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Competition effects within mixed stands

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Introduction

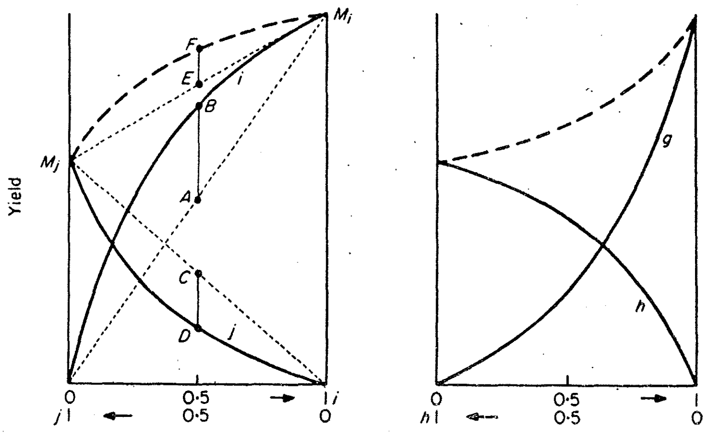
Among crop scientists there is a continued interest in mixed cropping. Most of the experiments reported here concern mixtures which were constituted in a rather arbitrary manner, the yields being compared with the yield of monocultures without further analysis. The experimental design would have been more sophisticated, the analysis more thorough and the focus on the search for overyield mixtures improved if the competition effects had been better quantified. Moreover, fallacies would have been avoided.

The most convenient model to analyse the competition effects within mixed stands is that introduced by de Wit in 1960 (Trenbath, 1978; Spitters, 1979, Chapter 3). With this model some fallacies in the interpretation of mixed cropping experiments will be exposed and some mechanisms for overyielding in mixtures will be discussed.

Design and interpretation of competition experiments

Competition between two species can be studied with a replacement series. A replacement series is the result of generating a range of mixtures by starting with a monoculture of one species and progressively replacing plants of that species with plants of the other species until a monoculture of the latter is produced. All monocultures and mixtures are grown at equal density.

The results of such an experiment are presented in a replacement diagram where for each species the yield per unit area is plotted against the proportion of the total number of seeds sown (Fig. 1). The yield of a species increases linearly with its relative seed frequency in the mixture when there is no competition or when both species are equally competitive (dashed lines from the x axis in Fig. 1(a)). The curves for actual yield in Fig. 1(a) (continuous lines from the x axis) deviate from linearity. Species i shows a convex curve, i.e. i has a higher yield in the mixture than expected if both species were equally competitive. Hence



(a) (b)

Fig. 1 Replacement diagrams (a) with the species with the higher monoculture yield as the stronger competitor and (b) with the species with the higher monoculture yield as the weaker competitor.

i is a strong competitor. On the other hand, the curve for species *j* is a weak competitor. These effects were quantified by de Wit (1960).

The species compete in the mixture for a limited amount of 'space'. The term 'space' summarizes all growth requisites like light, water and nutrients. Each species expands into its share of the total available space. The output yield (O) of a species in a mixture is considered to be proportional to the space (RY) acquired by that species:

$$O = RY \times M,$$

where M is the monoculture yield. The space occupied by the species is estimated as $RY = O/M$ and is called its 'relative yield' (de Wit and van den Bergh, 1965). When the species compete for the same limited growth requisites, the total available space equals unity.

The 'relative yield total' in a mixture of *i* and *j* is then

$$RYT = RY_i + RY_j = \frac{O_i}{M_i} + \frac{O_j}{M_j} = 1.$$

RYT is greater than one when the species compete for only a part of the space, i.e. when they are limited in part by different resources. We will see that this is a necessary but insufficient prerequisite for overyielding mixtures. In some reports the term 'land equivalent ratio' (LER) has been used for RYT, but in the calculation of LER the replacement principle has not always been used.

Pseudo benefit of mixed cropping

Two fallacious approaches are frequently found in the literature:
(a) mixtures are compared with monocultures growing in a stand that is half as dense, and (b) the success of mixed cropping is read from the difference between the total yield of the mixture and the mean yield of the monocultures.

Mixtures and monocultures at different spacings

In many of the experiments reported, mixtures have been established by adding the plant populations used in the monocultures. A simple example may illustrate the pitfall behind this 'additive scheme'. Consider two species that do not differ in yield and in density response. In the example of Fig. 2, they both yield 5·6 t ha^{-1} in monoculture at 100 plants m^{-2}. In an additive scheme, the mixture is grown at 200 plants m^{-2}. The yield of a species in this mixture equals its yield in monoculture when the species are equally competitive. Hence, from Fig. 2, we read 7·3 t ha^{-1} for the total yield of the mixture. The mixture yields 30 per cent more than either of the monocultures. However, the yield benefit is only due to a greater density and may also be obtained with the monocultures growing at the same density as the mixture.

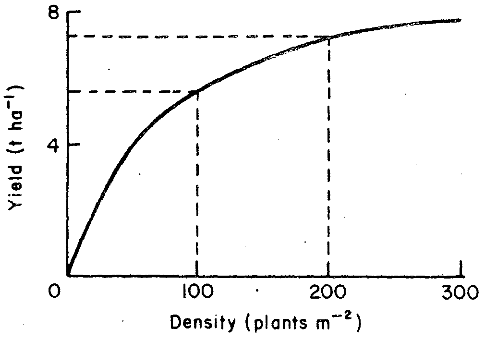


Fig. 2 The effect on yield of doubling the plant population.

Instead of the additive scheme a replacement scheme should be used, i.e. the mixtures should be established by replacing a certain proportion of one species with the same proportion of the other species, thus keeping the total density constant. From the replacement experiment RYT can be estimated. Only when RYT is greater than one can mixed cropping give a yield benefit, because in part the species occupy different spaces. For the space which the species do not have in common, the replacement experiment degenerates into a density experiment (Fig. 5; Berendse, 1979). This suggests that when RYT is greater than one, the optimal density is higher for the mixture than for either of the monocultures. This is supported by experimental evidence (Willey, 1979). The optimal spacing for the mixture may be determined in a separate experiment with the mixtures at different densities.

The density in the replacement series has, in general, to be in agreement with that used by farmers. However, the species may differ strongly in their optimal density. For example, Phaseolus beans are sown at twice the density of maize. The replacement diagram is then generated by substituting one maize plant with two bean plants (Willey and Osiru, 1972). In the equations, the density is expressed in 'plant units' with one plant unit equivalent to one maize plant and to two bean plants (de Wit, 1960, p. 63).

Difference between mixture yield and average monoculture yield

The yield of the 1 : 1 mixture is frequently compared with the average of the yield of the two monocultures (F vs E in Fig. 1(a)). A higher yield of the mixture is interpreted as argument for mixed cropping. However, when we consider the situation represented in Fig. 1(a), we see that the highest yield is obtained with a monoculture of species i (M_i). It can be shown that when two species compete for the same limited resources, i.e. $RYT=1$, the highest yield is produced with the better monoculture (de Wit, 1960).

On the other hand, when $RYT>1$, the species occupy in part different spaces so that a mixture may exploit the resources more efficiently than either monoculture and the mixture may yield more than the best monoculture. However, a value of RYT greater than one does not guarantee a better yield mixture (van den Bergh, 1968, pp. 6 and 8).

Often the farmer grows more than one crop, e.g. to guard against market risks and to spread labour peaks. We distinguish two situations: $RYT=1$ and $RYT>1$. When $RYT=1$, the same yield of each species may be obtained with monocultures as with a mixture, without changing the total area of land. The area fractions of the monocultures have to be taken equal to the relative yields of the species. In the situation presented in Fig. 3, the yields of the 1:1 mixture are reproduced by sowing 0·75 of the area with the stronger competitor i and 0·25 of the area with the weaker competitor j, both in monoculture. Hence, when

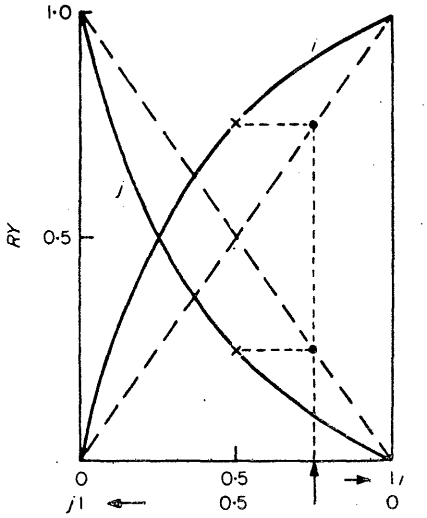


Fig. 3 Replacement diagram with relative yields showing that the yields of a mixture may be reproduced by growing the monocultures on the same area of land when $RYT=1$.

$RYT=1$ there is no advantage of growing a mixture instead of the monocultures.

When $RYT>1$, a larger area of land is needed to produce the same yield of each species with monocultures than with a mixture. The value of RYT measures the relative area under monocultures that is required to give the same yield of each species as in the mixture. Hence when $RYT>1$ mixed cropping may be of advantage. However, the industrial farmer usually chooses to grow the crops in monoculture for reasons of mechanization and management.

Comparison of the yield of the mixture with the mean of the yields of the two monocultures may lead to unjustified optimism with respect to the perspectives of mixed cropping. When $RYT=1$, a 1:1 mixture yields more than the average of the two monocultures when the stronger competitor is the species with the higher yield in monoculture (Fig. 1(a)), whereas the mixture yields less when the reverse is true (Fig. 1(b)). This is because the gain of the strong competitor ($B-A$ in Fig. 1(a)) and the loss of the weak competitor ($C-D$) in the mixture are proportional to their monoculture yields (M_i and M_j) (Spitters, 1979, Chapter 3). As already shown, there is no advantage in mixed cropping when $RYT=1$.

Real benefit of mixed cropping

As we have seen, mixed cropping may be of benefit only when $RYT>1$. The mechanisms resulting in $RYT>1$ were summarized by Trenbath (1976) and are well-known in mixtures of legumes and grasses. In the following, some other types of over-yielding mixtures are discussed and interpreted in terms of the de Wit model.

Nonsimilar growth periods

Mixed growing of species which differ in the time of their maximum demands on the growth factors extends the duration of resource exploitation. This mechanism will be explained with an experiment with potatoes (unpublished data of L. Sibma, CABO, Wageningen). The variety Tanja was planted on 5 May and the variety Multa on 5 May, 1 July and 1 August. The varieties were grown in monocultures and in 1:1 mixtures. The replacement diagram shows a convex and a concave curve when the varieties were planted at the same time (Fig. 4(a)). *RYT* was about unity indicating that the varieties competed for the same resources. When Multa was planted on 1 August, two density-response curves emerged in the replacement diagram (Fig. 4(c)) showing that neither variety felt the other's presence in the mixture. *RYT* was about 2. It was noted that by the time that Multa was established, Tanja was completely matured.

A similar experiment was done with the varieties Doré and Spartaan in a different year and at a different location. This time *RYT* was about 1 irrespective of the planting time of Spartaan (Figs. 4(d)-(f)). Hence the varieties compete for the same limited resources, even when Spartaan was established after Doré had matured. The replacement diagram for the latter situation (Fig. 4(f)) therefore shows a convex and a concave curve instead of the two density-response curves in the experiment with Tanja and Multa (Fig. 4(c)). Apparently, the early variety Doré consumed almost all of some limiting resource so that there remained little for Spartaan when it was established in the field in August.

In the second experiment where *RYT* was about 1, fertilizer was applied only before the first planting. On the other hand, in the first experiment with a large *RYT*, an additional dressing was given just before planting the late variety. This difference in fertilizer application may explain the discrepancy between the experiments. It illustrates that mixed cropping with species differing in growth-period results in a maximum yield benefit when the limiting resource is delivered

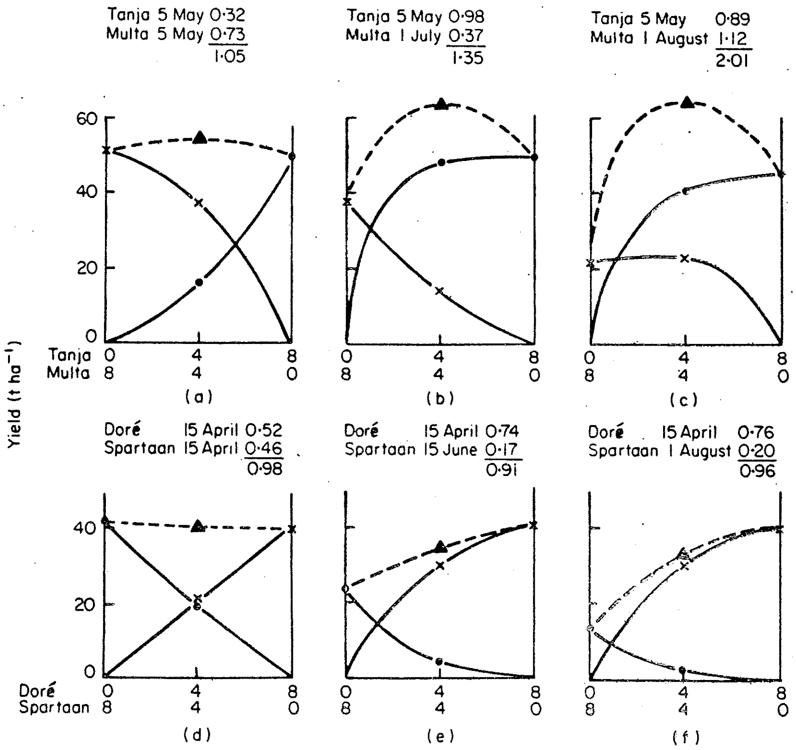


Fig. 4 The effect of intercropping an early-planted potato variety with a later-planted one on tuber yield at a population density of 8 plants m^{-2}. In the headings, the name of each variety is followed by the date of planting and the relative yield (RY).

continuously. This situation is most likely to be met under optimal conditions and with a supply of nutrients spread over the season, either by natural release or split dressing. On the other hand, when the limiting resource is depleted by the early species, i.e. $RYT=1$, the highest yield is obtained with the better monoculture and the mixture yields may be reproduced with monocultures on the same total area of land.

The previous principles are reflected in the types of mixtures found in areas differing in rainfall (Andrews and Kassam, 1976). In rain-fed agriculture with rainfall below 600 mm simultaneous cropping is practised with crops of similar maturity. Species with a retarded growth cycle are not found in the mixtures because they would have to mature under severe water stress. In contrast, crop mixtures involving different maturities are common in areas of rainfall between 600 and 1000 mm.

Here the slow-growing, later-maturing species generally tend to mature under better end-of-season moisture conditions. In areas with above 1000 mm of rainfall, multiple cropping both on the simultaneous and sequential principle is practised.

Figure 4(c) illustrates that an *RYT* of 2 can be approached only when the density of a stand is so high that the yield at half density approaches that at full density. A total population density of 4 plants m^{-2} gave an *RYT* of 1·71 as compared with 2·01 in Fig. 4(c). Hence for mixed cropping of species differing in their growth period, a greater density must be used than for growing monocultures.

The late-maturing species may not suffer too much by competition with the early species. The competitive relations in the mixture may be manipulated by the choice of variety of either species (Andrews, 1974) and by the time of planting. A small delay in time of establishment of a species may strongly reduce its competitive ability (Spitters, 1979).

Different rooting depths

In a mixture of two species differing in rooting depth, the deep-rooting species can draw on an extra supply of nutrients present in the deeper soil layer. A theoretical model for this situation was developed by Berendse (1979). The results of his experiments with the shallow-rooting grass *Anthoxanthum odoratum* and the deep-rooting herb *Plantago lanceolata* satisfy his model. The species share a common pool of nutrients in the upper layer where both are rooting. Therefore *RYT*=1 and the curves in the replacement diagram for the upper layer are convex and concave (Fig. 5). In the second layer, the replacement experiment degenerates into a density experiment for the deep-rooting species. In the combined replacement diagram (Fig. 5), *RYT* is greater than 1 and the curve of the deep-rooting species is S-shaped. It is assumed that the two soil layers are two strictly separated compartments and that the limiting resource is distributed homogeneously over both soil layers.

A mixture may yield more than the better monoculture only when the shallow rooting species is the more productive one in monoculture.

Multiple resource competition

Braakhekke (1980) elaborated a model for a situation where two species are limited by two different resources. Consider the extreme situation where species *a* is limited in its growth by element 1 and does

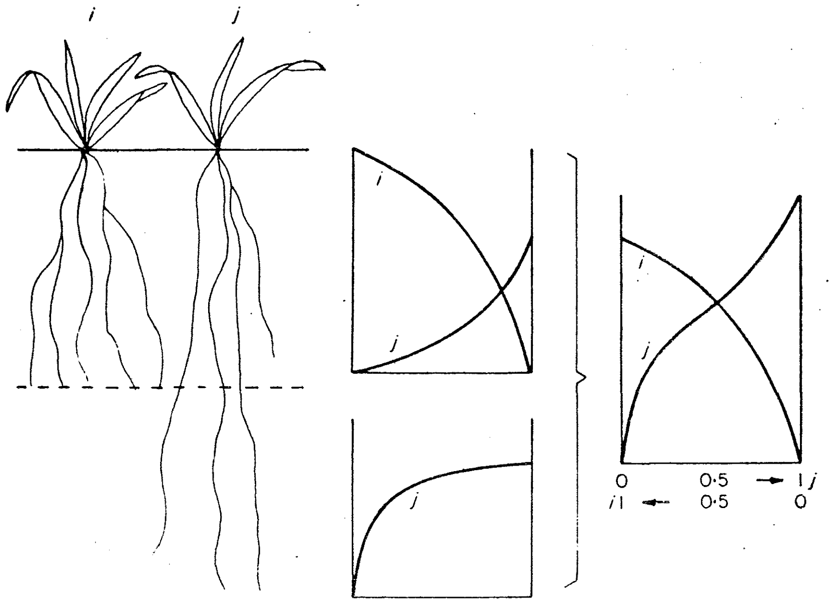


Fig. 5 Competition between a shallow- and a deep-rooting species interpreted as the combined effect of competition for the same resources in the upper soil layer and a density experiment with the deep-rooting species in the deeper soil layer.

not take up element 2 while species *b* is limited by element 2 and does not take up element 1. Neither species senses the others presence in the mixture, which results in two density-response curves in the replacement diagram (Fig. 6). *RYT* approaches the value of 2 at dense sowings which suggests a great advantage in mixed cropping.

The situation where both species *a* and *b* take up both of the elements 1 and 2 is more realistic. Suppose that the amounts supplied of each of the elements are completely taken up in the mixture and in the monocultures. The distribution of the elements among the species in the mixture satisfies the competition equations of de Wit (1960) which gives for each element an uptake replacement diagram with $RYT=1$ (Fig. 7, top). Yield is approximately linear with the uptake of the element that limits the growth ('Law of the minimum' of von Liebig). We obtain the yield replacement diagrams for element 1 limiting the growth of each species by multiplying the uptake curve of the species with its efficiency of resource utilization (Fig. 7, centre). These efficiencies are the slopes of the linear relations between yield and uptake and may be different for each species and for each element. Therefore, the yield replacement diagram when element 2 is the

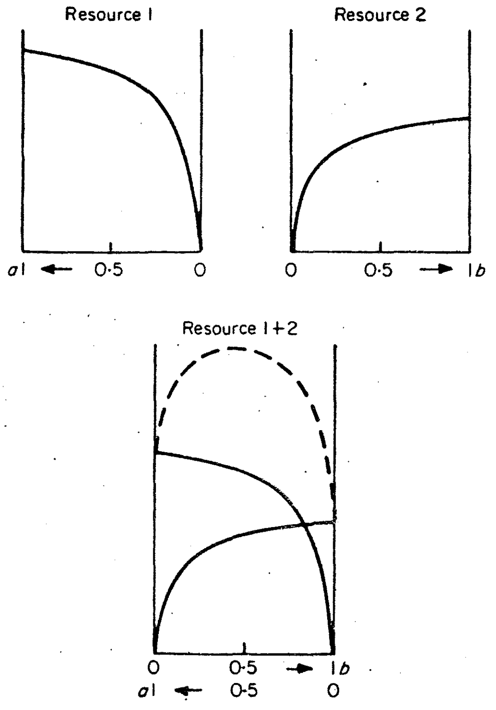


Fig. 6 Competition between species *a* and *b* when *a* is limited in its growth by resource 1 and does not take up resource 2 while *b* is limited by resource 2 and does not take up resource 1. The top diagrams are for the two resources separately whilst the bottom one shows the combined effect.

limiting growth factor may deviate from that for element 1 (Fig. 7, centre). In Fig. 7, the yield curve of species *a* for element 1 is consistently lower than that of *a* for element 2, so that the growth of species *a* is limited by element 1. On the other hand, species *b* is limited by element 2. Therefore, the yield replacement diagram is composed of the *a* curve for element 1 and the *b* curve for element 2 when the species compete for both resources (Fig. 7, bottom). We see that a mixture yields more than the better monoculture and *RYT* exceeds 1. The luxury consumption of non-limiting resources is reduced in the mixture compared with the monocultures so that the nutrients are used more efficiently in the mixture. Hence, mixed cropping may be of advantage when each species is the stronger competitor for the element that limits its own growth.

On the other hand, an *increased* luxury consumption in a mixture is found when each species is the stronger competitor for the element that

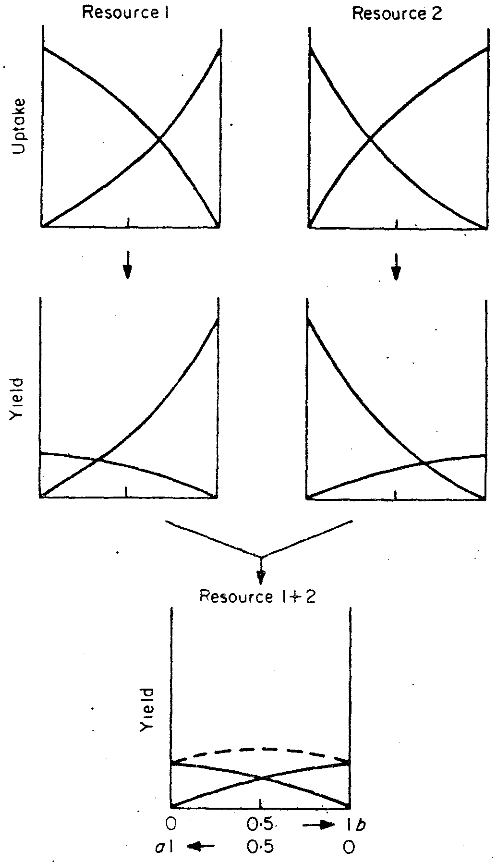


Fig. 7 Multiple-resource competition resulting in a yield benefit of mixed cropping. Diagrams at the top give the uptake of the two resources separately; diagrams in the centre represent the yields which would be achieved if the growth of both species were limited by the resource in question; diagram at the bottom gives the combined effect of competition for the two resources. (Data from Braakhekke, 1980.)

limits the growth of the other species (Fig. 8). Therefore, multiple-resource competition may explain a value of *RYT* smaller than one as well as the occurrence of allelopathic effects.

In conclusion, a mixture may outyield the better monoculture when the two species are limited in their growth by different elements and each species is the stronger competitor for the element that limits its own growth. The use of this mechanism for mixed cropping will be limited because the prerequisites are difficult to meet. Species differing

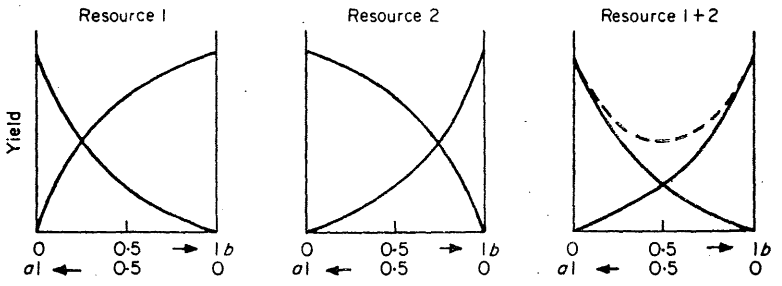


Fig. 8 Multiple-resource competition resulting in a yield loss of mixed cropping. Diagrams at the left and centre represent the yields which would be achieved if the growth of both species were limited by the resource in question; diagram at the right gives the combined effect of competition for the two resources. (After Braakhekke, 1980.).

strongly in competitive ability for limited resources and in their resource utilization efficiencies in an environment with a low fertility offer the greatest probability of finding such a mixture. The previous discussion of the model of Braakhekke (1980) illustrates primarily a way of thinking in the analysis of competition.

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