ECOLOGY, BEHAVIOR AND BIONOMICS

Tritrophic Analysis of the Coffee (*Coffea arabica*) - Coffee Berry Borer [*Hypothenemus hampei* (Ferrari)] - Parasitoid System

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Análise Tritrófica do Café (*Coffea arabica*) - Sistema Broca-do-Café
[*Hypothenemus hampei* (Ferrari)] - Parasitóide

RESUMO – Desenvolveu-se um modelo tritrófico de simulação para o cafeeiro (*Coffea arabica var. mundo novo*), a broca- do- café [*Hypothenemus hampei* (Ferrari)] e três de seus parasitóides. O modelo contém a dinâmica da planta estruturada por idade e massa e é influenciado por fatores edáficos e meteorológicos. Dados extensivos de matéria seca de plantas de cafeeiro foram coletados durante três anos e dados de campo sobre a dinâmica da broca foram observados durante um ano. Os trabalhos foram desenvolvidos na sede do IAPAR, Londrina, PR, Brasil. Estes dados foram usados para estimar as relações alométricas e os parâmetros de alocação de matéria mas os parâmetros para a broca e três dos seus parasitóides, foram baseados em dados resumidos da literatura. Níveis iniciais de fatores do solo (nitrogênio e água) e dados climáticos foram usados para executar o modelo. Este modelo é independente dos dados de campo, entretanto simula a dinâmica de ramificaçao, frutificação e crescimento da matéria seca das subunidades da planta. Resultados de simulação sugerem que, dos três parasitóides introduzidos para controlar a broca, somente o eulofideo adulto endoparasitóide (*Phymastichus coffea* La Salle) exibe caracteristicas demográficas para, potencialmente controlar as populações da broca . Os efeitos da colheita, a remoção dos frutos não colhidos (na planta e no solo), liberações inundativas de parasitóides e o uso de inseticidas com diferentes características de toxidez e persistência sobre a dinâmica da broca, foram avaliados. O modelo é flexível e fornece uma base sólida para incorporar novos conhecimentos, novas variedades e a biologia de novos inimigos naturais a nível mundial.

PALAVRAS-CHAVE: Insecta, broca-do-café, parasitóides, controle biológico, modelo tritrófico.

ABSTRACT – An age-mass structured multi-year tritrophic simulation model of the coffee (*Coffea arabica var. mundo novo*) - coffee berry borer

[*Hypothenemus hampei* (Ferrari)], borer - three parasitoid system was developed. Three years of extensive plant drymatter data and one year of field data on borer dynamics were collected at Londrina, PR, Brazil. The allometric relationships and parameter for plant drymatter allocation were estimated from the field data, but the parameters for borer and its three parasitoids were summarized from the literature. Initial levels of soil factors (e.g., nitrogen and water) and observed weather data were used to drive the model. The model is largely independent of the field data, yet it simulated the dynamics of plant branching, fruiting and drymatter growth of plant subunits. Simulation results suggest that of the three parasitoids commonly introduced to control the borer, only the eulophid adult endo-parasitoid (*Phymastichus coffea* La Salle) has the demographic characteristics to potentially regulate borer populations. The effects of harvesting, cleanup of abscised berries, inundative releases of parasitoids and pesticides with various toxicity and persistence characteristics on borer dynamics were evaluated. The model is very flexible, and may provide a sound foundation for incorporating new findings, new varieties, and the biology of new natural enemies worldwide.

KEY WORDS: Insecta, coffee, coffee berry borer, parasitoids, biological control, tritrophic modeling.

The economic value of coffee (*Coffea arabica* var. *mundo novo*) worldwide is about 15 billions dollars per year, and the exotic coffee berry borer [broca do café , *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae)] threatens it production in many areas. This pest was accidentally introduced to South America (Oliveira Filho 1927, Gallo *et al*. 1978), and the recent expansion of its range into Colombia, Central America and Mexico presents a vexing problem for biological control specialist (Baker 1984, Klein -Koch *et al*. 1988, Barrera *et al*. 1990a,b). Attempts to control borer using classical biological control and inundative releases have a long history (LePelley 1968, Cenicafe 1990, Orozco & Aristizabal 1996, Aristizabal *et al*. 1996), and several agencies in affected Latin American countries are currently introducing parasitoids and pathogens to control it (Hoyos & Aristizábal 1996).

In this paper, field data from Brazil on coffee growth and development and borer dynamics are summarized, and a tritrophic age-structured simulation model of the coffee system composed of coffee, borer and three exotic parasitoids is presented and used to analyze various scenarios for control of borer. The model simulates the dynamics of the plant, borer, two species of larval - pupal parasitoids (*Cephalonomia stephanoderis* Betrem and *Prorops nasuta* Waterston, family Bethylidae) and an adult endoparasitoid (*Phymastichus coffea* LaSalle, family Eulophidae). The bethylid parasitoids have been used extensively for inundative releases in many affected regions. A larval parasitoid, *Heterospilus coffeicola* Schemied (family Braconidae) is known, but it was not included in our analysis because of insufficient bionomics data (Toledo & Fonseca 1935). Tritrophic models that include the plant are being increasingly used to assess the efficacy of biological control agents (Gutierrez *et al*. 1988b, 1993, Mills & Gutierrez 1996, Gutierrez 1996), because failure to include it often cripples the utility of such models for evaluating pest management strategies.

Materials and Methods

Coffee. Field studies were conducted at the

Instituto Agronômico do Paraná (IAPAR) at Londrina, PR, Brazil (23° south latitude). A one-hectare plot of coffee (var. *mundo novo*) was planted at a density of two seedlings per hill in a 3x2-m grid on November 12, 1982. The seedlings had six pairs of leaves at planting and were grown under natural rainfall during the period March 10, 1983, to June 1, 1986. Three samples consisting of two plants from the same hill were taken at 20-day intervals. Each tree was dissected by branch into its component subunits (e.g., leaf, branch wood, mainstem and root and fruit). The taproot, but not the fibrous roots, was excavated. Fruit drymatter, but not berry numbers, were recorded. The plant material was dried in an oven at 60°C for three days and weighted.

Growth of individual branches continues for several seasons with fruits buds initiated from the prior year's growth. The current season's growth is distinguished from that of prior seasons by its green color. During development, each berry passes through a pre-flower bud period (assumed to be eight weeks) and four post flower growth phases (I-IV, Fig. 1, cf., Salazar *et al*. 1993) that vary in their relative preference to attack by borer (Cure *et al*. 1998).

Coffee Berry Borer. The phenology and abundance of borer life stages were estimated from 30 berry collected during the period February 7, 1986, to July 7, 1986. Ten stage III berries in the top, middle and bottom levels of the plant were selected at random. The berries were dissected and the number and age structure of borer were recorded. The numbers of adults killed by the pathogen *Beauveria bassiana* (Bals.) Vuill. were also recorded.

Initial Conditions of the Model. The initial conditions of the model include estimates of plant mass, age structure of all subunits and initial levels of animal populations and their age structure. Rough estimates of root zone volume, initial inorganic nitrogen and organic matter as well as soil water holding capacity and current content. The parameters of all animal species were summarized from the literature (see Tables 1and 2).

Daily weather data recorded at IAPAR included max-min temperatures (°C), mm rainfall, solar radiation in watts/m^2/day (see Fig. 2) and average km of wind per day were used to drive the model. Time and age in the model are in physiological time units (degree-days, *dd*) above the developmental threshold for each species. Non-linear developmental rate models can be used but data to characterize them are insufficient. A five-year simulation of the coffee system requires 15s on a 233 MHz microcomputer.

Phenology of Coffee Growth and Development. The plant drymatter data are plotted on physiological time (*dd* > 11.25°C, Fig. 3). The lines through the data were eye fit to emphasize trends. Comparisons with simulation results are presented in a later section.

Flower drymatter was first observed at about 5700 *dd* with a second flowering occurring at about 11000 *dd* (Fig. 3a). Plant vegetative growth (i.e., green wood and leaves) (3c,d)) slowed shortly after flowering began and coincided with the period of rapid phase II and III berry growth (Figs. 1, 3b). This slowing is seen as plateaus and later declines in leaf and green stem mass. Slowing of vegetative growth occurs because growing berries are stronger competitive sinks for photosynthate. As berries mature (phase IV), a second cycle of vegetative growth occurs followed by a larger second flowering (Fig. 3a). The field studies were terminated before the full effects of the second fruiting cycle could be observed.

Branching (Fig. 3e), mainstem node numbers, plant height and stem diameter (Fig. 4) slowed as vegetative dry matter growth slowed. Mainstem nodes were produced at a rate of one per 300 *dd* before time 6000 *dd*, but the rate slowed to one per 430 *dd* thereafter (a 43% decrease). Two lateral branches are produced at each mainstem node, and their rate of production similarly slowed.

Strong allometric relationships were found in the drymatter data (Table 3 and Fig. 5) con-

Table 1. Some parameters for tritrophic coffee systems model.

Coffee (*Coffea arabica* var *mundo novo*)	Coffee Berry Borer (borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae)	*Cephalonomia stephanoderis* Betrem (Hymenoptera: Betylidae)	(Hymenoptera: Bethylidae)	*Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae)
(see text)	0.25 immigration rate (adults/ plant/day) Fruit attack preferences 0.0; {pin head} 0.2; {fast growth} 0.4; {endosperm filling} 0.8; {mature} Borer ages in dd 0.0 - 52.0 {egg stage} 52.0 - 308.0 {young larvae} 308.0 - 380 {pupal stage} 380.0 - 505.0 {young - pre-ovipositing adults} 505.0 - 850 {older adults} Eggs / female / day = 2.5 or 0.241/dd Female biased sex ratio = 10:1 α = proportion of plant searched (see text) Temperature threshold = 11.25°C	Host preference for oviposition: prepupae and pupae Female biased sex ratio 3:1 Age in dd 0.0 - 52.0 {egg stage} 52.0 - 308.0 {larval stage} 308.0 - 390.0 {pupal stage} 390.0 - 1170.0 {adult stage} Host feeding demand =0.02 eggs per female per dd Oviposition rate = 0.1 eggs/ dd/female Initial number of adults (1.0) Immigration rate = 0.1{adults/ plant/day} α = search rate (see text) Temperature threshold = 13.7 °C *Prorops nasuta* Waterston	Host preference for oviposition: large larvae and pre pupae Female biased sex ratio 3:1 Ages in dd 0.0 - 24.0 {egg stage} 24.0 - 126.0 {larval stage} 126.0 - 336.0 {pupal stage} 336.0 - 1000.0 {adult stage} Host feeding demand =0.02 eggs per female per dd Oviposition rate = 0.1 eggs/ dd/female Initial number of adults (1.0) Immigration rate = 0.1 {adults/ plant/day} α = search rate (see text) Temperature threshold = 13.7 °C	Host preference for oviposition: pre-ovipositing adults Female biased sex ratio 20:1 Ages in dd 0.0 - 36.0 {egg stage} 36.0 - 276.0 {larval stage} 276.0 - 324.0 {pupal stage} 324.0 - 370.0 {adult stage} No Host feeding demand Oviposition rate = 0.56 {eggs/dd} Initial number of adults (1.0) Immigration rate = 0.1{adults/ plant/day} á = search rate (see text) Temperature threshold = 13.7 °C

Table 2. Quantitative information on borer and it's main parasitoids gleaned from the literature.

	Hypothenemus hampei Scolytidae	*Prorops nasuta* Bethilidae	*Cephalonomia stephanoderis* Bethilidae	*Phymasticus coffea* Eulophidae	*Heterospilus coffeicola* Braconidae
Fruit preferences	Green: Semi-ripe: Ripe = 1 : 2 : 3.6 (current study)	green :ripe : overipe = 1 :5 :15, oviposition in fruits is in proportions 1 :7 :28 (Toledo, 1942)	green :ripe : overipe = 1 :5 :15, oviposition in fruits is in proportions 1 :7 :28.	Probably green fruits	
Oviposition	Preference increases with increasing berry age to maturation.	On prepupae and pupae (Barrera *et al.*, 1989 ; Abraham *et al.* 1990)	On larvae and pre-pupae of the borer, not in pupae. (Abraham *et al.* 1990)	Attacks pre-oviposition CCB adults before extensive galleries are made	Prefers to lay egg when borer has begun laying
Number of eggs laid / host	The maximum number of borer eggs per fruit (ca. 30 eggs).	1 egg per host (Hempel, 1934)	1 egg per host	2 eggs per adult borer (Infante *et al.* 1992)	One egg is laid per berry, but hatching can eat up to 10 borer eggs per day (or equivalent mass of other immature stages). Kills adult borer before pupation. Adult survive 10 days of starvation (Toledo & Fonseca,1935).
Sex ratio	10:1	Probably same as *C. stephanoderis*	3 :1 (Barrera *et al.* 1989)	20:1 (Feldhege 1992)	
Maximum oviposition	up to 135 eggs	37 (Hempel, 1934)	63.4 (Infante & Luis, 1993)	17-18 (Feldhege 1992)	
Preoviposition period	6 days	13.8 (±2.69) (Abraham *et al.*, 1990)	9 (±0.62) (Abraham *et al.*, 1990)	0 (Infante *et al.*, 1994)	
Oviposition period	20 days	as per *C. stephanoderis*	50 days at 27C (Infante & Luis 1993)	2-3 days	
Study conditions	25°C, 90%RH	25°C, 90%RH	25°C, 90%RH		
Daily fecundity	2 - 3	1.25 -1.5	1.25 -1.5	8	
Egg developmental time	7 days	1.6 (Abraham *et al.*, 1990)	1.6 (Abraham *et al.*, 1990)	3.15 (Feldhege 1992)	
Larval developmental time	12 days	3.8 (Abraham *et al.*, 1990)	2.8 (Abraham *et al.*, 1990)	13.53 (Feldhege 1992)	
Prepupal development	2 - 3 days	3 (Abraham *et al.*, 1990)	2.9 (Abraham *et al.*, 1990)	3.93 (Feldhege 1992)	

Pupal developmental time	4 - 5 days	14 (Abraham *et al*., 1990)	15.6 (Abraham *et al*.,1990)	7.78 (Feldhege 1992)
Immature Developmental time	25-27 days	22.4 (Abraham *et al*.,1990)	23.20 (Abraham *et al*.,1990)	29.7 (Feldhege 1992)
Maximum number per berry	30	3.7 in mass rearing (Portilla &	3.2 in mass rearing (Portilla Bustillo, 1995)	& Bustillo, 1995)
Notes:		A parasitoids stays in a fruit until the brood matures. If no susceptible borer stages at time of attack, parasitoid stays and feed on borer eggs and young larvae preserving older stages for future parasitization.	As in *P. nasuta*, adults feed 2 to 11 days before eggs mature. Adults require 2 eggs or larvae, or two adults per day to survive (Koch, 1973).	Once a host is attacked it leaves the fruit to seek new hosts.

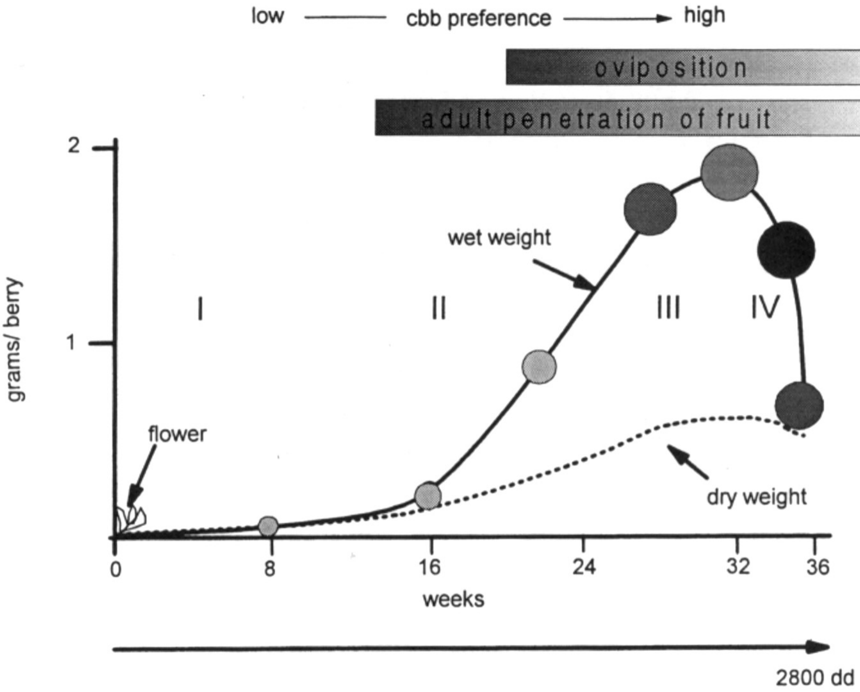

Figure 1. The patterns of growth of individual coffee berries from flowering to fruit maturity plotted on plant physiological time (cf., Salazar *et al.* 1993). Note that borer preference, penetration and oviposition favorability of fruits is also indicated (Cure *et al.* 1998).

firming the internal consistency of the data. Among the relationships are: the ratios of leaf area to leaf mass (Fig. 5a, 3.7dm^2: g); leaf mass to green branch mass (Fig. 5b, 3.06 g: g); plant height to stem diameter (Fig. 5c, 1cm: 0.315 cm); root mass to stem mass (Fig. 5d, 0.375 g: g); and branch mass to stem volume (Fig. 5e, g: cm^3). The strong relationship of fruit mass to brown branch mass (1.1g: g, not shown) suggests that roughly two 0.55g berries mature per g brown branch mass providing a rough estimate of the fruit initiation rate. No significant relationship was found between fruit mass and leaf mass, leaf mass and total branch mass, or green branch and brown branch mass. This occurred because when one is growing the other is not, and/ or subunits such as leaves abscise. Last, we note that the volume of stem increased monotonically with physiological time (Fig. 5f) with the slowing effects of fruit growth seen in the data. These allometric relationships provided important information to formulate the plant model.

Coffee Berry Borer Dynamics. Borer dynamics were studied for roughly 1600 *dd* on the plant's time scale, and the period is indicated by a horizontal line in the lower right of Fig. 3e. The percentages of fruits infested were the same in all strata of the plant (not shown) and exhibited a decreasing trend late in the sampling period (Fig. 6a). Most infested berries contained a single female (Fig. 6b), but an increase is seen as the season progresses due to a small number of multiple attacks (Fig. 6c) and the presence of new females that had

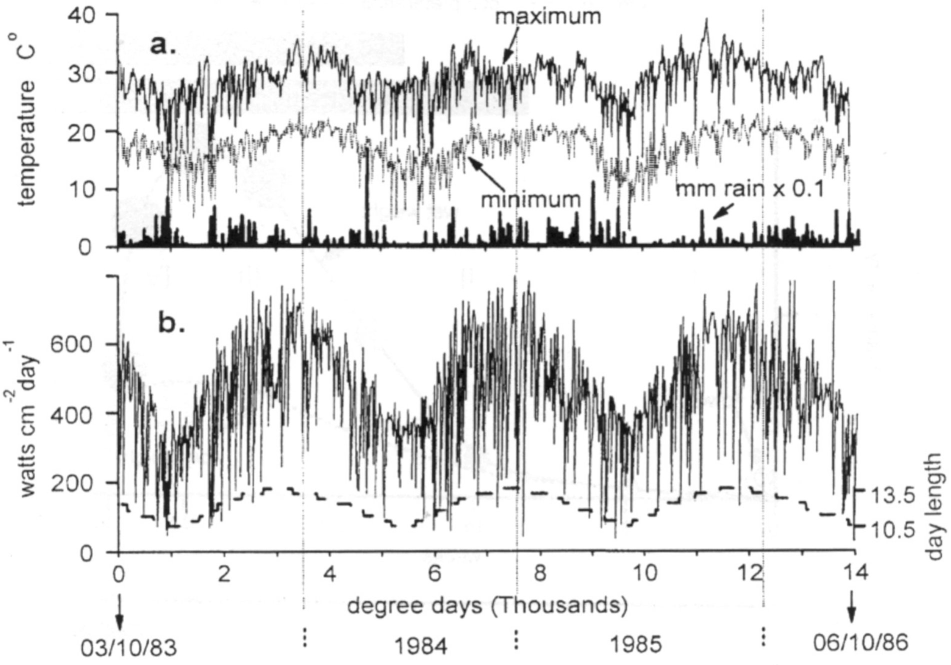

Figure 2. Weather data from Londrina, PR, Brazil for the period 6/10/1983 to 6/1/1986 (D/M/Y) used to drive the tritrophic coffee model.

not left to seek hosts. The number of old adults and the few killed by the fungal pathogen *Beauveria bassiana* (Bals.) Vuill. are shown in Fig. 6c.

The phenologies of borer life stages are shown in Fig. 7. Egg density increased to roughly 4.5 per berries (Fig. 7a) with the observed pattern being the net of eggs laid and losses due to mortality and hatching during the period between samples (see below). Most new adult borer leave the fruit on which they were reared, and this is verified by comparing their small numbers in the samples (<0.3 per berry, Fig. 7c) to the larger numbers of larval stages (Fig. 7b,c). A strong relationship of old females (*y*) per berry to total females per berry (*x*) was found ($y = -21.74 + 0.83x$, $r=0.95$, $n=59$), but only a weak relationship was found between new and old females ($r=0.26$).

In the absence of mortality, the number of egg (E) oviposited (Δe) in thirty berries during physiological time $\Delta t(t)$ at day t may be estimated as

$$\Delta e(t) = \left[\left(\frac{E(t)-E(t-1)}{2}\right)\Delta t\right] \Big/ DEL_{eggs}$$

DEL_{eggs} is the developmental time (*dd*) of the egg stage. The cumulative eggs laid is $E(t) = E(t-\Delta t) + \Delta e(t)$. Similar methods can be used for the other life stages, but we caution that this simple estimation procedure is useful only when the mortality rate is small. Distributed maturation time models with attrition are more appropriate for field studies (Fouque & Baumgärtner 1996).

A Systems Model for Coffee. Models of agricultural and other systems that have applications to field problems have been classed as engineering or demographic (Baumgärtner & Gutierrez 1989). Our model for coffee is a demographic model, and while it is far from a

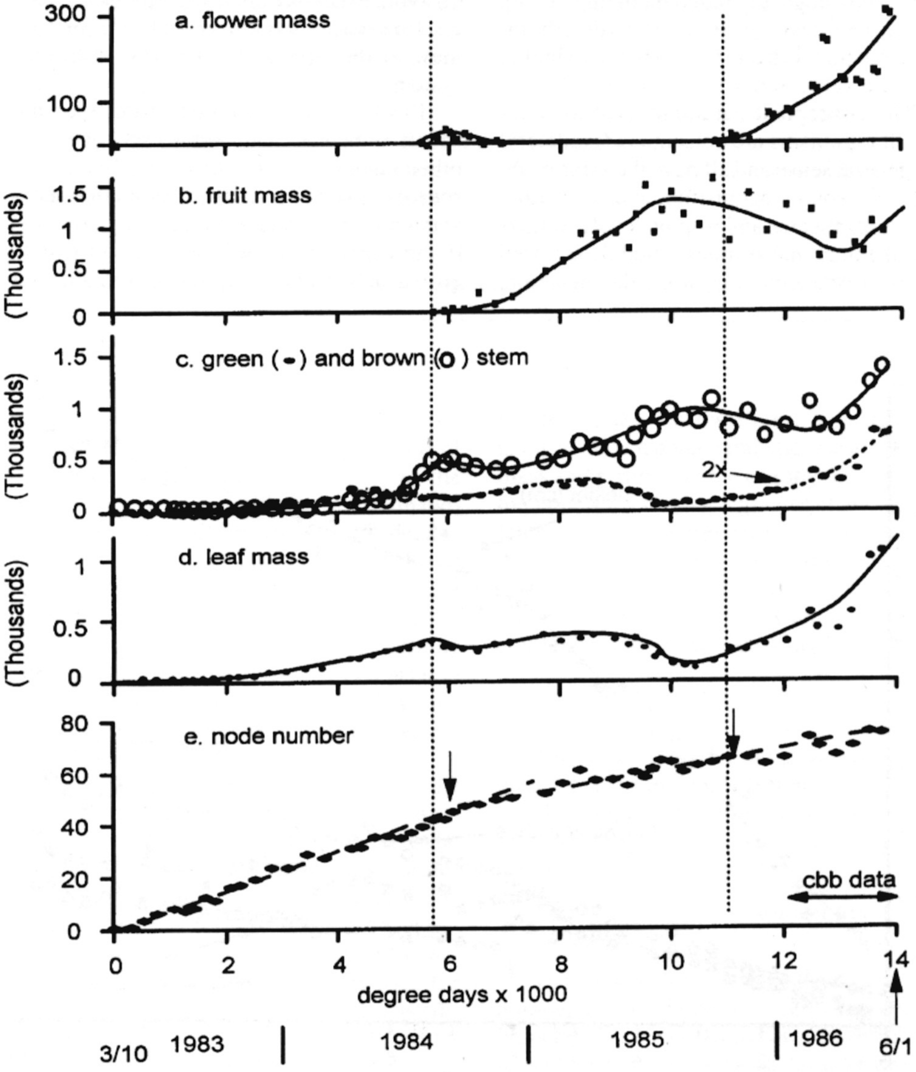

Figure 3. Whole plant coffee dry matter and branching data from Londrina PR, Brazil for the period 6/10/1983 to 6/1/1986. The data have been plotted on physiological time and lines have been eye-fitted to show trends: (a) flower drymatter, (b)leaf drymatter, (c.) green and brown stem drymatter, (d.) total fruit mass and (e.) number of branches. The data are means of six plants. The down turned arrows indicate pruning dates.

one to one description of nature, it is biologically rich. The early work of De Wit & Goudriaan (1978) and colleagues gave impetus to physiologically based modeling of crop growth and development, and indirectly influenced our work and its extension to higher trophic levels (Gutierrez and Wang 1977).

The conceptual paradigm used assumes that all organisms are consumers (predators) in a general sense and all have the same problems of resource acquisition and allocation. Across all species and trophic levels, similar type II functional response models are used for resource acquisition, while the metabolic pool model is used to allocate resources to growth and reproduction (i.e., the numerical response). These models are described below. To avoid excessive citations, interested readers are referred to Gutierrez (1996) for a review of this approach applied to tritrophic systems.

Briefly, leaves seek light, roots seek nutrients and water, and animals seek prey and other resources. All organism allocate resources in priority order to respiration, conversion costs of various kinds, reproduction if the organism is old enough and last to growth and reserves if resources remain after

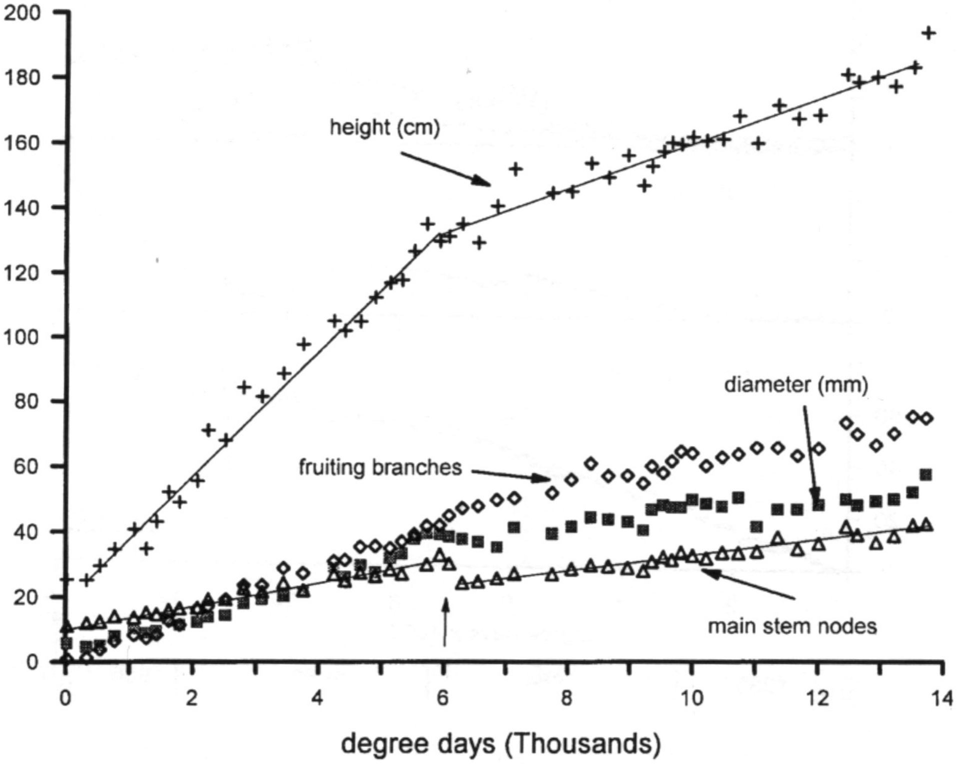

Figure 4. Data on plant height, branch and mainstem node number and stem diameter (see Figure 3).

Table 3. Regressions of six plant averages of different variables in the coffee data (n=56).

Leaf area (dm^2) on leaf mass (grams)	
leaf area = 3.75 leaf mass	
Leaf mass (g) on green wood mass (g)	
leaf mass λ - 7.78 + 3.065 green branch mass	r^2 =0.964
Plant height (cm) on stem diameter (cm)	
height = -4.17 + 0.315 diameter,	r^2 = -0.989
Root mass (g) on previous years stem mass (i.e., brown stem, g)	
root mass = -29.37 +.375 stem mass	r^2 = -0.966
Main stem node numbers on plant height (cm)	
nodes = -11.96 + 4.05 height	r^2 = -0.992
Fruit mass (g) on brown wood mass (g)	
fruit mass = -61.11 + 1.104 brown wood mass	r^2 = -0.878

satisfying all higher priority demands. A key element of the paradigm is that the ratio of the resource acquired (i.e., supply) to the maximum genetic assimilation rate (demand) (i.e., *S/D*) scales all growth - birth - death - aging rates from the maximum to the observed in all trophic levels. Shedding of excess fruit in plants and emigration rates in animals are related to the shortfall (1-*S/D*). The interplay of supply and demand is used at various levels (e.g., whole plant, branch and between competing sinks within a level). Computations of the S/D ratio are reviewed below.

The model simulates the dynamics of the whole plant, or with a simple Boolean instruction the dynamics of each branch. Here the greater detail of branch level dynamics is developed to accommodate future findings. The dynamics models for leaf, stem and root tissues are mass-age structured, while mass - number - age structured models are used for fruit (cf., Gutierrez & Wang 1977). Distributed maturation time age-structured population dynamics models (Vansickle 1977) are used to describe the time varying mass - age dynamics of all species. DiCola *et al*. (1998) reviews these and other related models. All branching levels utilize the same code to update subunit dynamics. With minor modification, the same code is used to model animal population dynamics.

Modeling the Coffee Plant. Key determinants of branch photosynthetic rate are its leaf mass and position in the canopy. Branches in the upper levels have a greater chance of intercepting light energy ($\varphi(t)$ = *cal* cm^{-2} day^{-1}) than those lower down. The proportion of light captured by a branch (*i*) depends on its leaf area index (LAI_i) defined as the ratio of leaf area to the area for plant growth ($A = 300\ dm^2$).

$$LAI_i = cL_i(t)/A \qquad [2]$$

The constant *c* (=3.7 dm^2g^{-1}) converts leaf mass (($L_i(t)$) to dm^2 of leaf area.

To compute the proportion ($\acute{a}_i(t)$) of light reaching level *i* that is intercepted, we use Beers Law.

$$\alpha_i(t) = (1 - e^{-0.805\ LaI(t)}) \qquad [3]$$

The constant *0.805* is the efficiency of light interception. Light not intercepted by higher branches filters in decreasing quantities to lower branches with some striking the ground. If we assume there are *n* branch levels, then the *LAI* for the whole plant is

$$0 < LAI_{tot} = (c\sum_{i=1}^{n(t)} L_i(t)) / A < 4.5 \qquad [4]$$

with the amount of light reaching the bot-

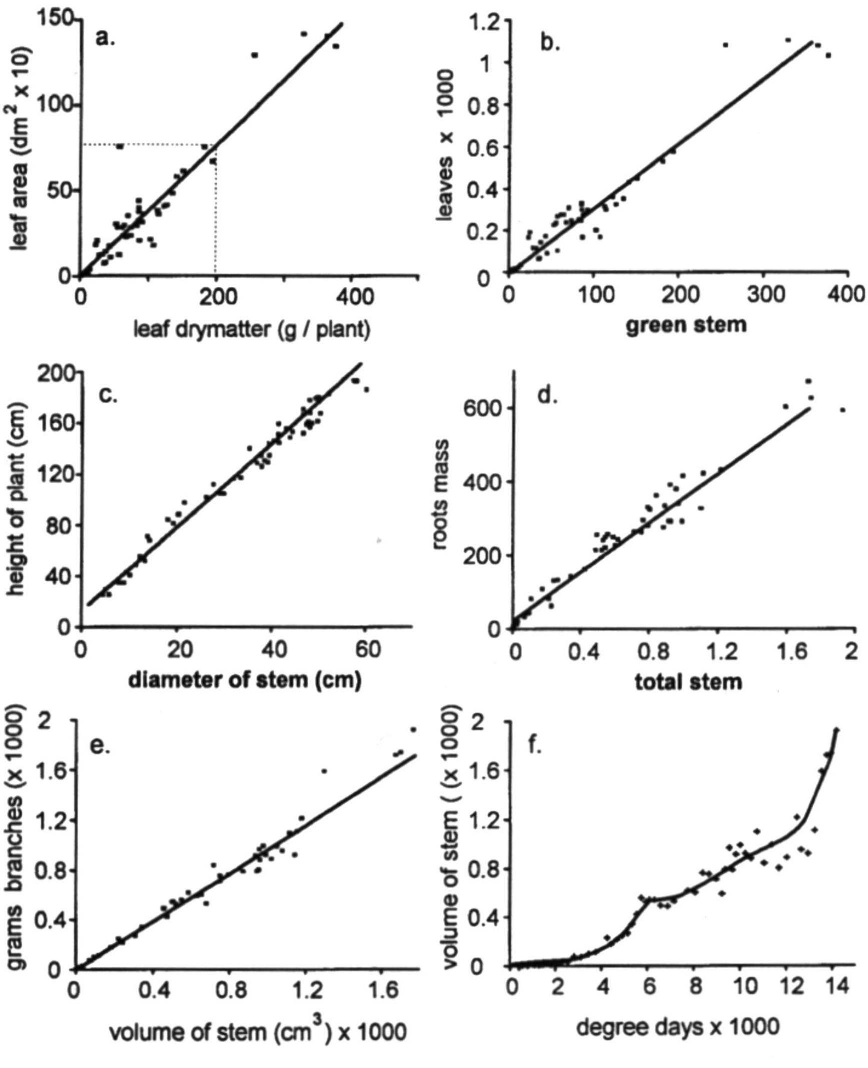

Figure 5. Allometric plant growth relationships: (a.) leaf area to leaf mass, (b.) leaf mass to green wood, (c.) plant height to stem diameter, (d.) root mass to stem mass, (e.) branch mass to stem mass and (f.) stem volume on physiological time.

tom or *nth* level ($\varphi_n^*(t)$) being

$$\varphi_n^*(t) = \varphi(t) \prod_{i=1}^{n-1} e^{-0.805\mathrm{LAI}_i(t)}. \qquad [5]$$

From predation theory, this is the probability of an initial quantity of light (prey) escaping interception (predation) from a series of branches (predators) acting in sequence. Graf *et al.* (1990) used a similar approach to compute the photosynthetic rate of rice in the face of competition from weeds of varying height.

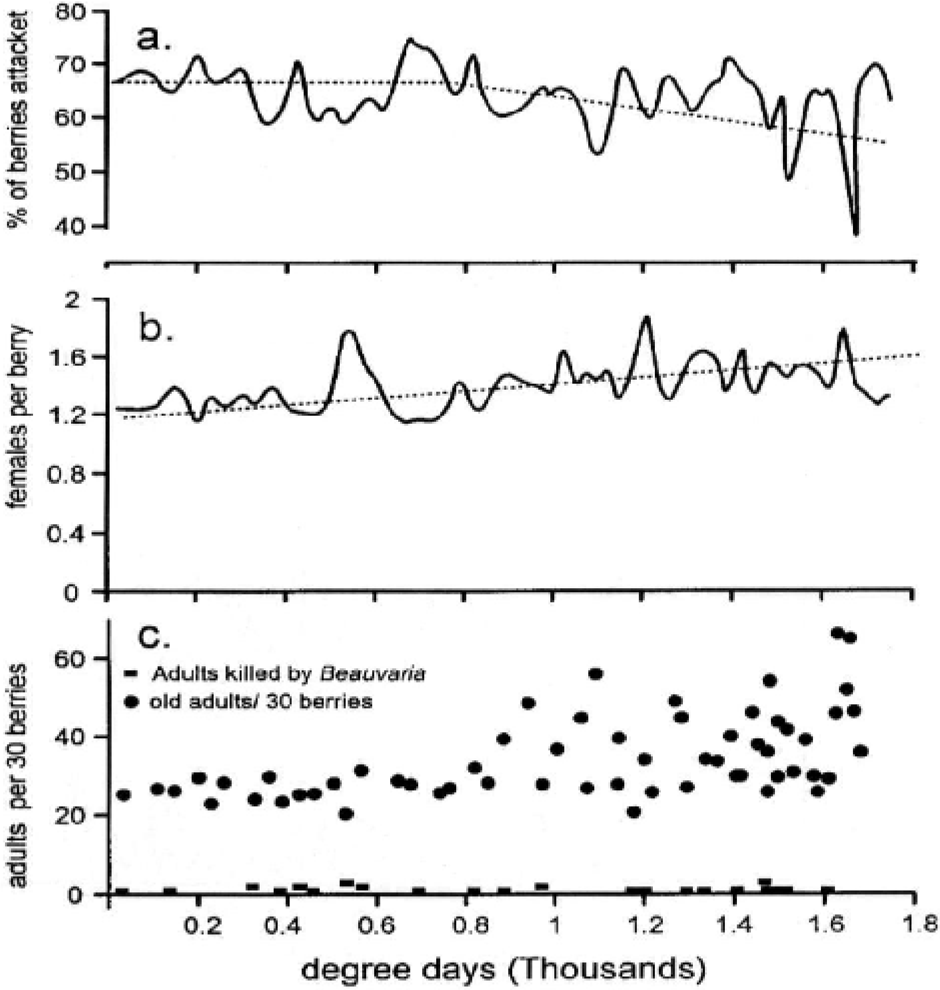

Figure 6. The percentage of coffee berries attacked (a.), the mean number of adult borer per berry (b.) and (c.) the number of old borer adults and those killed by the fungal pathogen *Beauveria* sp.

The amount of carbon fixed (S_i = supply) at time t by the *ith* branch level, assuming all other factors are non limiting (see below), is computed using a variant of Watt's (1959) functional response model

$$S_i(t) = (1 - e^{\frac{-\alpha_i(t)c\varphi_i^*(t)}{D_i(T(t))L_i(t)}})D_i(T(t))L_i(t) \; . \qquad [6]$$

Light energy ($\varphi_i^*(t)$) reaching the top of the *ith* level (see [5]) is converted to *g* of basic sugar by a constant (nCH_2O, Loomis & Williams, 1963). The function $D_i(T(t))$ is the maximum demand (production) rate of photosynthate per *g* of leaf ($L_i(t)$) at temperature *T* at time t. The demand includes the vegetative growth, costs of conversion and respiration plus the level's contributions to mainstem and root demands. As tissues age (transform to wood), the respiration rate goes to zero. Fruit growth and respiration demands

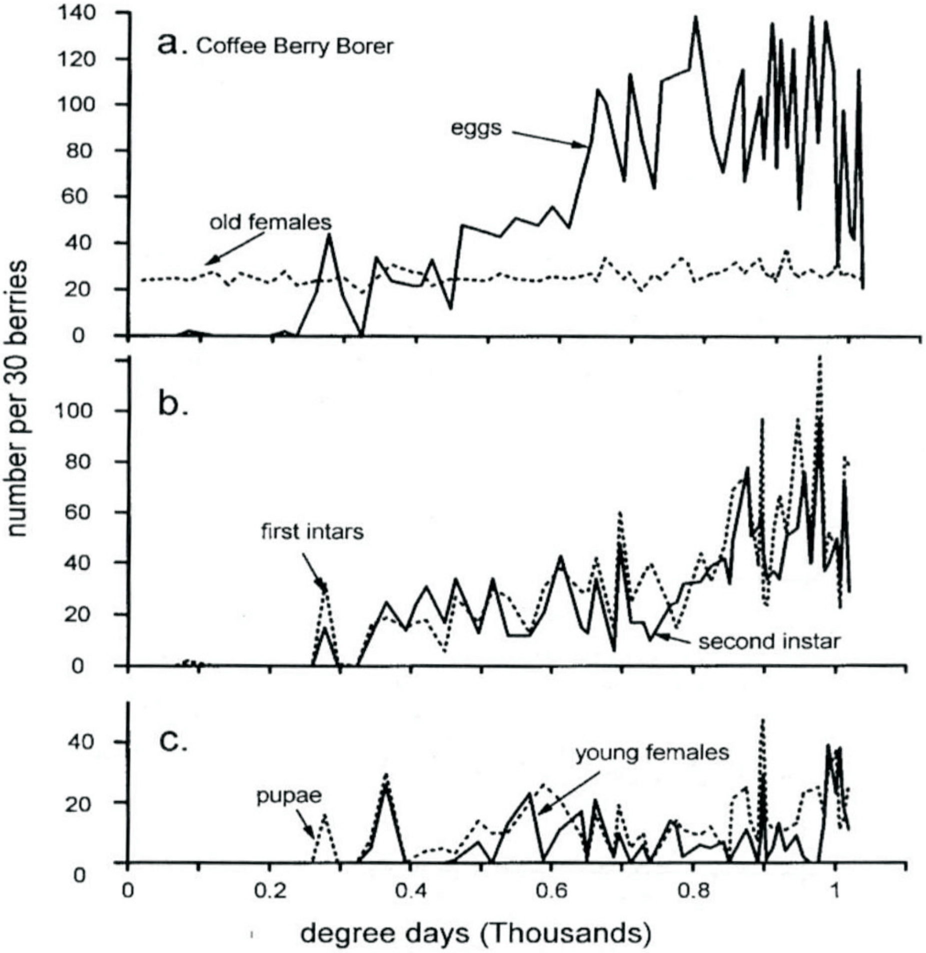

Figure 7. The phenology of borer immature stages: (a.) eggs and old adult females, (b.) first and second stage larvae, and (c.) pupae and young adult females.

are additional costs that have a high priority and are met at the expense of vegetative growth (see below and Gutierrez 1996). In simpler notation, we write [6] as

$$S_i(t) = h_i(u_i)D_i(T(t))L_i(t) \qquad [7]$$

Rearranging terms,

$$0 \le h_i(u_i) = S_i(t) / (D_i(T(t))L_i(t)) < 1$$

is probability that branch level i obtains resource demand level $D_i(T(t))L_i(t)$.

Shortfalls of other factors such as nitrogen and water affect the photosynthetic rate, and their acquisition are modeled using an analogous form of [6] (see Gutierrez *et al*. 1988a, 1996). The root area index replaces total LAI and the plant area for growth is replaced by the root zone volume (6m^3). The demand for nitrogen is proportional to the demand for carbon. A balance model follows the uptake and depletion rates of inorganic soil nitrogen, the decomposition of organic matter to absorbable nitrates, fertilizer applications and leeching. Reallocation of nitrogen is assumed to occur from old leaves before they are shed. Greater detail could be included but it was not necessary for our purposes.

The potential evapo-transpiration rate per plant (*ET(t)*) estimates the maximum demand for water at time *t*, and may be computed using a biophysical model (e.g., Ritchie 1972 or other model). The water balance model budgets all inflows (rainfall) and outflows including transpiration, evaporation from the soil surface, and flow-through and runoff.

The compounding effects of nitrogen ($(S/D)_N$) and water ($(S/D)_W$) shortfalls are included at the whole plant level as the product of their supply-demand ratios (i.e., $0<\phi(t)=(S/D)_n.(S/D)_w<1,$) (Gutierrez *et al*. 1993), and applied at the branch level as follows:

$$S_i^*(t) = ø(t)h_i(u_i)D_i(T(t))Li(t) \qquad [8]$$

The ratio $S_i^*(t)/D_i(T(t))L_i(t)$ now includes the effect nitrogen and water shortfalls. Similar methods have proposed to incorporate the shortfall effects of other essential resources in photosynthesis for plants and resource acquisition in animals (Gutierrez 1996).

Drymatter Allocation. In practice, resource acquisition and allocation occur simultaneously, but for simplicity and clarity the model is presented here in discrete form. If $S_i^*(t)$ is the photosynthetic rate of canopy level *i* at time *t* ([8]), it is allocated ([9]) in priority order to respiration ($r_i(T(t))M_i$) , fruit growth (R_i) and last to vegetative growth (G_i) and reserves (V_i).

$$R_i(t)+G_i(t)+V_i(t)=S_i^*(t)-r_i(T(t))M_i \qquad [9]$$

$r_i(T(t))$ is the temperature dependent per unit mass metabolic cost rate by all non-woody tissues (M_i), and includes the Q_{10} rule for respiration as well as conversion and other costs. In general, when fruit demands are positive, fruit growth occurs at the expense of vegetative growth. Some translocation of nutrients occurs between branching levels, hence S^* includes a portion (5%) of available reserves. Allocation of nutrients to competing demands occurs as follows.

If fruit demands (D_F) are larger than the supply minus respiration ($0 \geq S_F = S^* - rM \leq D_F$), reserve accumulation and vegetative growth including the production of new flower buds, mainstem nodes and branches cease, and fruit grow at $0 \leq S_F/D_F < 1$ times the maximum rate. In addition, fruit buds in which little investment has been made, are aborted at a rate ($1-S_F/D_F<1$). In coffee, buds are aborted early, but some shedding of older buds and berries may also occur (see Cure *et al*. 1998).

If, $S_F > D_F$, then $S_F/D_F = 1$ and maximum fruit growth occurs and the maximum vegetative growth (see above) is scaled by $0 \leq (S_v / D_v) = (S_F - D_F)/D_v < 1)$.

This simple discrete model captures the essence of the branch level allocation processes and in the aggregate the overall plant dynamics (Gutierrez & Wang 1977). The branch level *S/D* effects on fruit bud initiation rates and whole plant S/D effects on mainstem node and branch initiation are illustrated below.

Branch Fruiting Dynamics. Annually, flower buds (*F*) are initiated from the last year's fruit wood (W_i, i.e., brown wood of age ca. 3000-8,000 *dd*) (Mestre and Ospina 1994). The realized bud initiation rate ($\Delta F_i(W_i,t)$) at the *ith* mainstem node level at day *t* is

$$\Delta F(W_i(t)) = 0.011 \cdot W_i(t) \cdot \Delta t \cdot (S_{v,i}(t)/D_{v,i}(t)) \geq 0. \qquad [10]$$

Buds are initiated at a rate 0.01 W_i dd^{-1} scaled by the time varying branch level vegetative supply demand ratio ($S_{v,i}(t)/D_{v,i}(t)$) over a 200 *dd* period. Branch reserves no doubt influences the budding rate, but data were not available, hence we used W_I(t) as a surrogate.

Branch Initiation. All branches are assumed to contribute to mainstem growth, hence the whole plant S/D ratio is used to scale the rate of new mainstem node and branch initiation. This ratio is computed from the sums of the components of the branch level vegetative S/D ratios and is denotes by the subscript *v* outside of the bracket ($(S(t)/D(t))_v$). Under non-limiting conditions, new mainstem nodes (*n*) are initiated at the rate of one per 300 *dd* and branches (*B*) at one per 150*dd* . These values were observed before the first flowering cycle (see Fig. 3e). The effects of nutrient shortfalls on mainstem node ($\Delta n(t)$) and branching ($\Delta B(t) = 2.0 \Delta n(t)$) rates at time *t* during $\Delta t(t)$ are modeled as follows.

$$\Delta n(t) = \frac{\Delta t(t) \cdot (S(t)/D(t))_v}{300} \qquad [11]$$

In discrete form, the total number of mainstem nodes and branches time *t+1* are

$$n(t+1) = n(t) + \quad n(t) - X_n(t_x) \qquad [12]$$

$$B(t+1) = B(t) + 2.0 \,.\, \Delta n(t) - X_B(t_x) \qquad [13]$$

where $X_n(t_x)$ and $X_B(t_x)$ are the number of nodes and branches lost at pruning at times specified by $t=t_x$.

Some Additional Notes on S/D Effects. As plants become large, the S/D ratios of lower branches get progressively smaller causing branch growth and fruiting to slow. If the respiration rate exceeds the photosynthetic rate, the branch is assumed to die. This is a natural outcome of the model and readily accounts for the observed decreasing fruitfulness of lower branches and of whole plants (Mestre & Ospina 1994).

Biotic and abiotic factors affect either the supply or the demand side of the S/D ratios, and influence plant phenology and growth. Defoliators affect leaf area and cause wound healing losses that affect the supply side of the ratio. Feeding on older leaves may reduce respiration relative to the reduction in photosynthate production it causes. Feeding that opens up the canopy may result in a net increase in photosynthesis as light penetration is increased. Increases in temperature increase the respiration rate affecting the demand, but low levels of solar radiation, water or soil nutrients decrease the supply. Factors that reduce fruit numbers reduce the demand side of the ratio and may increase vegetative growth. Similar supply-demand relations are used to model the interactions of higher trophic levels with their resources (Gutierrez & Wang 1977, Wang *et al*. 1977, Gutierrez 1996). Coffee berry borer is a pest of the standing crop, and does not decrease the demand or reduce the supply.

Modeling Coffee Berry Borer and Its Parasitoids. Biology of the Coffee Berry Borer. The borer may be viewed as a parasitoid seeking fruit (hosts) under conditions of time varying fruit abundance and preference (Cure *et al.* 1998). A borer female attacks a single berry during its life time by burrowing into the calyx end (Montoya & Cárdenas. 1994, Fig. 1). Females may penetrate younger fruit, but gallery formation and oviposition are delayed until the seed coat begins to harden (late phase II or older berries). Females may also attack non-preferred phase I fruit, but the fruit may be shed (Cure *et al.* 1998). Older fruit may be shed providing an important refuge for borer between fruiting cycles.

At 22°C, the borer females produce two to three eggs day^{-1} for an average of 74.1 eggs (range 31-111) over a 20 day oviposition period (Bergamin 1943). The preoviposition period is 5-10 days and the duration of the egg, larval and pupal stages are 8.6, 15.9 and 7.6 days respectively (Bergamin 1943). The average life span is 156.6 days (82-282 day range). Mating of new females normally occurs with a sibling male in the same fruit within 2-3 days of eclosion. The ratio of female to male progeny is roughly 10:1. Both females and males are diploid but males are functionally haploid (pseudo-arrhenotokous, see Borsa & Kjellberg 1996). The lower threshold for development is 11.25°C (Costa & Villacorta 1989). These data are summarized in Table 1.

The Borer Fruit Attack Model. The total number of uninfested berry (*B*) weighted for preference is

$$\dot{B}(t)=\int_0^{a_{\max}}\vartheta(a)B(t,a)da \qquad [14]$$

The preference function 0< (a)≤1 is right skewed on fruit age (Cure *et al.* 1998, see Fig. 1). The number of previously attacked berries (subscript *a*) is

$$B_a(t)=\int_0^{a_{\max}}B_a(t,a)da \qquad [15]$$

The Fraser and Gilbert (1976) functional response model is used to estimate the number of uninfested fruit ($S_b(t)$, [16]) attacked. This model is the integrated parasitoid form of Ivlev's (1961) model that accounts for superparasitism (it is related to Watt's model, see Gutierrez 1996).

ϑ

$$S_b(t)=B(t)\left(1-e^{\frac{N_b(t,a_s)(1-e^{-\alpha_b(t)B(t)}}{B(t)}}\right) \qquad [16]$$

Because a female attacks only one berry during its lifetime, the population demand rate equals the number of seeking females $N_b(t,a_s)$ of physiological age a_s. The parameter α_b is the Nicholson & Bailey (1935) per capita search rate parameter. The attacks are allocated among the fruit age classes in a manner that reflects their abundance and preference.

The dynamics model keeps track of both infested and uninfested berries. Infested berries and the borer they host age physiologically over time, but the rate of maturation of adult borers in very young fruits slow dramatically until the seed coat begins to form. To accommodate this biology, borer females that attack fruits enter cells of a two dimensional distributed maturation time model corresponding to the age of berry attacked (row) and their own age (column). New eggs enter the first cell of borer age (column) in the row (age) of fruit inhabited by the female. Borer females and their progeny age along diagonal paths that depend on temperature and berry age (Stone & Gutierrez 1986, Gutierrez 1996). The model enables us to determine when infested fruits are sufficiently ripe for oviposition to occur, and to track borer aging, reproduction and population age- and mass-structure in all age fruit on the tree or those that shed on the ground. This model provides a convenient structure for linking berry-borer-parasitoid(s) dynamics (see below).

The Biology of Coffee Berry Borer Parasitoids. The biologies of the bethylid parasitoids (*Cephalonomia stephanoderis* Betrem and *Prorops nasuta* Waterstam) are very similar (Orozco & Aristizábal 1996, see Tables 1, 2 for details). Both must first find fruit having borer infestations. The adult bethylid females are thought to attack borer in only one berry during their life time. Once a parasitoid female finds a fruit and enters it, it host feeds on eggs and young larvae and oviposits externally on large larvae and/or pupae. The parasitoid may also kill the adult borer. *P. nasuta* prefers to oviposit on large larvae and prepupae and *C. stephanoderis* prefers late larvae, pre-pupae and pupae. Both species have a female biased sex ratio (3:1). The developmental time of *C. stephanoderis* is 23.2 days and that of *P. nasuta* is 22.4. The lower thermal threshold of *C. stephanoderis* is 13.8°C and the upper one is below 37°C restricting it development in very hot regions. The same threshold is assumed for *P. nasuta*, but incorporating the correct one when it becomes available is easy.

Feldhege (1992) and Infante *et al.* (1994) reviewed the biology of the eulophid adult-endoparasitoid (*Phymastichus coffea* La Salle). The parasitoid attacks borer adults in fruits before they have begun to oviposit. Average oviposition in the laboratory is 17 eggs over a two-day adult life span, but it is unlikely that this reproductive potential is met in the field. Two eggs are usually deposited per host, hence a female can potentially attack 8-9 borer adults in different berries during its life. The egg to adult period is relatively long (29.7 days), but the female has no discernible preoviposition period. A thermal threshold for development of 13.8°C was also assumed for this species, and is an important missing parameter. A female biased sex ratio of 20:1was observed in the field (Feldhege 1992), but a 3:1 ratio has been reported from laboratory experiments (Feldhege 1992, Infante *et al.* 1994). The consequences of both sex ratios were explored with the model.

The Parasitoid Attack Models. Parasitism is a two-stage process: Parasitoids must first find infested berries and only then can they attack borer life stages in them. The functional response models for the *kth* , (*k= P.n., C.s., P.c.*) parasitoid species finding borer in infested berries ($B_{a,k}$) of varying fruit and borer age preference are variants of [16].

$$S_k(t)=B_{a,k}(t)\left(1-e^{\frac{-D_k A_k(t)\left(1-e^{\frac{-\alpha_k(t)B_{a,k}(t)}{D_k}}\right)}{B_{a,k}(t)}}\right) \qquad [17]$$

The search rates for *C. stephanoderis* and *P. nasuta* females (e.g.,) were assumed 0.6 and that for *P. coffea* is 0.15. D_k is the per capita demand for berries by species *k* (see above). Information on borer density and age structure in each age class of fruit is readily available from the borer dynamics model, and provides estimates of parasitoid specific values for $B_{a,k}$ in [17]. This is important capacity as bethylid females enter an infested berry only after a gallery has been formed (late phase II and all phase III and IV and older fruit on the tree or on the ground) and in which borer reproduction is in full swing. In contrast, the eulophid *P. coffea* attacks borer adults in berries before the beetles have made an extensive gallery or are waiting for the host berry to ripen sufficiently for oviposition to begin.

After correcting for multiple parasitism, infested berries entered by each bethylid parasitoid are transferred to corresponding cells of similar parasitoid specific two-dimensional arrays where borer and parasitoid aging, reproduction as well as parasitoid host feeding are followed. Similar models are used for borer adults attacked by *P. coffea* and the parasitoids themselves. The age-structure of all species is easily estimated by the model. Competition between the bethylid parasitoids is symmetrical, but the inclusion of asymmetrical competition where one species is the consistent winner in cases of superparasitism is not difficult to compute using this system (Mills & Gutierrez 1996). Competition of the bethylids with the eulophid is indirect as the latter seeks only pre-ovipositing adult borer females.

Simulating the Plant Field Data. The plant model reproduced the observed drymatter data reasonably well (Fig. 8). The dry matter and number dynamics are regulated by the S/D ratios that respond not only to current weather conditions, but also to plant state variables, especially fruit growth dynamics The first brief period of flowering occurs at roughly 5500 *dd* (Fig. 3a, 8b). After flowering, each berry grow at a rate of 0.00003 g dd^{-1} for 1200 *dd* and then the rate increases 15 fold (0.0005 g dd^{-1}) for a further 1400 dd (calculated from Salazar *et al.* 1994). Although coffee berries are small they are numerous and their aggregate demand causes a shortfall in photosynthate. When this stress occurred, allocation switched from vegetative growth to fruit growth (see below). Figure 8c depicts the whole plant vegetative and fruit S/D ratios. The similarity in pattern and magnitude of the two ratios occurs because some branches have a heavy fruit load and other a small one. The S/D ratios rise and fall as internal allocation switching occurs. The number of fruit initiated is determined from the prior season's branch growth scaled by the vegetative S/D ratio (see Fig. 8b, equation [10]). Fruit size is determined by the branch level S/D ratio. On average, berries achieve a mass of 0.55 g drymatter.

The effect of fruit induced stress is also seen in the slowing of branch production (Fig. 8c). The rate was approximately linear during the first 6000 *dd*, but declined as the whole

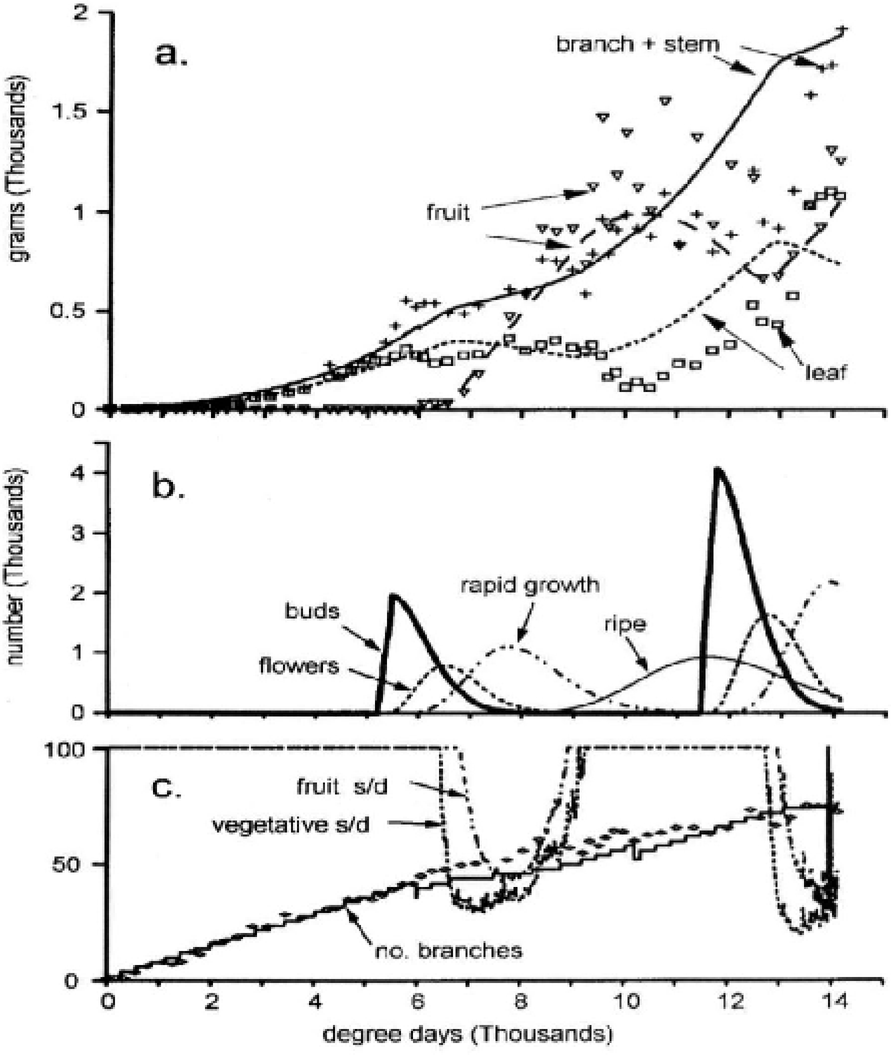

Figure 8. Simulation results: (a.) leaf, stem and fruit drymatter (observed and simulated), (b.) simulated fruit number (no data available), and (c.) simulated and observed branch numbers. The time-varying whole plant vegetative and fruiting supply-demand ratio are also shown in subfigure c.

plant vegetative supply-demand ratio declined (Fig. 8c). As the first crop of berries matured, the branching rate and other forms of vegetative growth increased until slowed by the second fruiting cycle at time 10,500. The time between the two cycles is roughly 5200 *dd* (see also Fig. 3). The predicted second cycle of flowering is much larger than the first amply illustrating how vegetative growth in the prior season affects the number of flowers in the current season.

A Simulation Analysis of the Interaction of Borer and Its Parasitoids. Numerous simulation studies were made, but for brevity only the more important ones are illustrated. The conclusions of others are reported without supporting graphics or tables. In our study, coffee berries were not harvested and remained on the tree until shed. This is not the normal situation. Cleanup of berries remaining on the tree after harvest and on the ground is also practiced to increase the yield and to reduce an important breeding resource for borer between fruiting cycles.

Borer Alone. The simulations covered a five-year period yielding three distinct peaks for borer that correspond with a lag to three fruiting cycles (Fig. 9). A high immigration rate (0.5 borer adults per day per plant) assured an early high infestation.

The Effects of Parasitoids. The bethylid species singly (Fig. 10a) or in combination (Fig. 10b) had little impact on simulated borer populations despite high parasitoid immigration rates relative to borer (0.25 parasitoids per plant per day versus 0.5 for borer), and high search rates ($\alpha_{C.\,s.} = \alpha_{P.\,n.} = 0.6$). In combination, the patterns remained the same but borer egg numbers increased slightly due to interspecific competition. Poor control occurs because these species have a low numerical response and each female attack borer in only one berry. Control of borer was little affected if the bethylid parasitoids were assumed to kill the borer female because its death limited future parasitoid numerical response. Increasing the immigration rate of the bethylid parasitoids was helpful, but control was not

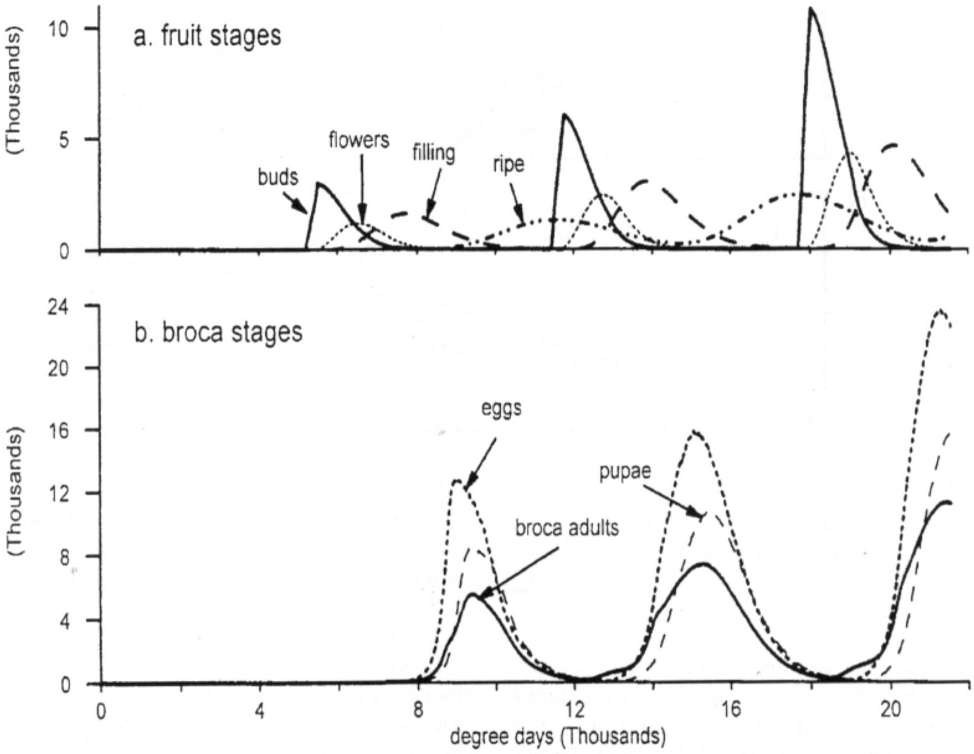

Figure 9. Simulated fruit (a.) and borer (b.) phenology over a five year period.

achieved except at very high rates.

In contrast, simulations with the adult endoparasitoid *P. coffea* indicated marked reductions of borer densities (Fig. 10c). This occurred despite a low search rate ($\alpha_{P.c.} = 0.06$) and an immigration rate a fifth that of the

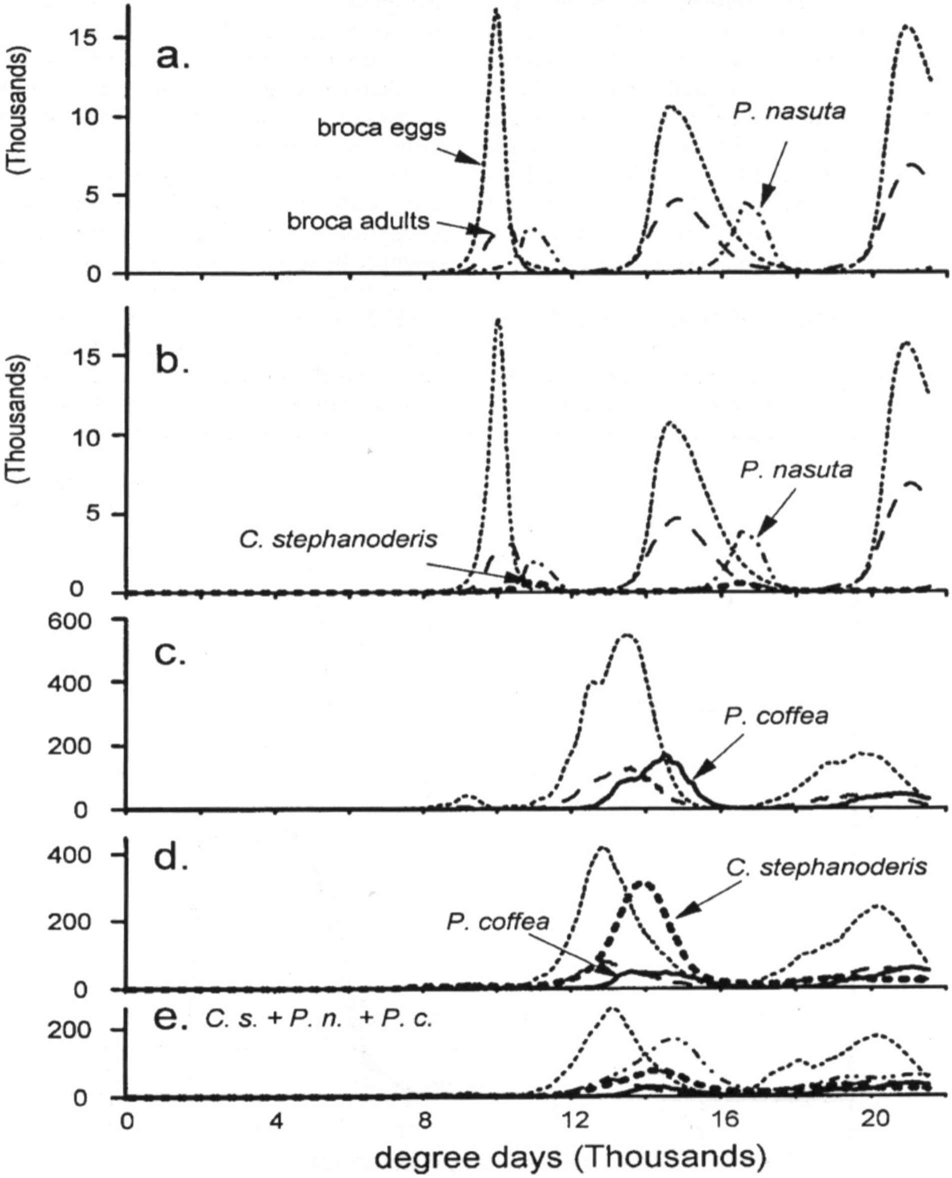

Figure 10. Simulated borer egg and adult dynamics as influenced by: (a.) *P. nasuta*, (b.) *P. nasuta* and *C. stephanoderis*, (c.) *P. coffea*, (d.) *C. stephanoderis* and *P. coffea* and (e.) all three parasitoids together. Note that the first letters of the scientific names are used as convenient.

bethylids. The predicted differences are dramatic and likely accrued because *P. coffea* attacks borer early in the season, it kills the adult borer female before it reproduces, it has a very high female biased sex ratio, and it can attack several fruits per day. Predicted borer densities were reduced and percentage berry infestation rates were low in the first fruiting cycle, increased to 50 percent in the second cycle (Fig. 11) and decreased in the third cycle (not shown). Control of borer improved when *C. stephanoderis* and/or *P. nasuta* were combined with *P. coffea* (Fig. 10d,e)

Percentage Infested Berries. In the absence of harvesting, cleanup and parasitism, borer quickly infested most berries (Fig. 11). The addition of the parasitoid *P. coffea* to the system suppressed infestation levels in the first fruiting cycle, but an outbreak to 45% occurred in the second cycle. An augmentative release of *P. coffea* per fruiting cycle proved disruptive and increased the percentage of infested berries (Fig.11).

C. stephanoderis is commonly used for inundative releases, hence the effects of two releases of 100 adult per plant 1000 dd apart during each fruiting cycle were evaluated.

In the absence of *P. coffea*, releases of *C. stephanoderis* reduced borer populations imperceptibly as the benefits were quickly swamped by borer's larger numerical response (not shown). The benefits of such releases would be greater at low borer densities because of a higher prasitoid to host ratio. Releases of bethylids were most useful in combination with *P. coffea* as a decline in berry infestation was especially dramatic in the sec-

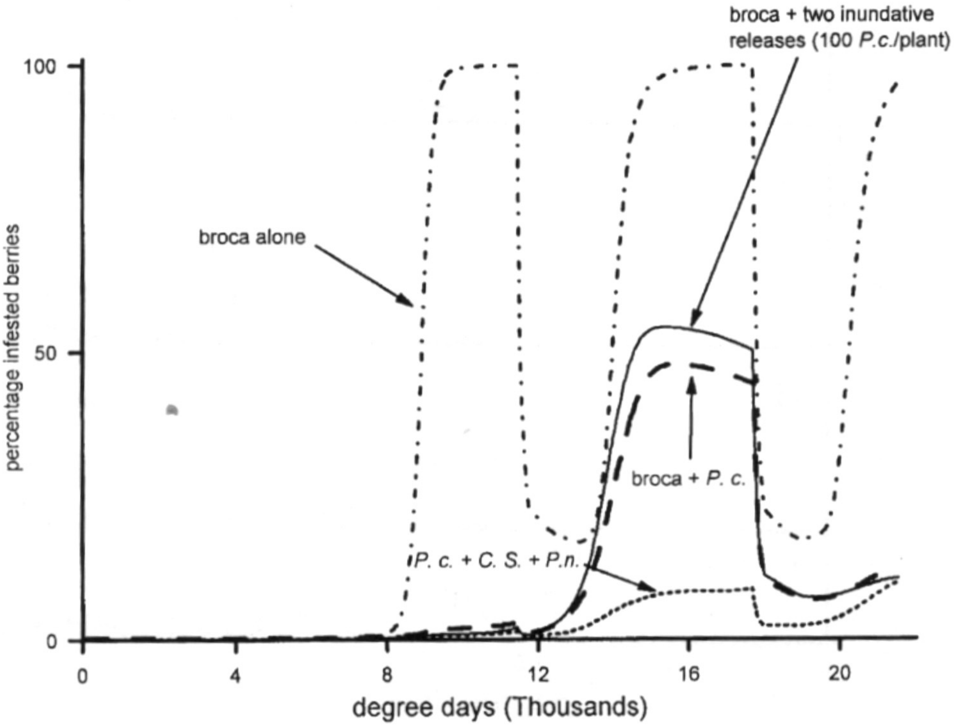

Figure 11. The simulated effects of berry infestation levels in the absence of parasitism, with parasitism by *P. coffea* and with two releases of 100 parasitoids per tree, and with all species of parasitoids present.

ond fruiting cycle (Fig. 11).

Agronomic Practices. Among the agronomic practices used to control borer are harvesting, cleanup of berries and pesticide use. The effects of these practices on the interaction of borer - *P. coffea* are reviewed below (Fig. 12). The interaction of borer and *P. coffea* will be the standard treatment (Fig. 12a) to which the addition of agronomic factors will be compared.

Harvesting and cleanup occur at about the same time and in our simulation study are assumed to be 95% efficiency. In the absence of parasitism, harvesting and cleanup have little impact on high borer populations (not

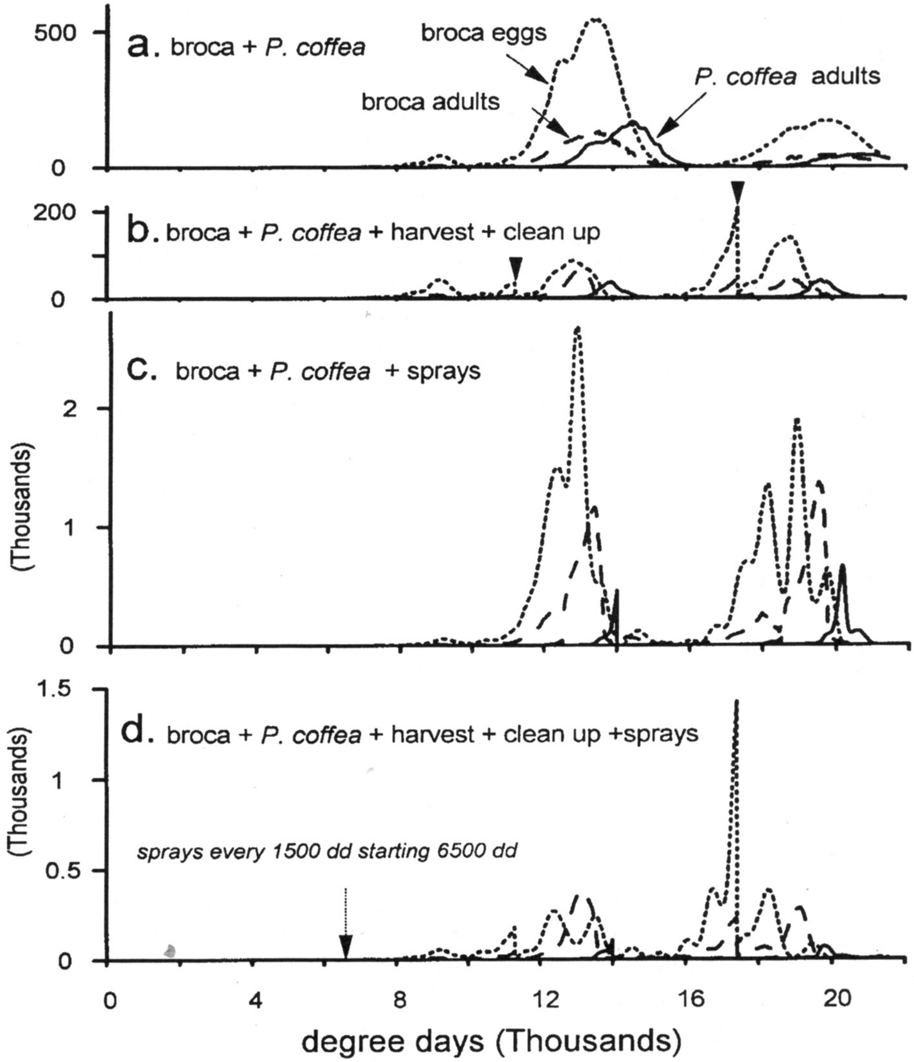

Figure 12. Simulation studies of (a.) borer - *P. coffea* dynamics, (b.) the same as (a.) but with 95 percent efficiency of harvest and clean, (c.) the same as (a.) with the added effects of a weak insecticide applied at 1500dd intervals, and (d.) the effects of all treatments.

shown) because: at harvest most berries are infested; the borer in them are near the end of their reproductive life; most adult progeny have emerged to seek uninfested berries; the remaining infested berries provide a large inoculum for the next fruiting cycle.

In the presence of *P. coffea*, the added effects of harvesting reduces peak borer populations at time 13,000 in Fig. 12a by approximately 40 percent (not shown) but the population doubles in the second peak at time 20,000 (not shown). This occurs because harvesting disrupts the parasitoid more than the borer. Borer populations, but not *P. coffea*, continue to build in shed fruit. Cleanup added to the effects of *P. coffea* lowers all borer peaks about 10% (not shown). This occurs because cleanup removes borer but has little impact on *P. coffea*. Combining harvesting and cleanup with *P. coffea* results in a substantial reduction of borer (Fig. 12a vs. 12b). The two agronomic practices complement each other by reducing borer numbers generally and eliminating most of the borer refuge in shed fruit.

An insecticide with a weak fumigant action is assumed to kill all free flying adults of all species. In addition, borer adults and the *P. coffea* life stages attacking them in shallow burrows are assumed killed. Borer sheltered deep within berries (and the bethylid parasitoids that attack them there) are assumed unaffected. In the absence of harvesting and cleanup, sprays applied at 1500dd intervals disrupt the regulatory power of *P. coffea* (Fig.12a vs. 12c) causing pest resurgence. Resurgence would be greater without the assumed background parasitoid immigration rate (not shown).

When a weak pesticide is combined with harvest, cleanup and *P. coffea*, the benefits of the cultural practices disappear (Fig. 12c vs. 12d). Insecticides having a strong systemic or fumigating action would increase control of borer (not shown), but may lead to pest resurgence, resistance and outbreaks of secondary pests (van den Bosch 1978). These effects are well known but are difficult to incorporate reliably in our model because the details of that biology are obscure.

Discussion

Despite considerable progress in developing sound biologically rich tritrophic models, models are not meant to be a one to one descriptions of nature. Furthermore, simulation models are not predictive instruments, their strength is heuristic and are most useful when they help identify important issues not easily amenable to experimentation and when they identify important data gaps (see text). Simulation models are not suitable for developing *optimal* strategies because they require brute-force enumeration methods to obtain the solution (Gutierrez 1996, appendix 3). However, simulation is useful for exploring interrelations of factors and the potential efficacy of different control tactics. This is the approach taken in this study wherein some strategic predictions arose.

In developing our coffee systems model, we used the metabolic pool paradigm that describes the processes of resource acquisition and allocation in all species cast in a mass-age-structured population context. The model captured the dynamics of coffee's vegetative growth and fruiting dynamics under conditions of south central Brazil, but the model can be easily extended to other coffee growing regions.

Berry production in our Brazilian data was cyclic and each cycle can be viewed as a standing crop. Fruiting cycles may overlap in regions such as Colombia, and the differences in fruit phenology no doubt affect borer-parasitoid dynamics (Arcila *et al.* 1993). Such interactions are difficult to evaluate in the field, but they are easily incorporated and evaluated in our model. The potential of two bethylids (*C. stephanoderis* and *P. nasuta*) and a eulophid (*P. coffea*) to control borer were evaluated. With a caveat, the model predicted that of the three parasitoids, only the adult endo-parasitoid *P. coffea* has the biological characteristics that may be sufficient to regulate borer populations. *P. coffea* attacks early in the fruiting cycle parasitizing borer adults that have not formed deep galleries; it has a very high female biased sex ratio; it does not host feed; its progeny are produced in many fruits; and host adults are sterilized before reproduction. We assumed that this parasitoid does not attack borer in shed berries and it has a very low search rate compared to the bethylids. Despite this, *P. coffea* was potentially the superior parasitoid even when its female biased sex ratio was reduced from the 20:1 observed in the field to 3:1 observed in the laboratory.

Mitigating factors restricting the effectiveness of the bethylid parasitoids are: the adults can begin their activity only after borer infestations develop in ripening fruits; each female attacks borer in only one fruit; they must host feed on eggs and young larvae to produce eggs reducing their potential future numerical response; and they are ectoparasitoids of older life stages. The activity of the bethylid parasitoids begins fairly late in the fruiting cycle, and borer's reproductive capacity and higher female biased sex ratio (10:1) easily overwhelm the parasitoids capacity to control them. Bethylid females are thought to kill the adult beetle, but when does this occur and do some borer continue to reproduce? Simulation suggests that it does not matter all that much to the efficacy of the bethylid parasitoids.

Coffee berry quality would appear to suffer less when the borer are attacked by *P. coffea* compared to those attacked by the bethylid. In the first case, the beetles may not have formed deep galleries before being killed, and the berries may not be greatly affected. In contrast, bethylids usually attack thriving colonies of borer that have made extensive galleries in berries, and hence berry quality must be lower and concerns about fungal toxins raised if these berries are processed.

Inundative and augmentative releases of *C. stephanoderis* are widely promoted, but simulation results suggest that this strategy is appropriate for low level borer infestations. This tactic needs to be explored further in the field, and its efficacy compared to the cost of parasitoid production.

Harvest and cleanup of remaining berries on the plant and ground remove large numbers of borer and parasitoids from the field creating a host free period that resets all populations at a much lower levels. In such cases, inoculative releases of parasitoids, especially of *P. coffea* early in the fruiting cycle may prove profitable. Poor cleanup may leave a large inoculum of borer in shed fruits that results in high levels of infestation of fruits in the next fruiting cycle.

Insecticides that do not have a strong fumigating or systemic action are likely not to be effective as they kill only adult borer and adult parasitoids seeking hosts. Such pesticides especially disrupt borer - *P. coffea* dynamics because all life stages are relatively susceptible. In contrast, bethylid adults and immature stages sheltered within fruit are relatively immune, but the parasitoids are relatively ineffective. Systemic or fumigant types of pesticides would be more effective in controlling borer but they could also adversely affect the action of the parasitoids resulting in pest resurgence, secondary outbreaks of other pests, and possibly resistance (van den Bosch 1978).

The use of pheromones was not explored fully, but pheromones for mating disruption would not be useful as borer is pseudo-arrhenotokous (the females mate with sibling male within the host fruit before emergence, Borsa & Kjellberg 1996). Pheromones that mask oviposition sites for borer or attract them to traps are a possibility that might profitably be explored.

Last we end on a cautionary note. Models are always incomplete and are at best guides to understanding complicated systems. Our simulation studies provide research direction but not specific predictions. Whatever general predictions are apparent should be taken with caution and evaluated further in the field. Most models normally examine narrow specific questions, and then are discarded. In our approach, we seek to make the model as general and flexible as possible to be able to incorporate future findings and answer unanticipated questions as they arise. The model is easily parameterized to simulate other varieties and species of pests and natural enemies. Weather and levels of edaphic factors drive the biological processes in the plant model making it independent of time and place. Similar time and place remarks apply to the models of the other species in the system. Together, these attributes make the model applicable to other coffee growing regions and other combinations of species throughout Latin America and elsewhere.

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