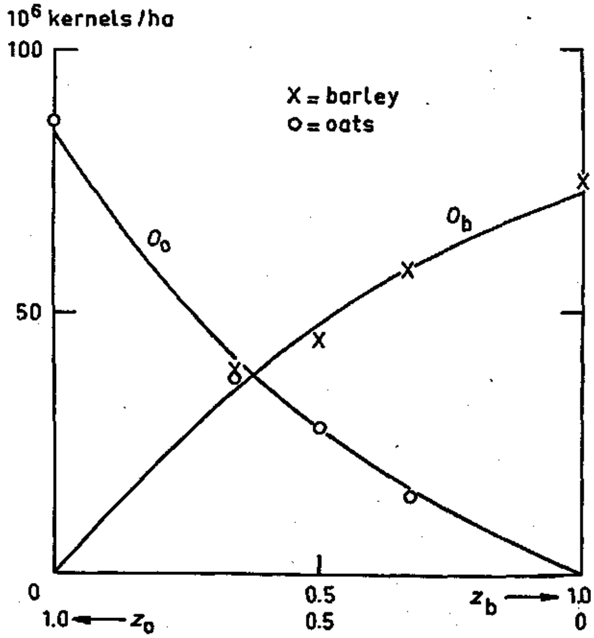

Fig. 2. The relative frequency of barley and oats in a sown mixture (horizontal axis) and yields (vertical axes).

The relative reproductive rate of barley with respect to oats is, from equation [2], equal to

$$\alpha_{bo} = k_{bo}\frac{M_b}{M_o} = 2 \times (72/83) = 1{\cdot}7$$

Thus, although the yield of barley in monoculture is lower than the yield of oats, in a mixture the proportion of barley relative to oats increases because the barley has an advantage as far as crowding for space is concerned, an advantage which is of small value in pure stands (the Montgomery effect). The curvature of the yield curves is governed by the value of the relative crowding coefficient (k).

Two grass species (competition model II or III)

It has been found that the number of tillers per unit area is a useful basis for calculating the reproductive rate.

An experiment with the species *Anthoxanthum odoratum* and *Phleum pratense* was carried out in climate chambers, mixtures being planted in Mitscherlich containers. To save time and labour, winter and summer treatments were reduced to 1 and 2 months, respectively.

The ratio of the number of tillers of the 2 grass species in the first winter is plotted against the ratio in the second winter in the ratio diagram of Figure 3.

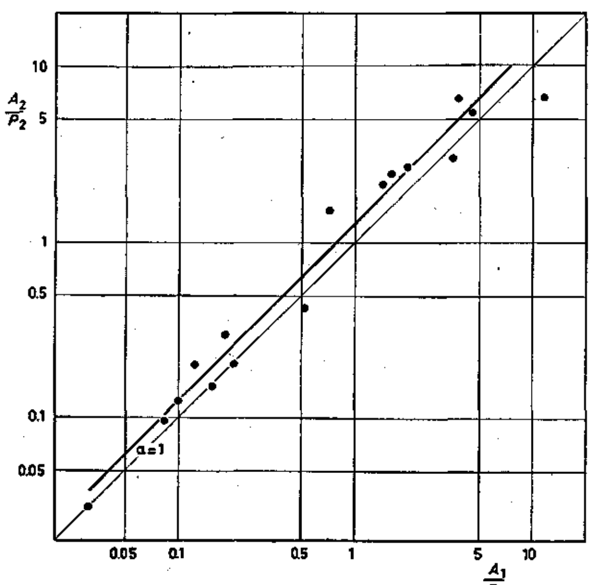

Fig. 3. Ratio of number of tillers of two species in the first winter (A_1/P_1) and in the second winter (A_2/P_2).

It appears that the relative reproductive rate of 1·3 is constant, so that these 2 grass species affect each other only by crowding for the same space under these conditions. The relative crowding coefficient of *Anthoxanthum* with respect to *Phleum* was found to be 0·82 and the numbers of tillers at the end of the cycle were 475 and 300 for *Anthoxanthum* and *Phleum* respectively.

In this case *Anthoxanthum* increases with time, in spite of the fact that the relative crowding coefficient of this species with respect to *Phleum* is less than 1.

Grass/clover (competition model IV)

A similar experiment was carried out with *Lolium perenne* and *Trifolium repens*. For the grass the number of tillers per unit area and for the clover the length of the stolons per unit area were used as a basis for calculating the relative reproductive rate.

The ratio of the length of stolons and the number of tillers in the first winter is plotted against this ratio in the second winter in the ratio diagram of Figure 4. One curve holds for a high light-intensity (6×10^4 ergs $cm^{-2}sec^{-1}$ from HPL 400w lamps) and the second curve for a low light-intensity (3×10^4 ergs $cm^{-2}sec^{-1}$ from TL-33 tubes).

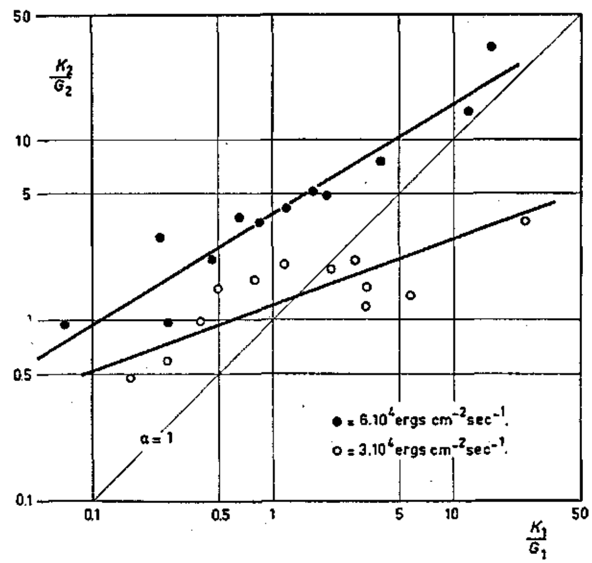

Fig. 4. Ratio of the lengths of stolons of *T. repens* to number of tillers of *L. perenne* in the first winter (K_1/G_1) and in the second winter (K_2/G_2) at 2 light-intensities.

The slope of both lines is $<45°$, probably because the grass benefits from nitrogen fixation by the clover.

The equilibrium point at high light-intensity is at a ratio of 35 cm stolons/number of tillers while at low light-intensity it is at a ratio of 1·5 cm stolons/number of tillers. This illustrates the large effect of light-intensity on the behaviour of clover in a mixture with grass.

Crop/weed (failure of competition model V)

The present approach can also be used to describe the effect of weeds on crop production. It has been supposed by Grümmer (3) that *Camelina* spp. produce some toxic substance which hampers the growth of *Linum* spp. *Linum usitatissimum* and *Camelina sativa* were grown by us at different ratios in Mitscherlich containers in the glasshouse and the number of seeds produced was determined. The result is represented in the ratio diagram of Figure 5. It appears that the observations are found around a line of 45°, with no deviations suggesting a slope $>45°$. There does not seem to be any toxic effect whatsoever.

The effect of different proportions of diseased plants in a healthy crop has been treated in a similar way. In case of non-infectious diseases, the results may be described by means of model II or III, while in cases of infectious diseases model V may be of value.

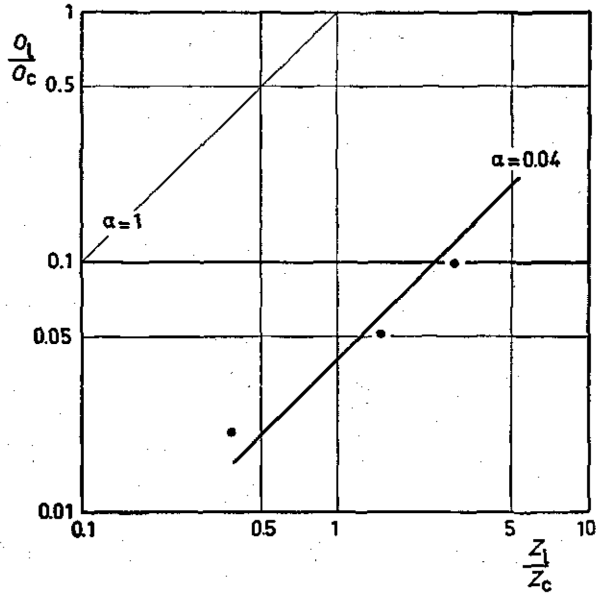

Fig. 5. Ratio of seed production (O_l/O_c) at different seeding ratios (Z_l/Z_c).

Physiological background

The term space as used in the present study on competition stands for the complex of growing factors associated with the space where the plant exists, and can be used without account being taken of the physiological background of growth.

In a further analysis it may be advantageous to consider the physiological processes which govern competition phenomena under different conditions.

Experiments to determine whether competition takes place above or below the soil surface, and the causal factors, have been started. A simple example is given here.

Lolium multiflorum was sown in two flat containers with a large surface. In one container root development was restricted to a small portion of the soil by placing the plants in glass tubes reaching to the bottom of the containers, while in the other container roots developed freely. The former treatment had little effect on the growth of the plants. After 3 months, *Lolium perenne* and *Festuca pratensis* were intersown in the stands of *L. multiflorum*, which were cut down at the same time to eliminate competition above the soil surface.

In the container in which the *L. multiflorum* plants were restricted a *Lolium perenne* plant formed 2·9 tillers and produced 48 mg of dry matter within 7 weeks. The corresponding figures were 1·1 tillers and 9 mg of dry matter in the containers where the roots spread freely. The figures for *F. pratensis* were 2·4 and 1·0 tillers and 38 mg and 5 mg dry matter, respectively.

It may be concluded therefore that competition in the soil was far more important than competition above the soil in governing the establishment of the later-sown species.

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