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ANALYSIS OF BIOLOGICAL CONTROL OF CASSAVA PESTS IN AFRICA. I. SIMULATION OF CARBON, NITROGEN AND WATER DYNAMICS IN CASSAVA

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SUMMARY

(1) A model for the growth and development of cassava, *Manihot esculenta* Crantz, as modified by weather, soil nitrogen and water is described, and used in later papers to evaluate damage by exotic cassava pests and the effectiveness of control by natural enemies.

(2) Analogous relationships between trophic level models at the population and per capita levels were exploited to develop a model that has a common mathematical form across trophic levels.

(3) The distributed delay model of Manetsch (1976) was used as the conceptual shell in describing the population dynamics of populations and of organism organ levels (e.g. leaves of plants, ova in animals).

(4) The Frazer–Gilbert functional response model from animal ecology was modified to predict rates of photosynthesis and nitrogen and water uptake in plants.

(5) Dry-matter partitioning in cassava as affected by solar radiation, temperature, and water and nitrogen stress was simulated and compared with three sets of field data.

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is a tuber crop native to South America. Cock (1985a) provides an overview of this crop, its uses and spread. Cassava was introduced to Africa in the 1600s where it quickly became an important food staple for nearly 200 million people. During the early 1970s, two important pests, the cassava green mite *Mononychellus tanajoa* (Bondar) (*sensu lato*) and the cassava mealybug *Phenacoccus manihoti* Mat.-Ferr. were accidentally introduced into Africa, and reduced tuber yields by 30–50% and severely reduced the quality of planting materials (Herren 1981; Herren, Lema & Neuenschwander 1983). The Africa-wide Biological Control Project (ABCP) (Herren *et al.* 1987) of the International Institute for Tropical Agriculture (IITA) at Ibadan, Nigeria was begun in the early 1980s. Biological control of *P. manihoti* by the introduced exotic parasitoid *Epidinocarsis lopezi* (De Santis) is thought to have a good chance of success over much of the cassava belt (Herren & Lema 1981; Herren, Lema & Neuenschwander 1983; Herren *et al.* 1987; Herren 1987) but *M. tanajoa* remains an unresolved severe problem (Yaninek 1985).

Classical biological control has been criticized because the effectiveness and consequences of introduced natural enemies have not been assessed (Howarth 1983). In this

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paper, a mathematical model of cassava is presented and used to examine the effects of abiotic factors on yield formation under pest-free conditions. This work extends the multitrophic level models proposed by Gutierrez *et al.* (1984, 1987) to include the dynamics of water and nitrogen utilization by plants. The effects of *P. manihoti* and *M. tanajoa* feeding damage on cassava yield, and the biological control of *P. manihoti* are examined in papers by Gutierrez *et al.* (1988a, b). The models provide a synthesis of the ongoing agronomic, ecological, and economic evaluation of the problem.

CONCEPTUAL FRAMEWORK

Development of crop and pest models is becoming commonplace (Jones *et al.* 1974a,b; Gutierrez *et al.* 1975, 1984, 1987; Gutierrez & Wang 1976; Wang *et al.* 1977; Curry *et al.* 1980; Wilkerson *et al.* 1983; Law 1983). The development of a sound plant model requires extensive field data, which fortunately exist for cassava (e.g. Veltkamp 1985; Schulthess 1987). The new data reported in Schulthess (1987) were used here.

Our model differs from most plant models in using population theory as a framework. It is a population dynamics model that incorporates plant physiology. The roots of our approach may be traced to Leslie (1945), von Foerster (1959), Hughes (1963), Gutierrez *et al.* (1975), Gilbert *et al.* (1976) and Wang *et al.* (1977). We recognize that our models have characteristics in common to methods proposed by de Wit & Goudriaan (1978) and the numerical methods proposed by Goudriaan (1973), but their methods were developed from systems theory (Forrester 1961) and not from population ecology.

The mathematical model (eqn (1)) proposed by Manetsch (1976) and modified by Vansickle (1977) for modelling distributed delay processes with attrition in general has been used by various workers to model insect phenology (e.g. Welch *et al.* 1978). It was adapted by Gutierrez & Baumgaertner (1984a,b) and Gutierrez *et al.* (1984, 1987) as the *shell* to model the dynamics of multitrophic interactions realistically. Here it is used to model the dynamics of cassava growth and development and, in later papers (Gutierrez *et al.* 1988a,b) to model the dynamics of several arthropods associated with cassava. The model (1) is a book-keeping device for accounting for changing rates of birth, death, net immigration and mass growth in cohorts of differing ages of a population; see Vansickle (1977) for details.

$$\begin{aligned}
 d\rho_{1,j}/dt &= x_j(t) - r_{1,j}(t) - \mu_{1,j}(t, \cdot)\rho_{1,j} \\
 d\rho_{2,j}/dt &= r_{1,j}(t) - r_{2,j}(t) - \mu_{2,j}(t, \cdot)\rho_{2,j} \\
 &\quad \cdot \quad \cdot \quad \cdot \quad \cdot \\
 &\quad \cdot \quad \cdot \quad \cdot \quad \cdot \\
 d\rho_{k,j}/dt &= r_{k-1,j}(t) - y_j(t) - \mu_{k,j}(t, \cdot)\rho_{k,j}
 \end{aligned}
 \tag{1}$$

Assume we are modelling the number dynamics of population *j* with cohorts $\rho_{i,j}$ of age $i = 1, 2, \dots, k$ the dynamics of which are described by eqn (1). The birth rate enters the population via $x_j(t)$ and those surviving age-specific mortalities $0 < \mu_{i,j} \leq 1$ (i.e. the net proportion of death, immigration and emigration) exit at maximum age as $y_j(t)$. This process could describe the birth and death dynamics of a population of plants, plant organs (e.g. leaves) or insects. The model is deterministic but simulates stochastic

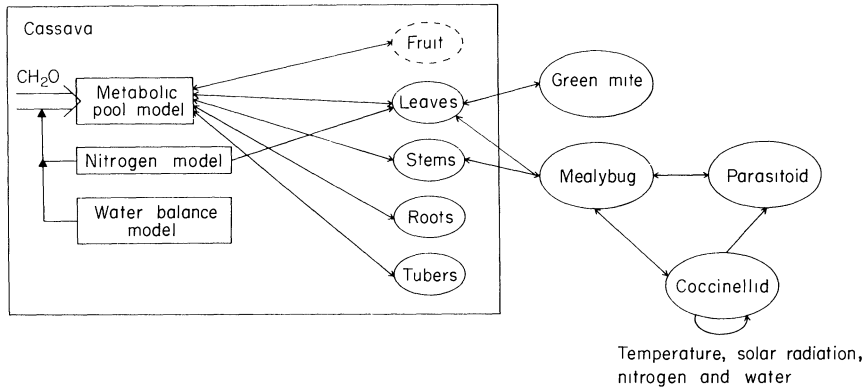


FIG. 1. Components of the cassava systems model.

development. Individuals of a cohort entering the population at the same time will have different development times through a life stage. Ageing occurs via flow rates $r_{i-1,j}$ from $\rho_{i-1,j}$ to $\rho_{i,j}$. The flow rate between two cohorts is a function of the average development time through the stage, the number of age categories (i.e. $k = (\bar{x}^2/s^2)$) and cohort density. If mortality is zero and if $k = 1$, the development times of a cohort would have a geometric distribution, while large values of k would produce an Erlang distribution of development times characterized by a delay to first emergence and a small variance about the mean emergence time. Of course, age-specific mortality greatly affects the pattern (see Vansickle 1977) and is an important component introducing realism into our models. A convenient time step for updating the model is 1 day, which in physiological time units (e.g. degree days, proportional development) may vary considerably. Time and age and all rates in the model are in degree day (DD) units.

If the age-specific mass $M_{i,j}$ dynamics (i.e. growth) of cohorts $\rho_{i,j}$ are also modelled, a parallel model (1) for mass flow is required with a common age index i linking it to the numbers dynamics model ρ . The net age-specific growth in $M_{i,j}$ occurs via $\infty < \mu_{i,j} \leq 1$ which suggests that negative growth is possible because of herbivory and respiration. If other attributes such as age-specific nitrogen dynamics ($N_{i,j}$) are assessed, yet another model is required with the same age index i . An efficient subroutine to update (1) including attrition may be obtained from A. P. Gutierrez.

Cassava model

This is a canopy model consisting of six linked population models of form (1) describing the age-specific dynamics of leaf numbers, their mass and nitrogen content, and the mass of roots, stems and tubers (Fig. 1). Reserves do not have age structure, and are modelled as a simple balance model described in a later section. A model for the population dynamics of whole plants linked to the plant organ models would be computation intensive and not required for a crop where all plants are the same age. The population dynamics models of two arthropod pests and their linkage to the appropriate plant organ models are described in Gutierrez *et al.* (1988a, b).

In the model, the production (birth) rates of new plant organs and their associated age-specific mass growth rates are conceptualized as follows. New leaves are produced over time, and each has a genetic potential for carbon (growth) assimilation. However, the

production rate of new leaves and the maximum growth *demands* of existing ones may not be sustained because of shortfalls in photosynthate production (*supply*) due to adverse weather or nutrient deficiency, pest damage and competition from other plant parts. The maximum growth demands of tuber, stem, root and reserve masses are assumed to be allometric to total leaf demand, and they accrue biomass at rates modified by the same supply–demand considerations that affect leaf production and growth rates. The parameters defining longevity of plant parts, and the maximum growth and production rates are given in the Appendix.

The sequence of computations performed during each time step (Δt) are those for (i) demand, (ii) photosynthesis, and (iii) dry-matter allocation, ageing and mortality.

Production and allocation of photosynthate

The production of new biomass (photosynthesis) by plants (eqn (3)) and its general allocation (eqn (2)) are analogous to the capture and assimilation of food by animals (i.e. supply) (Gutierrez, Baumgaertner & Hagen 1981). Leaves seek light, herbivores seek plants or plant parts, and carnivores (parasitoids) seek prey (hosts). These processes have been described by balance equation (2) in a general way for all trophic levels (n) represented as trophic level M_n acquiring resources from level M_{n-1} (Gutierrez, Baumgaertner & Hagen 1981; Gutierrez & Baumgaertner 1984a).

$$\begin{aligned} dA/dt &= \Theta_V(dG/dt + dv/dt) + \Theta_R dR/dt \\ &= \psi f[\psi, \Delta t, b(\omega, \eta, \cdot), s(M_L)] - z(\Delta t, \cdot) M_T + v^* \\ &= M^* - z(\Delta t, \cdot) M_T + v^* \end{aligned} \quad (2)$$

For plants: dA/dt = total assimilate; dG/dt = maximum vegetative growth rate (i.e. leaves + stems + tubers + reserves); dR/dt = maximum reproductive growth rate; dv/dt = maximum reserve growth rate; Θ_V = supply/demand ratio $0 < \Theta_V \leq 1$ for vegetative growth (see below and Wang *et al.* 1977); Θ_R = supply/demand ratio $0 < \Theta_R \leq 1$ for reproductive growth; ψ = $g \text{ CH}_2\text{O m}^{-2} \text{ day}^{-1} = 1.299 \text{ J cm}^{-2} \text{ day}^{-1}$ (Loomis & Williams 1963; Gutierrez *et al.* 1987); M^* = photosynthate produced during dt (i.e. the *supply*). The photosynthetic rate appears intermediate between C_3 and C_4 plants (Mahon *et al.* 1977 and the general estimates of Monteith 1978); $f(\cdot)$ = acquisition function (i.e. Frazer & Gilbert (1976) functional response model, where (\cdot) implies many factors); $z(\Delta t, \cdot)$ = metabolic cost rate per unit mass of plant mass (M_T); Δt = the change in physiological time (e.g. degree days above $13.5^\circ\text{C} = \Delta\text{DD}$); $b(\omega, \eta, \cdot)$ = maximum assimilate demand rate by all plant organs and respiration as modified by water (ω) and nitrogen (η) stresses described in later sections; $s(M_L)$ = proportion of light intercepted as a function of leaf mass; M_L = dry biomass of the leaves (L); M_T = dry biomass of all respiring tissues; v^* = reserves available daily.

Photosynthesis

Concave functions (e.g. $f(\cdot)$) have been used to estimate rates of photosynthesis, predation and parasitism (Evans 1975; Mack *et al.* 1981; Gutierrez, Baumgaertner & Hagen 1981; Gutierrez *et al.* 1987). The Frazer & Gilbert (1976) model (eqns (3,4)) is used here to predict photosynthetic rates (M^*) because of the convenient biological property that it is demand-driven and mathematically related to Nicholson–Bailey and Lotka–Volterra models from animal ecology (Gutierrez & Wang 1976; Gutierrez *et al.* 1987). Model (3) should be used when resource acquisition occurs with replacement (where

multiple attacks are possible; parasitism); eqn (4) should be used when resources are depleted without replacement (e.g. photosynthesis, nitrogen and water uptake and predation; Gutierrez, Baumgaertner & Hagen 1981). Note that the exponents are dimensionless numbers and $\psi = M_{i-1}$ (i.e. the lower trophic level in the general case).

$$M^* = \psi f(\cdot) = \psi [1 - e^{(-b\Delta t/\psi)(1 - e^{-s\psi/b})}] \quad (3)$$

$$M^* = b\Delta t f(\cdot) = b\Delta t [1 - e^{(-s\psi/b\Delta t)}] \quad (4)$$

All the variables have been defined above, but here we amplify the biological underpinnings of parameters b and s ; b is the major determinant of the photosynthetic rate in the model (Gutierrez *et al.* 1975; Wang *et al.* 1977) and equals the sum of all maximum growth and respiration demands by plant organs modified by ω and η . *The key feature of the model is that growth demands of stem, root, tuber and reserve in eqn (4) are related to leaf demand rates.* The total demand by leaves includes the demand of both new and existing leaves, and is computed as described below.

In the three-branched cassava variety (TMS 30572) studied, leaves are produced at each stem node, hence the leaf initiation rate per branching path ($\lambda(t)$) was estimated from field counts of node numbers of ten plants (Schulthess 1987). The initial number of branching paths (v) determines the architecture and the potential leaf production rate per plant. In TMS 30572, a maximum of three new branches is formed at each branching node (ζ), hence one would expect that the leaf production rate per plant would be initially $v\lambda(\zeta=0)$ and then increase $\gamma=3$ -, 9 -, 27 -fold etc. at subsequent branching levels. However, the field data showed that the rates were *c.* $v\lambda$, then $3v\lambda$, and $6v\lambda$ at maximum (Schulthess 1987). In the model, first branching ($\zeta(t_1)=1$) was assumed to occur at time t_1 when the ratio of the computed daily supply of photosynthate plus reserves (v) to the *total daily demands* (i.e. $\Theta^* = (M^* + v)/(b\Delta t)$) was 3. Subsequent branching occurs after a minimum of time has elapsed ($\Delta t^* = t - t_i > t_1/\Theta^*$, where i denotes the previous branching level) and $\Theta^* > 2$. First branching in unstressed cassava normally occurs at about 750 DD, but this may be delayed considerably under carbon (Θ), water (ω) and nitrogen (η) stresses.

$$\lambda(t) = \omega\eta\Theta\gamma(\zeta_i) v \lambda(t=0), \text{ where } \gamma = \begin{cases} 1 & \text{at } \zeta=0 \text{ given } \Theta^* \leq 3 \\ 3 & \text{at } \zeta=1 \text{ given } \Theta^* \geq 3 \\ 6 & \text{at } \zeta > 1 \end{cases} \quad (5)$$

The maximum age-specific leaf growth rate ($g_L(a)$, (6)) was estimated from field leaf-growth data (Schulthess 1987):

$$g_L(a) = \begin{cases} c \exp^{ca} & \text{for } 0 < a \leq 250 \text{ DD} \\ 0 & \text{for } a > 250 \text{ DD.} \end{cases} \quad (6)$$

where c is a fitted constant and DD is physiological age in degree days. Thus, the maximum total growth demand rate by all leaves (b_L) at time t may be computed as follows:

$$b_L(t) = \omega\eta \int g_L(a)h(a,t)da, \quad (7)$$

where $h(a,t)$ is the frequency of leaves of age $0 < a \leq 250$ DD at time t . The growth demand rates of other plant organs ($g_j(t)$), j =roots (R), reserves (RS), stems (S), tubers (T)) are assumed to be allometric to total leaf growth demand as follows:

$$\begin{aligned}
 & c_1 b_2 \text{ for } t \leq 900 \text{ DD} & (8) \\
 \text{stems} \quad g_S = & \begin{cases} c_1 b_L \text{ for } t \leq 900 \text{ DD} \\ c_2 b_L \text{ for } t > 900 \text{ DD} \end{cases} \\
 \text{tubers} \quad g_T = & \begin{cases} c_3 b_L \text{ for } t \leq 900 \text{ DD} \\ c_4 b_L \text{ for } t > 900 \text{ DD} \end{cases} \\
 \text{roots} \quad g_R = & c_5 b_L \\
 \text{reserves} \quad g_v = & c_6 b_L
 \end{aligned}$$

Fruit demands are small relative to the total weight of the plant (2.32 ± 1.12 g vs. 3000 g) and hence were not considered in the model. The total demand b in eqn (4) equals $(g_L + g_S + g_T + g_R + g_v)$. Because ω and η reduced the leaf demand b_L in eqn (7) and the other sink demands above, the rates in eqn (2) are the realized growth rates.

The search parameter s is an asymptotically increasing function (eqn (9)) of leaf area index (LAI) proposed by M. Monsi and T. Saeki (Evans 1975) to describe the proportion of light intercepted by plants. Leaf area is a linear function of leaf mass, and LAI is the ratio of the leaf area:area occupied by the plants at time t . The light extinction coefficient (ϕ) is easily measured in the field.

$$0 \leq s = 1 - \exp[-\phi \text{LAI}(t)] < 1 \quad (9)$$

Equation (9) is analogous to the random search Nicholson & Bailey (1935) functional response model, but as used here it is the search parameter in the Frazer & Gilbert model (3,4) which itself is a subcomponent of the metabolic pool model (2), the effects of which are embedded in the population dynamics model (1).

Biomass allocation

In the allocation scheme (2), metabolic costs $z(\Delta t, \cdot)$ are first subtracted from M^* , and the remaining photosynthate is allocated first to meet demands by reproductive organs, and then, if any remains, to vegetative growth and reserve demands (Gutierrez *et al.* 1975). The demand rates are factored by the supply–demand ratio (i.e. Θ) yielding actual growth rates $dx_j/dt = \Theta g_j$ as shown in eqn (2). Mass allocation in the mass models (1) occurs via terms x_j and $\mu_{i,j}$. The mass of new leaves enters the population via x_L , and net growth of older leaves occurs via $\mu_{i,L}$ (see eqn (1)). In stems, roots and tubers, new biomass enters the populations only via $x_j = x_S, x_R$ and x_T , respectively. In discrete form, the dynamics of mobile reserves $v(t + \Delta t) = v(t) (1 - \alpha) + \Theta g_v$, where α is the fraction of reserves used daily to meet demand shortfall for plant respiration, regrowth and *P. manihoti* feeding. Under severe stress, tuber mass may also be mobilized to meet these demands.

While this allocation scheme applies specifically to cassava, the analogies made by Gutierrez *et al.* (1987) between plant and animal growth demands show that the same scheme may be used to estimate the parameters for the different trophic levels modelled in Gutierrez *et al.* (1988a,b). One important difference is that, in animals, b must be corrected for egestion.

Effects of nitrogen on cassava

Insufficient uptake of nitrogen (N) reduces growth rates and yield and influences the dynamics of higher trophic level organisms (McNeil & Southwood 1978; Mattson 1980). Studies of N requirements of cassava (Fox, Tallyrand & Scott 1975; Obigbesan & Fayemi 1976; Dominguez, 1982; Howeler & Cadavid 1983; Cock & Reyes 1985; Howeler 1985)

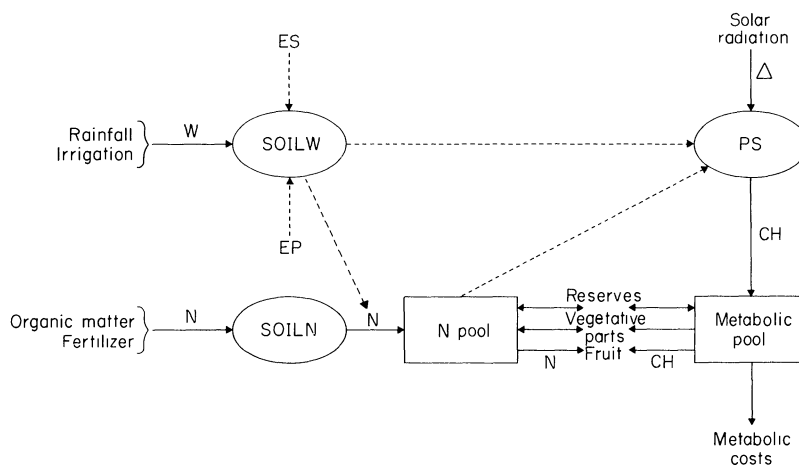


FIG. 2. The interaction of water and nitrogen with the metabolic pool model. Δ = light energy, CH = carbohydrates, N = nitrogen compounds, W = water, PS = photosynthesis, SOILW = soil water content, SOILN = soil nitrogen content, vegetative parts include leaves, stems, roots and tubers, ES = evaporation from the soil, EP = evapotranspiration of the plant; \rightarrow mass flows, $-\cdot-\cdot-$ effects.

indicate that cassava extracts large amounts of nutrients from the soil (e.g. 57 kg N ha⁻¹ per 25 t ha⁻¹ tuber yield), especially if leaves and stems are removed from the field at harvest (Howeler 1985). Generally, fertilizers are not applied to cassava crops because they are too expensive, and acceptable yields are obtained on fairly infertile soil. In many tropical countries, cassava is often planted on poor soil as the last crop in a rotation causing further severe depletion of soil nutrients (Cock & Reyes 1985). Application of up to 150 kg ha⁻¹ of N has been shown to enhance yields, but rates of 50–90 kg ha⁻¹ are more common (Cock & Reyes 1985). Large doses of N tend to produce leafy growth (high LAI) and to decrease root:shoot ratios (Fox, Tallyrand & Scott 1975). Increased concentrations of cyanogenic glycosides, which are converted to toxic hydrocyanic acid, are associated with high fertilization rates (Obigbesan & Fayemi 1976). Low soil fertility induces small leaves, and the efficiency of photosynthesis decreases with decreasing nutrient concentrations (Howeler 1985). In our model, the effects of N stress on biomass production are manifested via reductions in growth demands. This method gave better results than reducing photosynthesis, which is more common in such models.

Nitrogen balance model

Nitrogen and water (W) uptake at time t by plants are considered as predation processes. Figure 2 illustrates the effects of soil water on nitrogen uptake and photosynthesis, as well as the allocation of carbohydrate and nitrogen. The balance model (10) for the nitrate N mass acquired and assimilated (i.e. subscript N) is similar to the metabolic pool model (2) (Gutierrez, Baumgaertner & Hagen 1981), except that metabolic costs in units of N are not assessed but are included in $z(\Delta t, \cdot)$ in (2).

$$\begin{aligned} dA_N/dt &= dG_N/dt + dR_N/dt + dv_N/dt = \\ N^* &= \omega N_r f_N(N_r, \Delta t, b_{N,s}) + v^*_{N} \\ &= \omega N_r f_N(\cdot) + v^*_{N} \cdot \end{aligned} \quad (10)$$

N_r is the nitrogen available in the current root volume (i.e. subscript r); N^* is the N

absorbed by the roots; b_N is the maximum demand rate for N as a proportion of b in eqn (2) (cf. Howeler 1985); s is the proportion of the root zone penetrated by the roots and is assumed to be the same as the proportion of light intercepted by leaves; ω is the water stress index (see below); $f_N(\cdot)$ is the nitrogen version of the Frazer–Gilbert functional response model; v^*_N is the rate at which N can be reallocated from reserves and senescent plant parts to growing plant tissues. If defoliators were attacking the crop, s would retain the prior high value. The use of s assumes that the above-ground development of the canopy and the below-ground occupancy of root space occur in parallel. The mass of N (i.e. L_N) in leaves (L_i) of age i must be modelled using (1). The age-specific ratios (i.e. $0 \leq L_{N,i}/L_i \leq 0.05$) provide further descriptors of leaf quality and are important when linking herbivores to the plant model. $0 < \eta = N^*/b_N < 1$ is the nitrogen stress index in (2) that scales growth demand rates. The allocation priorities for N are the same as described above for the carbon balance model (2).

The balance model for available soil nitrogen is as follows:

$$N_N(t + \Delta t) = N_N(t) + \alpha_N N_o + N_A(t) - N^*(t) + v^*_N(t), \quad (11)$$

where N_N is total N in the maximum root volume, $\alpha_N N_o$ is the nitrogen released from organic matter (N_o) during Δt , α_N is a constant, N_A is the N in fertilizer applied at time t , N^* is the inorganic nitrogen taken up (10), and v^*_N is that recycled within the plant.

Water use in cassava

Cassava is drought tolerant (El Sharkawy & Cock 1984), but is extremely susceptible to excess water (Connor, Cock & Parra 1981). The latter factor is not included in the model. Positive responses to irrigation have been shown (Cock & Reyes 1985), especially in the first 2 weeks after planting.

Water concentration in plant organs is not modelled directly; only the water stress ($0 \leq \omega \leq 1$) and the soil water balance are calculated. The maximum plant evapotranspiration demand ($b_w = E_T$) for assumed non-limiting soil water conditions is estimated from the water balance model developed by Ritchie (1972). b_w is used in the water acquisition version of the Frazer–Gilbert model (12) to predict the water acquired (E^*_T). The water stress index ($0 \leq \omega = E^*_T/b_w < 1 = \text{water supply} : \text{demand ratio}$) is used to scale both the uptake rate of N (10) and the growth demand rates (2).

$$E^*_T = W_r f(W_r, b_w, s, LAI, \Delta t) \quad (12)$$

In the model, W_r is the water in the current root volume, b_w is the evapotranspiration demand, s in (2) is the search parameter, and Δt is physiological time. The maximum root volume is assumed to be 2.5 m^3 . The water available to the plant ($W_r(t)$) in a particular soil type at time t is that above the permanent wilting point (PWP, e.g. $-1.5 \text{ MPa} = 475 \text{ l m}^{-3}$) in the current root envelope (Connor, Cock & Parra 1981). The water holding capacity of the soil (W_{max}) at IITA in the maximum root zone is $1500 \text{ l per } 2.5 \text{ m}^3$. The soil volume is not layered, but the water is considered to be in a tank to which plants have access as the root volume expands as measured by s .

Water demand $b_w = E_T$ is computed using the Ritchie model and depends primarily on LAI and pan evaporation rate (E_p) estimated from solar radiation, temperature, and windspeed. The Ritchie model also predicts evaporation from the soil surface (E_s) and is used to complete the soil water balance model below (13). E_s is a function of solar radiation, wind, relative humidity, and the hydraulic properties of the soil, and

approaches zero as LAI increases. E_T in the model is computed before E_S (i.e. $0 < E_S \leq E_P - E_T$) which restricts its maximum.

The soil water balance model may be written as follows:

$$0 \leq W(t + \Delta t) = W(t) + P(t) - E^*_T(t) - E_S(t) \leq W_{\max}, \quad (13)$$

where the variable $P(t)$ is precipitation or irrigation at time t .

FIELD DATA

Extensive field data on the growth and development of the three-branched cassava variety TMS 30572 were collected in 1982–83 (*c.* every 2 months) and 1983–84 (weekly) at Ibadan, Nigeria (Schulthess 1987). Two plantings were studied in 1982–83. Cuttings (12 g) were planted in the field at 1 m^{-2} on 15 May 1983 at the beginning of the rainy season when the soil moisture was high. Two branching paths were allowed to develop on each cutting in 1982–83, but only one was allowed in 1983–84. Eight to ten plants were dug up and dissected into leaves, stems, tubers and roots. Plant samples were dried at 100°C for 1 week and weighed. All data shown in the figures are the means of ten plants. The 1983–84 data were more complete and will be emphasized here.

The daily weather data (maximum–minimum temperatures, solar radiation, rainfall and wind) from the IITA weather bureau were used to drive the simulation model. The time and quantity of rainfall was particularly relevant.

The cassava systems model was programmed in FORTRAN and requires *c.* 3 min to run 12 months on an IBM-PC/AT-compatible computer with a numerical coprocessor.

CASSAVA SIMULATION RESULTS

Dry-matter allocation

Rainfall was generally more frequent and abundant in 1983–84 than in 1982–83. A high initial soil water value of 1350 l was used for 1983. The planting of the second crop in 1982 was considerably closer to the dry season, hence 1250 l was used for the earliest 1982 planting and 1225 l for the late 1982 planting. This was the only adjustment made to the model.

1983–84

The 1983–84 field data (*cf.* Schulthess 1987) for dry-matter in leaves, stems plus roots, tubers, and cumulative leaf number (= node) are shown in Fig 3a,c. The drought period in 1983 was short as indicated by the patterns and quantity of rain. The simulated growth patterns of leaves, stems plus roots, and tubers (i.e. lines) were similar to the field data (symbols). Leaf dry-matter increased to *c.* 220 g plant^{-1} , then levelled off when the rate of leaf production equalled the abscission rate. Later, the mass of leaves declined as the rate of leaf production fell below the abscission rate. This occurred because the mass of respiring tissues in roots, stems and tubers continued to increase after the leaf canopy had reached maximum LAI. This resulted in maximum supply of photosynthate but increased respiration demands causing a shortfall in photosynthate supply (i.e. Fig. 3b, $\Theta = S/D = \text{daily supply} : \text{demand} < 1$).

The patterns of dry-matter accumulation in stem (plus root) and tubers were similar. The growth rate of all plant organs nearly doubled after 900 DD when the exponential

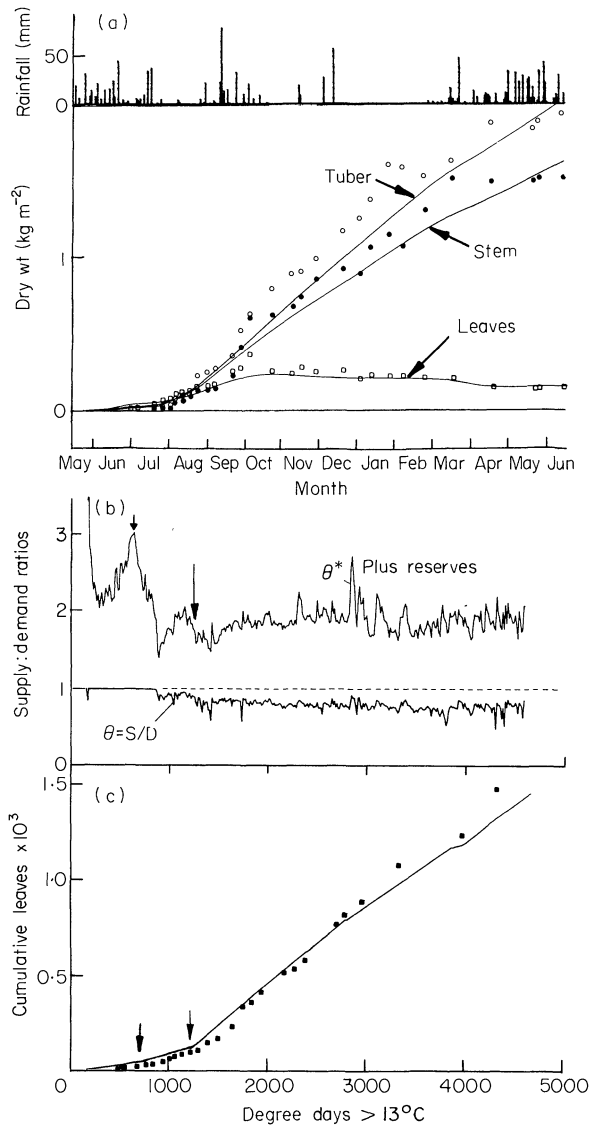


FIG. 3. Simulated (—) and observed (symbols) data for cassava growth and development at IITA, Ibadan, Nigeria in 1983-84: (a) rainfall and dry-matter accumulation; \circ = tubers, \bullet = stems, \square = leaves; (b) simulated ratio of daily photosynthate supply plus all reserves: daily demand (top line), and the ratio of daily photosynthate supply:demand (bottom line); (c) cumulative leaf (node) production. Note \downarrow in (b) and (c) indicating the times of the first and second branching.

growth phase began. Later, carbohydrate stress, due principally to high maintenance respiration costs and slight water and N stress, caused a decreased rate of dry-matter accumulation in all plant organs. The increase in the rate of leaf (node) production after branching (i.e. the down-turned arrows) is apparent in Fig. 3c. The production rate of leaves (nodes) decreased in response to carbohydrate stress as predicted by (5). The use of

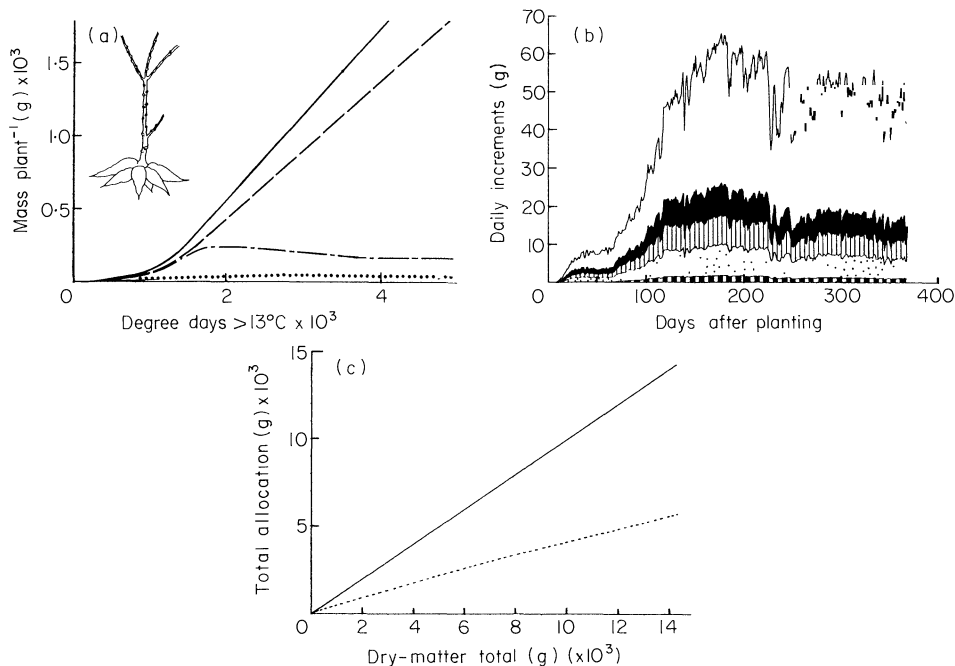


FIG. 4. Simulated dry-matter allocation in unstressed cassava at Ibadan, Nigeria in 1983–84: (a) dry-matter accumulation in leaves (---), stems (—), tubers (— —) and reserves (·····); (b) daily allocation rates to plant organs; ▨ = leaves, □ = respiration, ▩ = reserves, ▧ = stems plus roots, ■ = tubers; and (c) cumulative dry-matter allocation over time to respiration (—) and vegetative growth (----) (cf. Gutierrez *et al.* 1987).

the daily total supply: demand ratio ($\Theta^*(t)$) to regulate the time of branching, and $\Theta(t)$ to regulate the rate of growth and organ production proved quite adequate. Pests may affect either the supply or demand side of the ratio, and are included in both Θ^* and Θ (above and Gutierrez *et al.* 1975, 1988a, b).

Figure 4 shows simulated season-long (4a), daily (4b) and cumulative (4c) dry-matter allocation patterns, respectively (cf. Gutierrez *et al.* 1987). The gross, predicted daily photosynthetic rates are about the same as those reported by Mahon *et al.* (1977) and, despite the daily fluctuations due to weather, the allocation ratios remained relatively constant (Fig. 4c).

1982–83

The simulated phenological pattern of dry-matter allocation for two plantings in 1982–83 are shown in Fig. 5. Major discrepancies from the data in Schulthess (1987) are indicated as shaded areas. Drought stress caused considerable leaf loss in 1982 and tuber growth rates declined. The data were collected only every 2 months, hence the comparisons, while quite good, are qualitative. Despite this problem, the emerging patterns were similar in nearly all aspects to the field data. In the July planting, the model predicted more defoliation than observed and slightly higher yield, while the September patterns were reproduced well. In each case, the dominant factor was drought stress on plant part production. The large increase in leaf production after the drought in the

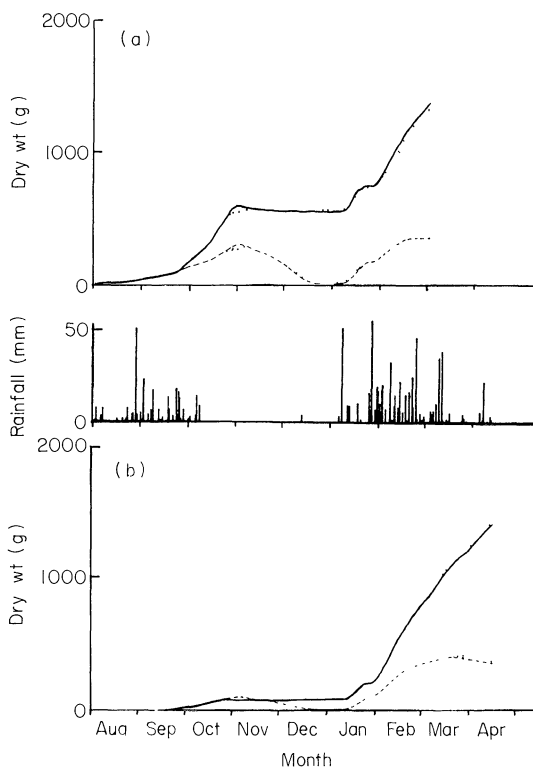


FIG. 5. Simulated and observed dry-matter allocation to leaves and tubers in cassava at Ibadan, Nigeria in 1982-83: planted (a) 15 July, (b) 15 September; (—) tubers, (-----) leaves. Deviations from data reported by Schulthess (1987) are shown as □.

September planting was obtained without modification of the model, and was due to a reduction in respiration costs due to stem and root lignification. The model's ability to reproduce the independent 1982-83 field data is reassuring but does not validate the model.

Effects of water stress

The 1983-84 weather data and the initial conditions were used to examine the effects of simulated water and N stress on growth and development. Using initial values in the Appendix, the simulated changes in soil water ($W = \text{SOILW}$), the permanent wilting point and the water stress index ($0 \leq \omega = \text{WSD} < 1$) are shown in Fig. 6a; $\omega < 1$ occurred only late in the season during mid-March (c. 3100 DD) when soil moisture was $< \text{PWP}$. Water stress was avoided when abnormal heavy rains occurred in normally dry November and December.

A 20% reduction in the observed rainfall pattern (Fig. 6b) caused simulated water stress in early February increasing in severity until the available water was $> \text{PWP}$ in early April. The simulated effects were very similar to those observed in the field in 1982-83 (Schulthess 1987).

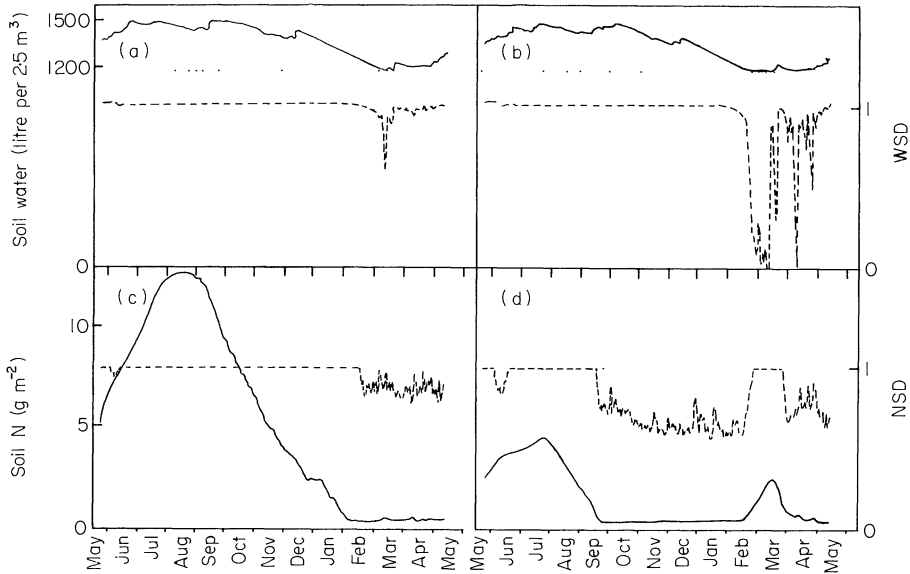


FIG. 6. Simulation of soil water and nitrogen at IITA, Ibadan, Nigeria in 1983-84: (a) soil water (—) and the water supply:demand ration ($\omega = \text{WSD}$, - - -) using observed rainfall data, (· · · ·) permanent wilting point; (b) simulation results using 80% of the rainfall; (c) soil nitrogen (—) and the N supply:demand ratio ($\eta = \text{NSD}$, - - -) under standard conditions; (d) at 50% soil N and 80% rainfall.

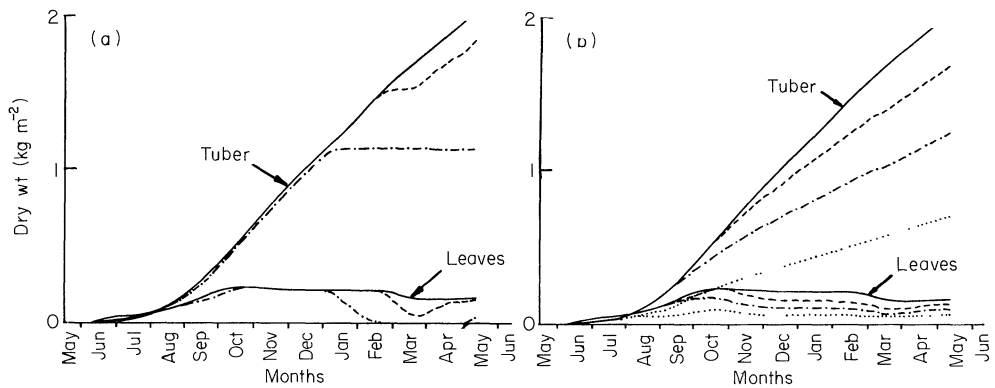


FIG. 7. Simulated leaf and tuber dry-matter production in cassava using 1983-84 temperature and solar radiation, but different proportions of observed (a) rainfall (— $\times 1$, - - - $\times 0.8$, · · · · $\times 0.6$) and (b) soil N conditions (— $\times 1$, - - - $\times 0.75$, · · · · $\times 0.5$, · · · · $\times 0.25$).

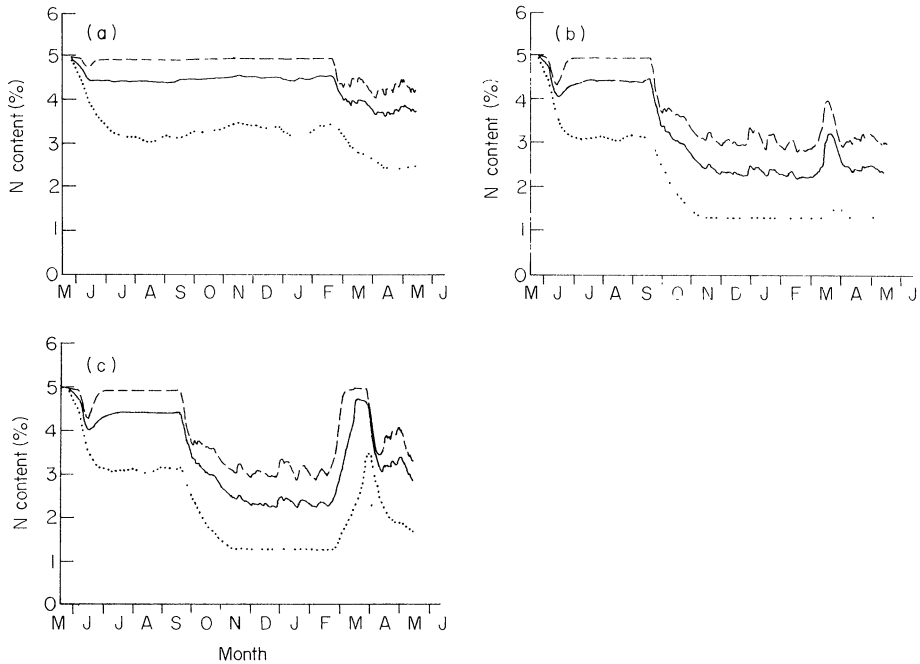


FIG. 8. Simulation of N content of fully expanded cassava leaves (— young, --- middle-aged, old) under (a) standard conditions, (b) 50% soil N and (c) 50% soil N and 80% rainfall.

Effects of nitrogen stress

The initial concentration of available soil N in 1983–84 was assumed to be 5 g m^{-2} , plus an additional 120 000 g of organic matter containing 5% N that decayed at a constant rate of $0.0027\% \text{ day}^{-1}$. The simulated levels of soil N from both sources above and the resulting N stress index ($0 < \eta = \text{NSD} \leq 1$) are shown in Fig. 6c. At the beginning of the season, soil N increased because the rate of uptake was less than the rate of decomposition of organic matter. Available N reached a maximum in April when the daily decay equalled the daily demand. After this, the uptake rate outstripped the decay rate, and the available soil N was nearly exhausted by the beginning of the dry season when a low equilibrium was finally reached. The predicted nitrogen stress was light during this period, fluctuating around 0.9.

The predicted effects of reducing rainfall by 80% and all components of soil N by 50% produced similar patterns for soil N and increased both η and ω stresses (Fig. 6d). ω stress caused cassava growth to stop in late February (Fig. 6b), resulting in an accumulation of N in the soil as the rate extracted declined below the organic-matter decay rate (Fig. 6d). This is seen as the small simulated peak in N in March.

Water and nitrogen stress on yield

Simulated ω and η stresses reduced yields by *c.* 2% and 6%, respectively, compared with simulated 1983–84 unstressed plants (Fig. 7). Because the effects were small, the results are not shown. Using initial N levels and the observed rainfall patterns, *c.* 1.9 kg m^{-2} of

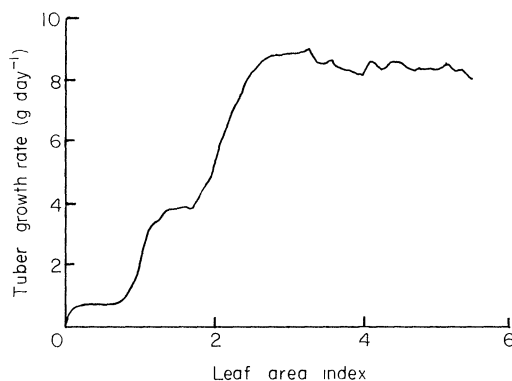


FIG. 9. Simulated tuber growth rates as a function of leaf area index using weather data from Ibadan, Nigeria for 15 May 1983 to 15 May 1984.

tuber mass were observed and predicted. However, a 20% reduction in rainfall severely decreased tuber growth towards the end of the dry season, while a 40% reduction caused growth to cease entirely and the plants to shed their leaves (Fig. 7a). No special mechanism was introduced in the model to accomplish this.

Reduced N, initial levels of organic matter and observed rainfall patterns in the model produced constant decreasing of dry-matter accumulation in tubers (Fig. 7b). The smooth patterns due to N stress contrast sharply with the abrupt changes in growth rates observed when rainfall was reduced. This results because N depletion rates are slower, and N reserves buffer abrupt changes in η unless N is applied. Tuber yields and mid-season leaf mass were roughly proportional to the decrease in available N (i.e. 0.86:1).

Leaf nitrogen content

The simulated N content in first fully expanded leaves, and middle-aged and old leaves in 1983–84 at three levels of initial N are shown in Fig. 8a–c. The results are in accord with data reported for cassava by Howeler (1985). The N content of young leaves remained high throughout most of the season in the high-N treatment (Fig. 8a), declining only with age as the N in them was extracted for reallocation to growing tissues. The maximum retained in old leaves was set to 1.3% (cf. Howeler 1985). However, with a 50% reduction in N, the simulated N in young and old leaves decreased sooner and to lower concentrations, and a higher proportion of N was extracted from older leaves (Fig. 8b). The simulation using 50% soil N and 80% of rainfall (Fig. 8c) was similar to the 50% N treatment (Fig. 8b), but the post-drought increase in leaf [N] was more apparent. The simulated reductions in rainfall caused considerable defoliation resulting in reduced uptake of N and a consequent accumulation of soil N from decaying organic matter during the drought period. As regrowth began after the dry season, higher concentrations of N were available resulting in the predicted increases in leaf N. The peak of N in Fig. 8b was smaller than that in Fig. 8c because the drought-induced respite in N demand was shorter. This latter simulation illustrates the compounding effects of water and N stresses on the uptake of soil N.

DISCUSSION

The simple plant model based on the production and growth rates of leaves and the allometric growth of other plant parts captured the main aspects of growth and development in cassava in three fields. The field data were not used for the most part to formulate the model. The addition of a simple dynamics model for N and water helped to explain the effects of rainfall patterns and levels of soil fertility on growth and yield formation. The model provides a reasonable base for examining the effects of pests on yield and of natural enemies on pests.

The model suggests that the partitioning coefficients for photosynthate allocation to all vegetative parts are relatively constant after respiration costs are subtracted. The results further suggest that tuber growth and reserve accumulation have the same priority as vegetative growth, and these sources of reserves may be used in times of carbohydrate stress to meet limited growth demands and all respiration demands. This is not new, but it is reassuring that the model confirms it. All attempts to redefine these priorities produced poor simulation results. The best simulation results were achieved when water and N stress were incorporated in the demand side of the supply:demand ratio, suggesting that they may limit sink strength (i.e. demand).

Several factors affect the net concentrations of available soil N. Among them are plant N uptake rates as modified by internal reallocation, regeneration of N from decaying matter and other biological and physical processes, and the effects of water stress on plant N uptake; especially during drought when the decay of organic matter may continue in the presence of reduced plant N uptake.

Over time, N in leaves and in other plant organs may vary drastically in response to depletion of soil N. This affects not only crop development, but also herbivore population dynamics via reduced fecundity, increased development times and higher intrinsic mortality rates (Mattson 1980; Wermelinger, Oertli & Delucchi 1985).

Water and N stress in the 1983–84 crop reduced tuber yields little compared with a simulated unstressed field. In 1983–84, there was an exceptionally short dry season interrupted by unusual and heavy December rains. In sharp contrast, water stress caused abrupt changes in leaf abundance as the production of new leaves declined or ceased and older leaves abscised. This slowed organ growth in 1982–83 and reduced yields by 50% compared with 1983–84. The model suggests that the effects of N stress are more gradual than those of water stress.

Changes in leaf quality during the season, including the post-dry season, have been measured in the field (Howeler 1985), and bioassayed in the field using *M. tanajoa* age-specific life tables (Yaninek 1985). The age-specific dynamics of leaf N predicted here are consistent with the results reported by Howeler (1985), while the predicted higher nutritional suitability of leaves after the dry season is consistent with Yaninek's (1985) results. The effects of [N] on the interactions of cassava and *P. manihoti* and *M. tanajoa* are examined in Gutierrez *et al.* (1988a, b).

Ideal plant phenotype

Field studies by agronomists and plant breeders often result in empirical evidence for breeding criteria for maximum-yielding plant phenotypes. Cock (1985b) at CIAT, Cali, Columbia proposed a graphical model for optimum growth rate of cassava as a function of LAI. The model suggested that growth rates could be enhanced by increasing photosynthetic efficiency and leaf longevity—a reasonable prediction. Sibly & Grime

(1986) used a graphical analysis to illustrate that the optimal investment in roots depended on the [N] in the soil. They concluded that the optimal costs increase as the concentration of available N increases. Applying the same analysis to photosynthesis in cassava suggests that greater costs should be incurred to increase leaf area as solar radiation increases but, of course, cassava can become light saturated. Such models are instructive, but leave out too many of the details. Both models are analogous to our allocation model (2) as written in less detail below.

$$dL/dt + dS/dt + dR/dt + dT/dt + dv/dt = \quad (14)$$

$$dP(M_{i-1}, \Delta t, LAI, b, s)/dt - dz(\Delta t, M)/dt$$

where $dP(\cdot)/dt$ is the rate of photosynthate produced and assimilated to tuber, leaf, stem, root, and reserves, respectively (T, L, S, R, v), minus respiration costs ($z(\cdot)$); Δt is physiological time, M is the mass of the plant; and M_{i-1} is the light energy available to the plant. After rearranging terms, the assimilation rate to tubers is:

$$dT/dt = dP(\cdot)/dt - dz/dt - dL/dt - dS/dt - dR/dt - dv/dt \quad (15)$$

$$dT/dt = dP(\cdot)/dt - dC/dt$$

where $dP(\cdot)/dt$ is a concave function as in Cock's (1985b) figure, but in our case it is a function of ψ , Δt , and LAI, and dC/dt is the sum of all other terms except tuber growth rate. It is now obvious that, if any or all of the minus terms are reduced and/or $dP(\cdot)/dt$ is increased, dT/dt is enhanced. Hence, not only should leaf longevity increase, but also the leaf production rate should decrease after the canopy reaches maximum LAI. Final tuber yield is the sum of all of the dT/dt over the season, which of course varies in length and in favourability to the plant and to pests, whose injuries to the plant are yet more negative terms (i.e. costs).

Cock's hypothesis suggests that the optimum ratios of growth rates of tuber:stem + leaves:total weight should be 1:1.6:2.6, while the model yielded ratios of 1:1.5:2.5 during the period of maximum growth rate (2000–2100 DD, 1983–84). Although our results are similar to Cock's predictions, it was difficult to test this hypothesis as the optimal LAI is expected to vary with weather which changes from year to year, and area to area; and each pattern would be expected to yield a somewhat different result. Our model suggests that maximum tuber growth rates occur near LAI 3 (Fig. 9), roughly the same as Cock's empirically estimated value. Of course, this may be fortuitous as the weather determines when the maximum is achieved.

The maximum-yielding variety or phenotype under optimum weather conditions might not be the most stable variety for subsistence economies where yield stability (i.e. lower yield and low variance) in the long term may be more important than high yields with associated possible high variance (Cock 1985a).

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APPENDIX

Manihot esculenta

Initial conditions

Soil water (litres 2.5 m^{-3})	1350
Organic matter (g m^{-2})	120000
Carbohydrate reserves (g cutting^{-1})	2.75
N reserves (g cutting^{-1})	0.084
Stems (g cutting^{-1})	3.25

Maximum parameters

Planting date	15 May 1983
Harvest date	15 May 1984
Albedo soil	0.055
Hydraulic conductivity (cm day^{-1})	0.05
Permanent wilting point (litres 2.5 m^{-3})	1190
Available soil N (g m^{-2})	5.0
Proportion of N in organic matter available (% day^{-1})*	0.0027
Development threshold ($^{\circ}\text{C}$)	13.0
Development time (DD) of	
leaves	900
stems†	500
roots†	500
Maximum leaf area index	4.5
ϕ in search rate s	0.68

Fitted constants for growth demands

Leaf production rate ($\lambda(t=0)$, eqn (5)) (DD^{-1})	0.057
c in $g_L(a)$ (eqn (6)) (DD^{-1})	0.0048
c_x parameters for $g_j(t)$ in eqn (7):	
c_1	1.0
c_2	1.5
c_3	1.0
c_4	2.0
c_5	0.25
c_6	0.30

* From dry-matter data of Schulthess (1987).

† Development time estimates are from initiation to lignification.