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Dynamic Simulation of Groundnut Rust: A Preliminary Model

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ABSTRACT

A first attempt to build a dynamic simulation model of groundnut rust is reported. The model involves two units: crop growth and development, and rust epidemic. Its structure is described, and its performances are presented. Simulated outputs were found fairly similar to observed rust severity and crop growth data from Adiopodoumé, southern Ivory Coast. The performances of the model may be considered to comply with the requirements expected from a preliminary simulation model. Directions for future improvements of the model are discussed.

INTRODUCTION

Groundnut rust, due to *Puccinia arachidis* Speg., and leafspots, due to *Cercosporidium personatum* (Berk. & Curt.) Deighton (late leafspot) and *Cercospora arachidicola* Hori (early leafspot), are causing two major foliar diseases in Western Africa, and especially in Ivory Coast (Savary, 1987*a*,*b*).

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The present study reports a first attempt to build a dynamic simulation model of groundnut rust, which is recently established in Africa. The objective is to acquire more insight in the quantitative aspects of groundnut rust epidemiology (Zadoks, 1972*a*). Crop growth and development were included in the model (Rabbinge & Rijsdijk, 1981), as were various components of resistance (Zadoks, 1972*b*). Due attention was given to leafspot diseases, which affect rust epidemics as well as crop growth.

STRUCTURE OF THE MODEL

General considerations

The system under study is a square meter of groundnut crop infected by rust. It is surrounded by a large number of identical systems, with identical attributes, such as development stage of the crop, leaf area index, and rust severity. The present model elaborates on an initial model by Zadoks (1971).

The model has two main units, one referring to the crop, with growth and development, and the other to the rust epidemic. The latter includes two subunits: rust lesion development and rust multiplication. Three categories of state variables are present: dry matter of plant organs, rust lesions and rust spores, which represent host growth, lesion development, and rust multiplication, respectively (Fig. 1). Weather data and leafspot data are handled as driving functions. The programme was written in CSMP (IBM, 1975).

The time step used in integration should be based on the time coefficients considered. As many processes are taken into account, with quite different time coefficients and with various feedbacks, the time step actually used must be a compromise between calculation time and deformation of results. This preliminary model uses a time step of 1 day. Processes with a time coefficient smaller than 1 day are incorporated into daily input features (Zadoks, 1971) by means of rules transforming complex processes into daily events (Waggoner, 1974; Rapilly & Jolivet, 1976). The biological day ran from 8 am to 8 pm, concurrent with the climatological day.

The host model

The host model used to simulate crop growth and development is SUCROS (Van Keulen *et al.*, 1982; Van Keulen & de Milliano, 1984). Four categories of organs are considered: roots, stems, leaves and pods, represented by their dry matter: *RTDM*, *SDM*, *LDM* and *PDM*, respectively (Table 1). Partitioning of carbohydrates produced by photosynthesis is modeled using

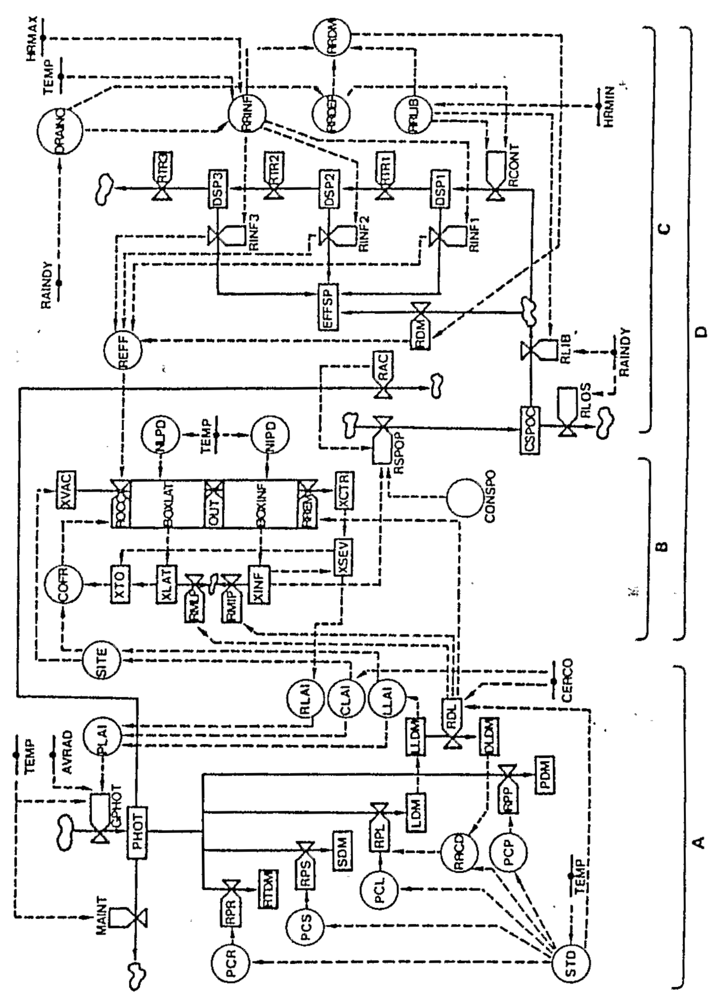

Fig. 1. Relational diagram of a preliminary simulation model for groundnut rust. A: crop growth and development sub-model, B: groundnut rust pustule development unit, C: rust multiplication unit, and D: rust sub-model. A, B, and C handle plant organ dry matter, sites and rust uredinospores as state variables, respectively. For symbol explanation, see Table 1 and text.

TABLE 1
List of Variables used in the Preliminary Simulation Model for Groundnut Rust

Variable	*Meaning of symbol*	*Units*
AMAX	Rate of assimilation of CO_2 at light saturation	$[kg_{CO_2}\,ha^{-1}\,h^{-1}]$
AVRAD	Actual daily radiation (400–700 nm)	$[J\,m^{-2}\,day^{-1}]$
CERCO	Cercospora leaf spot severity	[-]
CLAI	Fraction of *LAI* colonized by *Cercospora* sp.	$[m^2\,m^{-2}]$ or [-]
COFR	Correction factor	$[N_{site}\,N_{site}^{-1}]$ or [-]
CONSPO	Conversion coefficient of plant carbohydrate into spores	$[g_{DM}\,N_{sp}^{-1}]$
CSPOC	Canopy spore content	$[N_{sp}]$
CVF	Conversion factor of carbohydrates into plant dry matter	$[g_{DM}\,g_{CH_2O}^{-1}]$
CVFP	Conversion efficiency for pod dry matter	$[g_{DM}\,g_{CH_2O}^{-1}]$
DEPOX	Maximum deposition coefficient	$[N_{sp}\,N_{sp}^{-1}\,day^{-1}]$ or $[day^{-1}]$
DLAI	Fraction of leaf area index lost by defoliation	[-]
DLDM	Leaf dry matter lost by defoliation	$[g_{DM}]$
DMFR	Daily multiplication factor	$[N_{site}\,N_{site}^{-1}\,day^{-1}]$ or $[day^{-1}]$
DRAINC	Daily rain condition	[-]
DVS	Development stage	[-]
EFF	Efficiency of use of absorbed visible radiation for CO_2 assimilation at low light levels	$[kg_{CO_2}\,J^{-1}\,ha^{-1}\,h^{-1}\,m^2\,s]$
GPHOT	Gross photosynthesis rate	$[kg_{CH_2O}\,ha^{-1}\,h^{-1}]$
INEFD	Infection efficiency of the current day: ratio of the effective to the deposition spores	$[N_{sp}\,N_{sp}^{-1}]$ or [-]
LAI	Leaf area index	$[m^2\,m^{-2}]$ or [-]
LDM	Leaf dry matter	$[g_{DM}]$
LLAI	Living leaf area index	$[m^2\,m^{-2}]$ or [-]
LLDM	Living leaf dry matter	$[g_{DM}]$
LSPOC	Lesion spore content	$[N_{sp}\,N_{site}^{-1}]$
MAINT	Maintenance respiration rate	$[kg_{CH_2O}\,ha^{-1}\,h^{-1}]$
NIPD	Infectious period duration	[day]
NLPD	Latency period duration	[day]
PCL	Partition coefficient of leaves (a function of *DVS*)	[-]
PCP	Partition coefficient of pods (a function of *DVS*)	[-]
PCR	Partition coefficient of roots (a function of *DVS*)	[-]
PCS	Partition coefficient of stems (a function of *DVS*)	[-]
PDM	Pod dry matter	$[g_{DM}]$
PGNET	Net rate of photosynthesis	$[g_{CH_2O}\,day^{-1}]$
PHOT	Photosynthates pool	$[g_{CH_2O}]$
PLAI	Photosynthetically active leaf area index	[-]
PSIZE	Size (area) of one rust pustule	$[m^2\,m^{-2}\,N_{site}^{-1}]$
RAC	Rate of assimilate conversion into spores	$[g_{DM}\,day^{-1}]$
RADEP	Ratio for spore deposition	[-]
RAINF	Ratio for infection	[-]
RALIB	Ratio for spore liberation	[-]
RALIBX	Maximum ratio for spore liberation	[-]
RAINDY	Daily rainfall amount	[mm]
RCD	Rate of compensation for defoliation	$[g_{DM}\,day^{-1}]$
RDDS	Rate of spore dispersal (liberation and deposition), under unfavourable conditions for infection	$[N_{sp}\,day^{-1}]$
RDL	Rate of increase of the defoliated leaves dry matter	$[g_{DM}\,day^{-1}]$
RDM	Rate of daily multiplication. Daily inflow of efficient spores (favourable conditions)	$[N_{sp}\,day^{-1}]$ or $[N_{site}\,day^{-1}]$
REFF	Cumulated rate of infection deposited spores (efficient spores)	$[N_{sp}\,day^{-1}]$ or $[N_{site}\,day^{-1}]$
REFL	Reflexion coefficient of the canopy	[-]
RHMAX	Maximum daily relative humidity	[%]
RHMIN	Minimum daily relative humidity	[%]
RINF1-3	Rates of infection (under unfavourable conditions, three classes of survival of spores)	$[N_{sp}\,day^{-1}]$ or $[N_{site}\,day^{-1}]$
RLAI	Rusted leaf area index: fraction of living leaf area (*LLAI*) covered with rust postules	$[m^2\,m^{-2}]$ or [-]

(continued)

TABLE I—*contd.*

Variable	*Meaning of symbol*	*Units*
RLIB	Rate of spore liberation	[N_{sp} day^{-1}]
RLOS	Rate of loss of spores	[N_{sp} day^{-1}]
RMIP	Relative rate of mortality during the infectious period	[day^{-1}]
RMLP	Relative rate of mortality during the latency period	[day^{-1}]
ROCC	Rate of occupation of sites	[N_{site} day^{-1}]
RPL	Rate of partition to leaves	[g_{DM} day^{-1}]
RPP	Rate of partition to pods	[g_{DM} day^{-1}]
RPR	Rate of partition to roots	[g_{DM} day^{-1}]
RPS	Rate of partition to stems	[g_{DM} day^{-1}]
RRCD	Relative rate of compensation for defoliation	[g_{DM} g_{DM}^{-1} day^{-1}] or [day^{-1}]
RRCER	Relative rate of increase of cercospora leafspot severity	[day^{-1}]
RRDCER	Relative rate of defoliation due to cercospora leafspot	[g_{DM} g_{DM}^{-1} day^{-1}] or [day^{-1}]
RRDDS	Relative rate of spore dispersal (liberation and deposition, unfavourable conditions)	[N_{sp} N_{sp}^{-1} day^{-1}] or [day^{-1}]
RRDL	Relative rate of defoliation	[g_{DM} g_{DM}^{-1} day^{-1}] or [day^{-1}]
RRDM	Relative rate of multiplication (favourable conditions)	[N_{sp} N_{sp}^{-1} day^{-1}] or [day^{-1}]
RRDPHY	Relative rate of defoliation due to physiology of the plant	[g_{DM} g_{DM}^{-1} day^{-1}] or [day^{-1}]
RREM	Rate of removal of lesions from the infectious process	[N_{site} day^{-1}]
RRLOS	Relative rate of loss of spores	[N_{sp} N_{sp}^{-1} day^{-1}] or [day^{-1}]
RRMIVC	Relative mortality rate in the infectious stage (varietal coefficient)	[N_{site} N_{site}^{-1} day^{-1}] or [day^{-1}]
RRMLVC	Relative mortality rate in the latent stage (varietal coefficient)	[N_{site} N_{site}^{-1} day^{-1}] or [day^{-1}]
RSPO	Rate of sporulation	[N_{sp} day^{-1}]
RSPONI	Rate of spontaneous infection per *LAI* unit	[N_{site} m^{-2} m^2 day^{-1}]
RSPOP	Rate of spore production	[N_{sp} day^{-1}]
RSTART	Current rate of inflow of spontaneous infections	[N_{site} day^{-1}]
RTDM	Root dry matter	[g_{DM}]
RTR1-3	Rates of flow of surviving spores from the 1st to the 2nd to the 2nd to the 3rd, and from the 3rd stage to a 'death' stage	[N_{sp} day^{-1}]
SDM	Stem dry matter	[g_{DM}]
SITE	Number of sites	[N_{site}]
SITECO	Site coefficient: number of sites per *LAI* unit	[N_{site} m^{-2} m^2]
SLA	Specific leaf area	[m^2 g_{DM}^{-1}]
STEMP	Sum of temperature	[°C day^{-1}]
TEMPDY	Mean daily temperature	[°C]
TEMPN	Minimum daily temperature	[°C]
TEMPX	Maximum daily temperature	[°C]
THLD	Threshold of defoliated proportion of leaves for compensation for defoliation	[-]
VCSPOP	Varietal coefficient for spore production ($0 \leq VCSPOP \leq 1$)	[-]
VCIEFF	Varietal coefficient for infection efficiency ($0 \leq VCIEFF \leq 1$)	[-]
VCLAT	Varietal coefficient for the latency period duration ($VCLZT \geq 1$)	[-]
VCINF	Varietal coefficient for the infectious period duration ($0 \leq VCINF \leq 1$)	[1]
WTCOD	Wetness coefficient for deposition (a function of *DRAINC*)	[-]
WTCOIE	Wetness coefficient for infection efficiency (a function of *DRAINC* and *RHMAX*)	[-]
XCTR	Number of removed sites	[N_{site}]
XINF	Number of infectious sites	[N_{site}]
XLAT	Number of latent sites	[N_{site}]
XSEV	Accumulated number of infected and removed sites	[N_{site}]
XTO	Total number of occupied sites	[N_{site}]
XVAC	Number of available sites	[N_{site}]

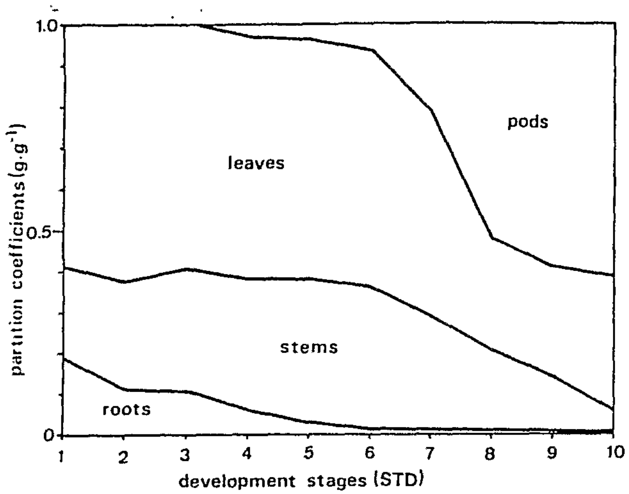

Fig. 2. Partition coefficients of groundnut. Data represent non-infected groundnut development and growth as measured at IIRSDA Experimental Station, Adiopodoumé (means of four replications at each of three sowing dates).

the partition coefficients *PCR*, *PCS*, *PCL* and *PCP*, respectively. The partition coefficients are functions of the development stage of the crop (*DVS*). Their values were measured in disease-free plots of an experiment conducted at IIRSDA Experimental Station, Adiopodoumé (Fig. 2). The development stage of the crop (*DVS*, after Boote, 1982*a*; Table 2) is a function of the accumulated mean daily temperature.

Leaf dry matter is converted into leaf area index (*LAI*) using a specific leaf area coefficient (*SLA*). Defoliation is physiological (development stage) and/or pathological (leafspot). The rate of defoliation (*RDL*) is proportional to the living leaf dry matter:

$$RDL = RRDL * LLDM$$

With physiological defoliation only, *RRDL*, equivalent to a relative death rate, is a function of *DVS* (H. Voortman & P. Raven (1984), unpublished data).

The rate of light-saturated apparent photosynthesis (*AMAX*) used in the model is that of Ketring *et al.* (1982):

$$AMAX = 38\, kg_{CO_2}\, J^{-1}\, ha^{-1}\, h^{-1}$$

The values for the efficiency of use of absorbed visible radiation for CO_2 assimilation at low light level (*EFF*) and the reflexion coefficient of the canopy (*REFL*) were the original ones (Ketring *et al.*, 1982, H. Van Keulen, pers. comm.) of the SUCROS model:

$$EFF = 0{\cdot}5\, kg_{CO_2}\, J^{-1}\, ha^{-1}\, h^{-1}\, m^2\, s, \text{ and } REFL = 0{\cdot}08$$

TABLE 2

Relation Between Accumulated Daily Temperature (*STEMP*) and Development Stages (*DVS*) of an Erect Short-cycle Groundnut Cultivar as Measured at IIRSDA Experimental Station, Adiopodoumé, Ivory Coast

Development stages[a]	*DVS*[b]	*STEMP*[c] *Minimum*	*STEMP*[c] *Maximum*
Emergence to first tetrafoliate unfolded on the main axis of the plant	1	0	279
Second to third tetrafoliate unfolded	2	279·1	463
Fourth to *N*th tetrafoliate unfolded	3	463·1	644
Beginning bloom: one open flower on the plant	4	644·1	823
Beginning peg: one elongated gynophore on the plant	5	823·1	1 000
Beginning pod (one swollen peg) to full pod (one pod reaching the dimension characteristic of the cultivar)	6	1 000·1	1 177
Beginning seed: one fully expanded pod containing visible seed primordium	7	1 177·1	1 413
Full seed: one fully expanded pod with its internal cavity filled with seeds	8	1 413·1	1 725
Beginning maturity: one pod showing pericarp or testa coloration	9	1 725·1	1 974
Full maturity: 2/3 to 3/4 of pods with pericarp or testa coloration	10	1 974·1	—

[a] From Boote (1982*a*), with slight modifications.
[b] Running value of *DVS* in the model.
[c] Accumulated daily mean temperatures from sowing date. Data are means of three replications (sowing dates).

Following Penning de Vries & Van Laar (1982), the conversion efficiency for growth of plant dry matter, *CVF*, is calculated as:

$$CVF = PCL * 0{\cdot}59 + PSC * 0{\cdot}62 + PCR * 0{\cdot}65 + PCP * CVFP$$

The conversion efficiency of pod dry matter (*CVFP*) is calculated from biochemical composition data (Ketring *et al.*, 1982: $CVFP = 0{\cdot}49\, kg_{DM}\, kg^{-1}_{CH_2O}$).

The rust model

The order of calculations

At each integration interval, calculations are executed in steps: (1) the amount of spores produced in the day under consideration, (2) the loss of spores leached to the ground by rain, (3) the proportion of the remaining spores liberated and deposited, (4) infections, leading to the production of latent lesions, and (5) accumulation of non-liberated spores in the canopy spore content (*CSPOC*).

The infection cycle

Following Zadoks (1971), four categories of sites (*SITE*) are distinguished: vacant, latent, infectious and removed lesions (*XVAC*, *XLAT*, *XINF* and *XCTR*). The rate of occupation of sites by rust is written as:

$$ROCC = REFF * COFR + RSTART$$

where *REFF* is the rate of infection of deposited spores, and

$$COFR = XVAC/SITE$$

is the correction factor. *RSTART* initiates the epidemic. *REFF* is the daily multiplication of the whole population of lesions and is calculated as the sum of rates of efficacy of spores dispersed under favourable conditions for infection (*RDM*) and of three age-classes of spores deposited under unfavourable conditions:

$$REFF = RDM + RINF1 + RINF2 + RINF3$$

DMFR is the daily multiplication factor per lesion (Zadoks, 1971):

$$DMFR = REFF/XINF$$

The total population of lesions is:

$$XTO = XLAT + XINF + XCTR$$

XSEV represents the population of visible lesions as determined by actual rust severity assessments:

$$XSEV = XINF + XCTR$$

Spore production

The spore content of the canopy, i.e. the amount of spores available for liberation, is calculated as an integral:

$$CSPOC = INTGRL\ (0., RSPO)$$

The rate of increase of the spore content of the canopy is:

$$RSPO = RSPOP - RLIB - RLOS$$

where *RSPOP* is the rate of spore production, *RLIB* the rate of spore liberation, and *RLOS* the rate of loss of spores due to rain leaching. The rate of spore production is a function of maximum (*TEMPX*), minimum (*TEMPN*), and average (*TEMPDY*) temperatures (Savary, 1985*b*). The resulting spore production is corrected by a varietal coefficient (*VCSPOP*), with a default value of 1· for a susceptible cultivar.

Spore loss by rain leaching

A rain shower on an infected groundnut canopy induces a flow of rust spores suspended in water dripping from leaves and running off the petioles and stems to the ground. Leaching was found to reach high values from 5 mm rainfall volume (*RAINDY*) upwards (Savary & Janeau, 1986). Three types of daily rain conditions (*DRAINC*) are considered: no rain, rainfall under 5 mm, and rainfall of 5 mm or more, which correspond to proportions of 0, 0·25 and 0·5 of the canopy spore content leached to the ground (Table 3).

Spore liberation

The rate of spore liberation is proportional to the canopy spore content (*CSPOC*):

$$RLIB = RALIB * CSPOC$$

RALIB is a function of the maximum relative rate under dry conditions ($RALIBX = 0{\cdot}16$; Savary, 1986). Dry conditions were defined by a minimum relative humidity (*RHMIN*) below 70% (Table 3; Mallaiah & Rao, 1982; Savary, 1986). *RALIB* also depends on the occurrence of rain. Slight rains ($RAINDY < 5$ mm) promote spore dispersal (Savary & Janeau, 1986; $RALIB = 1{\cdot}1 * RALIBX$), whereas heavy rains ($RAINDY \geq 5$ mm) impede spore dispersal ($RALIB = 0$).

Spore deposition on the canopy

Spore deposition is represented by its relative rate, *RADEP*. *RADEP* is proportional to the leaf area which contains sites, whether occupied or not, a maximum deposition coefficient (*DEPOX*), and a coefficient for canopy wetness (*WTCOD*). Deposition is taken to be three times higher on a wet than on a dry canopy (Chamberlain & Chadwick, 1972). *DEPOX* was derived from a study by Hirst & Stedman (1971), indicating that the depletion of a cloud of sugar beet pollen on a wheat crop due to deposition is about 1% per meter travel and per (dry) *LAI* unit. This figure corresponds to the average 0·8–1·4% depletion of an *Erysiphe graminis* spore flow per meter travel and per *LAI* unit (assuming $LAI = 3$) in a barley field (Aylor, 1982). These values represent spore deposition at mesoscale, over distances ranging from 1 to 10 m, i.e. within crop, between plant dispersal. When spore dispersal at microscale, i.e. within plant dispersal, is considered (Roelfs & Martell, 1984), the proportion of deposited spores takes larger values. A value of 0·03 for *DEPOX* was used.

TABLE 3

A Typology of Daily Weather Conditions used to Define Daily Weather Rules for Epidemiological Processes with Time-constants Smaller than 1 Day. *RAINDY*: Daily Rainfall (mm), *RHMIN*: Minimum Relative Humidity, *RHMAX*: Maximum Relative Humidity, *RRLOS*: Relative Rate of Loss of Spores by Dripping to the Soil (T^{-1}), *RALIB*: Relative Rate of Liberation of Spores under Dry Conditions (T^{-1}), *WTCOIE*: Wetness Coefficient of the Canopy for Infection Efficiency, *WTCOD*: Wetness Coefficient of the Canopy for Spore Deposition

Variables	*RAINDY* = 0				0 < *RAINDY* < 5	*RAINDY* ≥ 5
	0 < *RHMIN* < 70		*RHMIN* ≥ 70			
	RHMAX < 95	*RHMAX* ≥ 95	*RHMAX* < 95	*RHMAX* ≥ 95		
RRLOS	0	0	0	0	0·25	0·5
RALIB	*RALIBX*	*RALIBX*	0·5**RALIBX*	0·5**RALIBX*	1·1**RALIBX*	0
WTCOIE	0	1	0	1	1	1
WTCOD	1	1	1	1	3	3

Infection

Infection is represented by *RAINF*, the relative rate of infection. *RAINF* is proportional to the daily infection efficiency (*INEFD*), a wetness coefficient (*WTCOIE*), and a varietal coefficient for infection efficiency (*VCIEFF*), the latter having a default value 1· for a susceptible cultivar.

$$RAINF = VCIEFF * WTCOIE * INEFD$$

INEFD is the mean value of infection efficiencies calculated from three temperatures of the current day: *TEMPX*, *TEMPN* and *TEMPDY* (Savary, 1985*b*). Under laboratory conditions, *P. arachidis* spores may germinate and infect when relative humidity is 100% or when water is present on the leaf surface (Savary, 1985*a*). Under field conditions, a water-saturated atmosphere is assumed to coincide with the occurrence of water (rain or dew) on the foliage (Table 3). Dew is considered to occur when maximum relative humidity (*RHMAX*) is at least 95%.

Flows of spores (favourable conditions)

To simulate spore dispersal and rust spread, several phases were considered: spore liberation, spore deposition and infection of sites. Each of these phases can be defined by state variables: liberated and deposited spores, and latent lesions, related by flows with rates: rate of spore liberation, of spore deposition and of site infection. These rates can be made proportional to relative rates (dimension: $[T^{-1}]$: *RALIB*, *RADEP* and *RAINF*). Each of the considered processes, however, has time coefficients smaller than the time step chosen for the preliminary model (1 day). To be simulated within 1 day, their succession had to be summarized into a daily input feature, where the relative rates *RALIB*, *RADEP* and *RAINF* were considered as ratios (dimensionless), from which a relative rate of daily multiplication (*RRDM*, dimension $[T^{-1}]$) representing the daily fraction of the spores that successfully pass the dispersal and infection processes is calculated:

$$RRDM = (RALIB * RADEP * RAINF)/DELT$$

Favourable conditions are defined by: $RAINDY \neq 0$ or $RHMAX \geq 95\%$. The rate of daily multiplication under favourable conditions (RDM) is proportional to *RRDM*:

$$RDM = RRDM * CSPOC$$

Flow of spores (unfavourable conditions)

Under unfavourable conditions ($RAINDY = 0$ and $RHMAX < 95\%$), deposited spores enter a process of survival and maturation (Zadoks & Van Hees-Boukema, 1986; Van Hees-Boukema & Zadoks, 1986; P. D. de Jong &

L. Michaud, unpublished results). The rate of deposition of dry spores is calculated as:

$$RDDS = RRDDS * CSPOC$$

The relative rate of the process, *RRDDS*, takes a null value under favourable conditions ($RRDM > 0$); it combines the ratios for liberation and deposition when $RRDM = 0$:

$$RRDDS = INSW(-RRDM, 0\cdot, (RALIB * RADEP)/DELT)$$

Survival and maturation are modelled as a boxcar train without dispersion using *RDDS* as rate of inflow. The train has three boxes, each with three outflows: a rate of mortality (which allows to simulate survival), a rate of infection (which represents maturation of spores), and a rate of outflow to the next stage. The residence time in each stage is 2 days and the spores leaving the third box are considered dead. When favourable conditions occur, each of the three boxes is emptied, a proportion *RAINF* of the spores being efficient and the rest ($1\cdot - RAINF$) being eliminated. The infection efficiency in the second stage is twice that of the two other stages. Under unfavourable conditions, the contents of the first boxes are allocated to the next one every second day, while that of the third is brought to a sink of dead spores.

Latency and infectious period

Passage of rust lesions through these periods is simulated using boxcar trains according to Zadoks (1971), with some additional detail. Residence times in the latent (*NLPD*) and in the infectious (*NIPD*) stages are functions of daily temperatures (Savary, 1985*a*). Both are mean values of three daily calculations, using *TEMPX*, *TEMPN* and *TEMPDY*. The resulting residence times are corrected by variety-dependent factors (*VCLAT* and *VCINF*), with default values of 1· for a susceptible variety. Each boxcar train has a relative death rate which is a function of death rates due to cultivar resistance (*RRMLVC* and *RRMIVC*, default values: 0· for a susceptible cultivar), to physiological defoliation (*RRDPHY*), and to defoliation caused by leafspot disease (*RRDCER*). Exhausted sites (*XCTR*) accumulate with the rate of outflow from the infectious stage (*RREM*). *RREM* is corrected for defoliation.

Spontaneous infections

RSTART represents the background noise, the rate of inflow of effective spores from external inoculum sources into the considered crop. This rate of inflow is assumed to depend on the magnitude and distance of inoculum sources, which are beyond the limits of the system under consideration, and to be proportional to the (vacant) trapping area of the crop:

$$RSTART = RSPONI * (XVAC/SITECO)$$

where *RSPONI* is the rate of spontaneous infections per unit leaf area (an empirically estimated parameter, invariant per run) and *SITECO*, the number of sites per unit *LAI*.

Coupling

Hypotheses on the effects of rust and leafspot diseases on the physiology and growth of host plants

(1) *The groundnut rust pustule.* The occupied, sporulating site (*XINF*) is seen as a pustule (0·75 mm in diameter) surrounded by an apparently unaffected area (2·0 mm in diameter) which provides the energy needed for sporulation: the rust pustule is a sink for assimilates (Mendgen, 1981). A part of these assimilates is transformed into spores. A groundnut crop ($LAI = 4$) infected by rust at a 15% severity (approximately $1{\cdot}86 \times 10^6$ lesions m^{-2}) produces 1 to 3 kg spores ha^{-1} day^{-1} under moderately favourable conditions (200 to 600 spores per lesion day^{-1}; Savary, 1986).

The assimilates required for spore production are assumed to be directly derived from the net photosynthetic rate ($PGNET = GPHOT - MAINT$, where *GPHOT* represents the gross photosynthesis rate, and *MAINT* the maintenance respiration), before any partitioning to the growing organs. This effect is superimposed upon the reduction of photosynthetically active leaf area, represented by the accumulated areas of the pustules.

(2) *The cercospora lesion.* Three effects of the cercospora leafspots on the host are considered: (a) reduction of the rate of photosynthesis due to a reduction of photosynthetically active leaf area, (b) defoliation, and (c) compensation for defoliation. Cercospora lesions induce an acceleration of leaf senescence (Boote et *al.*, 1983), and defoliation. Defoliation due to cercospora lesions is represented by its relative rate, *RRDCER*, which is added to the relative rate of stage-dependent defoliation (*RRDPHY*) to compute the relative rate of defoliation of the canopy:

$$RRDL = RRDPHY + RRDCER$$

RRDCER was estimated as the difference between the relative rates of defoliation of untreated (infected) and treated plots (H. Voortman & P. Raven (1984), unpublished data). The regression equation:

$$RRDCER = 1{\cdot}72 \times 10^{-4} + 0{\cdot}01 \log_e(CERCO + 1)$$

which predicted *RRDCER* accurately in another, independent experiment ($p < 0{\cdot}05$, P. D. de Jong, 1986, unpublished data), was incorporated in the model.

Three hypotheses are introduced to simulate the compensation for defoliation: (a) the rate of compensation (*RCD*) is proportional to the amount of defoliation in the past 7 days (Jones *et al.*, 1982; Wilkerson *et al.*, 1984), (b) its relative rate (*RRCD*) depends on the development stage of the crop (Jones *et al.*, 1982), and (c) compensation occurs only when a threshold (*THLD*) is reached (Smith & Barfield, 1982), which depends on development stage. The model combines a decreasing relative rate of compensation with increasing development stage with a stage-dependent threshold for compensation.

Leaf area indexes

The coupling between *SITE*-variables and *LAI*-variables (Fig. 3) is provided by couplers (Zadoks & Rabbinge, 1985). The coupler in the *LAI* to *SITE* direction is *SITECO*, the number of sites per *LAI* unit. The value of *SITECO*, $3{\cdot}1 \times 10^5\ N_{site}\,m^2\,m^{-2}$, is derived from the estimated area of one site, calculated from the lesion density corresponding to the centre of the highest severity class in the standard area diagram for rust severity

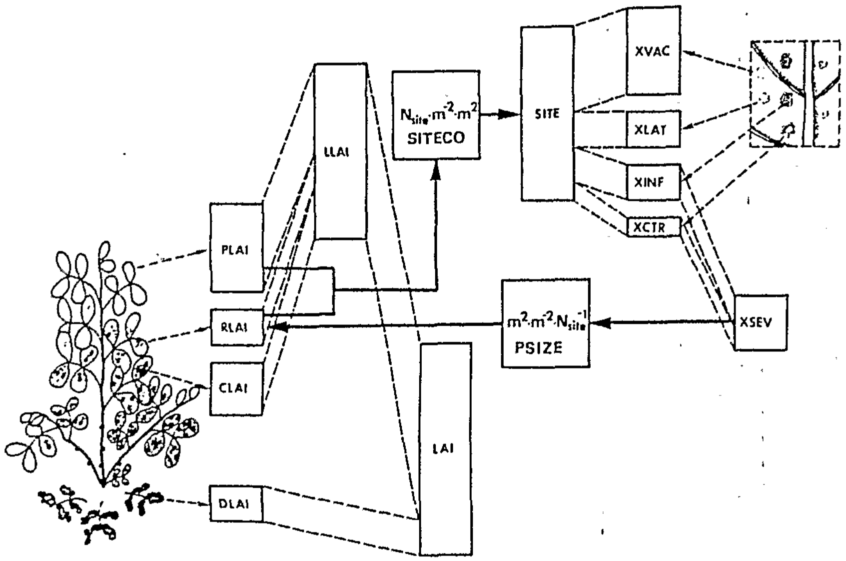

Fig. 3. Coupling between *LAI*- and *SITE*-variables, using *SITECO* ($3{\cdot}1 \times 10^5\ N_{site}\,m^{-2}\,m^2$, the number of sites per *LAI* unit) and *PSIZE* ($4{\cdot}4 \times 10^{-7}\,m^2\,m^{-2}\,N_{site}^{-1}$, the fraction of *LAI* unit per pustule) as couplers. For symbol explanation, see Table 1 and text.

assessment (Savary, 1987*a*). The coupler in the *SITE* to *LAI* direction is *PSIZE*, the fraction of *LAI* occupied by one pustule ($4{\cdot}4 \times 10^{-7}\,m^2\,m^{-2}\,N_{site}^{-1}$). The coupling mechanism allows to transform sites into *LAI* units and vice-versa.

The leaf area index (*LAI*) is divided into two major classes, dead (*DLAI*) and living (*LLAI*). The living leaf area index is subdivided into three sub-classes, photosynthetically active (*PLAI*), rusted (*RLAI*), and cercospora-blighted (*CLAI*). *RLAI*/*LLAI* corresponds with severity.

Effects of the host on rust

Crop growth affects pustule development and rust multiplication in two ways: (a) the number of spores caught by the canopy is proportional with its trapping surface, and (b) canopy growth makes new sites available for infection. The first of these effects is included in the calculation of the relative rate of deposition (*RADEP*), which is proportional to the leaf area index bearing sites (*LLAI–CLAI*). The second is included in the correction factor (*COFR*), which can be seen as the probability of an infectious spore to be deposited on a vacant site.

Interaction between rust and cercospora

Direct interaction between the two pathogens is seen in one way only: multiplication and radial growth of cercospora lesions leads to destruction of occupied (latent, infectious or removed) sites. An additional term for the relative rate of lesion mortality, the relative rate of increase of cercospora severity (*RRCER*), is, therefore, incorporated into the mortality rates in the latent, infectious and removed stages.

MODEL PERFORMANCES

Verification and sensitivity analysis

Simulated weather effects on the spore content of a lesion and on the daily multiplication factor

Daily variations of the lesion spore content (*LSPOC*, calculated as: *LSPOC* = *CSPOC*/*XINF*) and of the daily multiplication factor (*DMFR*) were studied as responses to faked daily variations of relative humidity (*RHMIN* and *RHMAX*), rainfall (*RAINDY*), and radiation (AVRAD). The results (Fig. 4) indicate strong dependence of *DMFR* on relative humidity and rainfall, according to the daily weather rules introduced into the model (Table 3). The variation of *LSPOC* indicates more complex relations with weather variables, and especially *AVRAD*. The model expects spore production to be negatively affected by a reduction of the rate of photosynthesis. Reductions of *LSPOC* are associated with low radiation (Fig. 4, arrows marked 1), heavy rainfall (3), or consecutive moderate rainfall (4), whereas it is increased by high radiation (2). High or low relative humidity appears to play a secondary role only. This verification run indicates that *LSPOC* is in

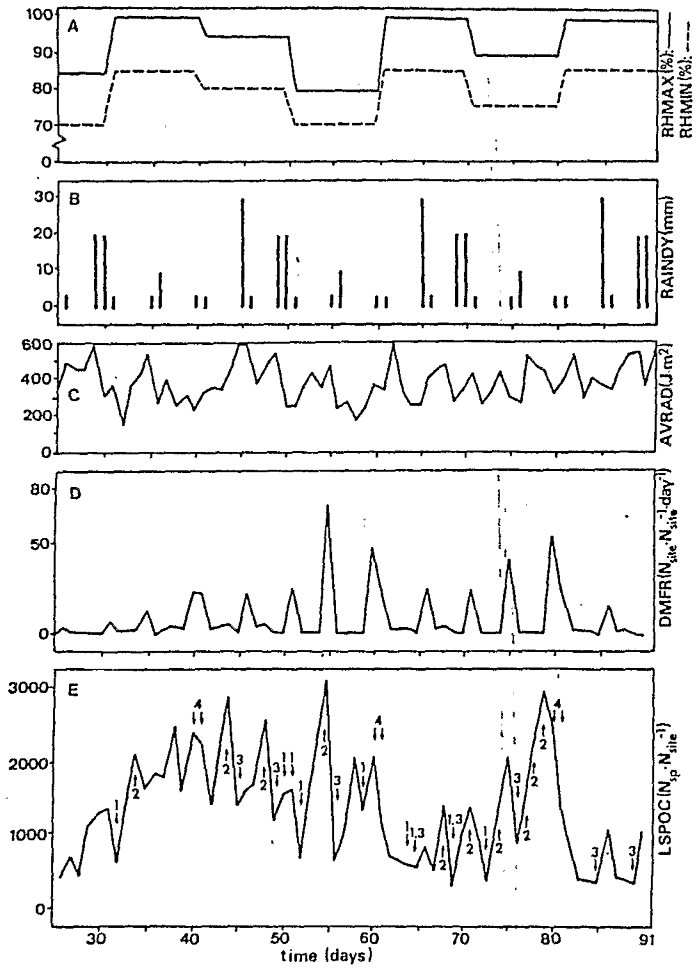

Fig. 4. Simulated variations of the daily multiplication factor (D: *DMFR* [day^{-1}]) and of the lesion spore content (E: *LSPOC* [$N_{sp}\ N_{site}^{-1}$]) as responses to faked variations of the relative humidity (A: *RHMAX* and *RHMIN* [%]), rainfall (B: *RAINDY* [mm]) and radiation (C: *AVRAD* [$J\ m^{-2}$]).

balance with a mean value of 1362 spores per lesion, which fits the range of minimum values measured in the field, following spore liberation under dry conditions (Savary, 1986), or rain-induced spore liberation (Savary & Janeau, 1986).

A simulation experiment about the effects of weather on rust epidemics
A simulation experiment was conducted to check the effect of weather on rust epidemics. The input variables consisted of three weather factors, each at three levels. The output variable characterizing the epidemics was the area under the disease progress curve (*AUDPC*). Inputs were rainfall patterns (Fig. 5, R1, R2 and R3), three levels of *RHMIN* and *RHMAX* (H1: 65–80, H2: 75–90 and H3: 85–98%), and three levels of *TEMPN* and *TEMPX* (T1: 23–27, T2: 21–31 and T3: 19–35°C). The effects of input variables could be assessed by their respective mean square values. The results indicated very strong effects of temperature (M.S. = 86·2), rainfall (M.S. = 73·6), and, to a lesser extent, of humidity (M.S. = 28·3). The response, as measured by *AUDPC*, to T and H decreased with increasing indices of these treatments, whereas the response to R followed an optimum pattern.

Effects of components of resistance on simulated groundnut rust epidemics
Following Teng *et al.* (1977), a simulation experiment was conducted using the levels of the varietal coefficients for infection efficiency, latency period, infectious period and sporulation intensity (*VCIEFF*, *VCLAT*, *VCINF* and *VCSPOP*, respectively) as treatments. Three levels of *VCLAT*, and two levels of *VCIEFF*, *VCINF* and *VCSPOP* were permutated. The levels of *VCLAT* were chosen to represent relative resistance indices (Zadoks, 1972*b*) of 0·, 0·25 and 0·5, respectively, i.e. *VCLAT* values of 1·, 1·33 and 2·, respectively. The levels of *VCIEFF*, *VCINF* and *VCSPOP* were chosen to represent relative resistance indices of 0· and 0·25, i.e. *VCIEFF*, *VCINF* and *VCSPOP* values of 1· and 0·75, respectively.

The resulting *AUDPC*s decreased with the increase of resistance indices corresponding to any of the considered components of resistance. The effect of *VCLAT* was very strong (M.S. = 97·1) whereas that of *VCIEFF* and *VCSPOP* were moderate (M.S. = 6·40 and 6·52, respectively), and that of *VCINF* (M.S. = 0·001) negligible.

Validation

To test the outputs of the model, the variables *LLAI* (living leaf area index) and *XSEV* (number of visible rust pustules per crop square meter) were chosen as representative of the crop sub-model and of the disease sub-model, respectively. Both were compared to data from field observations.

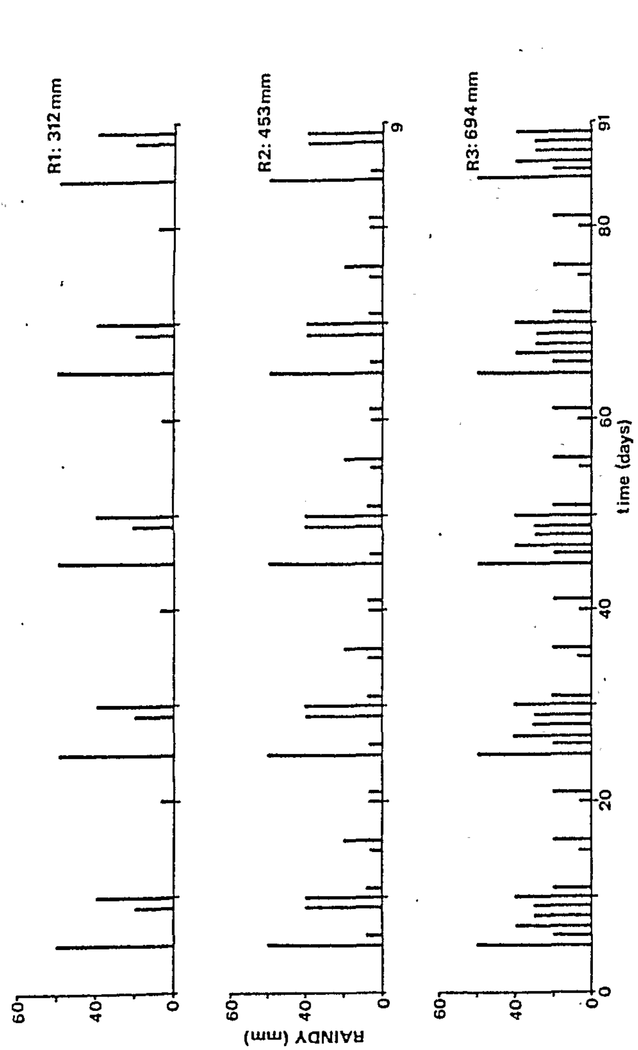

Fig. 5. Hypothetical rainfall profiles used in a simulation experiment (from top to bottom, treatments R1, R2 and R3).

A field experiment

The experiment (S. Savary & S. Ledermann, 1986, unpublished data) consisted of three blocks sown at three different dates (A: 12 May, B: 2 July and C: 23 July 1986), each block containing four replicates of paired (weekly treated with Chlorothalonil and non-treated) plots (3 × 3 m). The cultivar used was KH 149A, a short cycle, erect cultivar, planted at a density of 16·7 plants m^{-2}. Crop growth, rust and leafspot severities were assessed weekly on each replicate of the three blocks of the experiment.

Simulation runs

To simulate the course of rust epidemics in the field, the inputs required include weather data (*RAINDY*, *RHMAX*, *RHMIN*, *AVRAD*, *TEMPX* and *TEMPN*), information on the initial population of plants and of rust pustules and cercospora data. The initial population of plants is represented by the dry matter of roots, leaves and stems. Cercospora leafspot data are represented by *CERCO*, the weekly assessment of percentage leaf area covered by cercospora lesions. The rate of inflow of spontaneous infections per *LAI* unit, *RSPONI*, was estimated from the second assessment where rust severity was not null. This rate was kept constant from the estimated date of first infection till harvest.

The groundnut cultivar used was highly susceptible to rust. The values of the varietal parameters for susceptibility were inserted accordingly, using the statement:

PARAMETER VCIEFF = 1·, *VCLAT* = 1·, *VCINF* = 1·, *VCSPOP* = 1·,
... *RRMLVC* = 0·, *RRMIVC* = 0·

Comparison of simulated and actual results

The similarity between the simulated and observed values (Fig. 6) is not perfect but certainly encouraging. With one exception, the timing of the peaks is correct. With one exception again, the height of the peaks is correct, within a 10% limit. The upsurge of the simulated epidemic was about 1 week too early in two cases, and 1 week too late in one, but the slopes of the curves were simulated correctly. Simulation of the decline of epidemics is not yet fully satisfactory.

DISCUSSION AND CONCLUSION

Model structure

In building this preliminary model of groundnut rust, attention was given to the processes within the system, their hierarchy, their assembling with

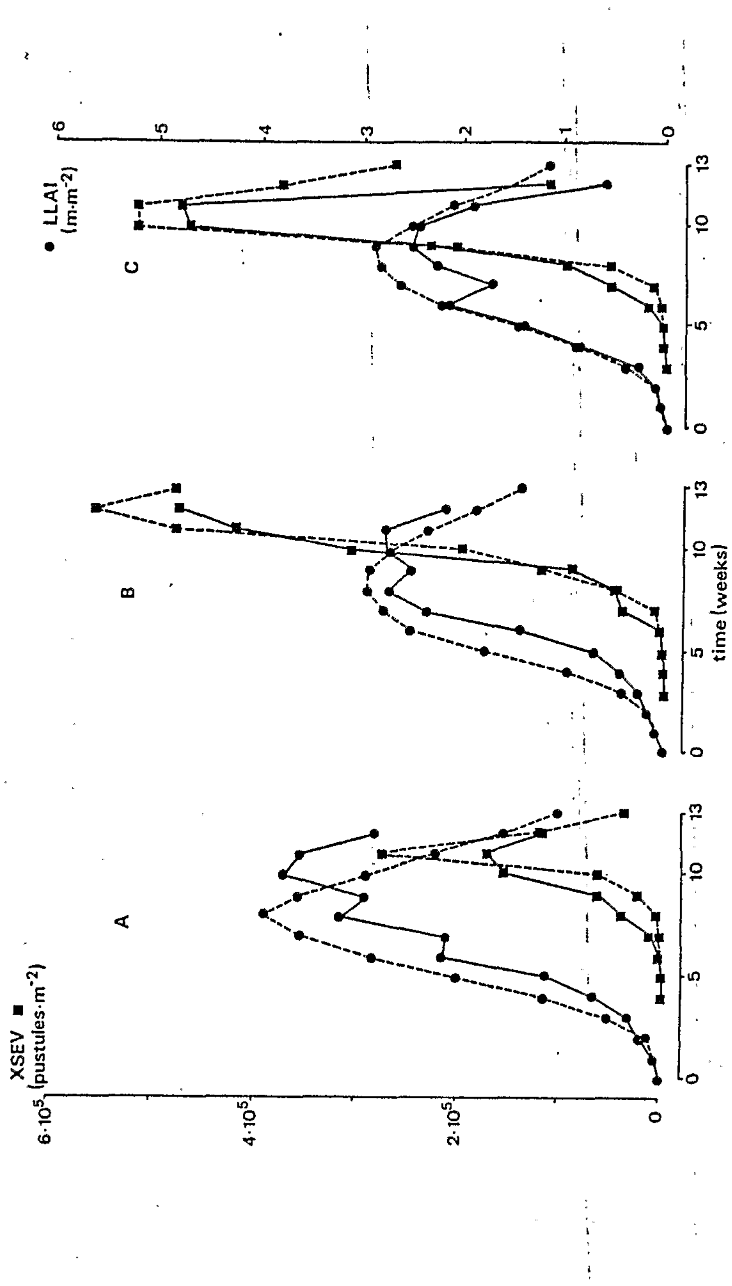

Fig. 6. Observed and simulated curves for canopy growth (*LLAI*) and groundnut rust pustule population (*XSEV*). ●——●: observed *LLAI*; ■——■: observed *XSEV*; ●- - -●: simulated *LLAI*; ■- - -■: simulated *XSEV*; A: block A (sown on 12 May); B: block B (sown on 2 July); C: block C (sown on 23 July). Abscissa: time elapsed since sowing date in weeks. Ordinates: leaf area indices (m^2 m^{-2}) and numbers of rust pustules per crop square meter (N_{site} m^{-2}).

explicit coupling hypotheses, and to convenient simulation techniques to represent them, rather than to the many factors that may affect a groundnut rust epidemic. Only those environmental factors which are assumed to exert major effects were introduced to allow an overall evaluation of the model. The model does not contain stochastic features.

Most simulation models, which try to describe dispersal in a two-dimensional (severity and time) space, including the present one, are facing representational difficulties (Teng, 1985). Furthermore, one pathogen may be subjected to several dispersal processes, each with its own time, space and efficiency attributes, corresponding to particular sets of environmental conditions (Zadoks & Schein, 1979). As groundnut rust spore dispersal was studied under dry (Mallaiah & Rao, 1982; Savary, 1986) and rainy (Savary & Janeau, 1986) conditions, an attempt is made to represent dry as well as rain-induced dispersal.

Spore production is represented as a function of variety, pustule age, and temperature. These factors are frequently used in simulation models (Teng & Bowen, 1985). Additional factors are, indirectly, those which affect the rate of photosynthesis, since sporulation is derived from the flow of carbohydrates fixed by the crop. Spore survival may be considered at three separate states: before liberation (in the pustule), during transport, and after deposition (Shrum, 1975; Teng & Bowen, 1985). Spore survival after deposition and spore maturation are introduced in the model, using some empirical data (P. D. de Jong (1986), unpublished results). Infection is introduced as a function of leaf wetness, which, in turn, depends on the occurrence of rain and on the daily maximum relative humidity (Table 3). The effects of temperature and variety on infection are superimposed. Latency and infectious periods are simulated according to Zadoks (1971), with temperature as the driving function. Both are modified by varietal characteristics, expressed as varietal coefficients.

Lesion spore content and daily multiplication factor

The results (Fig. 4) show that the simulated balance between spore production and spore liberation results in realistic value of the lesion spore content (*LSPOC*, Savary, 1986; Savary & Janeau, 1986). The results for *DMFR* (Fig. 4) indicate that the programme reacts adequately to the rules on weather relations (Table 3). *DMFR* varies from 0 to 5·60 (mean: 1·38) under dry conditions, from 1·3 to 72 (mean 27·2) when light rains occur, and takes zero value under heavy rainfall ($RAINDY \geq 5$ mm). The output of the model for *DMFR* is considered to be within the range of probable *DMFR* values, at least under dry conditions (four separate epidemics, $DMFR = 0$–$3{\cdot}36$, mean: 0·51, P. D. de Jong (1986), unpublished data).

Simulated weather effects on rust epidemics

A simulation experiment indicated that temperature and rainfall have strong, and relative humidity has moderate, effects on groundnut rust epidemics. Scarce rains, as well as heavy and numerous rain showers, or large daily temperature variations (and increase of daily mean temperature) are unfavourable to the development of epidemics. The conclusions reflect the information used to build the model. They are in agreement with results from an analysis of survey data on groundnut diseases in the farmers' fields in Ivory Coast (Savary, 1987*a*, *b*).

Simulated effects of components of resistance

Another simulation experiment indicates a hierarchy in the components of resistance. Among them, lengthening of the latency period has a strong effect, whereas reduction of the infection efficiency or of the sporulation intensity have but moderate effects on groundnut rust epidemics. Variation of the infectious period has negligible effects.

Comparable results were obtained by Zadoks (1971) and Teng *et al.* (1977). The similarity in conclusions should be ascribed to the similarity in system designs underlying the simulation models (Teng *et al.*, 1977; Teng & Bowen, 1985). The large value of the infectious period (up to 26 days, Savary, 1985*b*) probably contributes to minimize the effect of its reduction. For a necrotrophic pathogen (*Septoria nodorum* on wheat, Rapilly, 1979), the results of a comparison of components of resistance indicated that the latency period plays a secondary role only.

Comparison of model outputs with observed data

The data used to calculate the host's partition coefficients of the model were taken from the treated plots adjacent to the non-treated plots where the epidemics were measured. The procedure of validation, therefore, has not the same value for the crop sub-model as for the rust sub-model. Partition coefficients are functions of cultivar and development stage (Duncan *et al.*, 1978). Groundnut development is fairly independent of rust or leafspot (Boote *et al.*, 1983), at least until development stage 9 is reached (Bell, 1986). The values of the coefficients used in the model were similar to those of Forestier (1969) in Cameroon on cvr Minkong, which resembles the cultivar used in these experiments.

The population of rust pustules (XSEV)

A possible cause of discrepancy between model outputs and observed values of *XSEV* lies in the difficulty of estimating the early state of the considered pathosystem, and, especially, the early level of the epidemic due to spontaneous infections (Teng, 1985). The outputs of the model, however, do not indicate that major error was made in initializing the model (Fig. 6, especially B).

Several causes of the overall overestimate of *XSEV* by model outputs can be found in the structure and in the information used to build the model. *LLAI* is overestimated, and this leads to an overestimation of the correction factor (*COFR*), and thus of the rate of occupation of vacant sites, *ROCC*. The development of rust pustules described in the model is based upon studies on young, healthy leaves infected with young, highly infectious spores (Savary, 1985*a*,*b*). The use of these results to represent the development of rust pustules in the field entails the implicit assumption that optimum physiological conditions are met by both host and pathogen during the whole infection cycle. Another possibly important source of overestimation of *XSEV* is related to the defoliation of the canopy due to either plant physiology or leafspot effects. Due to the vertical distribution of pustules in the canopy (Savary, 1987*b*), defoliation more intensely affects the fraction of leaf area which bears the largest fraction of the population of pustules. This differential effect of defoliation on rust lesion mortality was not taken into account in this preliminary model without stratification of the canopy into different leaf layers.

Evaluation of the model

In view of its relative simplicity, the performance of this groundnut rust simulation model may be considered to comply with the requirements for a preliminary simulation model (Penning de Vries, 1982). The shapes of the simulated curves for *XSEV* and *LLAI* resemble the observed curves, although a tendency of the model toward overestimation is noted. The range of values taken by the simulated variables is not basically different from those taken by actual observations. According to the results, the present simulation model is considered to adequately simulate groundnut rust epidemics in optimum crop growth situations under the environmental conditions of southern Ivory Coast.

Perspectives

The necessity of a balance between details introduced into the coupled host and pathogen sub-models was discussed by Rabbinge & Rijsdijk (1981), Zadoks & Rabbinge (1985), and Teng (1985). In spite of the number of possible improvements in representing the groundnut rust cycle, their impact on the explanatory value of the model is probably minor when compared to the contribution of a more detailed host sub-model. Two categories of improvements can be considered.

The first set of improvements could be directed to a better description of canopy structure. Distinguishing several leaf layers in the groundnut crop canopy would allow consideration of vertical variations of microclimate characteristics (Zadoks & Schein, 1979), susceptibility parameters (Savary, 1987*c*), leafspot severity and life expectancy of the leaves. The introduction of vertical distribution of disease in the model would also be an important advantage for modelling crop losses due to groundnut diseases (Rabbinge & Rijsdijk, 1981).

The crop sub-model represents canopy growth under optimum conditions; host–pathogen interactions were therefore assumed to be reducible to few coupling statements. Both feedbacks and feed-forwards (Zadoks & Rabbinge, 1985) should, however, be considered in the coupling of host and pathogen in a detailed epidemiological model (Rabbinge & Rijsdijk, 1981). The introduction of additional relations between host and pathogen would require additional detail in both sub-models, and especially in the host sub-model. For instance, rust effect on pod set and pod filling (Bell, 1986) could be studied with considerable improvement when simulated yield results from successive cohorts of pods (Boote *et al.*, 1985).

The effects of plant water balance on rust lesion development (and vice versa, Zadoks & Schein, 1979; Rabbinge & Rijsdijk, 1981) could only be considered when plant water balance (Boote, 1982*b*) is introduced in the host sub-model. Such additions improve the realism of epidemiological simulation models, and bring in sight the analysis of yield losses in the multiple pathosystem: ground–rust–leafspot.

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REFERENCES

Aylor, D. E. (1982). Modeling spore dispersal in a barley crop. *Agric. Meteorol.*, 26, 215–19.

Bell, M. (1986). The effect of foliage pathogens on the growth of peanut (*Arachis hypogaea* L.) in tropical Northern Australia. *Aust. J. Agric. Res.*, 37, 31–42.

Boote, K. J. (1982*a*). Growth stages of peanut. *Peanut Science*, 9, 35–40.

Boote, K. J. (1982*b*). Peanut. In *Crop Water Relations*. ed. I. Teare & M. Peet, John Wiley & Sons, New York, pp. 256–86.

Boote, K. J., Jones, J. W., Mishoe, J. W. & Berger, R. D. (1983). Coupling pests to crop growth simulator to predict yield reductions. *Phytopathology*, 73, 1581–7.

Boote, K. J., Jones, J. W., Mishoe, J. W. & Wilkerson, G. G. (1985). Modeling growth and yield of groundnut. In *Agrometeorology of Groundnut*. ed. M. V. K. Sivakumar & S. M. Virmani, Niamey, pp. 243–54.

Chamberlain, A. C. & Chadwick, R. C. (1972). Deposition of spores and other particles on vegetation and soil. *Ann. Appl. Biol.*, 7, 141–58.

Duncan, W. G., McCloud, D. E., McGraw, R. L. & Boote, K. J. (1978). Physiological aspects of peanut yield improvement. *Crop Science*, 18, 1015–20.

Forestier, J. (1969). Développement de l'arachide hâtive en région forestière. *Cahiers ORSTOM, sér. Biol.*, 9, 33–63.

Hirst, J. M. & Stedman, O. J. (1971). Patterns of spore dispersal in crops. In *Ecology of the Leaf Surface*. ed. T. F. Preece, Academic Press, London, pp. 229–37.

IBM (1975). Continuous System Modeling Program III (CSMP III), Programme reference manual. IBM SH19-7001-3. Techn. Publ. Dept., White Plains, USA, 206 pp.

Jones, J. W., Barfield, C. S., Boote, K. J., Smerage, G. H. & Mangold, J. (1982). Photosynthetic recovery of peanuts to defoliation at various growth stages. *Crop Science*, 22, 741–6.

Ketring, D. L., Brown, R. H., Sullivan, G. A. & Johnson, B. B. (1982). Growth physiology. In *Peanut Science and Technology*. ed. H. E. Pattee & C. T. Young, Yoakum. pp. 411–57.

Mallaiah, K. V. & Rao, A. S. (1982). Aerial dissemination of urediniospores of groundnut rust. *Trans. Brit. Mycol. Soc.*, 78, 21–28.

Mendgen, K. (1981). Nutrient uptake in rust fungi. *Phytopathology*, 71, 983–9.

Penning de Vries, F. W. T. (1982). Phases of development of models. In *Simulation of Plant Growth and Crop Production*. ed. F. W. T. Penning de Vries & H. M. Van Laar, Pudoc, Wageningen, pp. 20–25.

Penning de Vries, F. W. T. & Van Laar, H. M. (1982). Simulation of growth processes and the model BACROS. In *Simulation of Plant Growth and Crop Production*. ed. F. W. T. Penning de Vries & H. M. Van Laar, Pudoc, Wageningen, pp. 114–35.

Rabbinge, R. & Rijsdijk, F. H. (1981). Disease and crop physiology: A modeller's point of view. In *Effect of Disease on the Physiology of the Growing Plant*. ed. P. G. Ayres, Cambridge University Press, Cambridge, pp. 201–20.

Rapilly, F. (1979). Simulation d'une épidémie de *Septoria nodorum* Berk. sur blé, étude des possibilités de résistance horizontale. *EPPO Bull.*, 9, 243–50.

Rapilly, F. & Jolivet, E. (1976). Construction d'un modèle (EPISEPT) permettant la simulation d'une épidémie de *Septoria nodorum* Berk. sur blé. *Revue de Statistique Appliquée*, 24, 31–60.

Roelfs, A. P. & Martell, L. B. (1984). Uredospore dispersal from a point source within a wheat canopy. *Phytopathology*, 74, 1262–7.

Savary, S. (1985*a*). Comparaison de différentes techniques d'infection de folioles d'arachide par *Puccinia arachidis Speg*. *Agronomie*, 5, 325–9.

Savary, S. (1985*b*). Effets du niveau de contamination et de la température sur quelques étapes du cycle de *Puccinia arachidis, Speg*. *Agronomie*, 5, 479–85.

Savary, S. (1986). Relative humidity and wind velocity associated with diurnal rhythmicity of aerial dispersal of *Puccinia arachidis* urediniospores. *Neth. J. Pl. Pathol.*, 92, 115–25.
Savary, S. (1987*a*). Enquête sur les maladies fongiques de l'arachide en Côte d'Ivoire. I. Méthode d'enquête et étude descriptive: Les conditions culturales et les principales maladies, *Neth. J. Pl. Pathol.*, 93, 167–88.
Savary, S. (1987*b*). Enquête sur les maladies fongiques de l'arachide (*Arachis hypogaea*) en Côte d'Ivoire. II. Epidémiologie de la rouille de l'arachide (*Puccinia arachidis*). *Neth. J. Pl. Pathol.*, 93, 215–31.
Savary, S. (1987*c*). Decrease by plant development and leaf age of susceptibility of groundnut to rust (*Puccinia arachidis*) in a susceptible cultivar. *Neth. J. Pl. Pathol.*, 93, 25–31.
Savary, S. & Janeau, J. L. (1986). Rain-induced dispersal of *Puccinia arachidis* studied by means of a rainfall simulator. *Neth. J. Pl. Pathol.*, **92**, 163–74.
Shrum, R. (1975). Simulation of wheat stripe rust (*Puccinia striiformis* West), using EPIDEMIC, a flexible plant disease simulator. Pennsylvania State Univ., Coll. Agric., Agric. Exp. Sta. Prog. Rep. 347, 41 p.
Smith, J. W. & Barfield, C. S. (1982). Management of preharvest insects. In *Peanut Science and Technology*. ed. M. E. Pattee & C. T. Young, Yoakum. pp. 250–325.
Teng, P. S. (1985). A comparison of simulation approaches to epidemic modelling. *Annu. Rev. Phytopathol.*, **23**, 351–79.
Teng, P. S. & Bowen, K. L. (1985). Disease modelling and simulation. In *The Cereal Rusts, Vol. II*. ed. A. P. Roelfs & W. R. Bushnell, Academic Press, New York, pp. 435–66.
Teng, P. S., Blackie, M. J. & Close, R. C. (1977). A simulation analysis of crop yield loss due to rust disease. *Agricultural Systems*, **2**, 189–98.
Van Hees-Boukema, E. M. & Zadoks, J. C. (1986). Postponed germination of *Puccinia recondita* urediospores deposited on wheat seedlings. II. Infectivity of urediospores after postponed germination. *Neth. J. Pl. Path.*, **92**, 71–80.
Van Keulen, H. & De Milliano, W. A. J. (1984). Potential wheat yields in Zambia. A simulation approach. *Agricultural Systems*, **14**, 171–92.
Van Keulen, H., Penning de Vries, F. W. T. & Drees, E. M. (1982). A summary model for crop growth. In *Simulation of Plant Growth and Crop Production*. ed. F. W. T. Penning de Vries & H. M. Van Laar, Pudoc, Wageningen, pp. 87–97.
Waggoner, P. E. (1974). Simulation of epidemics. In *Epidemics of Plant Diseases*. ed. J. Kranz, Springer-Verlag, Berlin, Heidelberg, New York, pp. 137–60.
Wilkerson, G. G., Jones, J. W. & Poe, S. L. (1984). Effect of defoliation on peanut plant growth. *Crop Science*, **24**, 526–31.
Zadoks, J. C. (1971). Systems analysis and the dynamics of epidemics. *Phytopathology*, **61**, 600–10.
Zadoks, J. C. (1972*a*). Methodology of epidemiological research. *Ann. Rev. Phytopathol.*, **10**, 253–76.
Zadoks, J. C. (1972*b*). Modern concepts in disease resistance in cereals. In *The Way Ahead in Plant Breeding*. ed. F. A. G. H. Lupton, G. Jenkins & R. Johnson, Eucarpia. Cambridge, pp. 89–98.
Zadoks, J. C. & Rabbinge, R. (1985). Modelling to a purpose. In *Advances in Plant Pathology. Vol. 3. Mathematical Modelling of Crop Diseases*. ed. C. A. Gilligan, Academic Press, London. pp. 231–44.

Zadoks, J. C. & Schein, R. D. (1979). *Epidemiology and Plant Disease Management*. Oxford University Press. New York, 427 pp.
Zadoks, J. C. & Van Hees-Boukema, E. M. (1986). Postponed germination of *Puccinia recondita* urediospores deposited on wheat seedlings. I. Ripening and longevity of urediospores with postponed germination. *Neth. J. Pl. Path.*, **92**, 57–69.