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ENERGY ACQUISITION AND ALLOCATION IN PLANTS AND INSECTS: A HYPOTHESIS FOR THE POSSIBLE ROLE OF HORMONES IN INSECT FEEDING PATTERNS

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Abstract

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A distributed delay age structure model is presented for plants and insects that describes the dynamics of per capita energy (dry matter) acquisition and allocation patterns, and the within-organism subunit (e.g. leaves, fruit, ova) number dynamics that occur during growth, reproduction, and development. Four species of plants (common bean, cassava, cotton, and tomato) and two species of insects (pea aphid and a ladybird beetle) are modeled. A common acquisition (i.e. functional response) submodel is used to estimate the daily photosynthetic rates in plants and consumption rates in pea aphid and the ladybird beetle. The focus of this work is to capture the essence of the common attributes between trophic levels across this wide range of taxa. The models are compared with field or laboratory data. A hypothesis is proposed for the observed patterns of reproduction in pea aphid and in a ladybird beetle.

Résumé

On a construit un modèle démographique avec distribution de délai applicable à des plantes et des insectes. Le modèle décrit la dynamique de l'appropriation et de la répartition de l'énergie (matière sèche) per capita, et la dynamique des nombres des sous-unités intra-organisme (ex. feuilles, fruits, oeufs). On a ainsi modélisé quatre sortes de plantes (fève, cassava, coton et tomate) et deux espèces d'insectes (puceron du pois et coccinelle). On utilise un sous-modèle commun d'acquisition (résponse fonctionnelle) pour estimer les vitesses journalières de photosynthèse des plantes et d'alimentation du puceron et de la coccinelle. Le but de ce travail est d'extraire les caractéristiques essentielles communes aux niveaux trophiques occupés par ces divers taxons. Les modèles sont comparés avec des données de terrain et de laboratoire. On propose une hypothèse pour expliquer les profils observés de reproduction du puceron du pois et de la coccinelle.

Introduction

The patterns of energy acquisition and assimilation by organisms must be in harmony with their ecological role in a biological system. To examine this requires the development of models of multi-trophic level interactions. The development of multi-trophic level models has been a goal of many population ecologists (May 1982; Gilbert *et al.* 1976; De Angelis *et al.* 1975; Gutierrez *et al.* 1981; Gutierrez, Baumgaertner *et al.* 1984; Gutierrez, Pizzamiglio *et al.* 1984).

Until recently, plant and animal demographers have viewed population processes from quite different perspectives, but this gap has narrowed (Gutierrez and Wang 1976; Wang *et al.* 1977; Gutierrez, Baumgaertner *et al.* 1984; Gutierrez, Pizzamiglio *et al.* 1984; Law 1983). For example, plant ecologists (Harper and White 1974; Harper 1979) proposed that populations of plants consisted of individual plants, each of which had populations of plant subunits with age structure. Animal ecologists (Gutierrez and Wang 1976; Wang *et al.* 1977; Curry *et al.* 1978) have used a series of linked von Foerster (1959) models to simulate the demography of cotton plants (*Gossypium hirsutum* L.) and plant subunit populations in the manner proposed by Harper and White. Growth, development, and reproduction in insects may also be viewed in a similar manner, as female insects have populations of ova or embryos growing within them that may have age structure. Immature growth and embryo production in insects (and other animals) are thus analogous to vegetative growth and fruit production in plants.

In this paper, a common model is used to simulate the dynamics of growth and development of common bean (*Phaseolus vulgaris* L.), pea aphid (*Acyrthosiphon pisum* Harris), cassava (*Manihot esculenta* Crantz), a ladybird beetle (*Hippodamia convergens* G.-M.), cotton, and tomato (*Lycopersicon esculentum* Mill.). In addition, the same functional response model from predation theory is used to predict photosynthetic rates in plants and predation and herbivory rates in insects (Gutierrez *et al.* 1981). The goal of the work is to examine the common patterns of energy allocation in widely separated taxonomic groups. A hypothesis is also proposed for the hormonal control of energy acquisition and allocation in insects.

Review of Mathematical Models

Population Dynamics. The von Foerster model used to simulate the dynamics of plant growth and development may be summarized as follows:

$$\delta N_j/\delta t + \delta N_j/\delta a = \mu_j(t,a)\, N_j(t,a) \qquad [1]$$

where N_j denotes the mass or number density function of the j^{th} plant or animal population or subunit population (e.g. j = plants, leaves, stem, root, fruit,. . .), and μ_j is the net birth–death rate of the population at time "t" of age "a" measured in temperature-dependent units (e.g. degree days, DD). An analytical solution for [1] given constant age-specific parameters is possible, and the numerical solution is equivalent to the Leslie (1945) matrix model (Wang *et al.* 1977). Sinko and Streifer (1967) provide a very readable summary of the mathematics of [1] and related deterministic age-structure models. Specific applications of this model to plant and poikilotherm population dynamics are reviewed by Wang *et al.* (1977), Curry *et al.* (1978), and Gutierrez *et al.* (1983).

In our model, species parameters vary with age and time and incorporate the detail of the biology in the term $\mu(.)$. The parameters that influence μ vary over time in response to changes in density, nutrition, natural enemy activity, physical and many other factors known to affect real population (Gilbert *et al.* 1976). Despite the mathematical intractability of these models, they have proven quite useful in examining many applied (Gutierrez *et al.* 1975, 1976; Gutierrez, Leigh *et al.* 1977; Gutierrez, Butler *et al.* 1977; Gutierrez, Baumgaertner *et al.* 1984; Gutierrez, Pizzamiglio *et al.* 1984; Wang *et al.* 1977; Wang and Gutierrez 1980; Cuff and Hardman 1980) and theoretical problems (Wang and Gutierrez 1980; Gutierrez and Regev 1983).

More recently, Gutierrez and Baumgaertner (1984*a*, 1984*b*) replaced the deterministic model [1] with a distributed delay model ([2], cf. Manetsch 1976; Vansickle 1977), and used it to simulate the stochastic development of cohorts of plants and insects.

$$\begin{array}{llll} \mathrm{d}N_{1,j}/\mathrm{d}t &= x_j(t) & - r_{1,j}(t) & - \mu_{1,j}(t,.)N_{1,j} \\ \mathrm{d}N_{2,j}/\mathrm{d}t &= r_{1,j}(t) & - r_{2,j}(t) & - \mu_{2,j}(t,.)N_{2,j} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \mathrm{d}N_{k,j}/\mathrm{d}t &= r_{k,j}(t) & - y_j(t) & - \mu_{k,j}(t,.)N_{k,j} \end{array} \qquad [2]$$

where x_j and y_j are the inflow and outflow rates of numbers or mass into the first and last age groups, respectively, in the j^{th} population, $r_{i,j}$ is the flow rate into the $i+1^{\text{th}}$ of k age categories, and $\mu_{i,j}(t,.)$ equals the net proportion of mortality, birth, immigration, and emigration in the i^{th} age group at time t. In the model, senescence of leaves in plants and ovaries in insects occurs as transition (ageing) rates through the distributed delay model [2]. Leaves lose their photosynthetic potential with age and insects lose their reproductive capacity. In the current application, N may be in number, mass, or energy units.

Examples of the application of this model to plant and insect demography and interactions are works by Gutierrez, Baumgaertner *et al.* (1984) and Gutierrez, Pizzamiglio *et al.* (1984). Bellows (1982) applied a distributed delay model which incorporated hazard rates to examine the dynamics of a laboratory population.

Metabolic Pool Model. The metabolic pool model for energy acquisition and allocation links the plant and subunit models (Jones *et al.* 1974; Gutierrez *et al.* 1976). On a per capita basis, the process of energy acquisition and allocation is modeled as follows (Fig. 1):

$$\begin{aligned} \mathrm{d}A/\mathrm{d}a &= \mathrm{d}G/\mathrm{d}a + \mathrm{d}R/\mathrm{d}a + \mathrm{d}O/\mathrm{d}a \\ &= M_{i-1}f(M_{i-1}, M_i,\tau,b,s)(1-\beta) - z(\tau)Mi + O^* \end{aligned} \qquad [3]$$

where M_{i-1} is the mass or energy in the $i-1^{\text{th}}$ trophic level available to the mass in the i^{th} trophic level to prey upon; $\mathrm{d}A/\mathrm{d}a$ is the per capita assimilation rate in terms of growth (G), reproduction (R), and/or reserves (O); τ is temperature; $f(.)$ is the predator functional response model [4]; b is the genetic maximum demand rate (see below); s is the predator search rate; $z(.)$ is the monotonically increasing metabolic cost rate as a function of temperature (τ); $O^* = \alpha O$ is the quantity of reserves used instantaneously to meet respiration costs; $\alpha \epsilon [0,1]$; β is the proportion of energy ingested that is egested. Of course, egestion does not occur in plants in a strict sense, but exudates and other compounds not used for growth, reproduction, or respiration could be included in β. Note also that $\mathrm{d}A/\mathrm{d}a = 0$ is the metabolic compensation point. The metabolic pool model suggests a priority scheme for allocation: first to respiration and egestion, then reproduction, and last to growth and reserves (Gutierrez *et al.* 1975, 1983; Wang *et al.* 1977). The sum of the maximum possible outflow or assimilation rates to growth, reproduction, and reserves corrected for respiration and egestion is the maximum genetically controlled demand rate (b), and the inflow from prey consumption or photosynthesis represents the realized supply rate (M^*). In the model, these maximum demand rates are multiplied by the appropriate level supply/demand ratio (e.g. $M^*/b \epsilon [0,1]$) to estimate the realized growth rates. This interplay between supply and demand has been the cornerstone regulating the allocation processes in our models (Gutierrez *et al.* 1975; Wang *et al.* 1977; Gutierrez and Baumgaertner 1984*a*, 1984*b*). In theory, the supply (i.e. the functional response, cf. Holling 1966) is always less than the demand ($M^* < b$), because the search process is imperfect even when conditions are nonlimiting. Gutierrez and Baumgaertner (1984*a*) discuss the role of multiple prey in this context.

The Frazer and Gilbert (1976) functional response model [4] was selected to estimate photosynthesis and prey acquisition rates (M^*) in plant and insect models, respectively, because the demand rate (b) is the major driving variable (Gutierrez and Wang 1976).

$$M^* = M_{i-1}f(.) = M_{i-1}\left[1 - \mathrm{e}^{(-b_iM_i\Delta t/M_{i-1})(1-\mathrm{e}^{-s_iM_{i-1}/b_i})}\right] \qquad [4]$$

where $\Delta t = \Delta DD$. In the limit, the F-G model approaches a Nicholson-Bailey model as

$M_{i-1}\rightarrow 0$, and a linear Lotka-Volterra model as both M_i and $M_{i-1}\rightarrow 0$ (Gutierrez and Wang 1976). This model more fully characterizes the range of observed predator–prey interactions (Frazer and Gilbert 1976). The model implies that at high resource availability, consumption is saturated; at lower resource levels, availability and not consumption is limiting; at very low levels, the encounter rate is low but linear, and the rate of change is at its maximum. Each of these attributes has a direct parallel in photosynthesis. For population development, true predators seek prey, herbivores seek plants or plant subunits, and plants seek light energy. Of course all levels may also seek other requisites (e.g. minerals), but for our purpose here these are assumed to be in adequate supply, unless otherwise indicated in the results section.

For plants, M_{m-1} is the light incident in their growing space, for the pea aphid M_{i-1} is the quantity of available plant sap dry matter, and for ladybird beetle it is the quantity of aphids in their search universe. For consistency of units in the model, the light energy falling per unit area (cal cm^{-2} day^{-1}) must be converted to dry matter equivalents (Gutierrez and Baumgaertner 1984*a*). Loomis and Williams (1963) estimated the theoretical maximum net photosynthesis per square metre per day at 500 cal cm^{-2} day^{-1} as 71 g CH_2O m^{-2} day^{-1}, or 129 g gross photosynthesis m^{-2} day^{-1}. Equation [5] shows the theoretical energy inputs and the mass components produced during photosynthesis.

$$6CO_2 + 12H_2O \xrightarrow{\Delta\ =\ 69\ \text{Einsteins}} C_6H_{12}O_6 + 6O_2 + 6H_2O \qquad [5]$$

Loomis and Williams (1963) suggest that 10.07 Einsteins (E) are required to produce 1 mol of CH_2O (30 g). This, as expected, is less than one-sixth the value required to produce 1 mol of glucose (180 g). In practice, a simple conversion constant (3.875) converts cal cm^{-2} day^{-1} to g CH_2O m^{-2} day^{-1}.

Prey capture rates (s in [3,4]) increase with predator (herbivore) size, hence s per unit predator mass [6] is characterized as follows:

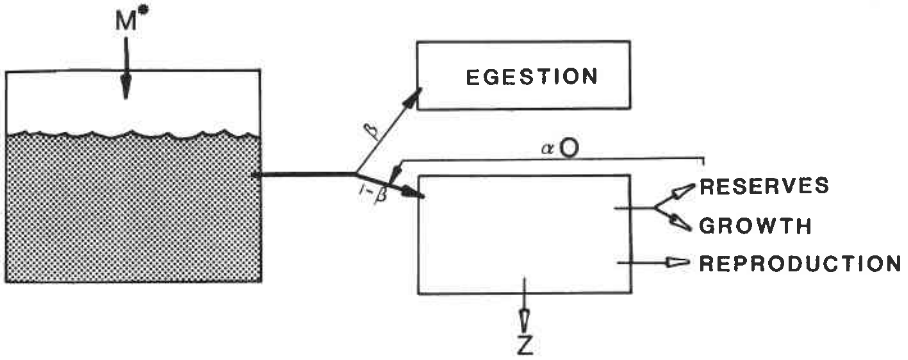
$$s = 1. - e^{-\gamma M} \in [0,1] \qquad [6]$$

where M is the predator mass and γ is the prey capture coefficient. Of course prey capture rates at the individual level are influenced by prey size, but the use of total predator mass attacking total prey mass simplifies the problem (Gutierrez, Baumgaertner *et al.* 1984). In this model, small predators would have little impact on populations of large prey (i.e. small demand rate), but large predators (i.e. large demand rates) could have a large impact on populations of small prey.

Similarly, light capture rates can be estimated using [6]. Leaf area is usually a linear function of leaf mass, and the proportion of light incident in the growing space of the plant that is intercepted by leaves increases with increasing leaf area (usually expressed as the leaf area index (LAI)). This relationship was described by M. Monsi and T. Saeki in 1953 ([7], Evans 1975), and it has the same form as [6] above.

$$s = 1. - e^{-\gamma' \text{LAI}} \in [0,1]. \qquad [7]$$

The light extinction coefficient (γ') is readily estimated in the field using light meter readings at different levels of the canopy. Hence s in [7] estimates the proportion of the potentially available light energy that falls on leaf surface, and is equivalent to Nicholson-Bailey search parameter (i.e. γ) in [6]. The use of this functional response model for photosynthesis was first proposed by Gutierrez *et al.* (1981), but Mack *et al.* (1981) independently pointed out the same shape properties of predation and photosynthesis models. Rectangular hyperbolic functions describing photosynthetic rates are common in plant physiology (e.g. Noggle and Fritz 1976). In this paper, linked models [2,4] are used to estimate photosynthesis and food acquisition rates for modeling per capita plant and insect growth and development. The extension of this model to plant and animal populations is given in Gutierrez and Baumgaertner (1984*b*). The effects of water, nitrogen, and other



$$A_i = R_i + G_i = M_{i-1} f(M_{i-1}, M_i)(1 - \beta_i) - Z_i M_i + O_i^*$$

FIG. 1. Generalized metabolic pool model for energy acquisition and allocation in plants and animals (see text for definitions of variables).

stresses are not reported in detail in this study because of the additional complexity they introduce. Their effects will be reported here as needed and in detail elsewhere.

Materials and Methods

Data to estimate plant model parameters were collected in field trials. The details concerning the source of the data, sites, planting and harvest dates, plant density, and source of weather data are given in Table 1. Table 2 summarizes the kinds of data collected for all species. The plants were protected from pest damage with insecticides as needed, but all other variables were not controlled. Dry matter data allocated to plant subunits as well as the number dynamics and age structure of fruits were collected for common bean, cotton, and tomato. Only dry matter, node (leaf) number, and branching pattern data were collected for cassava. In cassava, fruit mass is very small compared with the size of the overall plant, and is not considered here. Considerable energy is devoted, however, to tuber production in cassava.

The precise laboratory data published by Randolph *et al.* (1975) on energy allocation in pea aphid were used in this study. Laboratory data published by Gutierrez *et al.* (1981)

Table 1. Source of the biological and weather data, season lengths, thermal thresholds, and field plant density in the field

Species	Source of data	Season length	Thermal threshold (density)
Bean	Londrina, Pr., Brazil M.A. Villacorta, unpub.	9/2/82 – 12/8/83	5°C (6 m^{-2})
Cassava	Ibadan, Nigeria F. Schulthess, unpub.	5/13/83 – 5/12/84	13°C (1 m^{-2})
Cotton	Londrina, Pr., Brazil Gutierrez, Pizzamiglio *et al.* 1984	10/25/82 – 3/30/83	12°C (6 m^{-2})
Tomato	Davis, CA, USA L.T. Wilson, unpub.	2/22/82 – 8/5/82	10°C (6.6 m^{-2})
Ladybird beetle	Laboratory Gutierrez *et al.* 1981	—	6.1°C
Pea aphid	Laboratory Randolph *et al.* 1975	—	4.2°C

Table 2. Parameters estimated for model development

Plants	Insects
Fruits	**Ova/embryos***
a. Growth rate of buds	*a*. Growth rate of ova†,‡
b. Age of flower	*b*. Transition time between oogenesis and embryogenesis‡
c. Growth rate of fruits	*c*. Growth rate of embryos‡
d. Age at maximum size	*d*. Age at maximum size of an embryo‡
e. Shed windows of buds and fruits due to carbohydrate stress (supply/demand <1)	*e*. Age window of ova resorbed (supply/demand <1)
Vegetative growth	**Immature growth**
f. Growth rate of leaf, stem, and root before first fruiting branch (*i*)	*f*. Growth rate of immature before pupation† or the adult stage‡
g. Growth rate of leaf, stem, and root after (*f*) as a function of plant density	*g*. Pupal period (negative growth)†
h. Rate of bud production as a function of plant density	*h*. Rate of ova production†,‡
i. Age at first fruiting branch	*i*. Age at first reproduction†,‡

*See text.
†Holometabolous insects.
‡Hemimetabolous insects.

were used to model ladybird beetle growth and development. The ovisorption of young embryos occurs in sycamore aphid during periods of inadequate food (Ward and Dixon 1982), and a similar process is assumed in pea aphid and in the ladybird beetle.

In most cases, a small subset of each data set was used for model parameter estimation; hence true independent validation data sets were not available. This occurred because the enormous efforts required precluded the collection of the data at this time. Several data sets are available for cotton and the comparisons between simulated and observed values have been good (Gutierrez *et al.* 1975; Gutierrez, Pizzamiglio *et al.* 1984). Additional data are currently being collected for some of these species, but they will be reported elsewhere. No attempt was made to analyze the observed and simulated data statistically, because each parameter in the simulation model has error associated with it, and when used in simulation computations, the errors are compounded in unknown ways. Hence, the violation(s) of the assumptions of the statistical models would be more serious than the deficiencies of the relative comparisons presented here (Kvalseth 1985). Last, the major focus of this study was on model methodology, and only secondarily on specific applications.

Results

Field and Laboratory Data. For the plant species, the number and age structure of fruits and the dry matter dynamics are presented in Figures 2–5, and those for pea aphid and the ladybird beetle are given in Figures 6 and 7. The lines through data are simulation results. All of the data are average per capita values as indicated in the figure legends. Given the factors not included in the model (water, nitrogen,...) and the sampling and other sources of errors in the data, the simulation results were satisfactory.

Plant Data. In bean, cotton, and tomato, leaf and stem plus root production greatly slowed due to carbohydrate stress when the demand for dry matter in fruits increased sharply (i.e. the supply/demand ratio; Gutierrez *et al.* 1975) (Figs. 2, 4–5A). The declines in stem and leaf dry matter in bean and cotton after times 1100 and 1300 DD were due to the shedding of senescing leaves and petioles. Petioles are considered stem tissue, and are ca. 20% of

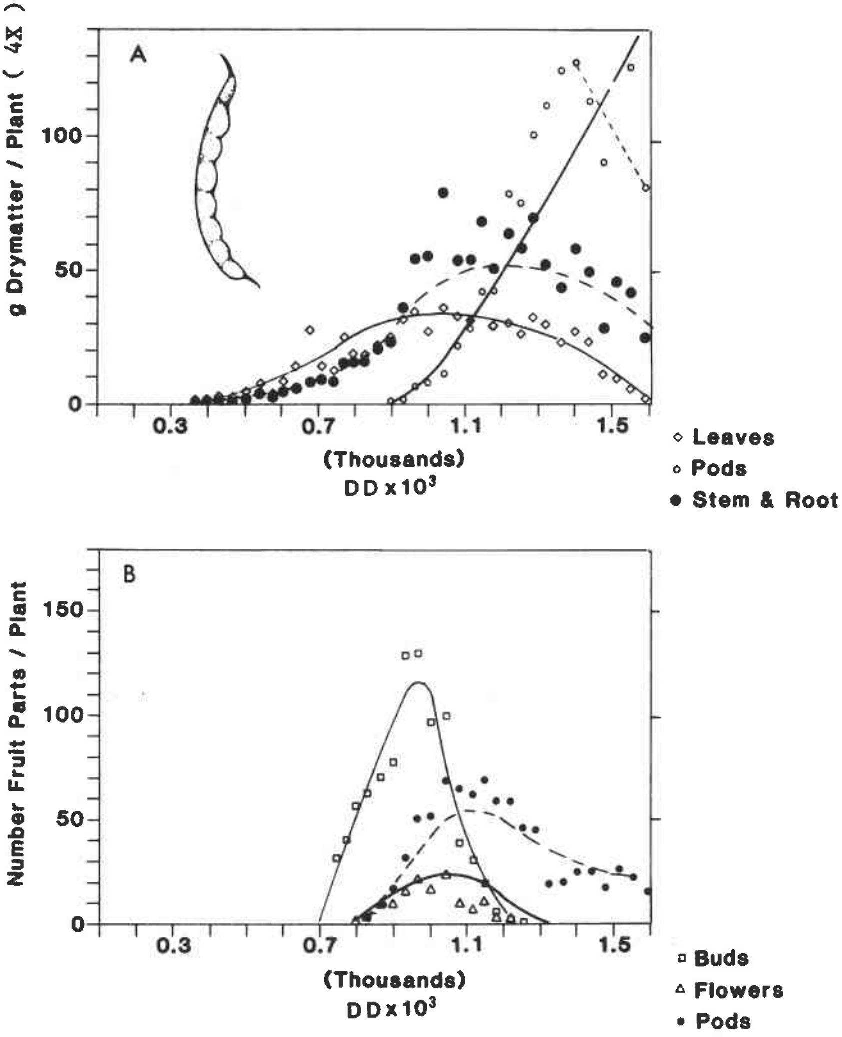


FIG. 2. Bean growth and development: (A) dry matter allocation (4 ×) to leaves, stem plus root, and fruit; (B) numbers (1 ×) of fruit buds, flowers, and pods. Averages for 10 plants are plotted on DD above 5°C using 1983 weather data from Londrina, Pr., Brazil. The lines represent simulated values (A.M. Villacorta, unpublished data). The late-season decline in fruit mass was not included in the simulation.

leaf weight. The bean and cotton plants suffered water stress which caused a faster than normal leaf abscission rate (Gutierrez *et al.* 1975). Water stress was not observed in tomato (Fig. 5A) because of available irrigation. The declines in late-season fruit dry matter in bean, cotton, and tomato are explained by the fact that mature fruits were not included in the field samples. In cassava (Fig. 3A), vegetative growth continued throughout the season, but slowed after time 3500 DD due to dry-season water stress. In the field, this stress may be severe enough to cause complete defoliation. No other serious discrepancies are seen in the comparisons.

The observed fruit number patterns for bean, cotton, and tomato are presented in Figures 2, 4–5B. In these species, the production of new fruits slowed or stopped due to carbohydrate stress when fruits began their rapid growth. This result is consistent with the

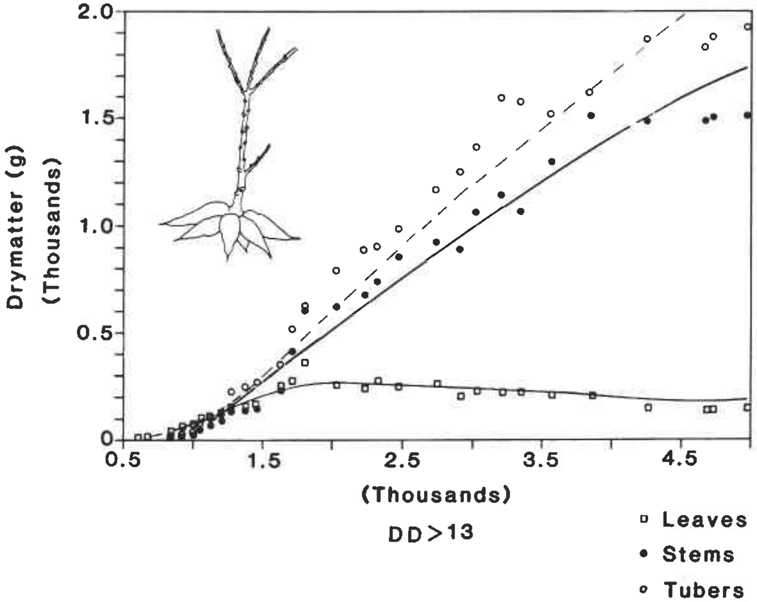


FIG. 3. Per plant cassava growth and development: dry matter allocation to leaves, stem plus root, and tubers. Averages of eight plants are plotted on DD above 13°C using 1983 weather data from the International Institute for Tropical Agriculture, Ibadan, Nigeria (F. Schulthess, unpublished data). The lines represent simulated values.

extensive data published for cotton by Gutierrez *et al.* (1975), and Gutierrez, Pizzamiglio *et al.* (1984*b*). In tomato, the numbers of postflower fruits reached nearly the same level as did small preflower buds. This occurred because rapid fruit growth was delayed 250 DD after flowering, and fruit abscission was delayed 900 DD when approximately 50% of large fruits began to be shed. The fruit dynamics patterns in bean and cotton are smoother because of shorter postflower delays in rapid fruit growth. As noted earlier, cassava fruit dynamics data were not available.

Insect Data. The complete data of Randolph *et al.* (1975) for pea aphid viviparae are shown as published Figure 6B. The height of each bar graph represents daily food consumption. The data are also plotted as cumulative values in Figure 6A. The data show that immature growth in aphids lasts approximately 10 days, and energy allocation to reproduction begins after a short prereproductive period. The data suggest that reproduction in pea aphid was limited by consumption which declined after day 16. The observed allocation ratios to respiration (32%), egestion (18%), and assimilation (50% to growth and reproduction) were nearly constant (Fig. 6C).

Data such as those shown in Figure 6C were not available for any of the other species. Data reported by Gutierrez *et al.* (1981) for the ladybird beetle *H. convergens* were used to parameterize that model. Data on dry matter allocation and reproduction were not available for the same females; hence only average data on reproduction were compared with model predictions. The relationship of the cumulative number of aphids eaten by a ladybird beetle at different constant food supply rates was linear in time (Fig. 7A). The numbers of eggs produced per female at three prey densities are shown in Figure 7B. The treatment of 40 aphids per day per beetle was equivalent to the conditions of the simulation study (i.e. the broken line in Fig. 7B). The proportions of prey captured at the different densities are depicted in Figure 7C, indicating that on average 5.6, 11.0, and 14.8 aphids were eaten per adult ladybird beetle female per day when fed 8, 24, and 40 aphids per day,

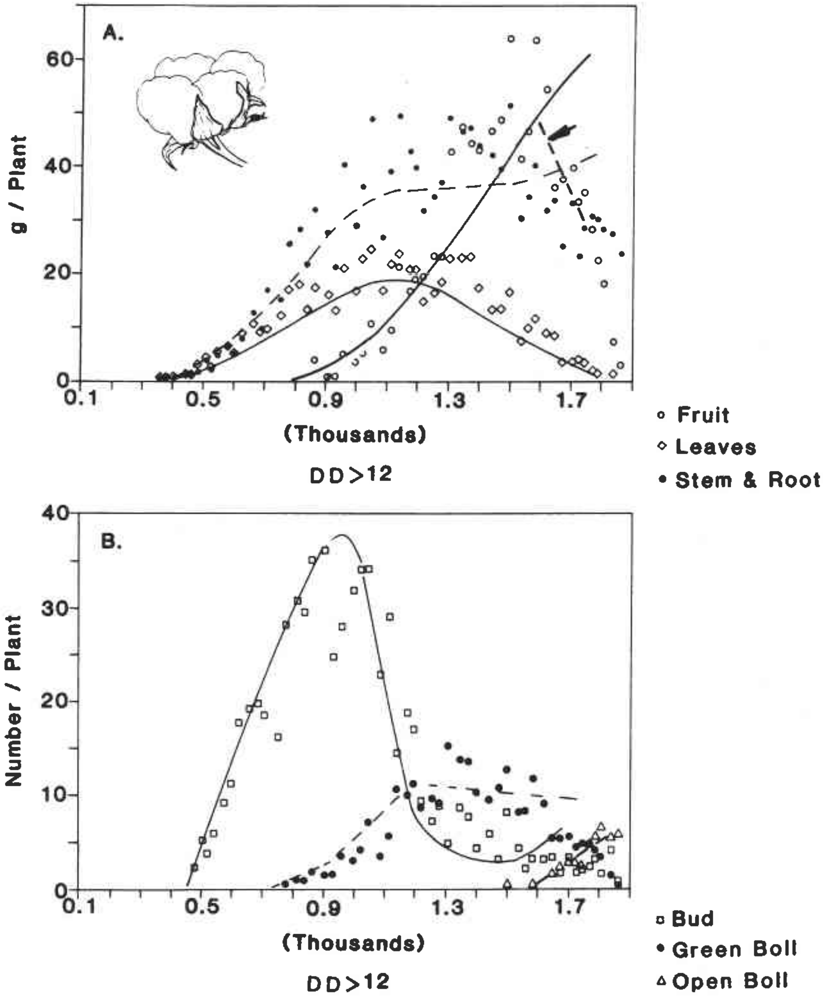


FIG. 4. Per plant cotton growth and development: (A) dry matter allocation to leaves, stem plus root, and fruits; (B) numbers of fruit buds, flowers, and green bolls. Averages of five plants are plotted on DD above 12°C using 1983 weather data from Londrina, Pr., Brazil (Gutierrez, Pizzamiglio *et al.* 1984). The lines represent simulated values. The late-season decline in fruit mass (i.e. arrow) was not included in the simulation.

respectively. Beetles fed fewer aphids were smaller, and they required fewer aphids to begin reproduction (Fig. 7B) because of lowered respiration costs. Approximately 0.35 mg of prey is required per day to meet basic metabolic costs per milligram of predator (Gutierrez *et al.* 1981). Thus larger beetles ate more, but also had higher metabolic costs.

Analysis of Simulation Results. Dry matter allocation patterns. The number of measurements on growth and development of each of the species was limited by time and resources. One of the important uses of the simulation models is to examine the intermediate products such as those painstakingly measured by Randolph *et al.* (1975) for pea aphid. Among these are the total biomass and numbers of fruits (ova) produced and shed, and the dynamics of energy production, allocation, and loss.

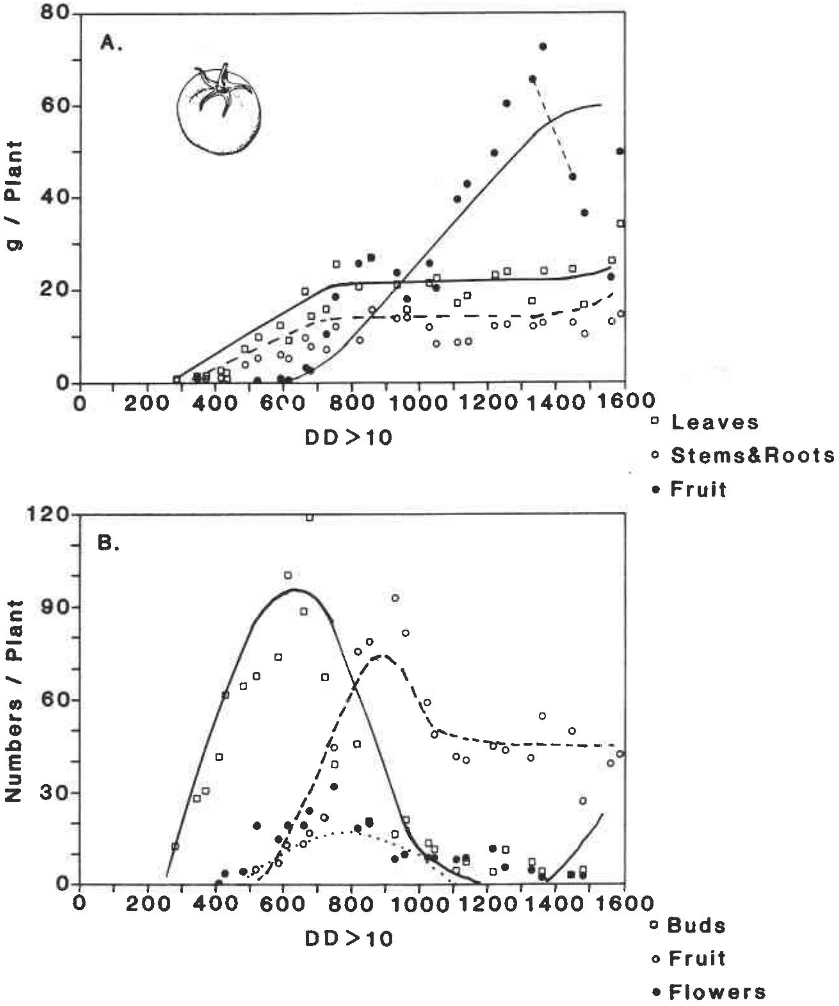


FIG. 5. Per plant tomato growth and development: (A) dry matter allocation to leaves, stem plus root, and fruit; (B) numbers of fruit buds, flowers, and large fruit. Averages of four plants are plotted on DD above 8°C using 1983 weather data from Davis, California (L.T. Wilson, unpublished data). The lines represent simulated values. The late season decline in fruit mass was not included in the simulation.

Plant data. As observed in the field data, plant subunits in bean, cotton, and tomato (Figs. 8, 10–11A) grow exponentially until fruits begin rapid growth causing sharp curtailment in growth rates. Relative to the dry matter retained, only a small amount is lost via shed fruit in these species. Cotton and tomato, in contrast with bean, have much lower leaf to stem ratios and their growth appears indeterminate as indicated by the second fruiting cycle. The model also predicts that bean may be kept growing vegetatively if enough fruits are removed to avoid carbohydrate stress. This prediction is consistent with field observations, and suggests that the definitions of determinate and indeterminate plants must remain flexible.

The model and the data suggest that cassava grows throughout the season without the sharp carbohydrate-stress-induced curtailments of vegetative growth observed in the other plant species (i.e. when demand becomes greater than supply). The slowing of leaf dry

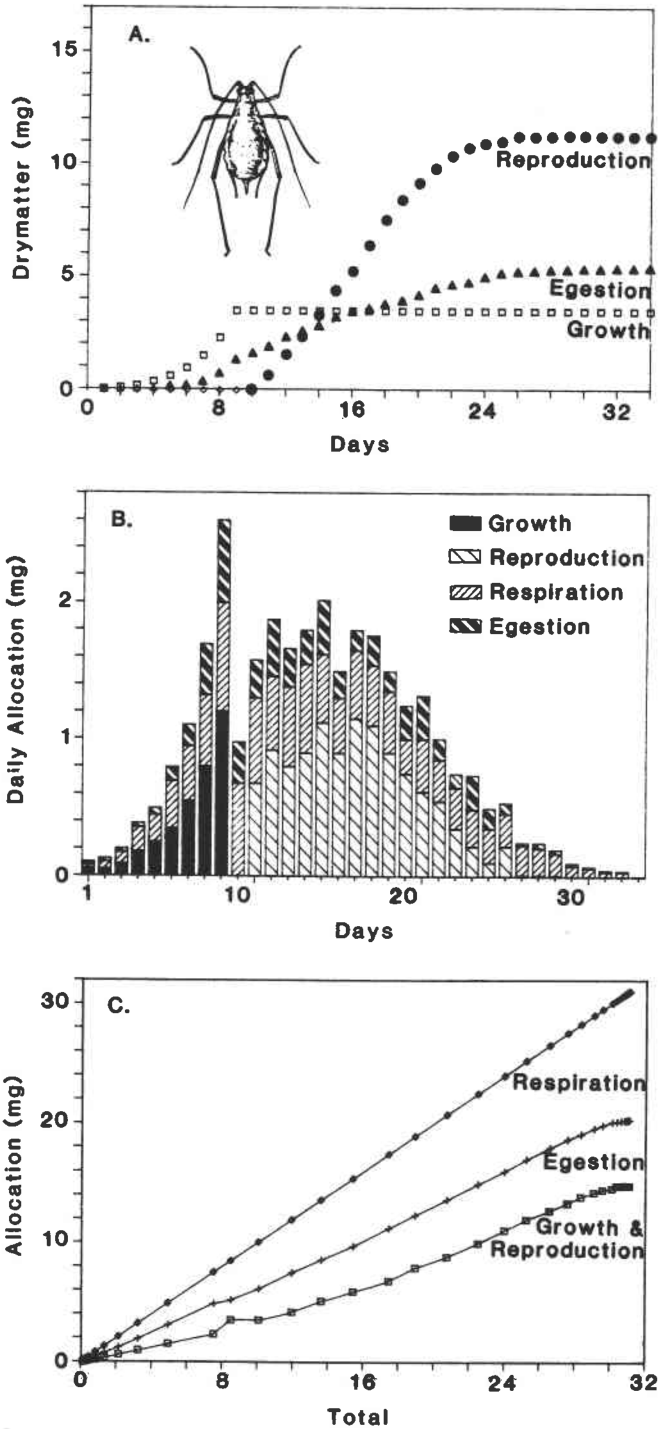


FIG. 6. Per capita pea aphid growth and development: (A) patterns of cumulative growth, reproduction, and daily available reserves; (B) daily dry matter allocation to immature growth, reproduction, egestion, and respiration; and (C) the allocation ratios. The data in (B) are presented as bar graphs on a daily basis at 21°C as published by Randolph *et al.* 1975.

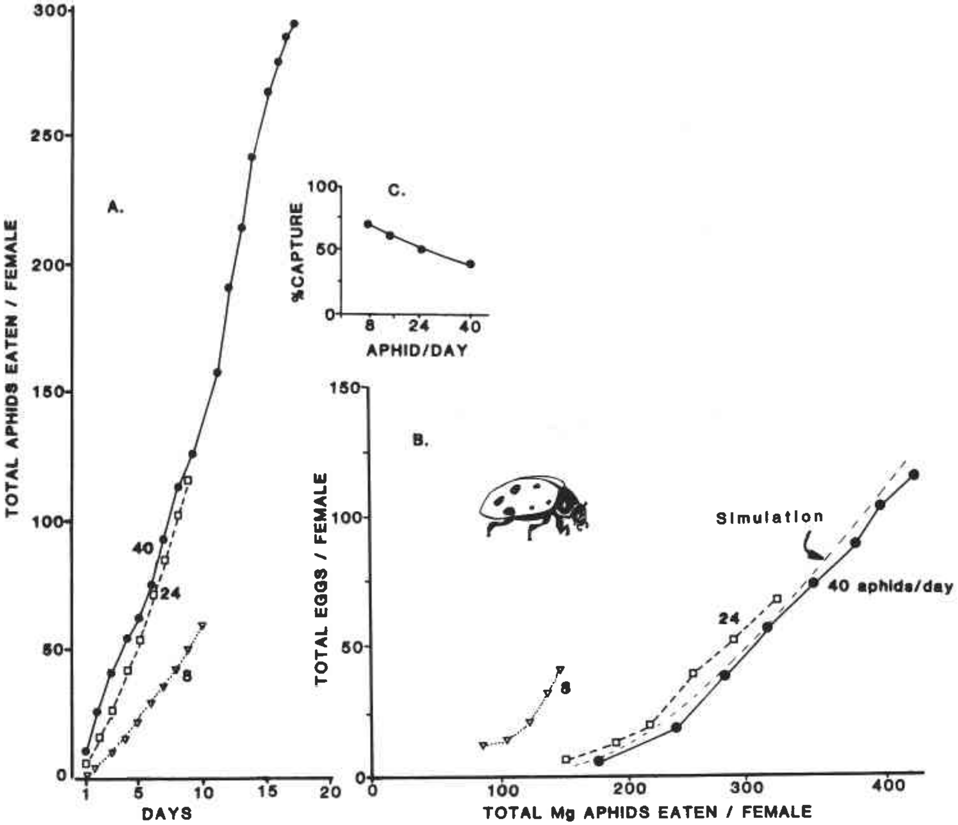


FIG. 7. Per capita ladybird beetle growth and development: (A) cumulative daily consumption of aphids; (B) cumulative production of eggs on cumulative consumption of aphids; and (C) the proportion of aphids offered that were eaten (A.P. Gutierrez, unpublished data). The results are from variable numbers of adults (10–20) kept at 25°C.

matter growth at time 1700 DD occurred when the rate of leaf production was equal to the death rate (i.e. at maximum leaf area index) (Fig. 9A). In cassava, demands of growing fruits for photosynthate are relatively small, and those of tubers are quite large. Tuber growth in the model is considered another form of vegetative growth, and all attempts to give it a higher priority met with failure.Tubers initially grew at about the same rate as did stem plus root. The increasing discrepancy over time between accumulated tuber and stem plus root dry matter was due to the fact that petioles were shed when leaves were shed. Slowing of dry matter accumulation in stem and tuber in the field occurred at about time 4000 DD due to increases in maintenance respiration without a concomitant increase in leaf production or retention. The simulation also predicted the slowing because the supply/demand ratio became less than unity at this time. Slight water stress did not occur in the field until after time 4200 DD. Cassava is very drought tolerant (Mahon *et al.* 1977), but water stress often occurs in the field during the dry season.

Insect data. Dry matter allocation patterns in pea aphid are similar to those measured by Randolph *et al.* (1975) (Fig. 12A). The patterns for pea aphid and the ladybird beetle (Figs. 12–13A) are also very similar to those of the plants studied here, but the allocation ratios (Figs. 12–13C) of reproduction to immature growth are much smaller in plants. Most insects do not reinitiate somatic growth after completing a reproductive cycle as

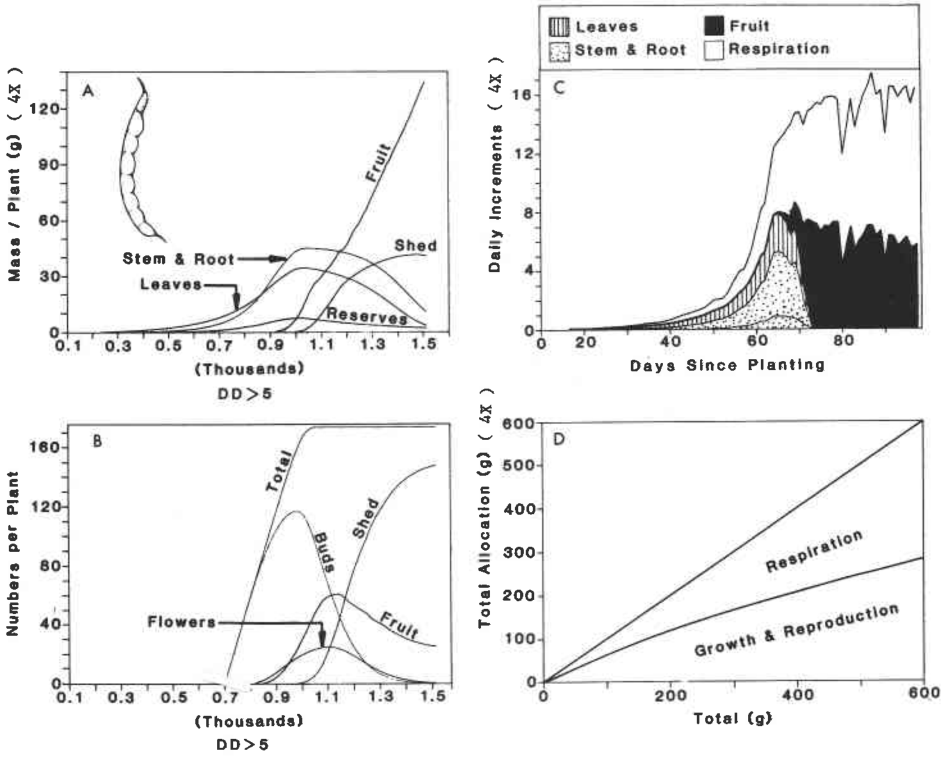


FIG. 8. Simulated bean growth and development: (A) dry matter allocation (4 ×) to leaves, stem plus root, reserves, and shed and retained fruit; (B) numbers (1 ×) of total fruits produced, fruit buds, flowers, pods, and total shed fruits; (C) allocation patterns (4 ×) to plant subunits; and (D) the allocation fractions (4 ×). The data were plotted on DD above 5°C using 1983 weather data from Londrina, Pr., Brazil (see also Fig. 2).

commonly observed, say in cotton. Reproduction may be determinate (e.g. pea aphid) or indeterminate (e.g. ladybird beetle).

Numbers of Reproductive Forms. Plant data. The simulated patterns of age structure and numbers of fruits in bean, cotton, and tomato are shown in Figures 8, 10–11B. The patterns of total fruit buds, small buds, large fruits, and shed fruits are similar between these species. In cotton, fruit buds are produced continuously after the time of the first fruiting branch until vegetative growth is inhibited by carbohydrate stress (Gutierrez *et al.* 1975). A large proportion of fruit initiated is shed in cotton and tomato, compared with bean. In cotton and tomato, small second regrowths of fruit buds are observed late in the season and are predicted by the model.

Insect data. New embryos were initiated by pea aphid viviparae until after peak progeny production, when despite abundant food, the feeding rate slowed and finally stopped (Randolph *et al.* 1975; Fig. 6B vs. 12B). The determinate reproductive pattern in pea aphid is similar to that of bean. In contrast, eggs were produced continuously by *H. convergens* females until they died of old age (Fig. 7B vs. 13C).

An aphid embryo is large relative to the size of the adult (4–5%), but a coccinellid egg is small compared with the size of the adult female (0.1%). The model suggests that food supply/demand stress affects the reproductive pattern in pea aphid more than in ladybird beetles where reproduction responds quickly to food supply. In contrast with pea aphid, the reproductive pattern in the long-lived ladybird beetle is indeterminate and similar

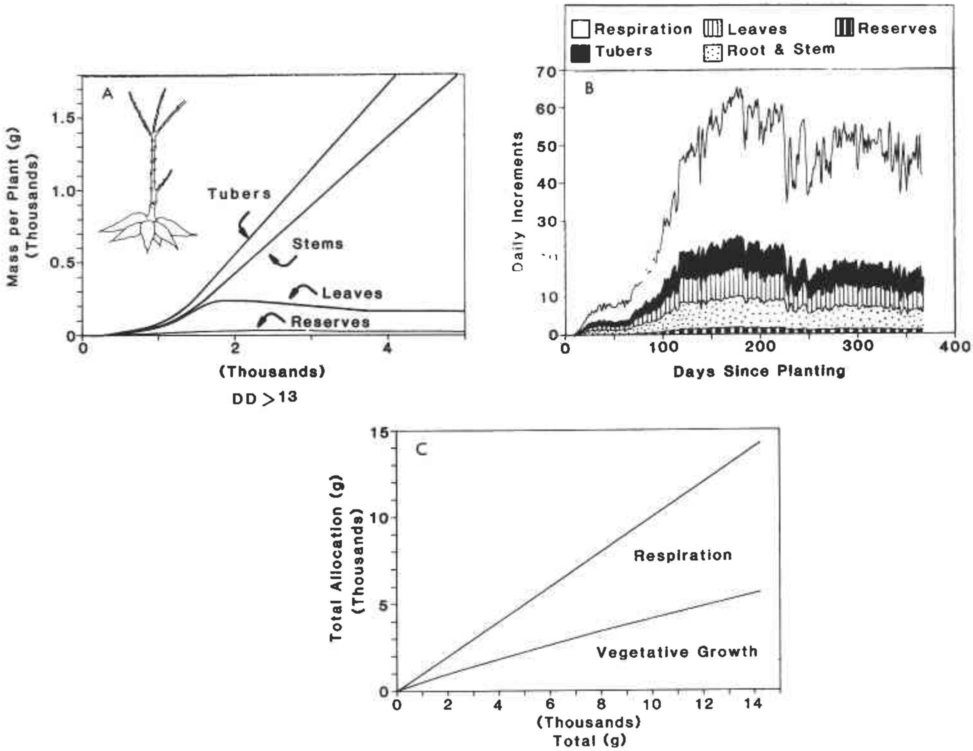


FIG. 9. Per plant simulated cassava growth and development: (A) dry matter allocation to leaves, stem plus root, and tuber; (B) daily allocation patterns to plant subunits; (C) allocation ratios. Data plotted on DD above 13°C using 1983 weather data from the International Institute of Tropical Agriculture, Ibadan, Nigeria (see also Fig. 3).

to that of plants such as Egyptian cotton, which produces and matures small fruits throughout the season.

As in plants, the predicted quantity of reproductive dry matter lost or resorbed is relatively small in the two insects, but in contrast with plants, the number of potential progeny aborted by the insects is also small.

Daily Allocation of Dry Matter. Daily dry matter acquisition and allocation data are generally not available in the literature, and validation data were available only for pea aphid (Fig. 6B). The results (Fig. 10C) show clearly the indeterminate growth habits of cotton where some late season vegetative and fruit regrowth is predicted. This contrasts with that observed for bean (Fig. 8C) where only one fruiting cycle occurs, and with cassava (Fig. 3B) which grows vegetatively throughout the season when conditions are favorable because no fruit-induced stress occurs. The daily allocation patterns for pea aphid (Fig. 6B vs. 12B) are determinate and similar to those of bean (Fig. 8C), but the patterns in ladybird beetle (Fig. 13C) are determinate for immature growth and indeterminate for reproduction. The fluctuations in the daily acquisition patterns for all species, except pea aphid, are due to daily fluctuations in their resource base (i.e. light energy for plants and aphid prey for the ladybird beetle) and to daily fluctuations in temperatures experienced by the species. The resource base for pea aphid, plant sap, was kept constant to facilitate comparisons to the Randolph *et al.* (1975) laboratory data.

Dry Matter Allocation Ratios. Daily rates of energy allocation show the dynamics, but a more meaningful picture of allocation emerges from plotting cumulative totals allocated

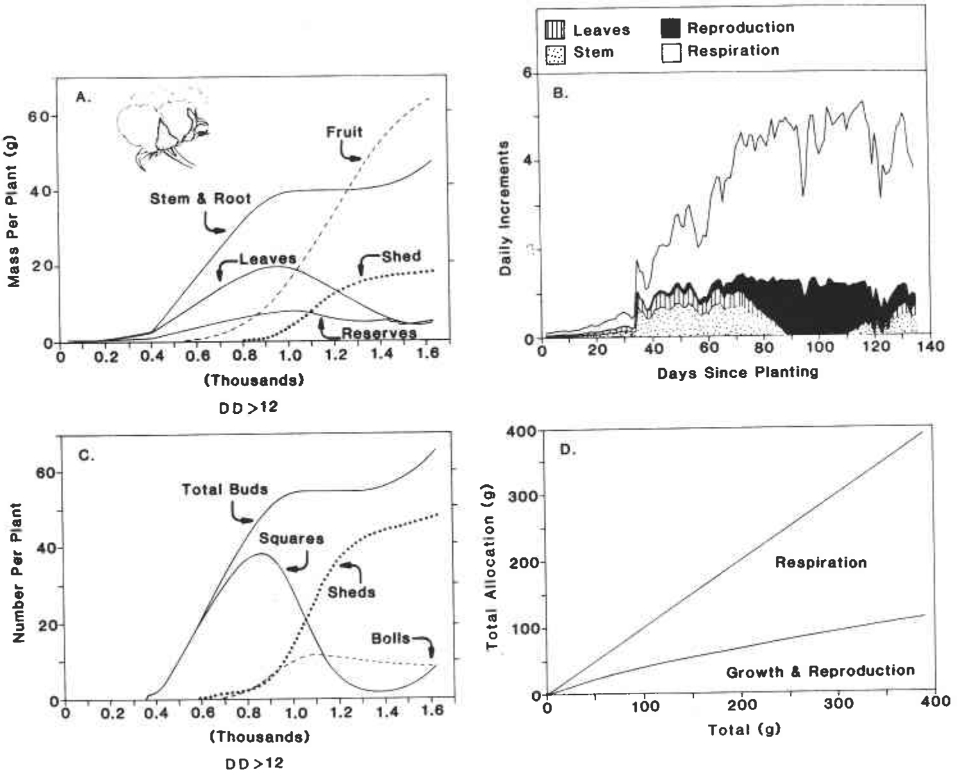


FIG. 10. Per plant simulated cotton growth and development: (A) dry matter allocation to leaves, stem plus root, reserves, and retained and shed fruits; (B) numbers of total fruits initiated, fruit buds, flowers, green bolls, and total shed fruits; (C) daily allocation patterns to plant subunits; and (D) allocation ratios. The data were plotted on DD above 12°C using 1983 weather data from Londrina, Pr., Brazil (see also Fig. 4).

to respiration, egestion (in the insects), and combined growth and reproduction (i.e. assimilation) to the total acquired (Figs. 8–13D). The results indicate that the allocation fractions are nearly constant in all species. This is very surprising in view of the fact that temperatures and resource base for many of the species were variable over time. Under constant conditions one would expect constant values as shown by Gutierrez and Baumgaertner (1984*a*) in their reanalysis of the Randolph *et al.* (1975) and pea aphid data.

Bean appears the most efficient of the plants, assimilating ca. 47% of the energy produced compared with 38% for cassava, 31% for tomato, and 27% for cotton. Excluding cassava, the same trends exist for fruit/vegetative allocation ratios. If one considers only the edible or economic components, cassava is by far the most productive. The high photosynthetic rates for cassava predicted by the model compare very well with those reported by Mahon *et al.* (1977). The ladybird beetle has a predicted maximum reproduction to growth ratio of 13.4:1, and that for pea aphid is 3.7:1. This greater apparent efficiency of the beetle occurred despite the suggestion that it is only 61.8% as efficient as pea aphid in converting host dry matter to somatic growth and reproduction. The predicted respiration rate per unit body weight is higher in the aphid than in the beetle, but the egestion rate is considerably higher in the beetle (Gutierrez *et al.* 1981). Unfortunately, the relevance of such predictions cannot be assessed in isolation, and must await the development of a systems model sufficiently complete to allow questions concerning their contribution to fitness to be asked in a more global ecological context (Gutierrez and Regev 1983).

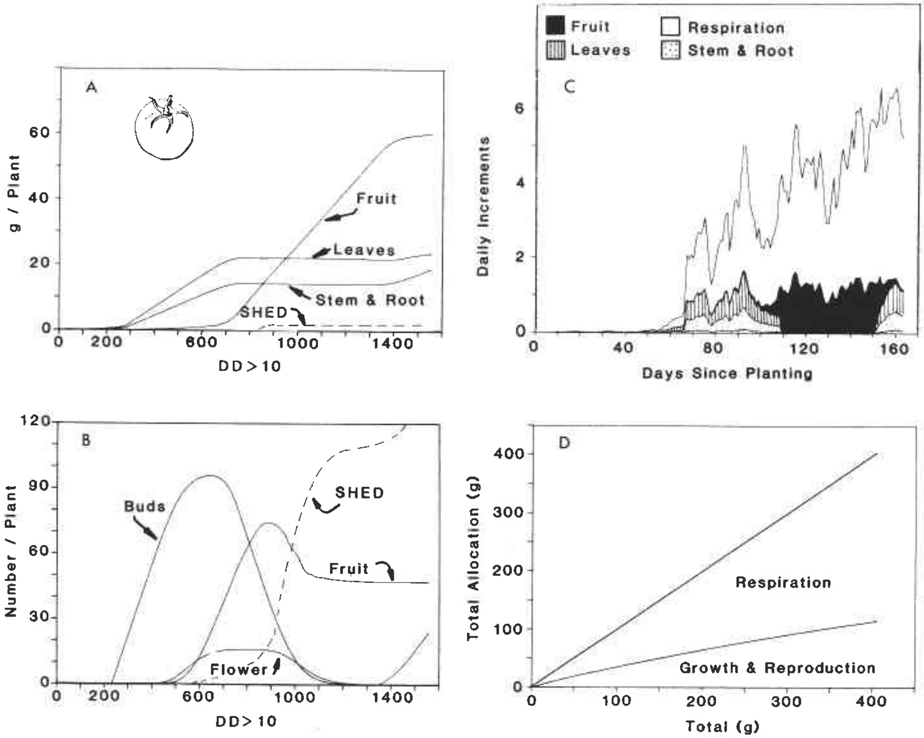


FIG. 11. Per plant simulated tomato growth and development: (A) dry matter allocation to leaves, stem plus root, and retained and shed fruits; (B) numbers of fruit buds, flowers, large fruits, and total shed fruits; (C) daily allocation patterns; and (D) allocation ratios. Data plotted on DD above 8°C using 1983 weather data from Davis, California (see also Fig. 5).

Discussion

The analogies between plant allocation processes during growth, development, and reproduction, and those in insects (possibly other animals) make possible the formulation of a general model for per capita growth and development. Ideally, the model should be sufficiently general so that only changes in parameter values should be required to simulate their development. This was demonstrated at the per capita energy acquisition and allocation level for bean, cassava, cotton, ladybird beetle, pea aphid, and tomato. The development of population level models are an extension of this (Gutierrez, Baumgaertner *et al.* 1984*a*), but the complication of species behavior and related phenology precludes generality at the population level at this time without modifications to accommodate it.

The significant contribution of this paper is the elaboration of a general model for prey acquisition and photosynthesis and its assimilation (cf. Gutierrez *et al.* 1981 and Gutierrez and Baumgaertner 1984*a*, 1984*b*), and the comparison of the model against data sets for six species in widely separated taxa. The model assumes that the processes of energy acquisition in both plants and animals are driven by genetically controlled age and time varying maximum demands for growth, reproduction, reserves, respiration, and egestion where appropriate, and that the assimilation process is driven by the supply of energy. The question then arises as to why growth and reproduction are determinate in some species in the presence of abundant food.

In plants, many different hormones affect the developmental process, but generally the allocation of photosynthate is thought to be controlled by hormone concentrations and

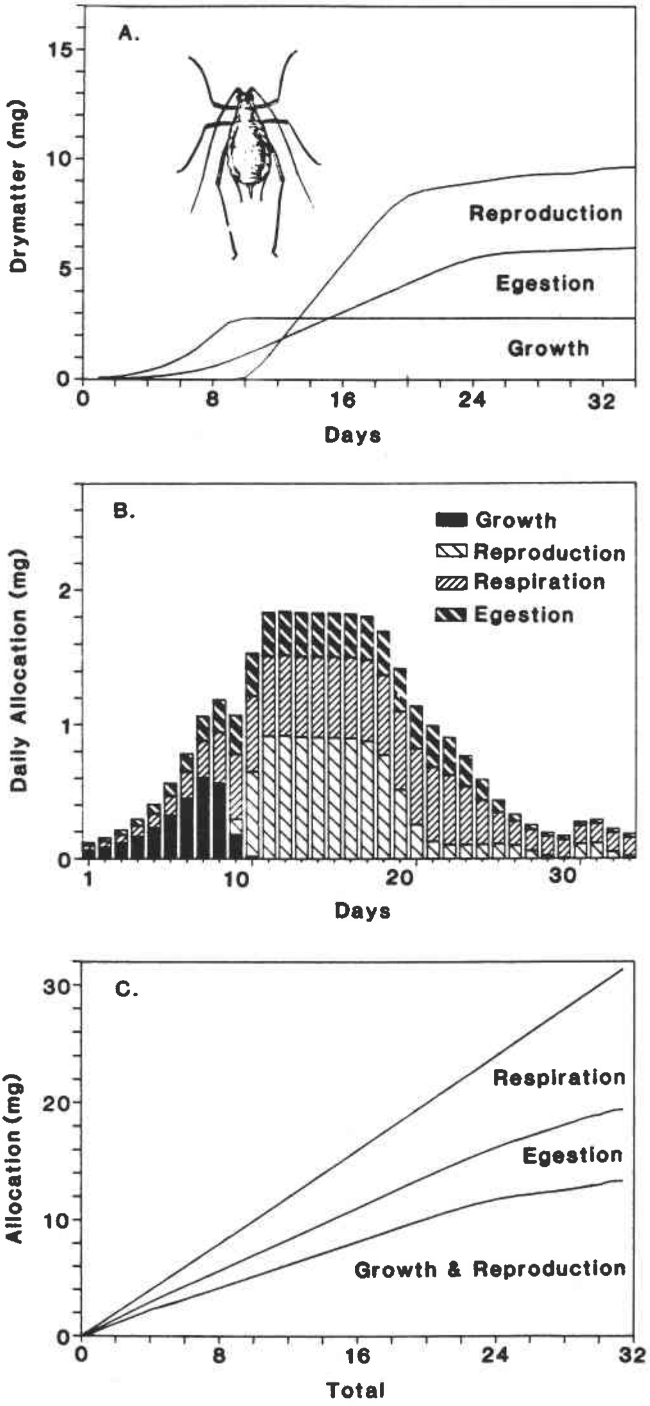


FIG. 12. Per capita simulated pea aphid growth and development: (A) patterns of cumulative growth, reproduction, and daily available reserves; (B) daily dry matter allocation to immature growth, reproduction, egestion, and respiration; and (C) the allocation ratios. Data are plotted on days as in Figure 6.

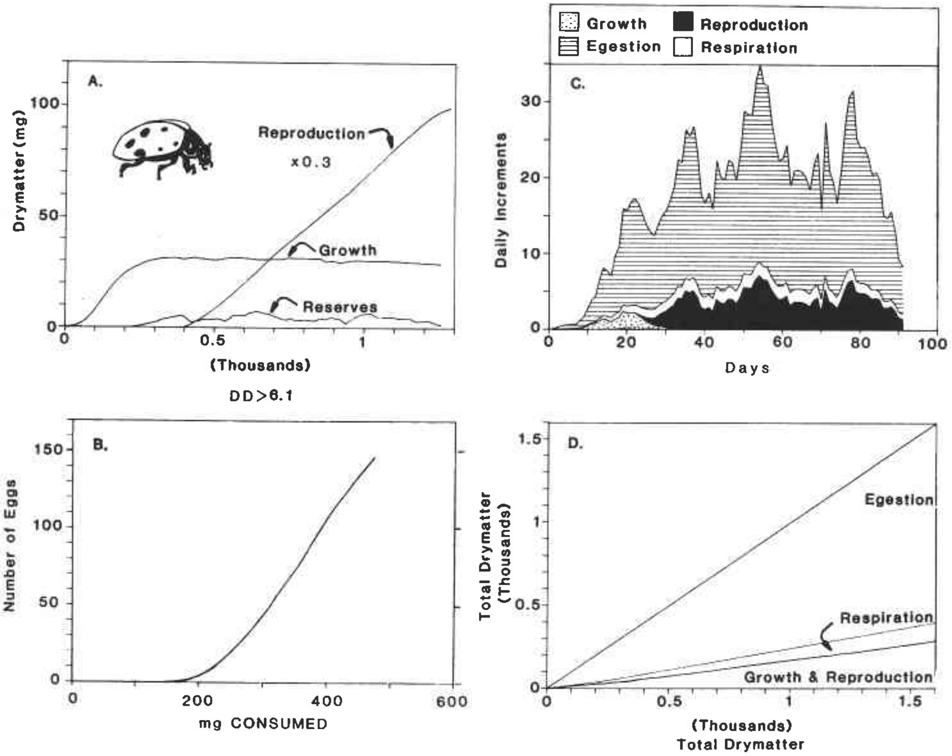


FIG. 13. Per capita simulated ladybird beetle growth and development: (A) patterns of cumulative growth, reproduction, and daily available reserves; (B) numbers of eggs produced on cumulative aphid consumption; (C) daily dry matter allocation to immature growth, reproduction, egestion, and respiration; and (D) the allocation ratios. Data in (A) are plotted on DD above 6.1°C, and those in (B) are plotted on days as in Figure 7.

by proximity to and strength of sinks (Noggle and Fritz 1976). For example, apical dominance in plants may suppress lateral bud growth, yet hormone production by embryonic tissues in fruits may produce sink strength sufficient to overcome apical dominance and cause a priority shift of photosynthate from vegetative to reproductive growth. The model is demand driven, suggesting that the stimulus for growth continues so long as the supply of photosynthate meets some of the growth demands. In some plants, additional growth cycles may occur after the fruits mature, provided weather remains favorable (e.g. cotton). Pruning of fruits from all of these species enhances vegetative growth. In other species such as cassava, vegetative growth continues at a rate proportional to the supply/demand ratio until respiration costs become larger than the supply or until unfavorable weather occurs. The model accommodates most of these phenological observations for the four plant species examined here.

In insects, the interplay between titers of juvenile hormone (JH), the molting hormone ecdysone (EC), and others during growth, development, and reproduction is well known (Chapman 1982). The titer of JH is generally higher at the beginning of an instar when somatic growth is greatest, and falls at the end during periods of differentiation. The reverse is true for EC. In reproduction, the processes of cell division (egg enlargement) and vitellogenesis (yolk accumulation) are stimulated by JH. In ladybird beetle females, eggs undergo only enlargement and vitellogenesis, and in aphids ova are produced that undergo further embryonic development within the female culminating in the deposition of walking nymphs. In aphids, the extra step in embryonic development could be considered an instar with initial high JH titer after vitellogenesis which declines as the embryo matures with a concomitant increase in EC titer. This kind of interuterine larval development is carried to an extreme in tsetse fly where a single larva matures to maximum size within the adult female, after which another reproductive cycle may begin.

A **hypothesis** for the observed determinate feeding pattern and allocation of assimilates in adult pea aphids is that the growing embryonic tissues produce JH which stimulates the adult to feed and makes the growing embryos the primary sinks for ingested nutrients. This implies that the hormones produced by the embryos escape into the mother's hemolymph and stimulate her feeding pattern. Thus, as several embryos mature within the mother, JH titer lessens and the increasing titer of EC prior to the emergence of the nymphs stimulates a slowing of the female's rate of feeding. This may occur when a large number of embryos reach maturity simultaneously, creating a situation where the EC-producing mass outweighs the younger JH-producing mass. Our hypothesis suggests that this stimulates the female not only to stop feeding, but also slows or stops further initiation of embryos. This hypothesis is supported by the aphid data, but unfortunately other data are not available in the literature to verify it. Increases in aphid fecundity associated with delayed topical applications of JH to adult aphids have been shown (Hardie and Lees 1985).

The hypothesis also appears to explain the reproductive pattern in the ladybird beetle, whose eggs do not have the last step in ova development seen in aphids. Hence according to the hypothesis, JH titers are expected to remain high and the female beetles should continue (as observed) to feed and to produce eggs until their ovaries become senescent, or food becomes limiting. Of course ladybird beetles are known to enter diapause in response to changes in diet (Hagen and Sluss 1966), but this aspect was not included in the model.

That hormones stimulate or trigger growth and development in plants and insects is well known, but the details are not entirely understood. Hormone production is genetically coded for activity times and levels specific to the life cycle of the species (i.e. at the individual level). The model simulates several aspects of organism growth and development, but the physiology underlying it is subsumed in the interplay between supply and demand. The model does not contain the dynamics of hormonal control, rather the use of the supply/demand ratio to control the allocation of assimilates is our convenient surrogate.

Ecological Context. The ecology and physiology of species are coevolved, and growth and reproductive strategies are reflections of that process. Fisher (1930) elegantly provoked this question, and stimulated considerable research interest in this area.

Domesticated plants show evidence that energy is conserved, as a cursory look at both the number and dry matter data for bean, cotton, and tomato reveals. Each of these species loses a large number of fruit buds, but relatively little dry matter is in them. These results are in accord with the empirical studies of Bookman (1983) on the cost of flower abscission and fruit aborting in milkweed (*Asclepias speciosa* Torr.). Their reproductive allocation conserves energy as well as compensation time, enabling the plants to compensate for fruit loss due to plant stress, herbivory, and other sources of fruit loss (Gutierrez *et al.* 1975; Wang *et al.* 1977; Gutierrez and Regev 1983). Herbivores (and higher trophic levels) themselves also appear to compensate for variable food supply at the individual level, but would appear to compensate for predation and parasitism at the population level.

Strategies conserving energy are important components in fitness maximization, but unfortunately domesticated plants are not ideal models for such studies. However, direct application of the cotton model to the analysis of fitness of sylvan cotton and boll weevil has been shown (Gutierrez and Regev 1983). Examining these questions in the context of fitness maximization is the ultimate goal of this research.

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