

## An alternative approach to the analysis of mixed cropping experiments. 2. Marketable yield

C. J. T. Spitters

Department of Theoretical Production Ecology, Agricultural University, P.O. Box 430, 6700 AK Wageningen, Netherlands

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### Summary

In a preceding paper (Part 1; Spitters, 1983), competition effects were estimated on the basis of biomass data. In the present paper, the effects of competition on the marketable yield are derived from those on biomass by means of the relation between per-plant biomass and harvest index. Besides, a method is presented to estimate competition effects and advantage of mixed cropping directly from the data of marketable yield. The effects of species composition and density of the population on advantage of mixed cropping, measured by the land equivalent ratio, is partitioned into (1) an effect due to better resource exploitation (niche differentiation), (2) a favourable influence of mixed cropping on harvest index, and (3) an effect due to density, which effect can also be achieved by growing the monocrops at a higher density. The approach is illustrated with the results of an experiment with mixed cropping of maize and groundnuts.

### Introduction

In Part 1 (Spitters, 1983) a model was introduced to analyse the competitive phenomena in mixtures. The approach was based on biomass, because biomass is a more direct measure of the distribution of limiting resources among the plants than yield of any plant part. However, in agronomical practice, not biomass but the yield of some desired plant parts is the aim of production. This yield is called the 'marketable yield'.

We cannot simply transpose our findings for biomass to marketable yield because the marketable yield/biomass ratio does not remain constant but may vary with plant density. This 'harvest index' decreases usually at high densities. In contrast to the asymptotic density-response curve for biomass per unit area (Spitters, 1983; Fig. 1a), for the marketable yield a parabolic curve is mostly found (Holliday, 1960).

Two methods may be applied. First, we may derive the trends for marketable

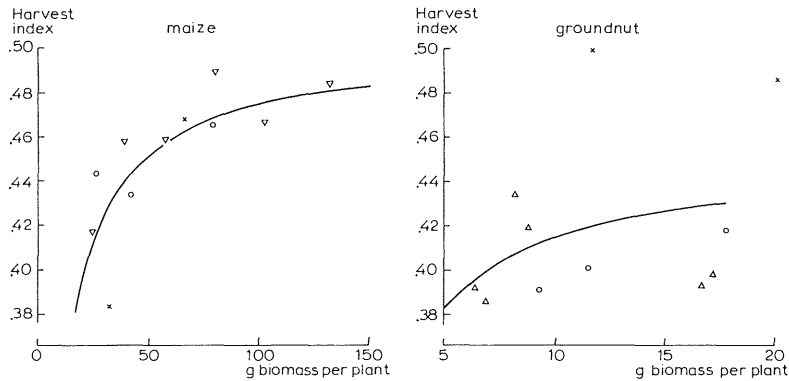


Fig. 1. Relation between harvest index of a plant and its competitive position, characterized by the biomass of that plant. The percentage of plants of the species in the total population is represented by:  $\nabla$  1-33 %,  $\circ$  34-66 %,  $\triangle$  67-99 %,  $\times$  100 %.

yield through the harvest index from the findings for biomass, where we describe the dependence of harvest index on population density as accurately as possible. Secondly, we may fit directly the data of the marketable yield with a parabolic curve. The indirect approach by means of the harvest index gives a better understanding of the mixture effects and is a more logical continuation of the analysis of the competitive phenomena so that this approach is presented first.

Both approaches will be illustrated with the results of mixed growing of maize and groundnuts. The experiments were described in Part 1 (Spitters, 1983). The data were kindly provided by W. C. H. van Hoof (Dept. of Tropical Crop Science, Agricultural University, Wageningen).

### Harvest index

Spacing experiments have shown that the harvest index is affected by plant density and, therefore, by interplant competition. Suppose that the effect of inter-specific competition on harvest index is similar to that of intra-specific competition. Then we may derive a single-pointed relation between the competitive position of a plant and its harvest index. In Part 1 (Spitters, 1983), the competitive position of a plant was quantified by its biomass. Hence, we read off the relation between harvest index and competitive position from a plot of harvest index against per-plant biomass.

In Fig. 1, that relation is described with a rectangular hyperbola. Maize gives a reasonable fit, but the relation for groundnut is much weaker.

Variation around the fitted curves may be caused by random error. Harvest index shows a large random variation: being a ratio of two quantities it includes the error of both quantities. However, variation around the curves may also be caused by deviation from the assumption that inter- and intra-specific competition have a similar effect on harvest index. For example, in another experiment, the harvest index of maize was much less reduced by inter-specific competition with groundnut

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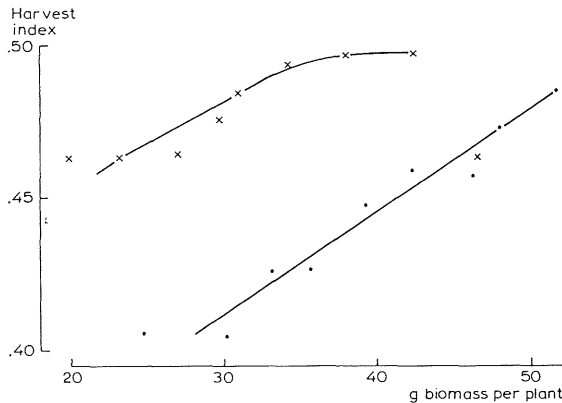


Fig. 2. Relation between harvest index and biomass per plant of maize in monocultures (●) and in mixtures with 16 groundnut plants  $m^{-2}$  (×). Data points come from populations differing in the number of maize plants  $m^{-2}$ .

than by intra-specific competition (Fig. 2). Plants of the same weight but originating from a different population may have a different harvest index when timing and nature of the competitive stress are different in the two populations. Timing during the ontogeny and nature of an environmental stress may greatly influence harvest index (review by de Ridder et al., 1981).

When such effects are consistent, one has to discriminate between the effects of inter- and intra-specific competition on harvest index. In that case the hyperbolic equation for the relation between harvest index and per-plant weight may be extended with the per-plant weight of the associated species (compare the extension of the density-response hyperbola in Part 1 (Spitters, 1983) to allow for inter-specific competition). Also other functions may be used, e.g. a multiple linear regression of harvest index on the logarithms of per-plant weight or on plant numbers of each species. In general, one should use the harvest index with caution.

### Assessing the advantage of mixed cropping

#### *Relative yield and land equivalent ratio*

The yield of a species in a population is expressed relative to its monoculture yield at a certain reference density. In analogy to Willey (1979), that *relative yield* of a species  $i$  is denoted by  $L_i$ . In general, the yield of the monoculture grown at the density which is recommended for local farmers is used as a reference. Within this frame the farmers weigh mixed growing of two crops against separate growing of the crops. Here, we set the recommended density of each species at 100 %.

Although two species may show a greatly different absolute yield level, through using relative yields with the monocrops at their recommended density as a reference, a comparable scale for both species is introduced.

The sum of the relative yields is called the *land equivalent ratio*. In a mixture of species  $i$  and  $j$ , the land equivalent ratio

$$LER = L_i + L_j = y_{ij}/y_{ii} + y_{ji}/y_{jj}$$

When  $LER = 1$ , the same yield of each species may be obtained with monocultures at recommended density as with a mixture, without changing the total area of land. The area fractions of those monocultures have to 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 mixture yield of each species with the monocrops. In other words, mixed cropping 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  $i$  is expressed relative to its yield in the monoculture from the same replacement series, the relative yield is denoted by  $RY_i$ ; 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.

#### *Search for maximum LER*

We may calculate the yields of groundnut pods and maize grain for a wide range of populations from (a) the competition parameters which we have estimated from the biomass data (Spitters, 1983, Fig. 3) and (b) the relation between harvest index and biomass per plant (Fig. 1).

Next we calculate for each population the relative yields  $L_m$  and  $L_g$  with respect to the yields of the monocrops at recommended density. For these monocrop yields, the values estimated by the model are used rather than the observed yields, so avoiding the random error of the observed monocrop yields, which would otherwise be introduced in each relative yield. But we risk a bias caused by a systematic deviation from the estimated trend in biomass and harvest index.

For each population we find a  $LER$  by summing up the relative yields. The  $LER$ s are presented in an iso- $LER$  diagramme where the  $LER$  is related to the plant density of each of the two species in the population (Fig. 3). The calculation for maize deteriorates at low population densities because of the negative estimate of  $b_0$  (see Spitters, 1983). We find a maximum value of  $LER$  of 1.5 in a mixture in which groundnut and maize are grown at 230 % and 80 % of their recommended monocrop densities, respectively. The  $LER$  shows a wide density optimum so that almost the same  $LER$ s are obtained with populations of much lower total densities. This is of practical significance because of the high costs of seed and low multiplication rate of groundnut. The highest  $LER$ s are always obtained with mixtures in which groundnut is present at a higher plant frequency than maize.

#### *Partitioning of LER to the underlying causes*

A value of  $LER$  greater than one points to an advantage of the respective popula-

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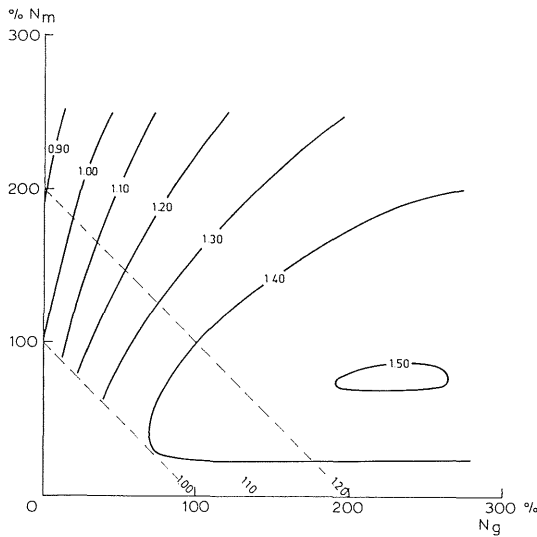


Fig. 3. Relation between maize density  $N_m$  and groundnut density  $N_g$  of a population and the LER of that population. LERs are represented by isocurves connecting populations with the same LER. The broken lines which join the axes represent replacement series with a total population density of 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.

tion in comparison to the monocrops at the recommended densities. 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 (Fig. 3), which is probably related to the high costs 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 (Fig. 3) and has nothing to do with advantage of mixed cropping.

2. *Real advantage of mixed cropping.* Whether mixed cropping leads to a real yield advantage that may be derived from the relative yield total in a replacement series. In a replacement series, the total population density is kept constant. When this total density equals 100 % of the recommended monocrop densities, RYT and LER are the same. This is the case in Fig. 4. 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 are used more efficiently in producing the desired plant parts than that is the case for either of the monocultures. The real advantage of mixed cropping can be partitioned into:

2a. *Favourable effect on harvest index.* When the species are not equally competitive, their per-plant weights in mixture will deviate from those in monoculture and so their harvest indices in mixture will differ from those in the monocultures (Fig.

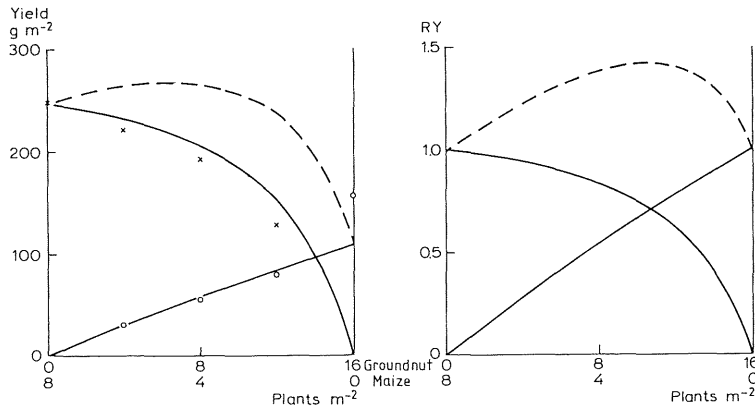


Fig. 4. Replacement diagrams with grain yield of maize and pod yield of groundnut per unit area (left) and with the yield of the species expressed relative to their yields in monoculture (right). One maize plant is replaced by two groundnut plants. Curves are those predicted with the model.

1). Interplant competition changes the competition for assimilates between the organs within a plant. Hence, even with  $RYT = 1$  for biomass,  $RYT$  for marketable yield may differ from one and may sometimes exceed the value one. The greater the  $RYT$  for biomass in a mixture, the greater tends to be the average weight per plant in that mixture. This contributes to a higher harvest index in the mixtures, if harvest index and per-plant weight are positively correlated as in Fig. 1.

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 mixed cropping on harvest index: the calculated  $RYT$  for marketable yield was 1.38 (Fig. 4) which is somewhat greater than the 1.35 for biomass. If there is a favourable effect of mixed cropping on harvest index, its contribution to the total advantage of mixed cropping will, however, be small in general.

2b. *Niche differentiation.* When total population density is kept constant and the effects of mixed growing on harvest index are removed, LER reduces to the  $RYT$  for biomass. In the mixtures of maize with groundnut  $RYT$  for biomass was greater than one. That points to a more efficient exploitation of the environment in the mixtures than in either of the monocultures. This indicates niche differentiation, with  $RYT$  being a workable measure of the degree of niche differentiation. We showed this niche differentiation between maize and groundnut already in Part 1 (Spitters, 1983) by a value greater than one for the product of the competition coefficients ( $b_{mm}/b_{mg})(b_{gg}/b_{gm})$ . Niche differentiation is, in general, an important reason of advantage of mixed cropping.

#### *Ratio of the species in the harvest product*

Up to now, we have searched for mixtures giving the highest LER. As known, a greater LER denotes that a greater area of land would have to be grown with monocrops to produce the same yield of each species as in the mixture. The higher the LER, the greater the advantage of growing the mixture.

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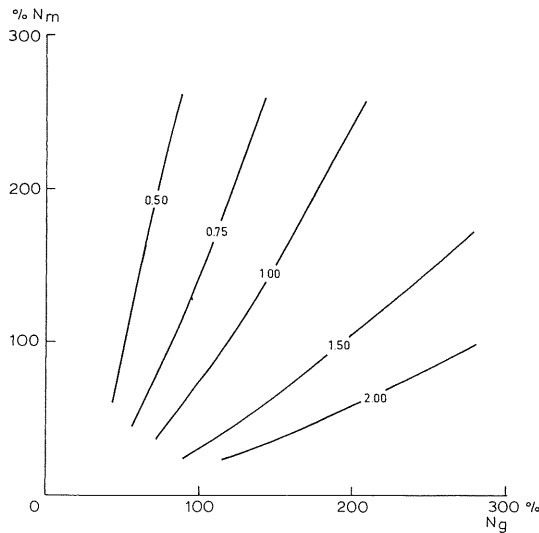


Fig. 5. Relation between maize density  $N_m$  and groundnut density  $N_g$  of a population and the yield ratio of that population. Yield ratios, defined as ratios of the relative yield of groundnut over that of maize, are represented by isocurves connecting populations with the same yield ratio. Plant 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.

However, a farmer often requests a distinct proportion of each species in the harvest product. Willey (1979, p. 3) discussed the different objectives with respect to this ratio. The yield ratio of the species may be presented by the ratio of either their absolute yields or their relative yields. By using relative yields, their yields are set on a comparable scale. The effect of the planting density of each of the two species in the mixture on the yield ratio (here expressed in terms of relative yields) is represented in a diagramme where populations with the same yield ratio are connected (Fig. 5).

The effect of species composition and density of the population on LER and yield ratio is evaluated simultaneously by projecting the iso-diagramme of the yield ratio (Fig. 5) on that of LER (Fig. 3).

Suppose that a yield ratio of 1.00 is desired. At this ratio, mixtures are found giving a LER which is substantially greater than one, although the peak LERs are observed in mixtures with a greater fraction of groundnut. To arrive at a yield ratio of 1.00, the densities of groundnut and maize should be about the same, with these densities being expressed relative to the recommended monocrop density of the species. As the recommended monocrop density of groundnut is two times that of maize, about twice as much groundnut seeds than maize kernels have to be sown to arrive at the desired harvest ratio. This illustrates the weaker competitive ability of groundnut.

**Direct analysis of data of marketable yield**

Instead of an indirect analysis of marketable yield by analyzing the data of biomass and harvest index, we may analyse directly the data of marketable yield by fitting an algebraic equation to these yield data. A general form of such a descriptive equation can be derived from the hyperbolic equations which we have used in the analysis of biomass and harvest index. Combination of these hyperbolic equations leads to the quadratic expression

$$1/w_{1m} = f_0 + f_1 (b_1 N_1 + b_2 N_2) + f_2 (b_1 N_1 + b_2 N_2)^2$$

where  $w_{1m}$  is the marketable yield per plant of species 1,  $b_1$  and  $b_2$  are the competition coefficients already used,  $f_0$ ,  $f_1$  and  $f_2$  are newly derived constants (see Appendix). This equation can be rewritten into a 4-parameter non-linear form as well as into a 6-parameter linear form (Appendix).

Both direct equations were applied to the yield data of groundnut and maize. The 4-parameter model showed a fit which was as good as that of the indirect model, which is a 5-parameter model (Table 1). The 6-parameter linear model gave the best fit. Evidently, a direct fitting of yield data gives a more accurate description of that data, measured by the percentage explained, than an indirect method. The more parameters are involved in the model the higher the percentage explained. (Be aware of overfitting when the number of data is only a little larger than the number of parameters).

With the fitted equation we may calculate yields and LERs for a range of populations. The results may be presented in an iso-LER diagramme alike Fig. 3.

It was already noted that the observed monocrop yield of groundnut is substantially higher than the monocrop yield which is predicted with the two-stage model (Fig. 4). The 6-parameter model makes better allowance for this relatively high monocrop yield of groundnut so that its predicted value is higher with this model. As a consequence, the 6-parameter model gives, compared to the two-stage model, lower values of LER, especially for mixtures with a high fraction of groundnut. The maximum LER is found to be 1.28 for a population consisting of 90 % of the recommended groundnut density and 80 % of the recommended maize density (compare this with Fig. 3).

The yield-based equation supplies an estimate of the competition effects, based

Table 1. The ratio of the competition coefficients, denoting how many plants of the second subscribed species have an equal effect as one plant of the first subscribed species on this first species, and the fraction of the observed variation in the reciprocal  $1/w$  of the marketable yield per plant which is explained by each of the three models. Data of groundnut (*g*) and maize (*m*).

	Ratio of competition coefficients		Fraction explained	
	$b_{gg}/b_{gm}$	$b_{mm}/b_{mg}$	$R^2_g$	$R^2_m$
Two-stage 5-parameter model	0.64	6.9	0.838	0.983
4-Parameter non-linear model	0.51	9.1	0.848	0.988
6-Parameter linear model	0.37	2.7	0.998	0.996



only on the yield data (see Appendix). These estimates agreed reasonably well with those based on the biomass data (Table 1). However, in general, only an indicative value should be adjudged to competition effects as estimated from data of marketable yield. These parameters are remotely derived ones with a large standard error. Moreover, the interpretation of the competition effects is biased when there are deviations in the experimental results from the assumptions where the two-stage model is based on.

In conclusion, the advantage of a direct fitting of the data of marketable yield is that (a) data of biomass are not required and (b) a more accurate description of the observed effects may be achieved. This better description of experimental data contributes to a more precise interpolation to untried populations. The direct analysis of yield data enables to discriminate between real and pseudo advantage of mixed cropping. It also provides a measure of the competition effects and of the degree of niche differentiation. However, these latter quantities have only an indicative value as they are based on a rather indirect way of estimating these effects.

A more reliable estimate of the competition effects is achieved with the two-stage model. That model gives also a better insight into the mixture effects because of the partitioning into the effects on biomass and harvest index.

### Discussion

The methods presented here enable one to estimate the competition effects and the degree of niche differentiation from a widely divergent set of populations. It gives insight into the observed effects of mixed cropping and it facilitates the recommendation for the optimal species composition and population density for mixed cropping. However, some notes have to be made, especially with respect to recommendations for farmers' practice. Not only the appropriateness of the mathematical model will be discussed, but also, and even more, the suitability of the type of mixed cropping experiments this paper deals with, i.e. experiments with mixtures of two species and a final harvest only.

In the indirect, stepwise approach, the marketable yields are calculated, by means of the harvest index, from the estimated trends in biomass. That gives a better understanding of how an advantage of mixed cropping is achieved. However, a precise prediction of marketable yields is important to arrive at recommendations on the optimal composition of populations for mixed cropping. In that situation the direct description of the yield data by fitting a parabolic curve through that yield data may be preferable. So both approaches are of value.

Both approaches consist of fitting a multiple regression equation through the data points. This facilitates interpolation to intermediate populations. Extrapolation outside the data range should be done only with great caution.

The observed results hold primarily for the situation studied. In another year, in another field or under different cropping practices the results may be different and therewith the optimum of composition and total density of the population. The sensitivity of the competitive relations for environmental conditions and cropping practices will be illustrated with the following. The outcome of competition is deter-

mined especially by the relative starting positions of the species. Relative differences in starting weight are maintained during growth, especially when the species have the same relative growth rate during early growth, the same height in course of time and an equal growing period. Under these assumptions, a species gains a twice as large proportion of the final total biomass of a mixed population either when that species is present with two times as many plants in the population or when its seedling weight is twice as large. A seedling weight that is two times larger is arrived at when its weight per seed is twice as large or when emergence is about 5 days earlier (Spitters, 1980). This emphasizes the necessity of periodic harvests to gain insight into the causal, physiological backgrounds of mixture effects. Experiments with a final harvest only, as is the case in most mixed cropping experiments, allow at most a 'mathematical' insight into the observed relations.

The model is directed towards the analysis of those mixed cropping situations where only a small number of species are involved. Especially in the humid tropics with a continuous growing season we find, however, compound farming systems with multiple cropping of sometimes several dozens of different species on the same piece of land (Okigbo & Greenland, 1976). For an analysis of those situations the model is not suitable.

In most mixed cropping experiments the analysis of yield per unit area in a given season is emphasized. A higher yield per unit area may be arrived at with a mixture than with the monocrops when the limiting growth resources are used more efficiently by the mixture. Examples are (a) the use of different nitrogen sources in mixtures of legumes and grasses or cereals and (b) a prolonged use of resources in mixtures of species differing in growing period, and in relay intercropping. However, the yields of the components of a mixture may also be influenced by other types of interspecific interaction than competition for growth resources: interference with the incidence of pests and diseases, windbreak, protection against high irradiance and low relative humidity, physical support for climbing species, and allelopathy. The model does account implicitly for this type of interactions, in so far they occur in the particular experiment, due to its empirical description of the effects of mixed cropping on yield. However, the biological interpretation, which is based on competition for growth resources, is biased by the latter type of interactions.

Apart from a higher yield per unit area in a given season, there are also other reasons why mixed cropping is practised.

a. Mixed cropping gives in general a quicker, greater and longer soil coverage. This contributes to a better control of soil erosion, which is of prime importance in maintaining the productivity of the soil, and to a better control of weeds.

b. A greater stability of yield over different seasons. When in a mixture one component is devastated by pests, diseases or adverse weather conditions, the other components may partly compensate for this yield loss. Minimizing these natural risks as well as the economic risks of price fluctuations is of prime importance for the small farmer to ensure food production and to protect his investments in labour, land and capital (if any). Mixed cropping may operate supplementary to crop diversification and phased planting in minimizing these risks.

Use of the land equivalent ratio (LER) is directed towards maximizing the pro-

ductivity per unit area. This fits in with the situation of those small farmers having the disposal of only a limited area of land. However, often other factors are scarcer than the area of land, for example labour during peak times of the multiplication rate of the planting material. In situations where the multiplication rate of grain crops is low, the productivity per kg seed is maximized rather than the productivity per hectare (Slicher van Bath, 1963). Taking the LER as a criterion would reduce the productivity per kg seed by recommending higher plant densities. We have met a similar situation for groundnuts in the experiment discussed. It is of particular importance in those vegetatively propagated species where the reproductive and the desired organs are the same.

An evaluation solely based on the LER neglects the requirements of the farmer on the amounts and ratios of the different crops in the harvest product. We made allowance for this by combining the results of the LER with those of the yield ratios.

The position of most of the small farmers is characterized by a high degree of self reliance and a strong dependence on the natural environment, due to their little technical and economical possibilities. This has led to the evolution of diverse and complex farming systems to fit in with these constraints. Consequently, cropping decisions of traditional farmers are influenced by different and more factors than are those of modern, high-technology farmers. Furthermore, there is a large variation in systems among regions which variation is not only the consequence of differences in the constraints dictated by the physical environment but also of different socio-economic and cultural backgrounds. That complexity is often not well understood by the agrarian technicians which are trained to perform in high-technology agriculture. This emphasizes the necessity of a regional agro-socioeconomic survey within the frame of a mixed cropping research project in order to understand what the farmers are doing, how they are doing it, and why they are doing it the way they are (see Hildebrand, 1976).

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### Appendix. Direct estimations from the data of marketable yield

#### *Basic regression equation*

The indirect analysis of marketable yield consisted of three equations.

1. A rectangular hyperbola for the relation between per-plant biomass  $w_t$  and plant density  $N$ . In linear regression form for species 1 in mixture with species 2:

$$1/w_{1t} = b_{1,0} + b_{1,1}N_1 + b_{1,2}N_2$$

where the regression coefficients  $b_{1,0}$ ,  $b_{1,1}$  and  $b_{1,2}$  characterize the competition effects (see Spitters, 1983).

2. A rectangular hyperbola for the relation between harvest index HI and per-plant biomass  $w_t$ . In linear regression form for species 1:

$$1/HI_1 = h_{1,0} + h_{1,1}(1/w_{1t})$$

where  $h_{1,0}$  and  $h_{1,1}$  are the regression coefficients.

3. Estimation of marketable yield per plant from biomass by means of harvest index:

$$w_{1m} = HI_1 \times w_{1t}$$

These three equations may be combined. This gives for the reciprocal of the marketable yield per plant of species 1:

$$1/w_{1m} = 1/(HI_1 \times w_{1t}) = b_0(h_0 + b_0h_1) + b_1(h_0 + 2b_0h_1)N_1 + b_2(h_0 + 2b_0h_1)N_2 + h_1(b_1N_1 + b_2N_2)^2 \quad (1)$$

where the first subscripts, denoting species 1, are omitted.

#### *Four-parameter non-linear equation*

Eq. 1 can be rewritten into the 4-parameter non-linear form:

$$1/w_{1m} = a_1 + a_2 N_1 + a_3 N_2 + \{a_4 N_1 + (a_3/a_2)a_4 N_2\}^2$$

The four parameters are estimated directly by a least-squares procedure from the data of the marketable yield. A weighted procedure is preferable (Appendix 1 of Spitters, 1983).

The parameters can be expressed in terms of the regression coefficients of the two-stage approach:

$$b_1/b_2 = a_2/a_3$$

$$b_0/b_1 = \{a_2 - (a_2^2 - 4a_1a_4^2)^{1/2}\}/2a_4^2$$

$$b_0/b_2 = (a_2/a_3) \{a_2 - (a_2^2 - 4a_1a_4^2)^{1/2}\}/2a_4^2,$$

$$h_0^2/h_1 = a_2^2/a_4^2 - 4a_1$$

for the interpretation of the parameters see Part 1 (Spitters, 1983).

*Six-parameter linear equation*

Eq. 1 can be recasted into the 6-parameter linear form:

$$1/w_{1m} = c_1 + c_2N_1 + c_3N_2 + c_4N_1^2 + c_5N_2^2 + c_6N_1N_2$$

The parameters are estimated by a multiple linear regression procedure.

The advantages of this equation over the non-linear equation are that a linear regression form is easier to handle and that, due to a greater number of parameters, a more accurate description of the data is arrived at.

Interpretation of the estimated parameters may be in terms of the above-mentioned ratios of  $b$  and  $h$ . Averaging is necessary because the six parameters carry information of four quantities only. In averaging the estimated ratios, a geometric average is preferable:

$$b_1/b_2 = \exp \{ \ln c_2/c_3 + \ln(c_4/c_5)^{1/2} \}$$

To account for the heterogeneity of variances, the  $c$  should be weighted to the reciprocal of their variances:

$$b_1/b_2 = \exp \{ [ \ln (c_2/c_3) / \text{var} \ln (c_2/c_3) + \ln (c_4 c_5)^{1/2} / \text{var} \ln (c_4/c_5)^{1/2} ] / \{ 1 / \text{var} \ln (c_2/c_3) + 1 / \text{var} \ln (c_4/c_5)^{1/2} \} \}$$

with as approximated variances:

$$\begin{aligned} \text{var} \ln c_2/c_3 &\approx (1/c_2^2) \text{var} c_2 + (1/c_3^2) \text{var} c_3 \\ \text{var} \ln (c_4/c_5)^{1/2} &\approx (1/4c_4^2) \text{var} c_4 + (1/4c_5^2) \text{var} c_5 \end{aligned}$$

The approximated variances are derived by the method of statistical differentials (Kempthorne & Folks, 1971, p. 130).

