Analysis of crop loss in the multiple pathosystem groundnut–rust–late leaf spot. II. Study of the interactions between diseases and crop intensification in factorial experiments

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Abstract Two factorial experiments were conducted to study the relationships between the intensification of the groundnut crop and the injuries of foliar diseases, in their effect on damage. In a first experiment, the overall damage caused by spontaneous levels of rust, early leaf spot and late leaf spot increased with intensification, represented by four successive levels. In a second experiment, the interactions between two input factors (cultivar potential yield and weed control) and manipulated levels of rust and late leaf spot were studied, using a double strip-plot design. Significant interactions were found, indicating a less than additive interaction between rust and late leaf spot injury on damage, and an increase of damage due to rust simultaneously with increasing cultivar potential yield and weed control. Cross-sectional and longitudinal analyses were conducted to check the effects of treatments on foliar growth and defoliation and to check the effects of disease treatments on epidemics. The results of analysis of variance were compared with the results of multiple regression analyses. The two experiments demonstrate that the damage due to varying injury levels of rust and leaf spot depends on the intensification level, that is, the production situation.

Keywords Factorial design; damage function; *Arachis hypogaea; Cercosporidium personatum; Puccinia arachidis*; crop loss; multiple pathosystem; crop damage

Introduction

Among the diseases that constrain groundnut production in West Africa, rust (*Puccinia arachidis* Speg.) and leaf spots (*Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton) are among the most frequent (Savary *et al.*, 1988). Groundnut is grown in a variety of production situations (De Wit, 1982), and the effect of production situation on damage function (Zadoks, 1985) is not known. Such information is needed to assess the outcome of protection measures and to foresee the consequences of future intensification of the crop in the regions where these diseases are present.

The concept of production situation refers to the combinations of environmental and agronomic conditions that govern crop production. Variation of production situations can be addressed in various ways, e.g. by replicating experiments over cropping seasons or locations (James, 1974), or considering crop intensification by means of input factors. The latter approach was considered here.

A factorial experimental design that specifically addresses interactions between pest constraints on yield was developed by Johnson, Radcliffe and Teng (1986). This design was adapted for the analysis of disease*disease, and disease*input factor interactions. In addition to the two diseases considered, two input factors were selected among the potential components of stepwise intensification of the crop (Busnardo, 1986), namely cultivar potential yield and weed control level. Weeds are a serious constraint to groundnut (Buchanan, Murray and Hauser, 1982; Ramakrishna and Ong, 1988) world-wide, and especially in the Ivory Coast (Marnotte and Busnardo, 1985).

The objectives of this study were (1) to test for an overall relationship between the intensification level of the crop and the multiple pathosystem terms of damage, in an initial experiment; in a second experiment (2) to study disease*disease and disease*input factor interactions, and (3) to examine further those methodological issues (Johnson *et al.*, 1986) that are associated with the use of factorial experimental designs in crop loss studies.

Materials and methods

Preliminary experiment

A preliminary experiment was established at the IDESSA Experimental Station, Ferkessédougou, in the savanna

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0261–2194/92/02/0110–11

region of the northern Ivory Coast on a gravelly, sandy clay loam. The experimental design was a split-split-plot (Gomez and Gomez, 1984), with groundnut varieties as main plots, crop intensification levels as subplots, and fungicide protection as sub-subplots, with three replications. The groundnut varieties used were KH149A, 69101 and RMP91, representing a range of cycle duration, from short ($\sim$90 days from sowing to harvest), medium (120 days), to long (145 days) cycles. Intensification levels were represented by four stages of an intensification process that has been recommended for this area (Busnardo, 1986): (1) no weed control, low crop density (6.25 plants m^{-2} for KH149A and 4.2 plants m^{-2} for 69101 and RMP91), and no fertilizer application; (2) regular hand-weeding, low crop density, and no fertilizer application; (3) regular hand-weeding, high crop density (12.3 plants m^{-2} for KH149A and 8.3 plants m^{-2} for 69101 and RMP91), and no fertilizer application; (4) regular hand-weeding, high crop density, and application of a fertilizer before sowing (NPK: 16-29-29 kg ha^{-1}).

The most prevalent weeds in the experimental area are *Pennisetum polystachion, Vernonia galamensis, Pennisetum* sp., *Ipomoea involucrata* and *Crotalaria* sp. Chlorothalonil (3.8 kg a.i. ha^{-1}), a contact fungicide with no reported physiological effect on groundnut, was sprayed on one-half of the sub-subunits on a fortnightly schedule. The sub-subunits were square, each side measuring 4.8 m, and separated by a 1 m wide uncultivated strip. The experiment was established approximately 3 weeks after the onset of the rainy season, on 26 June 1989.

Assessments of severities of foliar diseases were made every month. Observations were taken on three leaf layers (third, fifth and last attached leaves on the main stem, counted from the top) for rust and on two leaf layers (fifth and sixth attached leaves) for early and late leaf spot, using diagrammatic scales (Savary and Zadoks, 1992). Mean rust severity on each plant was corrected for the proportion of rust-infected leaves on the main stem. Mean rust and accumulated leaf spot severities were calculated for each individual plot from three sampled plants at each sampling date. Yields (kg dry pods ha^{-1}) were estimated within each plot, considering the outer rows and the first external plants on the rows as borders.

Second experiment

Experimental site and experimental design. The experiment was established at the IIRSDA experimental farm, Adiopodoumé, Southern Ivory Coast on sandy-loam soils. The experimental design used is a combination of two strip-plot designs (Johnson *et al.*, 1986), one strip-plot being assigned to intensification factors, in which another strip-plot was embedded and assigned to disease levels (*Figure 1*). The two intensification factors selected were cultivar potential yield, and weed control, set at three levels each, using three different groundnut cultivars (V1, V2 and V3), and simulating three weed-control levels (W1, W2, W3). The two diseases are rust (*P. arachidis*) and late leaf spot (*C. personatum*), manipulated so as to obtain two different levels of disease (R1 and R2, and S1 and S2, respectively).

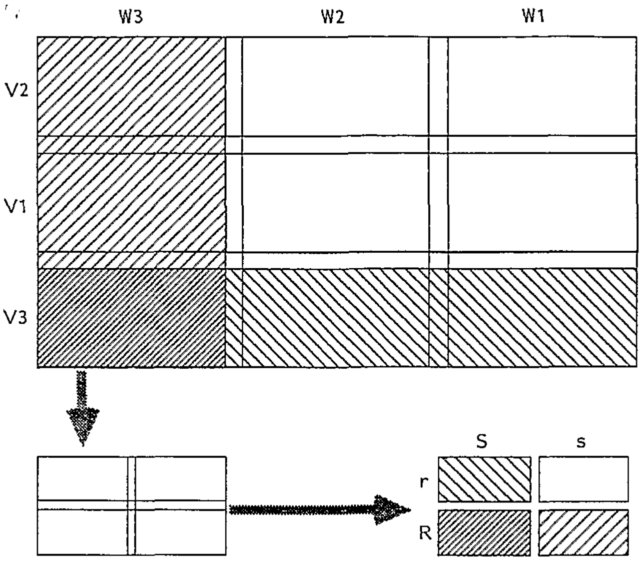

Figure 1. A factorial experiment designed to study groundnut yield in response to cultivar potential yield (three levels: V1, V2, V3), weed control (three levels: W1, W2, W3), rust (two levels: R, r) and late leaf spot (two levels: S, s). Lay-out of the first replication

The experiment had four replications and thus 144 individual plots, with five rows of 20 plants per plot. The distance between rows and between plants in the row was 0.4 m. Individual plots were separated by 1.2 m bare ground, and the replications by uncultivated strips 6 m wide. The total experiment occupied a land area of 4381 m^2. The outer rows and the first plants in the row were considered as border, and the 54 plants within the plots were considered for disease and yield assessment. Time was counted ($t=0$) from planting, on 16 May 1989.

Cultivars. The three groundnut cultivars were erect short-cycle plants (i.e. $\sim$90 days from planting to harvest): a local cultivar (V1), TMV2 (V2) and KH149A (V3). These cultivars represent increasing yield potentials. All three cultivars showed great susceptibility to *P. arachidis* (Savary, Subba Rao and Zadoks, 1989) and *C. personatum* (Subrahmanyam, McDonald and Gibbons, 1982). Previous experiments (S. Savary, unpublished) indicated similar patterns of epidemic development of the two diseases in the three cultivars.

Management of weed levels. The objective of the weed treatments was to establish three distinct levels of weed infestation that would mimic levels of weed infestation found in farmers' fields (Marnotte and Busnardo, 1985; Savary, 1986) and weed control frequencies. Among the most prevalent weeds in the experimental area were: *Mollugo nidicaulis, Oldenlandia corymbosa, Fimbristylis* sp., *Eleusine indica, Cyperus rotundis, Portula oleraceae, Amaranthus* sp., *Boerhavia diffusa* and *Digitaria* sp.

In the first weed treatment (W1) no weed control was applied. Regular hand-weeding (approximately every 15 days) was done at the third weed level (W3). In the second weed treatment (W2), selective hand-weeding was carried out, which was intended to limit the weed population to three species: *Mollugo nidicaulis, Oldenlandia corymbosa* and *Fimbristylis* sp. These three species were selected for their relatively prostrate habits, moderately profuse foliar growth, and reduced height compared with groundnut. Treatments W1 and W2 thus differed in weed density and in structure of the weed canopy.

Management of levels of the two diseases. The objective of disease management was to establish two distinct and independent levels of the two diseases by means of inoculations and fungicide sprays.

Rust inoculations were done twice, at $t=21$ and 32, using mixtures of rust urediniospores and kaolin dusted on to the plants of the inner three rows of individual plots (R2) as previously described (Savary and Zadoks, 1992). A mixture of spores and kaolin was applied at a rate of 250 mg per plot, with a spore density of 64 spores mg^{-1} for the first inoculation and 160 spores mg^{-1} for the second inoculation, i.e. ~300 and ~740 spores per plant, respectively.

Late leaf spot was inoculated twice, at $t=20$ and 29, spraying suspensions of spores (Savary and Zadoks, 1992) on the inner three rows of plots (S2). For the first inoculation, 50 ml at a density of 6 spores μl^{-1} (~5500 spores per plant), and for the second inoculation 40 ml at a density of 4 spores μl^{-1} (~3000 spores per plant) were sprayed on each plot.

Systemic fungicides were applied four times, starting at $t=31$. The fungicide used to control leaf spot (in S1 plots) was benomyl (Benlate) at a rate of 0.7 kg a.i. ha^{-1}, and the fungicide used to control rust (in R1 plots) was oxycarboxin (Plantvax) at a rate of 2.251 a.i. ha^{-1}. These fungicides had no side effects on the development, growth and yield of uninfected plants, as checked in a separate experiment using the same concentrations and spray schedule (F. Brissot and S. Savary, unpublished). To summarize disease management: R1S1 plots were sprayed with Plantvax and Benlate; R1S2 plots were inoculated with leaf spot and sprayed with Plantvax; R2S1 plots were inoculated with rust and sprayed with Benlate; R2S2 plots were inoculated with rust and leaf spot, and untreated.

Assessment of foliage growth, defoliation, weed infestation, severities of the diseases and yield. Observations were made at regular intervals ($t=17$, 27, 41, 51, 63, 76 and 86) in each plot, counts of attached and fallen leaves (leaf scars) on the main stem of three plants chosen at random in the three central rows, assessments of disease severity on these plants, and overall assessment of the weed infestation in the plot.

The mean number of total (attached and detached) leaves put out by the main stem at a given date was used as an estimate of the current total leaf area index ($tlai_i$, *Table 1*), using a functional relationship that was established and validated in a separate experiment, with the same cultivars at the same density, and in the same environment (Savary and Zadoks, 1992). The formula used is:

$$tlai_i = CD * (a * mt^{b}) * (c + d * \ln mt),$$

where mt is the total (attached and detached) number of leaves on the main stem, CD is crop density, and a, b, c, and d are parameters. The estimated total leaf area index and the proportion (p) of dead leaves on the main stem (assessed from the number of leaf scars) were then combined to produce an estimate of the detached ($p * tlai_i$) and attached ($(1-p) * tlai_i$) leaf area indices, assuming the proportion of defoliation on the main stem to be representative for the whole plant.

Table 1. List of variables

Acronym	Meaning	Units
$tlai_i$	Total leaf area index	$m^2 m^{-2}$
$dlai_i$	Dead leaf area index	$m^2 m^{-2}$
r_i	Rust severity	%
s_i	Leaf spot severity	%
wd	Mean rating for weed density	—
$tLAI$	Area under total leaf area index progress curve	$m^2 m^{-2}$ day
$dLAI$	Area under dead leaf area index progress curve	$m^2 m^{-2}$ day
R	Area under rust progress curve	%day
S	Area under leaf spot progress curve	%day
R_l	Log-transformed area under rust progress curve	—
S_l	Log-transformed area under leaf spot progress curve	—
Y	Yield of individual plot	kg ha^{-1}
Y_r	Reference yield for each VW combination, in each replication (R1S1 plot)	kg ha^{-1}

Weed infestation was assessed using the following key: 0, no weeds; 1, weeds cover 0–1% of the plot area; 2, weeds cover 1–5% of the plot area; 3, weeds cover 5–10% of the plot area; 4, weeds cover >10% of the plot area, but >80% of groundnut canopy dominates that of the weeds; 5, weeds cover >10% of the plot area, and >20% of the groundnut canopy is dominated by that of weeds. Disease assessments of rust (r_i) and late leaf spot (s_i) were made as described for the preliminary experiment.

Yield of each plot was estimated from the three central rows, where plants were harvested and their pods cleaned, dried in an oven (40–55°C) for 5 days, and weighed. Individual plot yields (Y) were expressed as kg dry pods ha^{-1}.

Analysis of data. Cross-sectional analyses (Zadoks, 1972) of variance were carried out on current values of four variables: total ($tlai_i$) and dead ($dlai_i$) leaf area indices, and rust (r_i) and leaf spot (s_i) severity. These analyses tested for (a) the appearance of effects of treatments, (b) interactions between treatments, and (c) specific effects of diseases on canopy growth and defoliation in the course of the season.

Analyses of variance were executed on variables representative of the overall growth of the canopy and of disease epidemics, for further study of the effects of, and interactions between, treatments (longitudinal analyses). Canopy growth and defoliation were represented by three variables – the areas under total ($TLAI$) and detached ($DLAI$) leaf area index progress curves, and the terminal ($t=86$) proportion of detached leaves (%def, see *Table 3*). The rust and leaf spot epidemics were represented by their respective areas under disease progress curves (R and S). Weed infestation was represented by wd, the mean of weed ratings in each individual plot. Areas under progress curves were calculated as $X=\sum \Delta t^* x_i$, where Δt represents the time interval between two assessments ($t_i - t_{i-1}$), and x_i the value of the appropriate variable on the ith observation (*Table 1*). Arcsine transformations were applied to %def (2 arcsine $\sqrt{(\%def/100)}$) and wd (2 arcsine $\sqrt{(wd/5)}$) and the analyses of variance, carried out according to the statistical design (Gomez and Gomez, 1984; Johnson *et al.*, 1986).

Data were further studied by means of stepwise linear regression analysis with backward selection of the variables. In a previous study (Savary and Zadoks, 1992), log-transformed areas under rust and leaf spot progress curves provided adequate descriptors of damage and yield. The areas under rust and leaf spot progress curves were thus transformed as $R_l = \ln(R+1)$ and $S_l = \ln(S+1)$. These variables were used to represent the injuries caused by the two diseases.

As the attainable yield (Zadoks and Schein, 1979) corresponding to each variety * weed-control level combination was unknown, an additional variable, the reference yield (Y_r) was considered, representing the yield of this combination at low rust and leaf spot levels (R1S1) within each replication. When considered within each data set pertaining to varieties across weed-control levels (Vk W –), Y_r incorporates effects of weed control and replications; when considered within each data set pertaining to weed-control levels across varieties (V–W1), Y_r incorporates effects of varieties and replications; and when considered over the whole data set (V–W–), Y_r incorporates effects of varieties, weed control and replications.

Results

Preliminary experiment

The short-cycle cultivar (KH149A) was harvested at the anticipated date, 90 days after sowing. In view of a severe drought, and the risk of pod loss at harvest, the two other cultivars (69101 and RMP91) were harvested simultaneously, 120 days after sowing.

Because of the irregular rainfall pattern at the beginning of the crop cycle, and the slow initial development of the crop, weed infestation was heavy in unweeded plots within one month after sowing. Overall development of foliar fungal diseases was strongly reduced in the protected sub-subplots, as indicated by the reduction of their respective areas under progress curves: early leaf spot, 2 vs 30 %days ($F=61.4$; 1,24 d.f.; $p<0.01$); late leaf spot, 4 vs 198 %days ($F=84.5$; 1,24 d.f.; $p<0.01$); rust, 6 vs 348 %days ($F=180$; 1,24 d.f.; $p<0.01$).

The experiment produced a wide range of yield values (*Figure 2*), from 521 to 1997 kg ha^{-1}. The analysis of variance indicated a significant effect of varieties ($F=13.7$; 2,4 d.f.; $p<0.05$), which was mainly attributable to a marked reduction in yield of cv. 69101 when no fungicide sprays were applied. There were no significant differences among varieties under fungicide protection ($F=1.51$). The effect of intensification levels on yield ($F=53.3$; 3,18 d.f.; $p<0.01$) was represented by an overall increase of 805 kg ha^{-1} throughout the intensification process. The increase was especially noticeable when weed control was incorporated (treatments 1 to 2, *Figure 2*), which accounted for an average increase of 420 kg ha^{-1}. The effect of fungicide sprays ($F=148$; 1,24 d.f.; $p<0.01$) was also strong, corresponding to an average increase of 531 kg ha^{-1}. The increase in yield by intensification was lower without fungicides (an increase from 550 to 1109 kg ha^{-1}) than with fungicides (from 834 to 1886 kg ha^{-1}). The effect resulted in a significant intensification level*fungicide interaction ($F=5.88$; 3,24 d.f.; $p<0.01$).

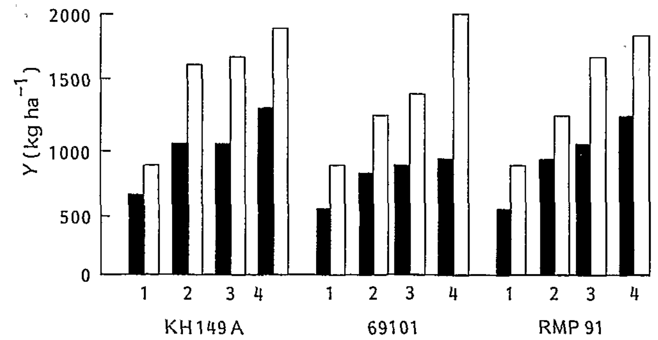

Figure 2. A preliminary experiment on yield reductions caused by early leaf spot, late leaf spot and rust on three groundnut cultivars (KH149A; 69101; RMP91) at various intensification levels (1–4; see text). Open bars: protected plots; closed bars: unprotected plots. Each bar is the mean of three replications

Second experiment

Development of rust and leaf spot epidemics. Rust epidemics were stronger in treatment R2 than in treatment R1 in all three cultivars (see e.g. V1, *Figure 3*), significant differences in r_i values appearing from $t=41$ onwards (*Table 2*), and resulting in very different mean areas under rust progress curves (R1: $R=192$ %days; R2: $R=808$ %days, $F=999$, $p<0.01$, *Table 3*). Rust epidemics were weaker in the presence of strong leaf spot epidemics (*Figure 3*), as indicated by the significant effect of S-treatment on rust severity appearing at $t=51$ (*Table 2*), and the ensuing reduction of area under rust progress curve; mean R values were smaller in S2 plots (337 %days) than in S1 plots (663 %days, $F=237$, $p<0.01$, *Table 3*). This reduction in R was stronger on strong rust epidemics, which is accounted for by the significant R*S interaction ($p<0.01$, *Table 3*). As a result, four categories of plots may be distinguished with regard to the area under the rust progress curve: R1S1, $R=278$ %day; R1S2, 105 %day; R2S1, 1048 %day; R2S2, 568 %day.

Leaf spot epidemics were stronger in treatment S2 than S1 (see e.g. V1, *Figure 3*). The difference appeared on $t=41$ (*Table 2*), and resulted in a large difference in the areas

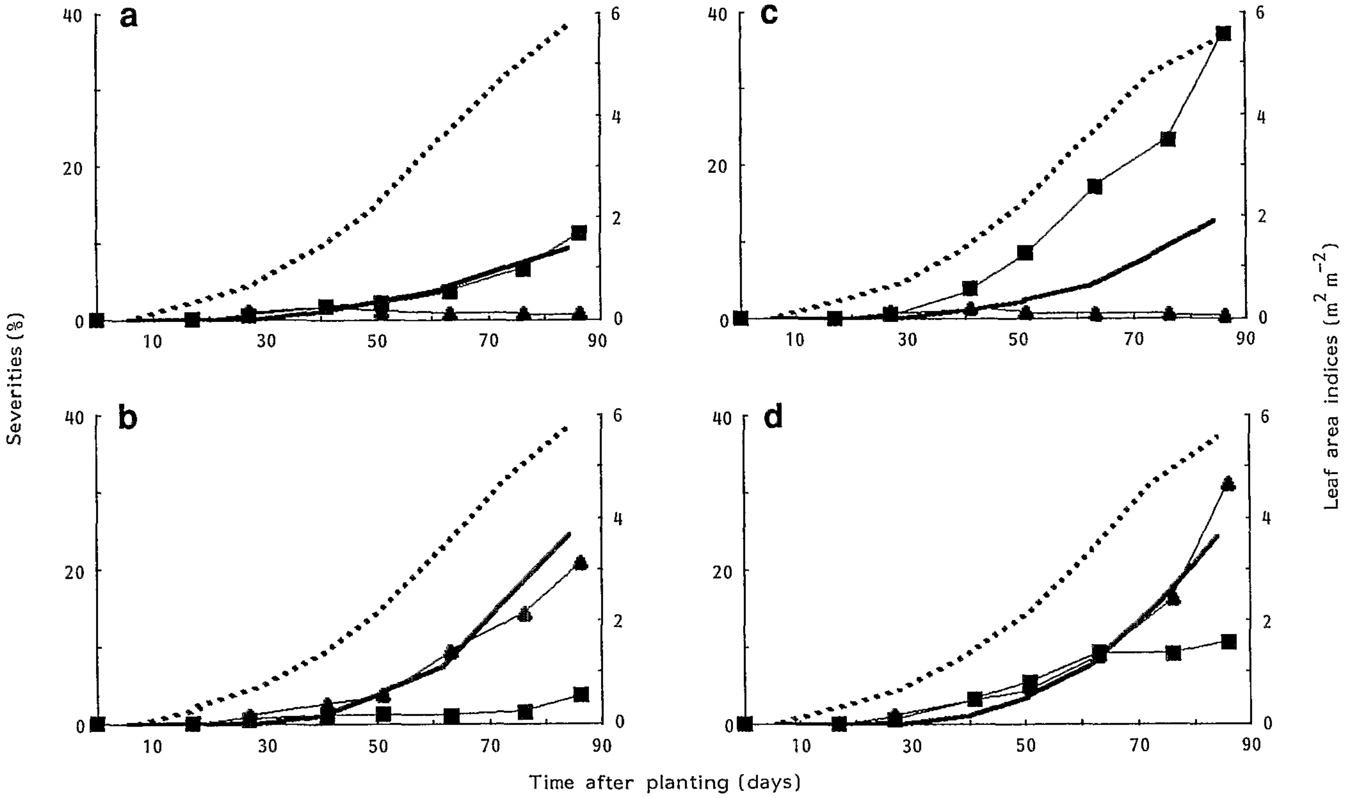

Figure 3. Second experiment: rust (r_i; ■) and late leaf spot (s_i; ▲) progress curves, and total ($tlai_i$; -----) and detached ($dlai_i$; ——) leaf area index progress curves for the local cultivar (V1). Each set of curves represents the variations for each combination of rust (R1, R2) and leaf spot (S1, S2) levels, averaged over three weed-control levels and four replications: a, V1R1S1; b, V1R1S2; c, V1R2S1; d, V1R2S2

Table 2. Second experiment: cross-sectional analyses of progress curves of the diseases, canopy growth, and defoliation

			Variance ratio values[b] at $t=$						
Variable	Source of variation	d.f.[a]	17[c]	27	41	51	63	76	86
r_i[d]	Cultivar	(2,6)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Weed control	(2,6)	n.s.	n.s.	n.s.	n.s.	n.s.	29.7**	66.4**
	Rust	(1,27)	n.s.	n.s.	125**	428**	307**	736**	514**
	Leaf spot	(1,27)	n.s.	n.s.	n.s.	53.0**	106**	133**	221**
s_i[d]	Cultivar	(2,6)	—[e]	n.s.	n.s.	14.4**	15.6**	26.7**	42.2**
	Weed control	(2,6)	—[e]	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Rust	(1,27)	—[e]	n.s.	n.s.	n.s.	n.s.	n.s.	7.85**
	Leaf spot	(1,27)	—[e]	n.s.	66.7**	228**	456**	374**	1240**
$tlai_i$	Cultivar	(2,6)	n.s.	n.s.	23.4**	9.64**	36.7**	63.1**	133**
	Weed control	(2,6)	n.s.	n.s.	n.s.	n.s.	n.s.	5.29*	7.71*
	Rust	(1,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	5.49*
	Leaf spot	(1,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
$dlai_i$	Cultivar	(2,6)	n.s.	n.s.	n.s.	9.02*	53.7**	18.1**	13.3**
	Weed control	(2,6)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Rust	(1,27)	n.s.	n.s.	n.s.	n.s.	n.s.	4.59*	16.3**
	Leaf spot	(1,27)	n.s.	n.s.	5.23*	80.3**	203**	264**	530**

[a]See *Table 4*; [b]variance ratio values were computed according to the appropriate d.f., main effect mean squares (M.S.) and error M.S. (see *Table 4*); [c]days after planting; [d]data were transformed into: 2 arcsine $\sqrt{(x/100)}$ before analysis; [e]no leaf spot on this date; n.s., not significant; *, $p<0.05$, **, $p<0.01$

under the leaf spot progress curves between the two treatments in all three cultivars (S1: $S=66$ %days; S2: $S=679$ %days; $F=318$, $p<0.01$, *Table 3*). On the last assessment date ($t=86$), leaf spot severity was lower in treatment R1S2 than in treatment R2S2, resulting in a significant effect of R-treatment on s_i at this date ($p<0.01$, *Table 2*), and in significant R and R*S effects on the areas under the leaf spot progress curves ($p<0.01$, *Table 3*). As a result, three categories of plots may be distinguished with regard to the area under the leaf spot progress curves: R1S1

Table 3. Second experiment: longitudinal analyses of explanatory variables of yield

Source of variation	d.f.[a]	Variables[b]					
		wd[c]	*R*	*S*	*tLAI*	*dLAI*	%def[d]
cultivar (V)	(2,6)	n.s.	n.s.	20.4*	230**	34.8**	n.s.
Weed control (W)	(2,6)	150**	13.7**	n.s.	6.05*	n.s.	n.s.
V*W	(4,12)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Rust (R)	(1,27)	n.s.	999**	9.16**	n.s.	9.01**	44.5**
R*V	(2,27)	n.s.	21.0**	n.s.	n.s.	n.s.	n.s.
R*W	(2,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
R*V*W	(4,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Leaf spot (S)	(1,27)	n.s.	237**	318**	n.s.	466**	527**
S*V	(2,27)	n.s.	8.34**	21.2**	n.s.	15.5**	3.80*
S*W	(2,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S*V*W	(4,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
R*S	(1,27)	n.s.	128**	12.5**	n.s.	18.0**	24.7**
R*S*V	(2,27)	n.s.	4.68*	n.s.	n.s.	n.s.	n.s.
R*S*W	(2,27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
R*S*V*W	(4,27	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a]See *Table 4*; [b]entries are variance ratio values computed according to the appropriate d.f., main effect and error M.S. (see *Table 4*). For acronym meaning, see *Table 1*; [c]mean weed density; data were transformed into 2 arcsine $\sqrt{(x/5)}$ before analysis; [d]terminal percentage defoliation; data were transformed into 2 arcsine $\sqrt{(x/100)}$ before analysis; n.s., not significant; *, $p<0.05$; ** $p<0.01$

($S=70$ %day) and R2S1 ($S=62$ %day); R1S2 ($S=633$ %day); and R2S2 ($S=725$ %day).

A significant cultivar (V) effect on leaf spot severity was apparent from $t=51$ onwards (*Table 2*), resulting in significant differences among all three varieties (V1: $S=360$ %days; V2: $S=547$ %days; V3: $S=210$ %days, $F=20.4$, $p<0.05$, *Table 3*). The differences were apparent only at high leaf spot levels, which is accounted for by a significant V*S interaction (*Table 3*).

A weed control effect was found on rust epidemics. This effect appeared at $t=76$ (*Table 2*) and corresponded to a reduction of rust severity with decreasing weed control. The significant overall effect on *R* ($F=13.7$, $p<0.01$, *Table 3*) was associated with a progressive decrease (W3: $R=568$ %day; W2: $R=486$ %day; W1: $R=445$ %day). An S*V interaction on *R* ($F=8.34$, $p<0.01$, *Table 3*) was found, which may account for differences in cultivar responses to leaf spot treatments, and their ensuing effect on rust epidemics. The result was that V3 had a stronger response to rust treatments, i.e. higher *R* values in R2 plots (918 %day), than V1 (736 %day) and V2 (733 %day).

Growth of the canopy and defoliation. The cultivars significantly differed in their growth from $t=41$ onwards (*Table 2*), that of V3 (KH149A) being less profuse than those of V2 (TMV2) and V1 (local cultivar). The area under the total leaf area index progress curve was significantly ($p<0.01$) smaller in V3 ($tLAI=162$ days) than in V2 ($tLAI=203$ days) and V1 ($tLAI=215$ days). A slight reduction in total foliar growth at high rust level was apparent at $t=86$ ($F=5.49$, $p<0.05$, *Table 2*), which did not influence the longitudinal analysis on *tLAI* (*Table 3*). Total foliar growth was significantly reduced at low weed control level, from $t=76$ onwards, resulting in a significant ($p<0.05$, *Table 3*) overall effect on *tLAI* (W1: $tLAI=184$ days; W2: $tLAI=195$ days; W3: $tLAI=201$ days).

Table 2 indicates that a significant effect ($p<0.05$) of leaf spot treatment on defoliation was apparent at $t=41$ onwards (*Table 2*), when significantly different leaf spot severities appeared. A significant effect ($p<0.05$) of rust treatment became apparent later in the season ($t=76$). Whereas the overall effect of leaf spot treatment on *dLAI* was large (S1: $dLAI=41$ days; S2: $dLAI=77$ days), that of rust treatment was small (R1: $dLAI=58$ days; R2: $dLAI=61$ days). Both effects were significant ($p<0.01$, *Table 3*). A significant R*S interaction on *dLAI* was found ($p<0.01$, *Table 3*), corresponding to a slight increase in defoliation with rust at low leaf spot level at the end of the cropping season (*Figure 3*).

A significant effect of cultivar on defoliation was apparent from $t=51$ onwards ($p<0.05$, *Table 2*). The overall defoliation was much lower in V3 (48 days) than in V2 (62 days) and V1 (68 days, $p<0.01$, *Table 3*). As this difference incorporated differences in canopy growth and in responses to leaf spot treatments among varieties, it was further analysed using the terminal percentage of defoliation, %def. No significant effect of cultivar on %def was found (*Table 3*). A significant S*V interaction on %def was, however, indicated ($p<0.05$), owing to a slightly higher proportion of defoliation in V3 (34%) than in V1 (30%) and V2 (29%) at low leaf spot level. The difference found in *dLAI* among cultivars should therefore be ascribed to differences in foliar growth (as represented by *tLAI*) with equivalent proportions of defoliation. In other words, the three cultivars differed in their response to leaf spot treatments (especially V3) in terms of leaf spot severity which, however, resulted in similar proportions of defoliation. Slight differences in %def between cultivars at low leaf spot level may be indicative of differences in carbohydrate remobilization at the end of the crop cycle, remobilization being higher in V3.

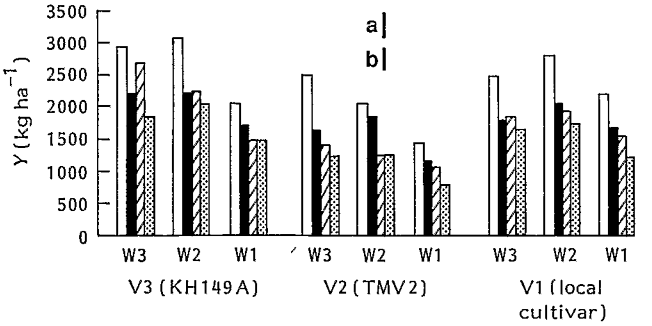

Figure 4. Second experiment: mean yields for each $V_kW_lR_mS_n$ combination. Each bar represents the mean of four replications: □, R1S1; ■, R2S1; ▨, R1S2; ▩, R2S2. The solid lines represent l.s.d. ($p<0.05$) for comparison (a) of rust treatments within one $V_kW_lS_n$ combination: 300 kg ha^{-1}; (b) of leaf spot treatments within one $V_kW_lR_m$ combinations: 377 kg ha^{-1}

Yield. *Figure 4* shows differences in mean yields of the three varieties. Reduced weed control and increasing levels of diseases obviously reduced yields of all three varieties. Apparently, V1 and V2 did not differ in their highest yields (W3R1S1), but yield decrease was more conspicuous in V2 than in V1.

The effect of cultivar (V) on yield was significant ($F=50.1$, $p<0.01$, *Table 4*), the three cultivars differing in their overall mean yields: V3, 2179 kg ha^{-1}; V1, 1938 kg ha^{-1}; V2, 1487 kg ha^{-1}. The effect of weed-control level (W) was significant ($F=46.9$, $p<0.01$). Yields in treatment W3 (2039 kg ha^{-1}) and W2 (2061 kg ha^{-1}) were higher than the yield at low weed-control level (W1: 1503 kg ha^{-1}). This suggests that the competition between weed and groundnut depended on weed density and on the structure of the weed canopy. Both rust and leaf spot treatments had significant effects on yield ($F=116$ and 137, respectively, $p<0.01$). The average yield reduction due to rust treatment was 2072 (R1) − 1664 (R2) = 408 kg ha^{-1}, and the average yield reduction due to leaf spot treatment was 2121 (S1) − 1614 (S2) = 507 kg ha^{-1}.

A significant V*W interaction was found ($F=3.73$, $p<0.05$), corresponding to differences in ranking of the cultivars with varying weed-control level. At low (W1) and medium (W2) weed-control levels, V1 and V3 had higher yields than V2; when high weed control (W3) was applied, V3 was significantly more productive than V1. The yield differences (W3 − W1) due to low weed control across disease treatments were 280, 582 and 745 kg ha^{-1} for V1, V2 and V3, respectively. In other words, V1 appeared to stand more weed competition than V2 and V3 (*Figure 4*).

The R*S ($F=26.4$, $p<0.01$) interaction corresponds to less than additive effects of the two disease treatments: the yield reduction due to a high rust level alone (at low leaf spot level and across weed-control levels) was 576 kg ha^{-1}, the yield reduction due to a high leaf spot level alone was 705 kg ha^{-1} and the yield reduction due to simultaneously high levels of the two diseases was 914 kg ha^{-1}.

The yield reductions associated with high rust level were increasing with increasing weed control (284, 362, and 576 kg ha^{-1} for W1, W2, and W3, respectively), which is accounted for by the significant ($F=5.28$, $p<0.05$) R*W interaction.

The response of cultivars to varying rust treatment and weed control combinations varied considerably as shown by the R*V*W interaction ($F=5.28$, $p<0.05$). In all three cultivars, increasing weed control at low rust level produced a consistent increase in yield; the increase, however, was greater in V2 and V3 (V1: 284 kg ha^{-1}; V2: 702 kg ha^{-1}; V3: 1059 kg ha^{-1}). The yield responses of cultivars to weed control at high rust levels were very different: whereas those of V2 (463 kg ha^{-1}) and V3 (431 kg ha^{-1}) were moderate, increasing weed control was associated with a sharp decline in yield in V1 (1196 kg ha^{-1}).

The final interaction, R*S*V*W ($F=3.56$, $p<0.05$), refers to variations between individual contributions of disease treatments to yield reductions, and their additive effects, depending on the cultivar*weed control combination. In V1, yield reductions due to high rust level alone increased moderately with increasing weed control, whereas yield reductions due to late leaf spot were independent of increasing weed control; in this cultivar, disease treatments had less than additive effects on yield reduction. In V2, yield reductions due to high rust level alone increased sharply with increasing weed control, as well as those due to late leaf spot level; in this cultivar, the effects of disease treatments were near-additive at low weed control, but strongly less than additive at high weed control. In V3, yield reduction due to high rust level alone increased moderately with weed control, but yield reduction due to high leaf spot alone decreased; in this cultivar, the effects of

Table 4. Second experiment: analysis of variance of yield

Source of variation	d.f.	M.S.	*F*	*p*
Replications	3	1378609		
V (cultivar)	2	5930544	50.1	<0.01
error (1)	6	118407		
W (weed control)	2	4793660	46.9	<0.01
error (2)	6	102179		
V*W	4	251288	3.73	<0.05
error (3)	12	67398		
R (rust)	1	5982147	116	<0.01
R*V	2	125666	2.43	n.s.
R*W	2	237451	5.28	<0.05
R*V*W	4	159968	2.99	<0.05
error (4)	27	51769		
S (leaf spot)	1	9263735	137	<0.01
S*V	2	116409	1.72	n.s.
S*W	2	73660	1.09	n.s.
S*V*W	4	87326	1.29	n.s.
error (5)	27	67657		
R*S	1	1021222	26.4	<0.01
R*S*V	2	10580	0.27	n.s.
R*S*W	2	59130	1.53	n.s.
R*S*V*W	4	138014	3.56	<0.05
error (6)	27	38741		
Total	143			

Table 5. Regression equations of yield (Y) on rust (R_l) and late leaf spot (S_l) injuries, and their interaction[a]

Weed control level and cultivar combination	Parameters of equations[b] a	b$_1$ (R_l)	b$_2$ (S_l)	b$_3$ (R_l*S_l)	r^2	p	n[c]
V1W1	9009	−957	−1085	129	0.89	<0.0001	16
V1W2	11404	−1240	−1381	175	0.74	<0.0001	16
V1W3	9584	−1063	−1134	151	0.79	<0.0001	16
V2W1	2351	n.s.	n.s.	−38	0.53	<0.005	16
V2W2	3150	n.s.	n.s.	−48	0.57	<0.001	16
V2W3	15901	−1928	−2116	279	0.79	<0.0005	16
V3W1	2344	n.s.	n.s.	−24	0.26	0.05	16
V3W2	10030	−1090	−1290	175	0.77	<0.0005	16
V3W3	5884	−421	−182	n.s.	0.61	<0.005	16
V–W–	8225	−812	−1003	120	0.44	<0.0001	144

[a]Regressions are of the shape: $Y = -a + b_1 R_l + b_2 S_l + b_3 R_l{*}S_l$; [b]parameters are significant at $p < 0.05$ at least; [c]number of individual plots used to test regression

Table 6. Regression equations describing the response of groundnut yield (Y) to varying levels of rust (R_1) and late leaf spot (S_1) injuries at varying levels of weed control and cultivar potential yield (Y_r)[a]

Weed control level and cultivar combination	Parameters of equations[b] a	b$_1$ (Y_r)	b$_2$ (R_l)	b$_3$ (S_l)	b$_4$ (Y_r*R_l)	b$_5$ (Y_r*S_l)	b$_6$ (R_l*S_l)	r^2	p	n[c]
V1W–	2040	2.08	n.s.	−780	−0.27	n.s.	89	0.70	<0.0001	48
V2W–	516	1.64	n.s.	n.s.	−0.07	−0.13	n.s.	0.74	<0.0001	48
V3W–	1556	1.68	n.s.	−589	−0.19	n.s.	71	0.57	<0.0001	48
V–W1	474	1.44	n.s.	n.s.	−0.06	−0.11	n.s.	0.76	<0.0001	48
V–W2	2482	1.61	n.s.	−723	−0.21	n.s.	77	0.82	<0.0001	48
V–W3	2895	2.09	n.s.	−902	−0.31	n.s.	103	0.59	<0.0001	48
V–W–	1829	1.48	n.s.	−495	−0.16	n.s.	44	0.71	<0.0001	144

[a]Regressions are of the shape: $Y = a + b_1 Y_r + b_2 R_l + b_3 S_l + b_4 Y_r{*}R_l + b_5 Y_r{*}S_l + b_6 R_l{*}S_l$; [b] parameters are significant at $p < 0.05$ at least; [c]number of individual plots used to test regression

disease treatments were less than additive at low weed control, but became near-additive at high weed control.

Multiple regression analyses. Yield variation was regressed on R_l, S_l and R_l*S_l for each combination of cultivar and weed-control level (*Table 5*). In five cases out of nine, the regressions showed significant contributions of interaction between rust and late leaf spot levels (R_l*S_l), in addition to significant R_l and S_l contributions. In one case (V3W3), the R_l*S_l term was not retained, indicating additive effects of the diseases on yield reduction. In three cases (V2W1, V2W2, and V3W1), the R_l*S_l term only was retained, the resulting regressions describing yield as decreasing with simultaneously increasing levels of the diseases. The overall regression (V–W–, $n = 144$ plots, d.f. = 140) accounted for 44% of total yield variation, and indicated a significant contribution of R_l*S_l, with a less than additive effect of the two diseases on yield reduction.

When yield variation is analysed in each cultivar across weed-control levels and levels of diseases (*Table 6*, V1W–, V2W–, and V3W–), the reference yield, Y_r, should be seen as the variation of yield attributable to weed-control levels and to replications. In V1 and V3, yield decrease was associated with increasing leaf spot intensity, and simultaneously increasing rust intensity and reference yield; in both equations a less than additive interaction effect of the two diseases on yield reduction was indicated. In V2, yield was described as decreasing with simultaneously increasing rust and leaf spot intensities, and reference yield.

When yield variation is analysed within each weed-control level across cultivars and levels of diseases (*Table 6*, V–W1, V–W2, and V–W3), Y_r should be seen as the fraction of yield variation attributable to differing cultivar potential yields, and replications. At low weed-control level (W1), yield was described as decreasing with simultaneously increasing R_l and Y_r and S_l and Y_r, the two diseases having additive effects on yield reductions. At weed-control levels 2 and 3, yield decrease was associated with increasing leaf spot severity, and with simultaneously increasing rust and reference yield. The interaction between diseases was significant and less than additive.

An overall description of the data was provided by a final equation (*Table 6*, V–W–), where Y_r accounts for variation in yield due to differing cultivar potential yields, weed-control levels, and replications. This regression showed that yield decreased with increasing leaf spot intensity, as represented by S_l, and with simultaneously increasing rust intensity and reference yield (Y_r* R_l), and that yield decrease was compensated by a less than additive effect of interaction between diseases.

Discussion

Preliminary experiment

The preliminary experiment demonstrated that fungal foliar diseases, as a whole, can inflict serious damage (Zadoks, 1985) to groundnut in the Ivory Coast, as indicated in previous reports (Savary, 1986). Fungal foliar diseases are major constraints to groundnut production world-wide (Porter, Smith and Rodriguez-Kabana, 1982), especially in West Africa (Savary *et al.*, 1988, Subrahmanyam *et al.*, 1991). In this experiment, three components of a multiple pathosystem were present – early leaf spot, late leaf spot and rust.

In addition to yield increase due to intensification and yield decrease due to diseases, this experiment indicated a significant intensification level*fungicidal protection interaction as shown in *Figure 2* by the increasing discrepancy between unprotected and protected yields throughout intensification in all three cultivars. Conversely, this experiment demonstrates that the damage due to the multiple pathosystem is increasing with improvement of the production situation (De Wit, 1982) by means of accumulation of inputs. Overall damage at the lowest intensification level was $834-550=284\,\mathrm{kg\,ha^{-1}}$ against $1886-1109=777\,\mathrm{kg\,ha^{-1}}$ at the highest.

The small difference in yield between short- and long-cycle cultivars found in this experiment should be ascribed to unfavourable rainfall conditions at the end of the cropping season, which did not allow long-cycle cultivars to achieve their potential yields. Short and irregular rainy seasons, a major constraint to groundnut production (Gibbons, 1980) is a common environmental feature faced by farmers in the savanna regions in West Africa (Savary, 1986).

Second experiment

Evaluation of conclusions drawn from ANOVA on yield. As the objective of the second experiment was to compare and analyse the effects of differences in disease injuries on yield at varying intensification levels, checks for the effect of treatment on disease levels (Johnson *et al.*, 1986) and comparison of results from ANOVA with those from regression were needed.

Analysis of yield variance showed that rust and leaf spot injuries on damage were less than additive (*Table 4*, R*S interaction). The area under the rust progress curve (R) was reduced when the leaf spot level was high (significant S-effect on R, *Table 3*) and this reduction was stronger at high than at low rust level (significant R*S effect on R, *Table 3*). The area under the leaf spot progress curve (S) was significantly modified by the level of rust, S being slightly increased in R2S2 plots in comparison to R1S2 plots (*Figure 3*). A negative interaction effect of diseases on yield reduction was confirmed by regression of disease variables on overall variation of yield in the total set of data (*Table 5*, V–W–).

Analysis of variance showed an interaction between rust injury, cultivar, and weed-control level on yield (*Table 4*, interaction R*V*W). The effect was interpreted as an increase in yield with increasing weed control in all three cultivars at low rust level – this increase being smaller in V1 – as opposed to a moderate increase in yield with weed control in V2 and V3 at high rust level, whereas yields were decreased with increasing weed control at high rust level in V1. The area under the rust progress curve increased with increasing weed control (significant W-effect on R), and V3 was more responsive to rust treatment than V1 and V2 (significant V*R interaction on R, *Table 3*). The final regression equation (*Table 6*, $n=144$) indicates a significant contribution of $R^{*}Y_{\mathrm{r}}$ to yield variation, where Y_{r} incorporates increase in yield due to weed control and cultivar potential yield.

The third-order interaction (R*S*V*W) has been interpreted in terms of interaction of rust and leaf spot injuries on damage in the various V*W combinations. This interpretation does not fit with the regression equations (*Table 5*) built for each of these combinations (see e.g. V3W3). However, comparison of equations in *Table 5* indicates that the relationship between rust and leaf spot varied among these combinations.

Overall results. In practice, treatments R1 and R2, and S1 and S2 did correspond to very different levels of both diseases. The overall regression equation (*Table 6*) representing the complete data set does not contradict the main conclusions drawn from ANOVA, that (1) rust and leaf spot injuries had less than additive effects on damage, and (2) damage due to rust increased with simultaneously increasing weed control and cultivar potential yield.

Origin of within-plot interaction between disease levels. Rust epidemics were weaker in R2S2 plots (high rust and leaf spot levels) than in R2S1 plots (high rust and low leaf spot). In R2S2 plots, the slowing down of the rust epidemic is mainly attributable to defoliation induced by leaf spot. In R2S1 plots, the rust epidemic may have been enhanced by a suppression of rust antagonists in the phyllosphere by benomyl (Skajennikoff and Rapilly, 1981).

The slight but significant reduction of late leaf spot epidemics in R1S2 plots compared with R2S2 may be due to a slight control effect of oxycarboxin on leaf spot (R1S2), and/or an increased susceptibility to leaf spot of plants with strong rust infection (R2S2). Such an effect is not documented in the case of rust–late leaf spot relationships, but is documented in other pathosystems, e.g. brown rust (*Puccinia recondita*) – glume blotch (*Septoria nodorum*) on wheat (Van der Wal, Shearer and Zadoks, 1970; Van der Wal and Cowan, 1974).

Injury–damage relationships. In the second experiment, a slight reduction in overall foliar growth was associated with high rust level. This reduction was apparent at the end of the crop cycle only. Although it should not be considered as a major damage component *per se*, it may reflect reduced growth of other plant organs, especially roots, which might have had strong effects. High rust levels were also associated with slight defoliation at the end of the crop cycle which probably had not contributed substantially to rust damage. Damage caused by rust in this experiment should probably be attributed to a diversion of carbohydrates to fungal growth and spore production (Savary *et al.*, 1990), and, possibly, to a disturbance of the water balance in rust-infected plants, due to reduced root growth and increased transpiration (Martin and Hendrix, 1966; Van der Wal and Cowan, 1974; Cowan and Van der Wal, 1975).

Marked defoliation was associated with the appearance of significant differences in leaf spot severity between high and low leaf spot treatments. Defoliation was already initiated at low leaf spot severity (Plaut and Berger, 1980; Backmann and Crawford, 1984). The cultivars differed in their response to leaf spot treatment (S*V interaction on the area under the leaf spot progress curve *S, Table 3*), but this interaction was not reflected in yield data. No significant cultivar effect on the proportion of defoliation (%def) was found, indicating a similar proportion of defoliation at high leaf spot level (S2) in all three cultivars. Different leaf spot severities had similar effects on defoliation and on yield reduction, suggesting that defoliation was indeed a major component of the damage incurred by leaf spot to the crop. In addition to reduction of photosynthetically active leaf area due to lesion multiplication, several other damage components have been documented in late leaf spot on groundnut, including reduced root growth (Teare *et al.*, 1984), reduced photosynthetic efficiency, reduced stem dry weight, and translocation to developing pods (Boote *et al.*, 1980).

Intensification levels and damage function. The second experiment occupied a fairly large area, and heterogeneity of the soil could not be avoided. As a result, rather large differences in replication mean yield occurred (range: 1680–2090 kg ha^{-1}). These differences are incorporated in Y_r, and the regression equations that can be derived may be considered as representative of the relationships between yield and disease injuries over a range of reference yields.

The final regression equation of *Table 6* (V–W–, $n = 144$) conveniently describes the yield response to disease injuries and intensification levels in the second experiment. In a previous study (Savary and Zadoks, 1992), a similar regression equation was built using attainable yield (Y_a), i.e. the yield of disease-free plots. It was of the shape:

$$Y = a + b_1\,Y_a + b_2\,Y_a{*}R_l + b_3\,Y_a{*}S_l + b_4\,R_l{*}S_l$$

and was indicative of a significantly increasing contribution of rust and leaf spot to crop losses with simultaneously increasing attainable yield.

The yield difference: $D = Y_r - Y$, can be considered as representative of the damage caused to the crop by diseases. A further stepwise regression analysis yielded the damage function:

$$D = -4910 + 709\,R_l + 848\,S_l - 138\,R_l{*}S_l + 0.014\,Y_r{*}(R_l{*}S_l)$$

($r^2 = 0.58$, d.f. = 139), where all parameters are significant at $p < 0.0001$. This equation indicates significant contributions of rust and leaf spot injuries, and a less than additive interaction of injuries on damage. The last term, $Y_r{*}(R_l{*}S_l)$, indicates an overall increase of damage with simultaneously increasing injuries and reference yield.

Conclusions

The two experiments demonstrate that the damage due to varying levels of foliar diseases in groundnut is related to intensification levels, i.e. production situation. The increase in damage with intensification shown in the first experiment was due to three different pathogens, which were not manipulated. The second experiment suggests that rust might contribute most to yield reduction. Both experiments indicate that disease control measures in groundnut should be adapted to (1) the expected levels of the diseases, (2) the production situation, including intensification level of the crop, and its economic objectives. To optimize disease control, damage and action thresholds (Zadoks, 1981, 1985, 1987) have to be devised for each component of the pathosystem, the thresholds 'shifting' from one production situation to another.

An alternative approach might be considered, based upon corresponding types of production situations, and patterns of the multiple pathosystem, each type being associated with one management strategy. The relevant methodology has yet to be developed, applying, for example, discriminant analysis (Francl *et al.*, 1987), and/or correspondence analysis (Savary, 1986; Savary *et al.*, 1988).

Acknowledgements

The authors are grateful to F. Brissot (IIRSDA, Ivory Coast) for assistance in field work and Ir Van Wijk (Department of Mathematics, Wageningen Agricultural University) for assistance in statistical analyses. The first author is grateful to the Department of Phytopathology, Wageningen Agricultural University, for the facilities provided during this research.

This research was supported in part by a fellowship provided to the first author by the International Agricultural Centre, Wageningen, the Netherlands.

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Received 22 October 1990
Revised 23 July 1991
Accepted 23 July 1991