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MODELLING COMPETITION EFFECTS IN INTERCROPPING SYSTEMS

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Summary

Two approaches of modelling competitive interactions are discussed: a regression approach and an eco-physiological approach. In the regression model, the relationship between yield and plant density of the different species in the mixed stand is described by an empirical regression equation. In the eco-physiological model, the competition process itself is described in due time on the basis of the underlying processes of resource acquisition and utilization.

The regression model can be used as a simple procedure to analyse intercropping experiments, especially in trials with only a final harvest. The regression model and a simple version of the eco-physiological model seem to be the most appropriate types of model for assessing optimum intercropping combinations. However, for understanding of the competitive interactions, the dynamic eco-physiological approach is indispensable.

1. INTRODUCTION

When two or more crops are simultaneously grown on the same field, they compete for the available growth factors of light, water and nutrients. This competition obeys to certain principles, which can be described by mathematical formulae that can be integrated into computer models.

Broadly spoken, two types of competition models can be identified:

- (1) regression models, in which the competition effects are described by some empirical regression equation;
- (2) eco-physiological models, in which the dynamics of the competition process are described from the underlying physiological processes of acquisition of light, water and nutrients, and the utilization of these resources into the production of biomass and marketable yield.

Many regression models to describe interplant competition have been developed; with reviews being given by Trenbath (1978), and Spitters (1979). Willey (1979) reviewed some of the regression approaches with respect to their use in intercropping research. On the other hand, only a few eco-physiological models to describe the competition process have been published, e.g. by Spitters & Aerts (1983), Spitters (1984, 1989a,b), van Gerwen et al. (1987).

In this paper, we only discuss a single regression model

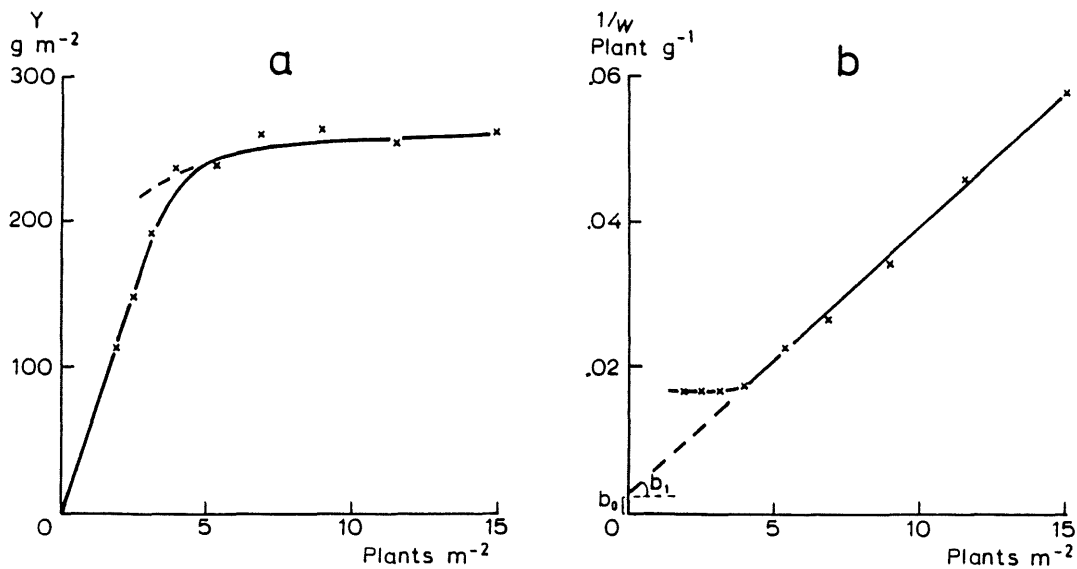


Figure 1. Density response of maize. Plots of (a) biomass per unit area and (b) the reciprocal of per-plant biomass against plant density.

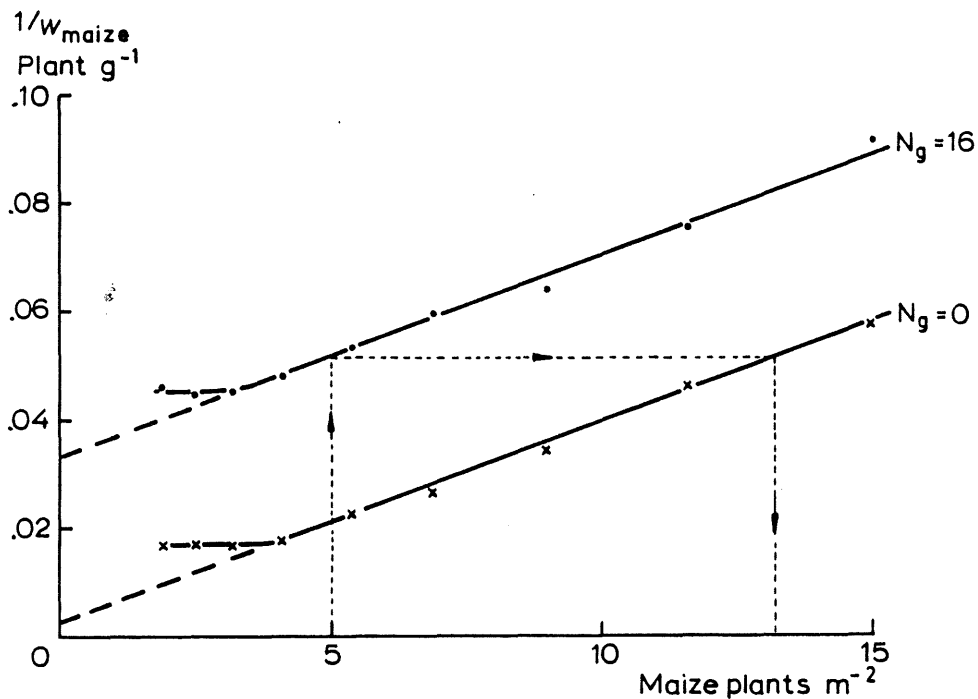


Figure 2. Addition of 16 groundnut plants ($N_g = 16$) to a monocrop of maize ($N_g = 0$) had the same effect on maize as adding 8 maize plants. Thus for a maize plant the presence of two groundnut plants was similar to the presence of one other maize plant. Because of the parallel lines, the substitution holds independent of the relative frequencies of the species and independent of total population density.

and a single physiological model, which we consider to be among the most suitable models to describe competitive interactions in intercropping systems. Pros and cons of both approaches will be discussed.

2. THE DESCRIPTIVE, REGRESSION APPROACH

Over a wide range of densities, yield of total biomass and often also yield of a certain plant organ are asymptotically related to plant density (Holliday, 1960; Donald, 1963); the relationship being characterized by a rectangular hyperbola (Shinozaki & Kira, 1956; de Wit, 1960, 1961). This equation for intra-specific competition was expanded by Suehiro & Ogawa (1980), Wright (1981) and Spitters (1983a) to allow also for effects of inter-specific competition. This regression model will be discussed, using the parameterization of Spitters (1983a). The relationships are illustrated with results of an experiment in which maize cv. Kretek and groundnut cv. Gajah were grown in monocultures and mixtures at a range of plant densities on East Java, Indonesia. The data were kindly provided by W.C.H. van Hoof and collected during a co-operation project between the Agricultural University, Wageningen and the Brawijaya University, Malang, Indonesia (van Hoof, 1987; Spitters, 1983a,b).

2.1 The hyperbolic yield-density function

Crop biomass is related to plant density according to

$$Y = N / (b_0 + b_1 N) \quad \text{or} \quad 1/W = N/Y = b_0 + b_1 N \quad (1)$$

in which Y is the biomass yield (g m^{-2}), N the plant density (plants m^{-2}), W the average weight per plant (g plant^{-1}), and b_0 and b_1 are regression coefficients. The parameter $1/b_0$ is the apparent weight of an isolated plant, and $1/b_1$ is the asymptote of the relationship between Y and N and thus measures the apparent maximum yield per unit area (Figure 1). At very wide spacing, there is no interplant competition so that the per-plant weight remains constant with decreasing density, and does not increase as is suggested by the hyperbolic equation. The observed biomass of an isolated plant is therefore somewhat smaller than the apparent biomass estimated by $1/b_0$ (Figure 1b).

According to Equation 1 and Figure 1b, $1/W$ is linearly affected by adding plants of the same species. That suggests that adding plants of another species also linearly affects $1/W$, and Figure 2 gives credit to this assumption. Hence, for species 1 in the presence of species 2 is

$$\begin{aligned} 1/W_{12} &= b_{10} + b_{11}N_1 + b_{12}N_2 \quad \text{or} \\ Y_{12} &= N_1 / (b_{10} + b_{11}N_1 + b_{12}N_2) \end{aligned} \quad (2a)$$

and for species 2 in the presence of species 1

$$1/W_{21} = b_{20} + b_{22}N_2 + b_{21}N_1 \quad \text{or}$$

$$Y_{21} = N_2 / (b_{20} + b_{22}N_2 + b_{21}N_1) \quad (2b)$$

Where the first subscript indicates the species whose yield is being considered, and the second subscript its associate. In Equation 2a, b_{11} measures the effect of intra-specific competition, while b_{12} measures the effect of inter-specific competition. The ratio b_{11}/b_{12} characterizes the relative competitive ability of species 1 and species 2, with respect to the effect on the yield of species 1. Figure 2 shows that the addition of 16 groundnut plants to a monocrop of maize had the same effect on $1/W$ of maize as addition of 8 maize plants. Thus for a maize plant, the presence of two groundnut plants was similar to the presence of one other maize plant.

2.2 Niche differentiation

Applying the analysis to the results of an other experiment with maize and groundnut (Figure 3), gave for the per-plant biomass of maize the regression equation:

$$W_m = 1 / (-0.001 + 0.0020N_m + 0.0003N_g) \quad (3a)$$

and for groundnut:

$$W_g = 1 / (0.024 + 0.0024N_g + 0.0038N_m) \quad (3b)$$

Hence, for this data set, one maize plant and 6.9 groundnut plants had an equal influence on the average weight per plant of maize ($6.9 = 0.002040 / 0.000296$ being the extended form of $0.0020 / 0.0003$ of the above equation for W_m). We may say that maize senses the presence of one maize plant as strongly as the presence of 6.9 groundnut plants. For groundnut the presence of one maize plant was equivalent to the presence of 1.6 ($= 0.0038 / 0.0024$) other groundnut plants. The influence of a maize plant, expressed relative to the influence of a groundnut plant, was therefore greater for maize itself than for groundnut. Intra-specific competition was greater than inter-specific competition. So, the species were only partly limited by the same resources; they partly avoided each other. This is defined as niche differentiation. In mixtures of grain crops, such as maize, with legumes, such as groundnut, niche differentiation is the rule.

In mathematical terms: there is niche differentiation when $b_{11}/b_{12} > b_{21}/b_{22}$ or, in other words, when the double quotient $(b_{11}/b_{12}) / (b_{21}/b_{22})$ exceeds unity. For the maize/groundnut experiment, we find a value of $6.9 / 1.6 = 4.3$. This double quotient may be written as the product $(b_{11}/b_{12}) \times (b_{22}/b_{21})$, which characterizes the degree of niche differentiation.

2.3 Estimation of the regression coefficients

The competition coefficients can be estimated from the linearized form for $1/W$ (Equation 3) by linear regression. However, when plant weights (W) are normally distributed, the reciprocals ($1/W$) show a skewed distribution and their

variances increase with an increase in plant density. This heterogeneity of variances biases the estimation of the competition coefficients. To meet the assumption of homogeneity of variances, the competition coefficients are therefore estimated better from Equation 2 by non-linear regression of Y on the plant densities, which can easily be performed using a statistical computer package (e.g. Genstat). When a wide yield range is covered in the experiment, the yields tend to be distributed log-normally. In that case, the competition coefficients are estimated using non-linear regression to fit the logarithm of yield to the logarithm of the right-hand side of Equation 2.

2.4 The parabolic yield-density function

The above regression model is based on a hyperbolic form for the yield-density relationship, which usually holds for biomass and in many species for marketable yield as well. In several crops, however, marketable yield responds to density according to a parabolic shape of curve, i.e. at high density yield decreases with further increase of plant density (Holliday, 1960; Willey & Heath, 1969). When these high densities are considered, the model has to be extended, either by introducing a quadratic polynomial term (Spitters, 1983b) or by introducing a power term (Firbank & Watkinson, 1985).

In the power function approach, Equation 2a for the inverse per-plant weight of species 1 in competition with species 2 is expanded as

$$1/W = (a_0 + a_1N_1 + a_2N_2)^{a_3} \quad (4)$$

and in the quadratic polynomial approach as

$$1/W = a_0 + (a_1N_1 + a_2N_2) + a_3(a_1N_1 + a_2N_2)^2 \quad (5)$$

where the a 's are regression coefficients to be estimated. The meaning of these coefficients, being different for both equations, can be derived from the original publications.

In many situations, however, the hyperbolic relationship (Equations 1 and 2) satisfies and the introduction of additional parameters, like in Equations 3 and 4, is redundant and may result in imprecise estimates of the individual parameters due to over-parameterization.

2.5 Assessing optimum intercropping combinations

The regression approach facilitates interpolation to intermediate populations, and can therefore be a tool in assessing the optimum intercropping combination in the environment considered. This will be illustrated with the data of maize grain yield and groundnut pod yield.

Relative yield and land equivalent ratio The yield of a species in a population is expressed relative to its

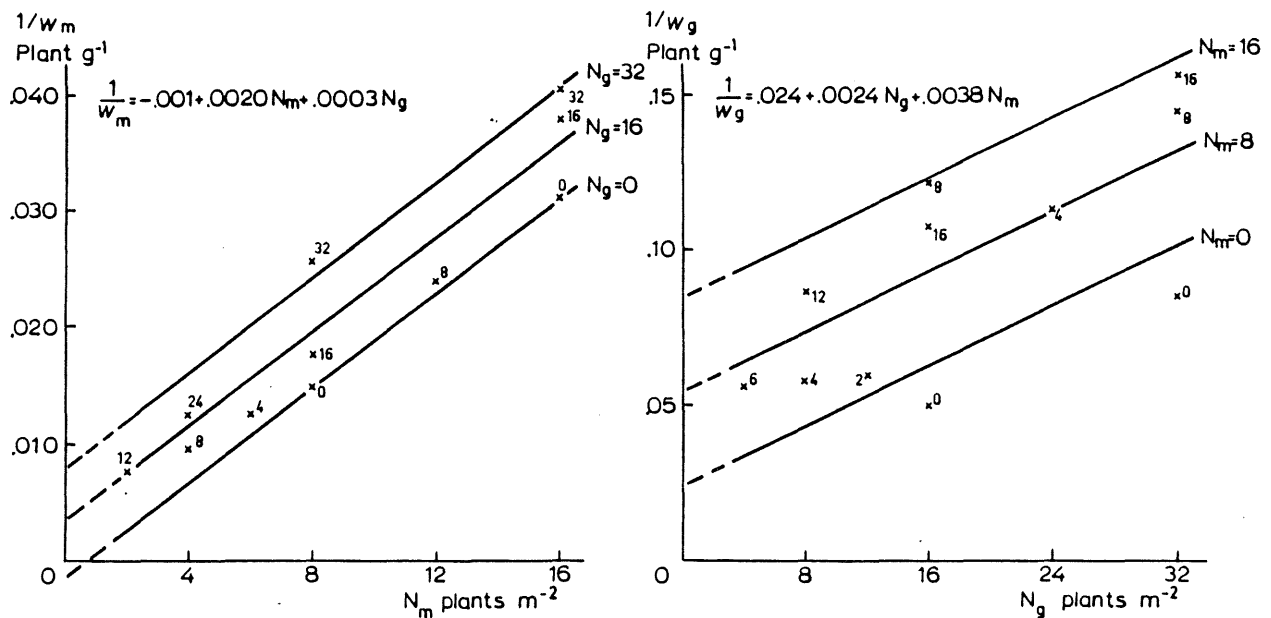


Figure 3. Effect of number of maize plants (N_m) and number of groundnut plants (N_g) on the reciprocal of per-plant biomass of maize and on that of groundnut. In the plot with $1/W_m$, subscripts of data points denote N_g , while in the plot with $1/W_g$ subscripts denote N_m . Curves are those fitted to the regression model.

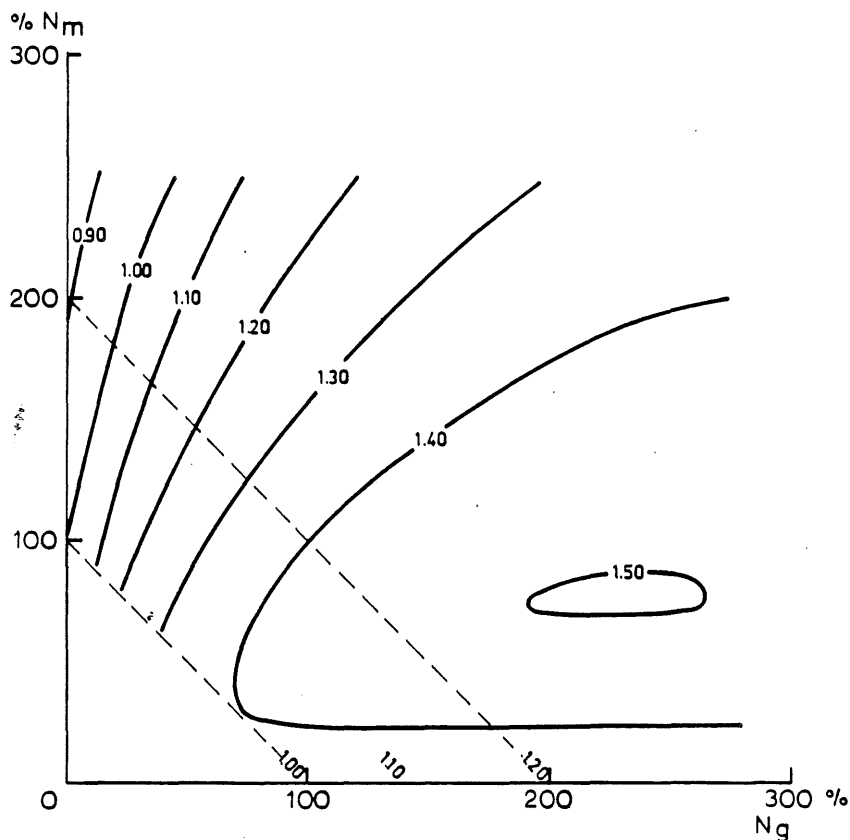


Figure 4. Relationship between maize density N_m and groundnut density N_g of a certain stand and the LER of that stand. LERs are represented by isocurves connecting stands with the same LER. The broken lines, joining the axes, represent replacement series with a total population density of 100% and 200%, respectively. The intersections of these lines with the iso-LER curves show RYT in the respective replacement series. Plant density is expressed as a percentage of the local recommended density of the monocrops: 8 plants m^{-2} for maize and 16 plants m^{-2} for groundnut.

monoculture yield at a certain reference density. This relative yield of a species 1 is denoted by L_1 . Usually, the yield of the monoculture grown at the density which is recommended for local farmers is used as a reference. Hence, mixed growing of two crops is weighted against separate growing of the crops. Here, we set the recommended density of each species at 100%.

The sum of the relative yields is called the land equivalent ratio (Willey, 1979; Mead & Willey, 1980). In a mixture of species 1 and 2, the land equivalent ratio

$$LER = L_1 + L_2 = Y_{12}/Y_{11} + Y_{21}/Y_{22} \quad (6)$$

When $LER = 1$, the same yield of each species can be obtained with monocultures at recommended density as with a mixture, without changing the total area of land. The area functions of those monocultures must be taken equal to the relative yields of the species. Hence, when $LER = 1$ there is no advantage in growing a mixture instead of the monocultures.

When $LER > 1$, a larger area of land is needed to produce the same yield of each species with monocultures at recommended density than with a mixture. The value of LER expresses the relative area under monocrops that is required to give the same yield of each species as in the mixture. For example, when $LER = 1.20$, 20% more land is required to reproduce the intercrop yield of each species with the monocrops. In other words, intercropping gives a yield advantage of 20% compared to growing both the monocrops at recommended density. However, often a part of this benefit can also be achieved by growing the monocrops at higher density, and sometimes the highest yield is achieved with the better monocrop.

When the mixture yield of a species 1 is expressed relative to its yield in the monoculture from the same replacement series, the relative yield is denoted by RY_1 ; the sum of the relative yields is called relative yield total and is denoted by RYT (de Wit & van den Bergh, 1965). The use of RY and RYT assumes that mixtures and monocultures are all part of the same replacement series. A replacement series is the result of generating a range of populations 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 (de Wit, 1960).

The yields of the groundnut pods and maize grain were predicted for a wide range of populations, using the regression equation fitted to the data according to the quadratic model of Equation 5. Next, for each population the relative yields L_m and L_g with respect to the yields of the monocrops at recommended density were calculated. The LER 's, obtained by summing the relative yields, were presented in an iso- LER diagramme where the LER is related to the plant density of each of the two species in the population (Figure 4). Over a wide range of intercrop combinations, LER exceeded unity, pointing to an advantage of intercropping over growing the monocrops at the recommended densities.

Partitioning of LER to underlying causes What are the reasons of the high values of LER?

(1) Density effect The locally recommended density of groundnut appears too low to give a maximum yield (LER values on N_y axis of Figure 4), which is probably related to the high cost of seed of groundnut. Therefore, a part of the high LER of the mixed populations is accounted for by an increased density of groundnut. This yield advantage would also be achieved by growing the groundnut monocrop at a higher density (Figure 4) and has nothing to do with advantage of mixed cropping. In such cases, it is of paramount importance to study why the recommended density is lower than the density for maximum yield.

(2) Real advantage of mixed cropping Whether intercropping leads to a real yield advantage that may be derived from the relative yield total in a replacement series, because there the total population density is kept constant (de Wit, 1960). When this total density equals 100% of the recommended monocrop densities, RYT and LER are the same. This is the case in Figure 5. We see that RYT is greater than one and so a greater LER is achieved with mixtures than with monocrops, even without increasing the population density. It shows that in the mixtures the available resources were used more efficiently in producing the desired plant parts than that was the case for either of the monocrops. The real advantage of intercropping can be partitioned into:

(2a) Favourable effects on harvest index The ratio between the marketable yield of a species and its total biomass is termed the harvest index. This ratio may be influenced by density. The effective density experienced by a species in mixture is, however, different from that experienced at the same plant density in monoculture. Thus, RYT values for marketable yield may differ from those for biomass. In the mixture where maize and groundnut were grown both at 50% of their monocrop density, there was a slight increase of RYT due to a favourable effect of intercropping on harvest index: the calculated RYT for marketable yield was 1.38, which is somewhat greater than the 1.35 for biomass.

(2b) Niche differentiation When total population density is kept constant and the effects of intercropping on harvest index are removed, LER reduces to RYT for biomass. In the mixtures of maize with groundnut, RYT was greater than one, pointing to a more efficient exploitation of the environment in the intercrops than in either of the monocrops. This indicates niche differentiation, with RYT being a workable measure of the degree of niche differentiation, supplemental to the previously discussed product of the competition coefficients $(b_{mm}/b_{mg}) \times (b_{gg}/b_{gm})$.

2.6 Dynamic regression models

The previous model describes the competitive relations at only a single harvest; it is a static model. A better understanding of the competitive interactions is gained by considering the dynamics of the process. Three dynamic

regression approaches are envisaged.

(1) Estimating the time course of competition parameters from density experiments where both monocrops and intercrops are harvested at intervals. For each harvest, the competition parameters are estimated from the biomass yields of the species, using Equation 2. The smoothed time courses of the individual parameters may subsequently be used to predict the biomass evolution of the species for various intercropping combinations, i.e. performing interpolations over time and populations (Spitters et al., 1989). This approach requires, however, laborious experiments.

(2) Estimating the time course of competition parameters from density experiments where only monocrops are harvested at intervals. De Wit c.s. showed that, under certain assumptions, the competition effects in mixture may be estimated from the density response of the species as monocrop (Baeumer & de Wit, 1968; de Wit & Goudriaan, 1974; Spitters & van den Bergh, 1981). The density effects are fitted to Equation 1 for each harvest, and the time trend of the parameters is inferred from the results of subsequent harvests.

(3) Estimating competitive relations from growth curves of free-growing plants and closed canopies. The growth rate of a free-growing plant, not influenced by neighbours, was interpreted by Spitters (1981; Vissers, 1981) as a measure of the rate with which the species can occupy the 'space' that is still available at that particular moment. The growth rate of the species in a mixed canopy was assumed to be proportional to the fraction of the space it occupies; the total available space being measured as the growth rate of a canopy fully covering the ground.

The above dynamic approaches are more or less variants to the well-known Lotka-Volterra equations, which are generally applied in animal ecology to describe inter-specific competition. Compared to the eco-physiological model to be discussed, this approach has however several disadvantages: a relatively high degree of abstraction, parameters that are biologically much less lucid, difficulties in coping with special cases (such as intermittent droughts, and incidence of pests and diseases), inflexible for further expansion, and mathematically more complex. A dynamic regression approach is therefore not recommended for intercropping research.

3. THE ECO-PHYSIOLOGICAL APPROACH

Inter-plant competition can be defined as that mutual interaction between the plants in which they restrict each others' growth by capturing growth-limiting resources for one another. The competition process can therefore be described in terms of the distribution of the growth-limiting factors over the species in mixture and the way each uses the acquired amounts in dry matter production. A review focussing on intercropping was given by Trenbath (1976, 1986). Here, we will discuss a simple eco-physiological model of competition for light (Figure 6). A further discussion of this model is

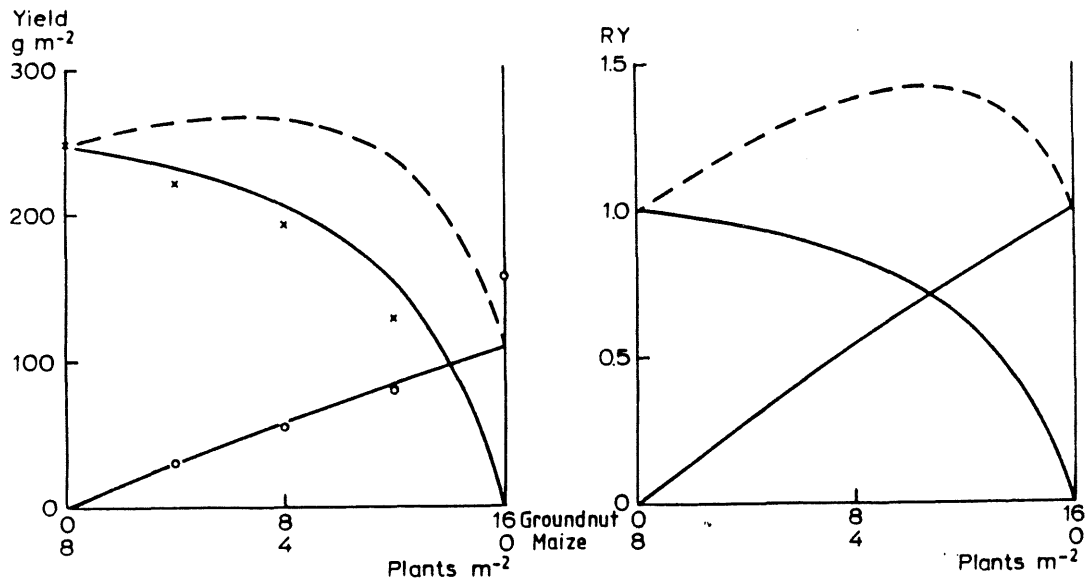


Figure 5. Replacement diagrams with grain yield of maize and pod yield of groundnut per unit area (left), and with the yield of the species expressed relative to their yields in monoculture (right). One maize plant was replaced by two groundnut plants. Curves are those predicted with the model.

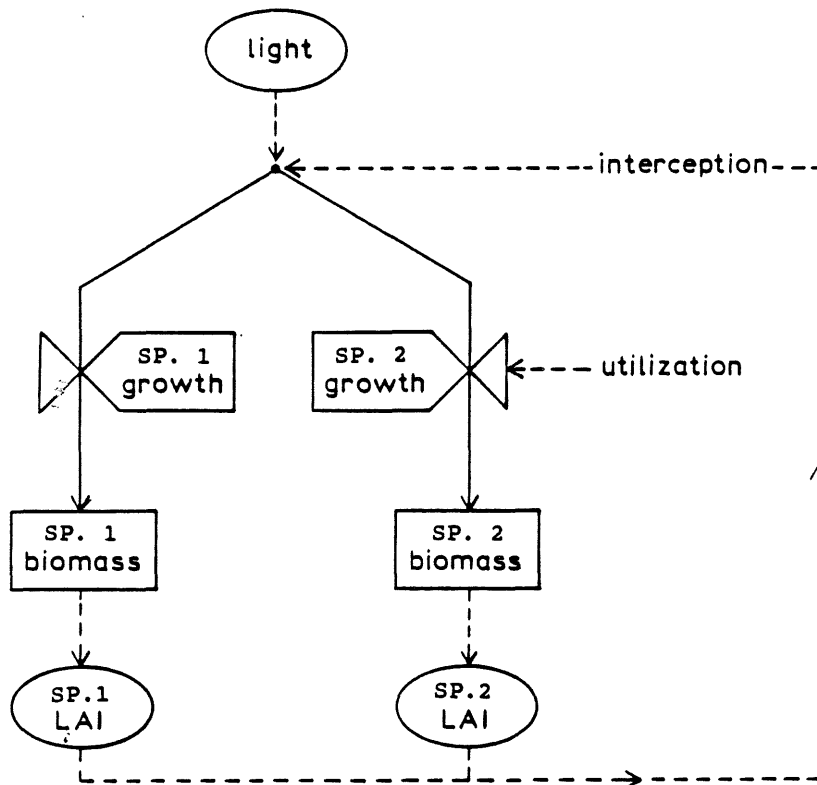


Figure 6. Simplified scheme for the simulation of competition for light between two species.

found in Spitters (1984, 1989b). For the more comprehensive versions of the model, we refer to Spitters & Aerts (1983) and Spitters (1989a).

3.1 A simple model of competition for light

The growth rate of a canopy is more or less linearly related to its light interception (review by Gosse et al., 1986). Since light interception is exponentially related to total leaf area, the growth rate of the canopy is

$$\Delta Y = (1 - \exp(-k.L)) \cdot PAR_0 \cdot E \quad (7)$$

in which ΔY is the daily growth rate ($g\ m^{-2}d^{-1}$), L the leaf area index ($m^2\text{leaf}\ m^{-2}\text{ground}$), k the extinction coefficient, E the average light utilization efficiency ($g\ d.m.\ MJ^{-1}$), and PAR_0 the incoming photosynthetically active radiation ($MJ\ m^{-2}d^{-1}$). Incoming PAR (wave bands 400-700 nm, 'light') amounts to 50% of total incoming solar radiation (350-3000 nm).

In a mixture of identical species, each species intercepts an amount of light which is proportional to its share in the total leaf area. Following the proportionality between growth and light interception, Equation 7 gives for the growth rate of species 1 in mixture with species 2:

$$\Delta Y_1 = \frac{L_1}{L_1 + L_2} (1 - \exp(-k.L_1 - k.L_2)) \cdot PAR_0 \cdot E_1 \quad (8)$$

where the subscripts refer to species 1 and 2, respectively.

The share of a species in total growth increases, however, when it intercepts more light per unit of leaf area. This is achieved with a greater extinction coefficient, e.g. due to a more horizontal leaf angle distribution, and with a greater plant height. In the distribution term of Equation 8, the leaf areas are then weighted to their respective light absorption. In mixture of short and tall species, the light interception is set proportional to the light intensities at half of the plant heights. For species 1:

$$\Delta Y_1 = \frac{l_1 \cdot k_1 \cdot L_1}{l_1 \cdot k_1 \cdot L_1 + l_2 \cdot k_2 \cdot L_2} (1 - \exp(-k_1 \cdot L_1 - k_2 \cdot L_2)) \cdot PAR_0 \cdot E_1 \quad (9a)$$

Assuming the leaf area of a species evenly distributed over its plant height (Figure 8) gives for the relative light intensity of species 1 at half of its height (H_1):

$$l_1 = \exp\left(-\frac{1}{2}k_1 \cdot L_1 - \frac{H_2 - \frac{1}{2}H_1}{H_2} k_2 \cdot L_2\right) \quad H_2 > \frac{1}{2}H_1 \quad (9b)$$

In a more detailed approach of competition for light, the light profile within the canopy is simulated and light utilization is calculated for each canopy layer separately

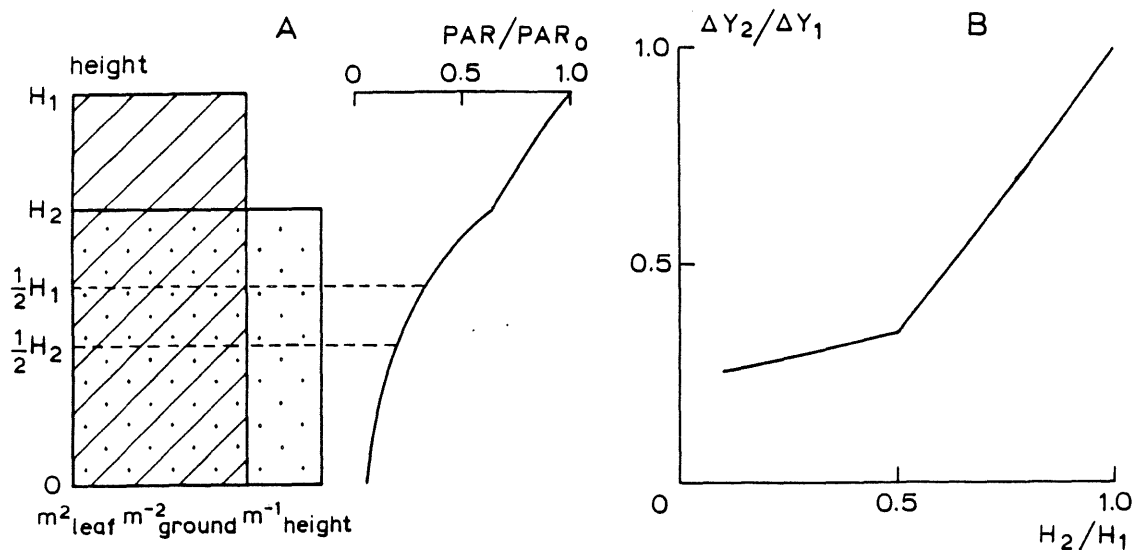


Figure 7. Schematic representation of the simple procedure of modelling competition for light.

a. The share of each species in total light interception is assumed to be proportional to its leaf area, weighted by the light intensity at half of its plant height. This intensity is calculated from the exponential light profile (PAR/PAR_0), assuming a uniform distribution of leaf area over plant height (H) for each species.

b. The ratio between the simulated growth rates of the two species in mixture as a function of their relative plant heights. Each of the species had a leaf area index of 2.

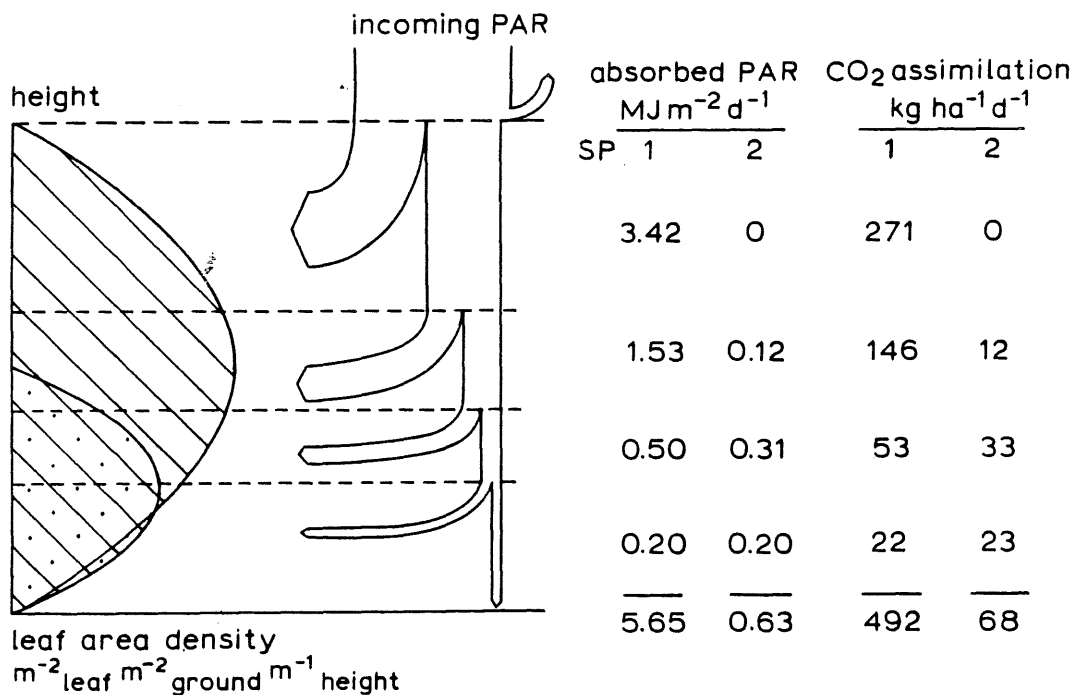


Figure 8. In the comprehensive model, the canopy is divided into a number of horizontal layers and illumination intensity and CO_2 assimilation rate are calculated for each species for each layer separately, accounting for the leaf area distribution of the species over their plant height. In this example, the tall and short species had a leaf area index of 3 and 1, respectively.

(Figure 9; Spitters & Aerts, 1983; Spitters, 1989a). For that, the canopy is stratified into various, horizontal height layers. The illumination intensity at the various heights is derived from the exponential light profile. This is done for sunlit and shaded leaf area separately, taking into account the profiles of both the diffuse and direct light flux. From the photosynthesis-light response of individual leaves, the rate of CO_2 assimilation per unit leaf area is calculated for each species and for each layer separately. Multiplication by the leaf area of the species in the layer gives its assimilation rate in that layer. Summation over the various canopy layers and over the hours within the day gives the daily assimilation rate of each species in the mixture. After subtraction of respiration losses, the daily growth rates are obtained.

The above approach assumes a random distribution of the leaf area of the various competitors in the horizontal plane. In intercropping, however, the leaf areas of the different species are often grouped into distinct structural entities, such as plant rows and tree crowns. When the deviation from a random distribution of leaf area becomes too serious, an expansion as presented by van Gerwen et al. (1987) may be followed. For that, the dimensions of the structural elements are defined, so that the fraction of the incoming light flux intercepted by the elements can be calculated, taking into account the mutual shading of the individual elements. Subsequently, the absorbed fraction of the intercepted flux is calculated from the leaf area index within each structural element.

In the simple model, leaf area is calculated by multiplying the accumulated biomass at time t (Y_t) by the leaf area ratio (LAR_t , m^2g^{-1}) at that time:

$$L_t = \text{LAR}_t \cdot Y_t \quad (10a)$$

This assumes that leaf area growth is limited by dry matter growth. Before canopy closure, however, leaf area growth is usually restricted by the potential rates of cell division and expansion, which depend on temperature rather than on the supply of photosynthates. In this early phase, leaf area growth is more or less exponential. As will be discussed later, the competitive ability of a species is strongly determined by its early growth. Therefore, a more accurate procedure is followed in which leaf area is assumed to increase exponentially till the beginning of mutual shading at a LAI of 0.75:

$$L_t = N \cdot 'L_0 \cdot \exp(R \cdot t) \quad L_1 + L_2 < 0.75 \quad (10b)$$

where N is the plant density (plants m^{-2}), $'L_0$ the apparent leaf area per plant at emergence ($\text{m}^2 \text{plant}^{-1}$) found by logarithmic extrapolation of leaf area data, R the relative growth rate of leaf area ($\text{m}^2\text{m}^{-2}\text{d}^{-1}$), and t the time in days after plant emergence. For tropical areas, R is best expressed per day, but for temperate climates R is better expressed per

unit degree-day.

Both leaf area ratio (LAR) and plant height (H) are a function of phenological development. They are therefore introduced as a function of days (in tropical climates) or as a function of degree-days (in temperate climates) after plant emergence.

In the detailed model, the total daily growth rate is partitioned to leaves, stems, roots and storage organs, according to keys which are a function of the development stage of the species. Leaf area growth is calculated from the dry weight increment of the leaves and the specific leaf area of the new leaves, while the decrease in leaf area due to senescence is also taken into account. Simulation of early leaf area growth is further improved by calculating leaf area per plant from leaf appearance rate and the final size of the successive leaves.

In the simple model, crop yield is obtained by multiplying the simulated final biomass of the crop by a fixed harvest index, which is the ratio between the marketable yield and the total biomass. For crops with a distinct density-dependence of harvest index, this parameter can be introduced as a function of the average biomass per plant (Spitters, 1983b).

In the foregoing, competition for light was discussed. Stress conditions are accounted for by using a multiplication factor for the light utilization efficiency (E). This factor takes a value between 0 and 1, and its value can be assessed from the observed or expected yield level of the monocrops.

Many models have been published to describe the effect of drought and nutrient shortage on crop growth. Most of the simple approaches can easily be attached to the competition model to describe the growth reduction of the intercrop as a whole. However, when soil moisture or nutrients are in short supply, uptake of these elements by an individual species in the mixture will be related to its share in total root length. Especially when the competing species differ markedly in their leaf area to root length ratio, these differences have to be accounted for. For a simple procedure to expand the model to account for competition for soil moisture and nutrients, including effects of root competition, we refer to Spitters (1989a).

3.2 Sensitivity analysis

The afore-described model is used to illustrate the effect of various morpho-physiological attributes on the competitive ability of a wheat-like species. For that, two isogenic lines were assumed to grow in an $\frac{1}{2} : \frac{1}{2}$ mixture and in monoculture. Total stand density was 200 plants m^{-2} , and both species started with a leaf area of 1 cm^2 per plant at emergence. The relative growth rate of leaf area during the juvenile phase was 0.15 d^{-1} . The leaf area ratio decreased linearly from a value of 150 cm^2 leaf area per gram plant weight at emergence

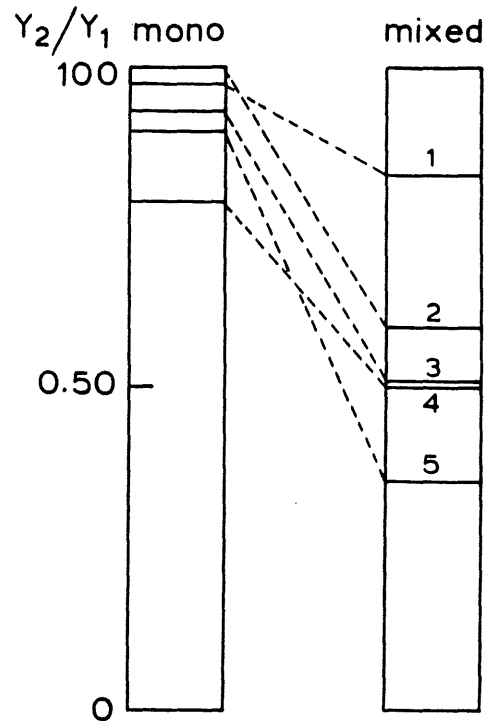


Figure 9. Simulated effect of single attributes on the ratio in biomass production of two isogenic species (Y_2/Y_1), grown in mixture and as monocultures. For species 1, the concerning attribute was enhanced to a value of 120% of that of species 2. Attributes: 1) initial leaf area per plant, 2) plant height, 3) extinction coefficient, 4) light utilization efficiency, 5) leaf area ratio.

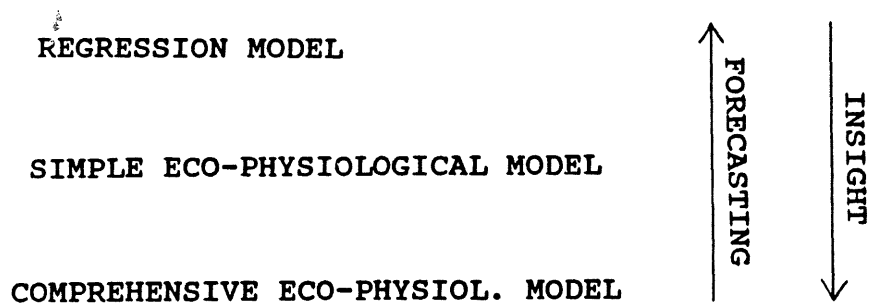


Figure 10. Regression models and simple eco-physiological models give the more accurate predictions of effects of intercropping, whilst eco-physiological models, and in particular the more comprehensive ones, give the better insight into the underlying principles of competitive interaction in intercrops.

to zero at full ripeness, 100 days after emergence. The light extinction coefficient was 0.7, and the light utilization efficiency amounted to 3 gram of dry matter formed per MJ of intercepted light. Plant height increased from 1 cm at emergence to 1 m, 80 days later. Incoming PAR averaged $8 \text{ MJ m}^{-2} \text{ d}^{-1}$.

In subsequent simulation runs, one attribute value for the first species was increased by 20%, so that in any run the species differed in only a single characteristic. The results of the sensitivity analysis are depicted in Figure 9. All attributes affected the yield of the species much more when it was grown as an intercrop than when it was grown as a monocrop. As intercrop, the advantage of an 20% greater leaf area at plant emergence was maintained over the whole growing period, while in monoculture it had a much smaller effect. This emphasizes the paramount importance of the starting position of a species in intercropping, and it also stresses the importance of accurate initialization in competition models. In mixture, the biomass production of a species increased more than proportional after increasing its light absorption per unit leaf area - either by taller plants or a greater extinction coefficient -, its utilization of the absorbed light, or its leaf area formed per unit plant weight.

4. DISCUSSION: USE AND LIMITATIONS OF THE COMPETITION MODELS

Models can be used either to predict expected effects in new situations or to improve our understanding of the studied system.

4.1 Predicting intercropping effects

The regression model facilitates the interpolation between the experimental data and thus the derivation of predictions of optimum intercrop combination and plant density (Figure 4). The competitive relations may, however, greatly vary from field to field, especially due to differences in the starting position of the different species (Figure 9). This variation in initial position is a major source of uncertainty when extrapolating the regression to other environments, and complicates the derivation of rules for farmers' practice.

In the eco-physiological models, many factors are accounted for, and so one might expect that these models, in particular the comprehensive ones, give the better predictions. This is, however, not the case. These models contain many functions and parameters, each with its own uncertainty, and these uncertainties accumulate in the simulated final yield. Simple models give therefore the more accurate predictions, in particular when their parameters are estimated from many experiments under the conditions where the model has to perform. Hence, in forecasting the effects of intercropping, we can better rely upon a simple eco-physiological approach than on a comprehensive one, and often even a regression approach may give the best result (Figure 10).

4.2 Understanding the competitive interactions

The regression model is useful as a first analysis of results of intercropping experiments, as it summarizes the experimental data with a minimum number of parameters. Moreover, some biological interpretation can be attached to the regression parameters. However, to expose the underlying principles of the competition process, an eco-physiological approach is indispensable. The presented physiological model offers a frame for the design and analysis of intercropping experiments aiming such an understanding.

In principle, the comprehensive models give the more thorough insight, but these may become so complex that others than the modeller himself cannot grasp anymore the structure of the model and the simulation results. The simple eco-physiological models are therefore better suited for the analysis of intercropping experiments and the transfer of the insights obtained.

4.3 Limitations to the use of models in intercropping research

The treated models essentially describe the effect of the plant numbers of the individual species on their yields in mixed stand. Hence, they can only assist in that part of the decisions on cultivation practices that deal with such a yield-density relationship, and usually only in relatively simple intercropping combinations. They don't give answer to the many other considerations involved in intercropping, in casu the other agronomical aspects (like a more complete ground coverage to control soil erosion), as well as the economic and sociocultural factors (e.g. Hildebrand, 1976; Lynam et al., 1986; Bradfield, 1986).

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