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Analysis of crop loss in the multiple pathosystem groundnut–rust–late leaf spot. I. Six experiments

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Abstract A series of six experiments was conducted to study the relationships between production situation, injuries, and damage in the groundnut–rust–late leaf spot pathosystem. The production situation, represented by attainable yields, was varied by replicating the experiments over seasons and incorporating several input factors at different levels. Injuries, represented by log-transformed areas under disease progress curves, were manipulated by means of inoculations and fungicide applications. The resulting database was used to develop damage functions, represented by yield and relative damage response surfaces, using multiple regression analysis. The corresponding equations indicate significant interactions between attainable yield and injuries on actual yield and relative damage. Further analysis indicates that injury–damage relations differ in rust and late leaf spot: whereas damage due to late leaf spot was mainly related to reduction of green leaf area and defoliation, damage due to rust was attributable to different mechanisms in addition to reduction of green leaf area. The negative interaction between the injurious effects of the two pathogens was ascribed to this difference.

Keywords Crop management; crop loss; intensiveness; multiple pathosystem; West Africa; *Arachis hypogaea; Cercosporidium personatum; Puccinia arachidis*; crop damage

Introduction

Detailed studies on yield-determining factors have been conducted, mainly to develop predictive models for yield (Stynes, 1980; Wiese, 1982). The resulting multiple regression models incorporate information on crop status, pests and diseases. Descriptors of crop inputs and cropping techniques account for the yield that could have been attained in the absence of yield-reducing factors such as pests, i.e. attainable yield (Zadoks and Schein, 1979).

Most tropical food crops are confronted with several pests (*sensu lato*), in various production situations (Zadoks and Schein, 1979; Moreno, 1985). A production situation can be seen as the combination of yield-determining and yield-limiting factors (De Wit, 1982a,b; Rabbinge and De Wit, 1989), and can be represented by an attainable yield. In general, the assumption of no interaction between the injuries induced by the components of a system of pest constraints on damage (yield loss, Zadoks, 1985) may not be valid (Teng, 1983). A larger issue is whether the overall effect of pest injuries on damage will change depending on the production situation.

Analysis of the relationships between attainable yield and damage induced by components of a system of constraints should address the following questions: (1) given a production situation, as represented by a given attainable yield, will management of one or more components of the system of constraints allow increase in actual yields; (2) will increasing attainable yield due to intensification of agricultural practices correspond to an increase in the overall damage, and if so, which of the constraint components will contribute most to this increase? Answers to these questions are prerequisites to the management of constraints, including the use of damage and action thresholds (Zadoks, 1985, 1987).

Groundnut is an example of a tropical crop with a wide range of production situations and many disease constraints in West Africa (Subrahmanyam *et al.*, 1985; Savary *et al.*, 1988). Foliar fungal diseases are particularly important, and the relationships between injury and damage have been documented (Boote *et al.*, 1980; Subrahmanyam *et al.*, 1984; Bell, 1986; Savary *et al.*, 1990), as well as some of the interactions between diseases (Cole, 1982; Savary *et al.*, 1988).

The objective of this study is to provide an overall description of the relationships between attainable yield, injuries, and damage in the pathosystem groundnut – rust (*Puccinia arachidis* Speg.) – late leaf spot (*Cercosporidium personatum* (Berk. & Curt.) Deighton) which is of particular importance in humid and sub-humid groundnut cropping regions of West Africa (Savary *et al.*, 1988).

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Table 1. Description of six experiments on crop losses due to foliar disease in groundnut

Experiment code	Dates: Planting	Dates: Harvest	Treatments confounded with blocks (input factors)	Management of epidemics of diseases: Inoculation methods: Rust	Inoculation methods: Leaf spot	Fungicide applied[a]: C	RS	Rs	rS	rs[b]
W	14 December 1987	14 March 1988	Three levels of water control (dry season) ● 14 mm twice a week till harvest ● 14 mm twice a week till 67 days after planting ● 14 mm twice a week till 50 days after planting	inoculated potted plants	infected leaves spread on soil	CHL	CHL from 57 days after planting onwards			
H	25 April 1988	25 July 1988	Three levels of weed control ● careful hand-weeding during crop cycle ● sowing of weeds[c] 3 weeks after sowing; half of rows hand-weeded ● same; no weeding during crop cycle	inoculum dusted on plots	infected leaves spread on soil- + spore suspension sprayed on plots	CHL	CHL from 48 days after planting onwards			
F1	13 October 1988	11 January 1989	Three levels of fertilizer ● no input ● lime: 600 kg ha^{-1}; NPK: 50-90-90 kg ha^{-1}; manure: 15 t ha^{-1} ● lime: 900 kg ha^{-1}; NPK: 80-144-144 kg ha^{-1}; manure: 15 t ha^{-1}	inoculum dusted on plots	spore suspension sprayed on plots	CHL	CHL from 53 days after planting onwards			
F2	13 March 1989	12 June 1989	Three levels of fertilizer ● no input ● NPK:30-54-54 kg ha^{-1} ● NPK: 60-108-108 kg ha^{-1}	inoculum dusted on plots	spore suspension sprayed on plots	CHL	—	—	—	—
D	13 March 1989	12 June 1989	Three crop densities ● 6.25 plants m^{-2} ● 10 plants m^{-2} ● 16 plants m^{-2}	inoculum dusted on plots	spore suspension sprayed on plots	CHL	—	—	—	—
V	24 August 1989	23 November 1989	Three varieties ● local short-cycle cultivar ● TMV2 ● KH149A	inoculum dusted on plots	spore suspension sprayed on plots	CHL	—	BNL	PLX	BNL + PLX

[a]CHL: chlorothalonil (3.8 kg a.i. ha^{-1}; weekly sprays); BNL: Benlate (0.7 kg a.i. ha^{-1}; bimonthly sprays); PLX: Plantvax (2.25 l a.i. ha^{-1}; bimonthly spray); [b]C, control; RS, high rust + high leaf spot; Rs, high rust + low leaf spot; rS, low rust + high leaf spot; rs, low rust + low leaf spot; [c]*Oldenlandia corymbosa*; sowing carried out on previously weeded plots

Materials and methods

Disease treatments

Five disease treatments were considered: low rust and leaf spot (rs), high rust and low leaf spot (Rs), low rust and high leaf spot (rS), high rust and high leaf spot (RS), and a control (C) where both diseases were eliminated by means of the contact fungicide chlorothalonil. Effects of this fungicide on growth, development, and yield of uninfected groundnut plants have not been reported. Each experiment consisted of three blocks in which the treatments were randomly assigned to 4 × 4 m plots. Within each block, plots were separated by a 2 m bare-ground row.

Description of experiments

Six experiments were successively conducted from late 1987 to late 1989 (*Table 1*) at the IIRSDA experiment station, Adiopodoumé, Ivory Coast. In order to enhance variation of yield, and of yield response to diseases, a series of input factors was selected, and applied at three different levels. One factor was assigned to each experiment, and its three levels were applied to the three blocks, one level per block: the first experiment (W) involved three levels of water control, the second (H), three levels of weed control, the third (F1) and fourth (F2) three levels of fertilizer input, the fifth (D) three levels of sowing density, and the sixth three cultivars differing in potential yields (V).

Plant material

In all experiments (*Table 1*) except the last (V), a local, short-cycle (~90 days from sowing to harvest) erect cultivar was used, susceptible to both rust and leaf spot. In the last experiment, this cultivar was used in one block whereas the two other blocks were planted with TMV2 and

KH149A, short-cycle erect varieties with higher yield potentials. The three cultivars are about equally susceptible to rust and to late leaf spot. KH149A is more sensitive to defoliation induced by late leaf spot.

All experiments except the fifth were sown at the same density, with equal spacing between rows and plants in the row (0.4 × 0.4 m). In experiment D, blocks had different densities: 6.25 (0.4 × 0.4 m), 10.0 (0.4 × 0.25 m), and 16.0 (0.25 × 0.25 m) plants m^{-2}. Replacements were made at emergence in order to obtain the desired crop density.

Disease epidemics

Both rust and late leaf spot are endemic in the southern Ivory Coast. Early leaf spot (*Cercospora arachidicola*), present in some experiments, never exceeded 0.01% severity. Disease levels were manipulated to enhance spontaneous epidemics in the plots where disease had to reach high levels, and reduce them to minimum levels in the control plots (C). Chlorothalonil (3.8 kg a.i. ha^{-1}) was sprayed weekly in these plots to control rust and leaf spot.

Rust development was enhanced in treatments RS and Rs either by placing potted plants inoculated in the greenhouse at the centre of each plot for a period of 3 days (experiment W), or by dusting each plant with 50 mg of a mixture of kaolin and rust spores containing 500 spores mg^{-1} (all other experiments). Two outside rows of plants were left uninoculated as borders. Inoculations were carried out twice, at an interval of 1 week, at dusk from development stage V3 until development stage R1. Inoculum was maintained in the greenhouse on detached leaflets placed on moist filter paper in Petri dishes (Savary, 1985).

Leaf spot development was enhanced in treatments RS and rS either by placing infected leaves on the soil after sowing (experiments W and H; approximately 5 g infected leaves m^{-2}), or by spraying the plants at dusk with a spore suspension containing 20–60 spores μl^{-1} of a Triton X-100/water (0.0001 %, v/v) solution (experiments H to V). Inoculations with *C. personatum* were carried out at the same development stages as with *P. arachidis*.

In experiments W, H and F1, an attempt was made to reduce interplot interference by both pathogens towards the end of the crop cycle by spraying chlorothalonil on all plots from ~50 days after sowing, onwards. In experiment V, a strong late leaf spot epidemic spontaneously developed on all plots except controls. Three sprays at 15-day intervals with systemic fungicides were superimposed on inoculations (*Table 1*), with Plantvax (oxycarboxin; 2.251 a.i. ha^{-1}) in treatments rS and rs and Benlate (benomyl; 0.7 kg a.i. ha^{-1}) in treatments rs and Rs. These two fungicides had no significant effect on crop growth, development rate, and yield of disease-free plants when tested in a separate experiment (F. Brissot and S. Savary, unpublished data).

Disease assessments

Rust and leaf spot severities were assessed weekly in three leaf layers on five plants chosen at random in each plot, using diagrammatic scales (Savary *et al.*, 1988). The estimated rust (r_i) and leaf spot (s_i) severities at each assessment (i) were used to calculate the areas under disease progress curves R and S (*Table 2*) in each plot:

Table 2. List of variables

Acronyms	Meaning	Units
R	Area under rust progress curve	%day
S	Area under late leaf spot progress curve	%day
R_l[a]	Rust injury: $R_l = \ln(R+1)$	—
S_l	Late leaf spot injury S: $S_l = \ln(S+1)$	—
$TLAI$	Area under total leaf area index (LAI) progress curve	$m^2\ m^{-2}$ day
$DLAI$	Area under detached LAI progress curve	$m^2\ m^{-2}$ day
$LLAI$	Area under attached LAI progress curve	$m^2\ m^{-2}$ day
$GLAI$	Area under green LAI progress curve	$m^2\ m^{-2}$ day
$GLAI_l$[b]	Log-transformed GLAI: $GLAI_l = \ln(GLAI+1)$	—
$TLAI_a$	Attainable LAI: TLAI value in the protected plot (C) in each block	$m^2\ m^{-2}$ day
$DLAI_a$	Attainable DLAI	$m^2\ m^{-2}$ day
$LLAI_a$	Attainable LLAI	$m^2\ m^{-2}$ day
Y_a	Attainable yield: yield of the protected plot (C) in each block (all other experiments, and combined data set)	$kg_{dry\ pod}\ ha^{-1}$
Y	Yield of individual plot	$kg_{dry\ pod}\ ha^{-1}$
RD	Relative damage	%

[a]All logarithms are Napierian; [b]other log-transformed LAI-variables were not used directly

$$R = \sum_{i=1}^{h} (t_i - t_{i-1}) r_i \text{ and} \tag{1}$$

$$S = \sum_{i=1}^{h} (t_i - t_{i-1}) s_i \tag{2}$$

where t_i and t_{i-1} denote dates of the ith and $i-1$th assessments, and t_n (=90 days after planting) denotes harvest date.

Crop development and growth

Development stages were assessed weekly, and development speeds, calculated as the number of stages passed per day, were calculated for stages R1 (flowering), R4 (full pod), and R6 (full seed; Boote, 1982) for each plot.

In all plots, the number of attached and detached leaves (leaf scars) were counted weekly on the main stems of the five plants chosen for disease assessment. Total number of leaves put out per plant and mean leaf area (from three leaves on the main stem) were estimated weekly on one selected plant of the protected plots. These data were combined to estimate the total number of leaves put out per plant (n_t) and the mean area of one leaf (l_a) from the total number of leaves (m_t) on the main stem in the unprotected plots:

$$n_t = a^* m_t^{\,b} \text{ and } l_a = c + d\ln(m_t), \tag{3)(4}$$

where a, b, c and d are parameters, n_t and m_t are leaf numbers, and l_a is the mean area of one leaf. Equations (3) and (4) were combined to calculate an estimate of the total leaf area index ($tlai_i$) at date t_i:

$$tlai_i = CD^* n_t^* l_a \quad (5)$$

where CD is the crop density in the considered plot. Estimates for parameters a, b, c, and d were made for the local groundnut cultivar at usual crop density (experiments W, H, F1, F2, and D, block 1), and at high densities ($CD = 10$ and 16 plants m^{-2}, experiment D, blocks 2 and 3).

Equations (3), (4), and (5) were used to estimate *tlai* values in the corresponding unprotected plots from weekly mean total of leaves (m_t) per main stem. It was further assumed that the mean area of detached leaves equalled the mean area of the total leaf population emitted by the plants, and that defoliation of the main stem represented defoliation on the whole plant. Using the mean proportion of detached leaves per main stem, p, the detached ($dlai_i$) and attached ($llai_i$) leaf areas per plot were calculated as

$$dlai_i = p^* tlai_i, \text{ and } llai_i = (1-p)^* tlai_i \quad (6)(7)$$

and the areas under total ($TLAI$), detached ($DLAI$), and attached ($LLAI$) leaf area index progress curves were calculated.

The green (apparently non-infected) leaf area index was calculated as

$$glai_i = \{1 - [(r_i + s_i)/100]\}^* llai_i \quad (8)$$

and the area under the green leaf area index progress curve ($GLAI$) was calculated.

Yield assessment

Dry pod yield per plot was determined by the weight of pods produced by plots excluding the borders, after drying (45–65°C for 5 days in an oven) and cleaning. When needed (experiments WD and F1), a sample of healthy pods was taken to estimate mean dry weight of undamaged pods in each plot, and correct yields for millipede injury and/or *Botryodiplodia* rot.

General procedure for data analysis

The concept of response surface was first introduced to study the relationships between damage, disease, represented by its various levels, and the development of the crop (DVS), hence the process of yield build-up through its various components (Teng and Gaunt, 1980; Teng, 1985): damage = F(disease, DVS). As the objective is to analyse the yield response to the largest possible range of DVS and disease combinations, the corresponding methodology – response surface analysis – lays stress on the number of treatments over replications (Teng, 1985, Shane and Teng, 1987).

Two-way analyses of variance and step-wise multiple regression analyses were performed within each experimental set, and on the complete series of experiments. Damage due to rust and leaf spot can be viewed as a two-stage process, leading first to a destruction of foliage and/or reduction of photosynthetically active leaf area, which then results in yield reduction (Subrahmanyam *et al.*, 1984; Bell, 1986). The relationships between foliage characteristics and yield were examined, and the above hypothesis on injury/damage relationships in groundnut foliar diseases was evaluated. In a final stage, the relations between treatments and yield were analysed.

Regression analyses

Step-wise regression analyses were performed using selected variables to be explained and sets of explanatory variables (Butt and Royle, 1974; Teng and Gaunt, 1980; Draper and Smith, 1981; Madden, 1983), the latter being introduced simultaneously and selected in a backward process.

Two variables were chosen to represent yield and damage variations: these were the harvested dry pod yield per plot (Y, *Table 2*), and the damage (RD) relative to the attainable yield (Y_a), i.e. the yield of the protected plot (C) in the block corresponding to each plot:

$$RD = [(Y_a - Y)/Y_a]^* 100 \quad (9)$$

To analyse the effects of diseases on leaf area indices in the six experiments, additional explanatory variables had to be introduced to account for the variation across blocks (input factors) and across experiments. The chosen variables are the characteristics of the foliage in protected (C) plots in the respective block, i.e. attainable accumulated total, detached, and attached leaf area indices ($TLAI_a$, $DLAI_a$, and $LLAI_a$, respectively). The areas under rust (R) and leaf spot (S) progress curves, and their product (R^*S) were introduced as explanatory variables. The regressions which were tested have the general shape:

$$\_LAI = f(\_LAI_a, R, S, R^*S) \quad (10)$$

where $\_LAI$ and $\_LAI_a$ represent $TLAI$ and $TLAI_a$, $DLAI$ and $DLAI_a$, or $LLAI$ and $LLAI_a$.

Logarithmic transformation of both R and S considerably increased the proportion of variation of relative damage (RD) accounted for by linear regression when compared with untransformed variables ($r^2 = 0.57$ and 0.35, vs 0.41 and 0.13 for R and S, respectively). Log-transformed areas under disease progress curves were therefore used as operational definitions of the injuries over the crop cycle. Logarithmic transformation of $TLAI$ also significantly increased the proportion of yield variation accounted for by linear regression ($r^2 = 0.50$ vs 0.40). Log-transformed areas under disease progress curves, $R_l = \ln(R+1)$ and $S_l = \ln(S+1)$, and leaf area indices progress curves, $\_LAI = \ln(\_LAI + 1)$, were used to analyse the variation of yield (Y) and relative damage (RD).

To analyse the whole set of data from the six experiments, an explanatory variable was needed to account for variation in yield and relative damage among blocks (input factor levels) within each experiment, and across experiments. The chosen variable was the attainable yield Y_a corresponding to each individual plot. The shapes of the tested equations are:

Table 3. Effects of disease treatments on areas under disease progress curves, leaf area indices and yield

Variable[a]	Treatment[b]	Experiment[c] W	H	F1	F2	D	Y
R	rs	263 c[d]	352 c	85 b	296 c	386 c	187 b
	RS	353 d	402 d	171 c	463 d	547 d	389 c
	rS	183 b	286 b	42 b	207 b	262 b	81 ab
	Rs	455 e	505 e	442 d	796 e	845 e	633 d
	C	3 a	8 a	0 a	1 a	1a	1 a
S	rs	220 c	102 b	136 c	152 b	135 b	38 a
	RS	270 d	234 c	477 d	519 c	445 c	287 b
	rS	340 e	263 c	459 d	387 c	363 c	245 b
	Rs	165 b	115 b	64 b	105 ab	75 ab	15 a
	C	14 a	4 a	0 a	1 a	1 a	7a
TLAI	rs	172 a	152	143	240	344	212
	RS	150 b	146	137	231	329	199
	rS	167 a	158	149	245	332	204
	Rs	146 b	164	143	232	320	198
	C	163 a	159	146	254	343	203
DLAI	rs	33 c	44 b	20 b	54 b	58 b	33 b
	RS	35 cd	44 b	42 c	79 d	108 c	51 c
	rS	36 d	51 b	40 c	65 bcd	102 c	50 c
	Rs	29 b	48 b	24 b	61 bc	92 c	37 b
	C	6 a	7 a	2 a	21 a	13 a	7 a
LLAI	rs	140 b	108 b	123 b	187 b	285 b	179 ab
	RS	112 c	102 b	96 d	152 c	220 c	147 c
	rS	131 b	108 b	109 c	180 b	230 c	154 c
	Rs	116 c	117 b	119 b	171 bc	228 c	161 bc
	C	157 a	152 a	145 a	233 a	330 a	196 a
Y	rs	1156 b	548 b	881 c	2592 b	2737 b	2756 b
	RS	1076 bc	466 b	800 d	1821 c	2243 bc	2244 c
	rS	1129 bc	445 b	968 b	2613 b	2580 bc	2288 c
	Rs	867 c	561 b	778 d	2071 c	2181 c	1809 d
	C	1782 a	902 a	1102 a	3131 a	3507 a	3283 a

[a]As in *Table 2*; [b,c]as in *Table 1*; [d]entries are means of three replications (blocks); numbers followed by different letters are significantly different according to their l.s.d. ($p<0.05$) after a two-way analysis of variance

$$Y=f(Y_a, R_l, S_l, Y_a*R_l, Y_a*S_l, R_l*S_l) \quad (11)$$
$$RD=f(R_l, S_l, Y_a*R_l, Y_a*S_l, R_l*S_l) \quad (12)$$

In the regression for *RD*, Y_a was not incorporated as an explanatory variable, because it is already included in the calculation of *RD*.

Results

Estimation of total leaf area index

The equations developed to estimate *TLAI* enabled 91, 94 and 86% ($p<0.01$ in all cases) of the variation of the estimated total leaf area index at usual, medium, and high crop density, respectively, to be accounted for in a series of observations representing a complete crop cycle in experiment D. The equation for $CD=6.25$ m^{-2} was further evaluated in experiment V to predict total leaf area indices in the three cultivars used. The results indicated significant r and high r^2 values (0.94, 0.92 and 0.91 for the local cultivar, TMV2 and KH149A, respectively, with $n=20$ observations), and non-significant bias in the predicted leaf area indices (slopes and intercepts not significantly different from 1 and 0, respectively).

Analysis of variance of yield across experiments

Each experiment incorporated one block where levels of input factors were set to default levels, i.e. sub-optimal water (W) and weed (H) control, no fertilizer input (F1 and F2), low crop density (D) and low cultivar potential yield (V). These blocks were used as replications of the five disease treatments applied, and the corresponding yields, submitted to two-way ANOVA. The results indicated strong experiment ($F=48.9$, $p<0.01$) and disease treatment ($F=10.3$, $p<0.01$) effects on yields. Further comparison of means using the Newman–Keuls test indicated that two groups of *Y*-values only were to be considered according to this design: protected plots (C; $Y=2233$ kg ha^{-1}) and unprotected (rs, RS, rS, Rs; $Y=1642$, 1437, 1592, 1403 kg ha^{-1}, respectively).

Effects of disease treatments on intensity of diseases, leaf area indices and yield

Disease intensities. A good overall protection was obtained in all six experiments against both diseases (*Table 3*, treatment C), as represented by their respective areas under progress curves (*R* and *S*). Rust intensities were highest in plots where it had been inoculated (treatments Rs and RS) than in treatments rS and rs. However, rust intensities were higher when leaf spot was low. Therefore, four distinct levels of rust were obtained in the unprotected plots.

Leaf spot intensity showed similar patterns, i.e. higher intensities where it had been inoculated (rS and RS), and

Table 4. Regression equations for the complete data set

Variables to be explained and explanatory variables[a]	Equations	r^2	d.f.	p
1 *TLAI*= f(*TLAI*$_a$, *R*, *S*, *R***S*)	$TLAI = 15.6 + 0.93\,TLAI_a - 0.020\,R$; p: <0.0001, 0.005	0.96	87	<0.0001
2 *DLAI*= f(*DLAI*$_a$, *R*, *S*, *R***S*)	$DLAI = 1.54 + 0.77\,DLAI_a + 0.063\,R + 0.086\,S$; p: <0.0001, <0.0001, <0.0001	0.67	86	<0.0001
3 *LLAI*= f(*LLAI*$_a$, *R*, *S*, *R***S*)	$LLAI = 44.2 + 0.77\,LLAI_a - 0.067\,R - 0.095\,S$; p: <0.0001, <0.0001, <0.0001	0.92	86	<0.0001
4 $Y = f(Y_a, R_l, S_l, Y_a{*}R_l, Y_a{*}S_l, R_l{*}S_l$	$Y = 143 + 0.96\,Y_a - 0.055\,Y_a{*}R_l + 0.020\,Y_a{*}S_l - 9.70\,R_l{*}S_l$; p: <0.0001, <0.0001, 0.10, 0.08	0.92	85	<0.0001
5 $RD = f(R_l, S_l, Y_a{*}R_l, Y_a{*}S_l, R_l{*}S_l)$	$RD = 1.94 + 0.0011\,Y_a{*}R_l - 0.0020\,Y_a{*}S_l + 1.32\,R_l{*}S_l$; p: <0.001, <0.0001, <0.0001	0.62	86	<0.0001
6 $RD = f(R_l, S_l, GLAI_l)$	$RD = 57.3 + 5.88\,R_l - 11.6\,GLAI_l$; p: <0.0001, 0.03	0.59	87	<0.0001

[a]As in *Table 2*

reduced intensities where high rust levels were present. Both rust and leaf spot intensity patterns therefore indicate competition effects in unprotected plots.

Total leaf area indices. The area under total leaf area index (*TLAI*) strongly differed among experiments. Whereas differences in *TLAI* can be related to differences in crop density in experiment D and to differing cultivars in experiment V, they can be ascribed to differences in crop establishment and environment in the four first experiments. Effect of disease treatment is not apparent from these data, except in the first experiment (W), where canopy growth was reduced in treatments RS and Rs. Reduced foliage growth in the presence of high rust levels is also suggested in experiments F2 and D.

Detached leaf area index. *Table 3* indicates that defoliation, as measured by *DLAI*, was strongly increased whenever any noticeable disease level was present; high defoliation levels were observed at low disease levels (rs), which in some instances were not significantly different from the maximum defoliation levels (experiments H and D). Defoliation was usually highest at high leaf spot level, irrespective of the preset rust level (experiments W, F1, F2, and V).

Attached leaf area index. As a combination of the above effects, living leaf area (*LLAI*) was highest in protected (C) plots. Living leaf area was lowest when both diseases were present at high (RS) levels in all six experiments.

Yields. Strong differences in yield (*Y*) among experiments were observed. Block effects, superimposed to levels of input factors (not shown) very much varied among experiments; it was significant in experiments W, F2 and V ($p < 0.05$ at least), and in some cases corresponded to wide variation in mean block yields (W: 654–1574; F2: 2261–2691; and V: 1924–3146 kg ha^{-1}). Highest yields were obtained in protected plots, and strongly varying relative damage (*RD*) levels were observed among experiments (W: 35–51%; H: 37–51%; F1: 12–29%; F2: 17–42%; D: 22–38%; V: 16–45%). The lowest yields were obtained at high rust (Rs) or high rust and leaf spot (RS) levels.

Development rate of the crop. Whereas significant effects of disease treatments were observed on yield, no significant differences in development rate of the crop among treatments were found in any experiment.

Regression equations

Relationships between leaf area indices and disease intensities. Equation (1) (*Table 4*) indicates that rust intensity as expressed as the area under disease progress curve (*R*) significantly reduces the overall growth of foliage. On the other hand, Equation (2) of *Table 4* indicates that rust and leaf spot severity additively contribute to defoliation, as the interaction term (*R***S*) did not significantly contribute to the description of *DLAI* variation. Alternatively, Equation (3) of *Table 4* indicates that both diseases contribute additively to the reduction of the living leaf area.

Relationships between yield or relative damage, and disease injuries and attainable yield. With the difference of the presence of a contribution of Y_a to Equation (4), which can be seen as a correcting factor for variation of average yield among experiments, Equations (4) and (5) (*Table 4*) have the same shape. Both include three interaction terms that can be interpreted in the same way. These equations are built using the log-transformed areas under disease progress curves for rust (R_l) and leafspot (S_l). In Equation (4), the contributions of $Y_a{*}S_l$ and $R_l{*}S_l$ are low ($p = 0.10$ and 0.08, respectively), and should be considered as trends

Table 5. Correlation matrix[a] between yield (Y) and relative damage (RD) and explanatory variables[b]

	Y	R_l*S_l	Y_a*S_l	Y_a*R_l	S_l	R_l	Y_a	RD
Y_a	0.89	−0.01	0.69	0.69	−0.07	0.04	1	—
R_l	−0.30	0.91	0.55	0.68	0.77	1		0.75
S_l	−0.31	0.93	0.60	0.44	1			0.60
Y_a*R_l	0.36	0.58	0.88	1				0.40
Y_a*S_l	0.43	0.62	1					0.29
R_l*S_l	−0.31	1						0.72
Y	1							−0.48

[a]$r(p<0.05)=0.21$; $r(p<0.01)=0.27$ (d.f.$=89$); [b]as in *Table 2*

only; they were, however, retained for reasons of symmetry.

In the absence of significant R_l and S_l contributions, R_l*S_l terms can be viewed as combined rust and leaf spot injury effects in reducing yield [Equation (4)] or increasing relative damage [Equation (5)]. Y_a*R_l terms can be interpreted as decreasing yield [Equation (4)] or increasing relative damage [Equation (5)] with simultaneously increasing rust injury and attainable yield, i.e. more than proportional rust effects when attainable yield is increasing. Alternatively, Y_a*S_l terms can be interpreted as increasing yield [Equation (4)] or decreasing relative damage [Equation (5)] with simultaneously increasing leaf spot injury and attainable yield, i.e. less than proportional leaf spot effects with increasing yield.

However, owing to the strong correlation between R_l and S_l (*Table 5*, $r(R_l, S_l)=0.77$, $p<0.0001$), these interpretations must be completed as follows: Y_a*R_l incorporates strong effects from leaf spot injury [$r(Y_a*R_l, S_l)=0.44$], as well as Y_a*S_l from rust injury [$r(Y_a*S_l, R_l)=0.55$]. Therefore, Y_a*R_l terms can be seen as more than proportional effects of both injuries on yield reduction and relative damage increase, whereas Y_a*S_l terms can be seen as less than proportional ones. The hypothesis is put forward that these latter terms are related to increasing defoliation, which in turn reduces damage due to rust.

Suggestion for a simplified injury–damage relationship. A significant linear correlation ($r=-0.51$, $p<0.0001$) was found between the log-transformed green leaf area index ($GLAI_l$) and relative damage (RD); the corresponding equation is:

$$RD=201-34.5\ GLAI_l\ (r^2=0.26)$$

$GLAI_l$ incorporates reduction of living area index due to defoliation, and reduction of photosynthetically active leaf area due to multiplication of both rust and leaf spot lesions, i.e. mechanistic effects of diseases on foliage. In order to test for the presence of additional effects of both diseases, leaf spot and rust injuries were incorporated in the equation as explanatory variables: the R_l contribution significantly increased the proportion of variation accounted for by the resulting regression [*Table 4*, equation (6), $r^2=0.59$].

Discussion

The experiments

These experiments were primarily conducted to establish a database on the relationships between groundnut yield and injury induced by foliar diseases at varying attainable yield and disease levels, rather than to measure the effects of one particular disease in one given set of environmental conditions. A large variation in attainable yield was needed (1) to incorporate in the database an overall amount of information on crop status that would cover a range as wide as possible (James and Teng, 1979; Wiese, 1982), and (2) to address yield response to disease constraints in a range of cultural practices that may be considered to represent a range of production situations (Rabbinge and De Wit, 1989). This was obtained by replicating the experiments in varying climatic conditions, and by incorporating input factors which were superimposed on blocks in each experiment.

The need for the experiments to be representative of current husbandry in the farming systems (Zadoks and Schein, 1979; Teng, 1985) was met by incorporating in them one block where input factors were set to default levels, i.e. involving cropping techniques and means (e.g. local cultivar, hand sowing, and hand weeding) that are available at farm level (Busnardo, 1986; Savary *et al.*, 1988). Similarly, input factors were selected among candidate components of an intensification process of the crop (e.g. fertilizer inputs, high-yielding varieties, higher sowing densities; Busnardo, 1986), or among factors that exhibit strong variation in current crop husbandry (e.g. water and weed control; Marnotte and Busnardo, 1985; Savary *et al.*, 1988).

In many respects, the data set produced by these experiments is midway between sets that would have produced a survey on crop loss, where a sample of fields would have been selected from a series of farms in various regions (De Datta *et al.*, 1978; Stynes, 1980; Wiese, 1982), or that are needed to establish a preliminary portfolio (Large, 1966) on injury/damage relationships. The reason for this choice is that, in addition to the need for large variation in attainable yield, variation of two key constraints to groundnut production had to be managed simultaneously.

Regression analyses

An overall description of the data set used in this study can be provided by the additional equation:

$$Y = 567 + 0.74\ Y_a - 20.9\ RD\ (r^2 = 0.96,\ \text{d.f.} = 87,\ p < 0.0001).$$

Yield variation can primarily be described as a response to increasing attainable yields and damage caused by diseases. *Table 5* indicates that 23% of yield variation only was accounted for by relative damage ($r(Y, RD) = -0.48$), whereas 79% was accounted for by attainable yield. Further analysis enables interactions to be identified.

Strong interaction between rust (R_l) and late leaf spot (S_l) injuries ($r = 0.77$, *Table 5*) should essentially be ascribed to very strong differences in intensities of diseases among protected (C) and unprotected (rs, Rs, rS, and RS) plots (*Table 3*). When compared with the levels of diseases in the protected plots, differences between inoculated and uninoculated plots in rust intensity (r vs R treatments), or in leaf spot intensity (s vs S treatments), although significant, appear marginal. This database lacks the presence of plots with either low rust or leaf spot levels, or plots with null levels of one disease and very high levels of the other (0S and R0). Such disease patterns could not be obtained in the chosen experimental design owing to endemicity of diseases and interplot interferences.

Low correlations between attainable yield and rust or leaf spot injuries [$r(Y_a, R_l) = 0.04$ and $r(Y_a, S_l) = -0.07$, *Table 5*] indicate that injuries were not significantly related to experiments (i.e. the overall effect of management of diseases among the six experiments produced similar disease treatments), or crop input factors superimposed on blocks. $Y_a{*}R_l$ and $Y_a{*}S_l$ interactions on yield or relative damage can therefore be interpreted as modifications of relationships between crop and injuries, rather than consequences of crop management on disease levels.

Equations (5) and (6) (*Table 4*) represent yield and relative damage response surfaces to varying attainable yield, rust and leaf spot injuries. *Figure 1* shows the variation of the yield response surface with varying attainable yields. Considering the three ($Y_a{*}R_l$, $Y_a{*}S_l$, and $R_l{*}S_l$) interaction terms present, these equations indicate (1) a decrease in yield (increase in relative damage) due to increasing levels of both injuries ($R_l{*}S_l$ terms), (2) a more than proportional effect of rust injury with increasing attainable yield ($Y_a{*}R_l$ terms), and (3) a less than proportional effect of leaf spot injury ($Y_a{*}S_l$ term).

Significant correlation between R_l and S_l, however, implies that interaction between attainable yield and rust injury ($Y_a{*}R_l$) also incorporates more than proportional effect from leaf spot on yield decrease and relative damage [$r(Y_a{*}R_l, S_l) = 0.44$, *Table 5*]. This interaction may therefore be interpreted as an overall increase in relative damage (decrease in yield) with simultaneously increasing attainable yield and injuries of both diseases.

Alternatively, interaction between attainable yield and leaf spot injury [$Y_a{*}S_l$, *Table 4*, Equations (4) and (5)] also incorporates less than proportional effect from rust on yield and relative damage [$r(Y_a{*}S_l, R_l) = 0.55$, *Table 4*].

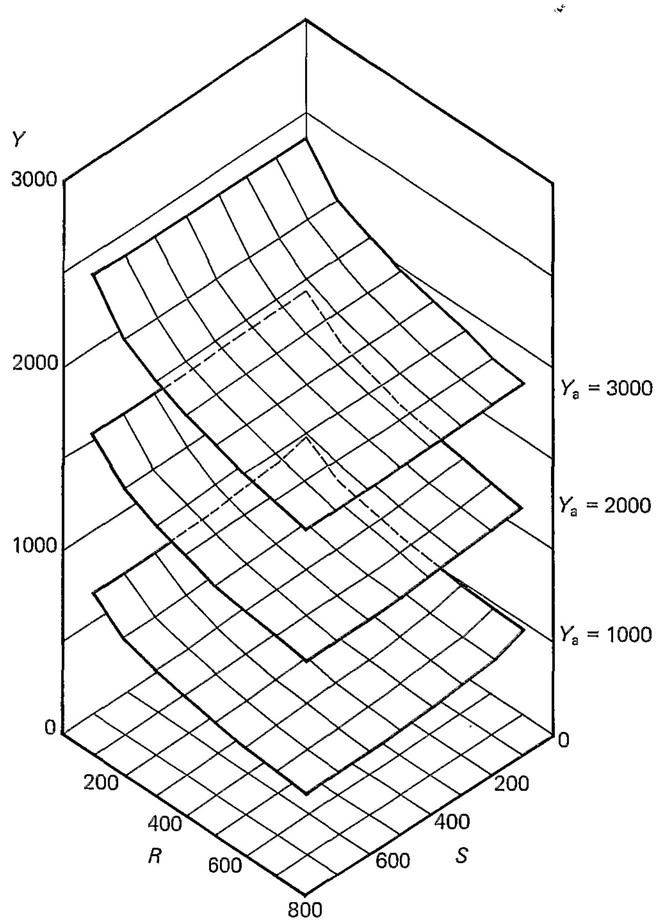

Figure 1. Groundnut yield response surfaces to varying rust and leaf spot intensities at different attainable yields. The graph is based on Equation (4) (*Table 4*), which describes a stronger effect of rust than of leaf spot on yield reduction. Note the variation in response surface shape, i.e. steeper and flattened yield reduction with increasing rust and leaf spot intensities, respectively, when the attainable yield increases: *R*, rust intensity (area under rust progress curve, in %days); *S*, leaf spot intensity (area under leaf spot progress curve, in %days); *Y*, yield (kg ha^{-1}); Y_a, attainable yield

Equation (6) suggests that injury/damage relationships in rust and leaf spot differ. The $Y_a{*}S_l$ interaction may therefore be interpreted in terms of less than additive relationships between injuries due to the two pathogens.

Equation (6) (*Table 4*) describes relative damage as decreasing with increasing amount of green (apparently uninfected) tissue ($GLAI_l$), with an additional term representing rust injury (R_l). $GLAI_l$ accounts for defoliation [*Table 4*, Equation (2)] and reduction of photosynthetically active leaf area (Teng and Gaunt, 1980; Teng, 1985; Johnson, Teng and Radcliffe, 1987), due to multiplication of both diseases. It also accounts for reduced foliage growth with increasing rust severity [*Table 4*, Equation (1)]. This term therefore represents the proposed mechanistic hypothesis, that damage increases with reduction of green leaf area index (Subrahmanyam *et al.*, 1984; Bell, 1986). The additional R_l term indicates that injury/damage relationships are more complex, and that this hypothesis does not account for damage components in the case of rust. These components refer to host photosynthate diversion towards rust spore production (Savary *et al.*, 1990) and, possibly, increased transpiration and increased drought susceptibility due to reduced root growth. Again, correlation between rust and late leaf spot injury suggests that additional damage components may also be considered in the case of leaf spot, such as reduced photosynthetic efficiency, and self-shading effect of the lesions in the canopy (Boote *et al.*, 1983).

In spite of the significant contribution of rust intensity (R) in Equation (2) (*Table 4*), whether rust was actually responsible for extensive defoliation in these experiments is questionable. Whereas there is strong evidence of defoliation caused by late leaf spot infection in groundnut (Plaut and Berger, 1980; Boote *et al.*, 1983; Backmann and Crawford, 1984), and descriptions of the possible underlying processes (at least for early leaf spot infection; Ketring and Melouk, 1982), rust-induced defoliation at the experimental level has not been documented. Defoliation develops at low leaf spot levels (Backman and Crawford, 1984); the statistical relationship between rust intensity and defoliation may therefore be attributed to the contrast between protected plots (C), where no or little leaf spot developed, and protected ones with varying levels of both diseases.

If this is the case, the injury/damage relationships involved in these experiments could be summarized as follows: late leaf spot predominantly caused defoliation, reduced the photosynthetically active leaf area in the canopy, and possibly induced additional injurious effects to apparently uninfected tissues; rust, in addition to reducing the photosynthetically active leaf area and reducing foliage growth, was predominantly responsible for a lessening of green tissues as a source of carbohydrates.

Theoretical considerations on the appropriateness of transformation of explanatory variables

A discussion on the advantages and disadvantages of transforming explanatory variables in multiple regression analysis has been provided by Butt and Royle (1974), Teng and Gaunt (1980), and Choong-Hoe Kim and MacKenzie (1987).

A variety of transformations have been applied to variables representing disease epidemics at one stage of their development (single-point models) before their incorporation into crop loss models (e.g. Teng and Gaunt, 1980). In most cases the transformation applied was intended to account for a curvilinear response curve. In so doing, the objective was not a mere increase in the proportion of damage variation accounted for by regression, but rather a better representation of injury/damage relationships.

Area under the disease progress curve (AUPC), as producing a measurement of the overall constraint exerted during the whole crop cycle (Van der Plank, 1963), with dimension [(disease proportion) × time] has very seldom been transformed before incorporation in crop loss models. Madden *et al.* (1981a), and Madden, Pennypacker and Kingsolver (1981b) incorporated AUPC values in a non-linear crop loss model derived from the Weibull distribution, which, in the particular case of leaf spots on groundnut, produced a positively skewed curve.

The purpose of the transformations applied to variables in this study was to increase their individual explanatory value and correlation with yield and relative damage, thereby accepting the risk of increasing the complexity of the regression and diminishing its overall transparence (Neter and Wassermann, 1974). The underlying assumption of transforming AUPC values of both rust and leaf spot was that increases of the overall injury over the crop cycle have a less than additive effect on damage. Alternatively, increase of the accumulated leaf area index was assumed to produce a less than additive increase in yield. Such hypotheses have not been documented.

On the other hand, less than additive effects of injury at one given time of the crop cycle have been documented (Tammes, 1961; Zadoks and Schein, 1979; Madden *et al.*, 1981a); alternatively, the relationship between leaf area index and yield is accounted for by radiation attenuation through the crop canopy, and conforms to the Lambert–Beer law (Gardner, Pearce and Mitchell, 1985; Waggoner and Berger, 1987). An alternative to the use of the log-transformed area under variable progress curves (R_l, S_l and $GLAI_l$) is therefore to use the area under log-transformed variables (lR, lS, and $lGLAI$). The new regressions are:

$$RD = 5.60 + 0.54 \times 10^{-5} lR^* Y_a - 0.72 \times 10^{-5} lS^* Y_a + 0.43 \times 10^{-4} lR^* lS$$

($r^2 = 0.66$, d.f. $= 86$, $p < 0.0001$, all coefficients significant at $p < 0.0001$)
and:

$$RD = 16.96 + 0.33 lR - 0.18\, lGLAI$$

($r^2 = 0.64$, d.f. $= 87$, $p < 0.0001$, coefficient for lR and $lGLAI$ significant at $p < 0.0001$ and $p < 0.04$)

where

$$lR = \sum_{i=1}^{h} (t_i - t_{i-1}) ln(r_i + 1),$$

$$lS = \sum_{i=1}^{h} (t_i - t_{i-1}) \ln(s_i + 1), \text{ and}$$

$$lGLAI = \sum_{i=1}^{h} (t_i - t_{i-1}) \ln(glai_i + 1).$$

These equations have the same shape as those previously discussed [*Table 4*, Equations (5) and (6)], indicating that data transformation at the crop cycle or epidemic level – longitudinal effects – is equivalent to transformation at the daily level – cross-sectional effects – for the purpose of this statistical description.

Conclusion

Response surface analysis (Teng and Gaunt, 1980) and factorial experiments (Johnson, Radcliffe and Teng, 1986) may be considered as possible avenues to address relationships between production situation, pest constraints, and damage. Production situation, including intensiveness (Zadoks and Schein, 1979) at the field level may be represented by the attainable yield of the crop, which can be introduced either as a factor of experimental designs, or one of the explanatory variables defining the response surface, as in this study.

The primary objective of the study was to test for, and describe patterns of, relationships between attainable yield, disease constraints and damage in a particular multiple pathosystem. Each plot was considered as a unique combination of the corresponding variables (Teng, 1985; Shane and Teng, 1987), yield and damage being considered as response surfaces to the explanatory variables. The response surface concept (Teng and Gaunt, 1980) might be transposed to the considered relationships, in a conceptual model, as:

$$\text{relative damage} = F(Y_a, X_1, ..., X_n) \qquad (13)$$

where $X_1, ..., X_n$ are injuries. In practice, we are dealing with two diseases only, and the complex relationships between variables appears to be reducible, in a descriptive regression equation, to first-order interactions:

$$\text{relative damage} = a + b_1 Y_a{*}R_l + b_2 Y_a{*}S_l + b_3 R_l{*}S_l \qquad (14)$$

The successive experiments were linked together by use of attainable yield (Y_a) as an explanatory variable. Y_a accounts for differences between experiments and differences among blocks and levels of input factors within experiments, i.e. for production situations. Variation in Y_a was therefore obtained through a variety of causes, which effects and interactions with other explanatory variables were not specifically addressed. More information is needed to document the effects of environmental conditions prevailing in each experiment, and input factors. These results must therefore be considered as an overview of a series of effects, most of them very complex.

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