

MATHEMATICAL SIMULATION MODEL OF THE VELVETBEAN CATERPILLAR. I. DESCRIPTION OF THE MODEL¹

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ABSTRACT - A mathematical simulation model was developed for the velvetbean caterpillar (*Anticarsia gemmatilis* Hübner, 1818), main Brazilian defoliator pest of soybeans, in order to consolidate existing information and also to verify research needs. Available information presented in Brazilian or international literature, plus data recorded in reports of Embrapa were used. Seven sub-models were developed to comprise the major simulation model considering the insect, the soybean plant, migration of moths, insecticide application, predation and parasitism, entomopathogens and environment. Working hypotheses, equations generated and developed, parameters and fundamentals of the mechanisms for study are presented. Although without validation, the results furnished by the model are considered normal when compared with observed field populations of the insect.

Index terms: insecta, biology, ecology, damage, modeling, simulation.

MODELO DE SIMULAÇÃO MATEMÁTICA DA LAGARTA-DA-SOJA. I. DESCRIÇÃO DO MODELO

RESUMO - Foi desenvolvido um modelo matemático de simulação da lagarta-da-soja (*Anticarsia gemmatilis* Hübner, 1818), o principal inseto desfolhador da soja no Brasil, com os objetivos principais de consolidar as informações existentes sobre o inseto e verificar as necessidades de pesquisa sobre o mesmo. Foram utilizadas as informações disponíveis na literatura brasileira e internacional e registros de relatórios da Embrapa. Sete submodelos foram desenvolvidos para compor o modelo principal, considerando o inseto, a soja, migração de mariposas, aplicação de inseticida, predação e parasitismo, entomopatógenos e ambiente. As hipóteses de trabalho, as equações geradas e desenvolvidas, os parâmetros e os fundamentos dos mecanismos de abordagem de cada uma das etapas são apresentados. Apesar de o modelo ainda não haver sido validado, os resultados por ele fornecidos são considerados normais quando comparados com os levantamentos do inseto efetuados em condições de campo.

Termos para indexação: insetos, biologia, ecologia, danos, modelagem, simulação.

INTRODUCTION

The velvetbean caterpillar (VBC) *Anticarsia gemmatilis* Hübner, 1818 (Lepidoptera:Noctuidae)

is considered a key defoliator of soybeans in tropical and subtropical areas, especially under conditions of soybean production in Brazil and the south-eastern United States (Turnipseed, 1972; Turnipseed & Kogan, 1976; Panizzi et al., 1977; Gazzoni et al., 1981). The presence of this insect on the Brazilian farms requires early insecticide applications on the cultivations. The impact of broad-spectrum insecticides on natural biological control may provoke a disequilibrium in the agroecosystem, generating favorable conditions for next generations of the VBC, or for outbreaks of other insect pests of soybeans. Minimum use of brand insecticides is one of the most important objectives of the implementation of the soybean Insect Pest Management (IPM) as recom-

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mended to Brazilian growers (Schmitt et al., 1979). By practicing IPM, these growers were able to save between US\$ 500 to US\$ 3,000 million dollars, according to the economic approach adopted to calculate growers' savings (Gazzoni, 1994). Other advances are not measured in monetary savings, but in a lower impact upon a complex of predators and parasitoids of soybean fields as in the biological control of VBC through the use of its polyhedrosis virus (Moscardi, 1989).

The nature of any IPM program is based on its continuous development. But as scientists add more information to the system, the trend is to make it so complex that integration of raw information, obtained under specific conditions, become more difficult over time. This is one of the advantages of simulation models, used to integrate specific information into a system. Shepard (1980) recommended special attention to modeling activities in the context of a nationwide coordination of soybean IPM. Also, modeling is a key to systemic research, an approach to agricultural research aiming for global answers to technological demands of growers.

The velvetbean caterpillar is a full metamorphosis insect, passing through four distinct stages of development: egg, larva, pupa and moth. Eggs are individually laid by moths at night, with marked preference for the underside of soybean leaves, stems, petioles and pods (Watson, 1916). The egg has a hemispheric shape, flat on the bottom. It is initially pale green, turning reddish-brown just after larval hatching (Ellisor, 1942). The egg stage may last from 3-5 days.

Larval stage normally presents six instars but, according to environmental conditions, five to seven instars might be observed (Watson, 1916; Reid, 1975; Moscardi, 1979). Larvae of 1st and 2nd instars only scratch soybean leaves. From the 3rd stage, larvae feed on the entire surface of leaves, including nerves (Watson, 1916). Just after hatching, larvae measure 2-3 mm; at the end of the 6th instar they can reach 40-50 mm. Small larvae are green, and large larvae may show green or black body color (Watson, 1916; Guyton, 1940). Dark larvae are always associated with high insect density. Larvae heads are greenish, and white strips are found along the body of the larvae (Kuitert, 1967). Four abdomi-

nal pairs of legs are found on the larvae. These parameters are conditioned by temperature, as established by Moscardi (1981a).

Before transformation to pupae, larvae of the last instar stop feeding, shrink to 20-25 mm, and the body color turns pink. This period is described as pre-pupa. Movement of the larvae is very slow while they migrate to the soil, where the pupation occurs inside a cell made of rests of leaves, petioles or other small parts of plants. Complete larval stages last 12-15 days.

Pupae are dark brown, measuring 18-20 mm long by 4-6 mm in diameter. This stage lasts 9-10 days (Kuitert, 1967). The moth may present several wing colors (brown, yellow, gray), but a straight line linking extremes of the wings is always observed. Sexual maturity is reached 2-3 days after moth emergence. The mating ritual includes emission of sexual pheromone by female at evening and reproductive activities are concentrated between 3-5 days after emergence (Greene et al., 1973). Oviposition may start at the same night of mating and can last the entire period of life of the adult female, but intensity of egg laying is dramatically reduced after the first days (Leppla, 1976; Leppla et al., 1977; Moscardi, 1979; Moscardi 1981b). A mated female under optimal environmental conditions can lay up to 1,000 eggs throughout her life.

Velvetbean caterpillar larvae feed on soybean leaves, but under extreme conditions (100% of leaf area loss) some were observed feeding on petioles and pods (Kuitert, 1967). Early instars (1st to 3rd) had low consumption capacity, while 40% of total area is fed during the 6th instar (Strayer & Greene, 1974). According to Reid (1975), total leaf area consumed by a single larva was 100 cm², but Moscardi (1979) and Moscardi et al. (1981) demonstrated a dependence of leaf area consumption on the stage of the soybean plant (quality of food). As a consequence of leaf area loss, a reduction in soybean yield may occur. Meanwhile, several scientists have proved that soybean has a special ability to recover from this damage, depending on the stage of development of the plant when defoliation was applied (Dungan, 1939; Kalton et al., 1949; Weber & Caldwell, 1966; Todd & Morgan, 1972; Turnipseed, 1972; Gazzoni, 1974; Thomas et al., 1974; Gazzoni

& Minor, 1979; Gazzoni & Moscardi, 1998). Higher absolute yield production is associated with defoliation applied at vegetative stages, while pod and seed filling stages are the most sensitive to defoliation. Gazzoni & Moscardi (1998) observed a trend to intense recovery of soybean leaf area when low to medium defoliation levels were applied at vegetative stages. At full bloom only low levels of defoliation induced short recovery times, while defoliation applied at seed filling stage had the effect of reducing intensity of natural leaf area loss.

The association of densities of insect feeding, leaf area consumed and soybean yield was studied by Strayer (1973). Under the conditions of his work, the economic damage level for the reproductive stage of soybeans was found to be 18% defoliation or 18 large larvae per meter of row, being almost the double for vegetative stage (33% defoliation or 36 large larvae per meter of row). For Brazilian conditions, 30% defoliation on the vegetative stage or 15% on the reproductive stage is recommended, while 20 large larvae per meter of row is the economic damage level for the whole soybean cycle (Gazzoni et al., 1981).

Correa et al. (1977) studied seasonal abundance and distribution of velvetbean caterpillar at six locations where soybean is cultivated in Brazil. As a general rule, the insect population peaked in January for areas situated in the North and in February for the most southern sites. However, dynamics of the insect populations strongly depended on environmental conditions such as weather, time of planting and natural enemies.

When environmental conditions are favorable, natural enemies can maintain VBC populations under the economic damage level during the soybean season, making the use of chemical insecticides unnecessary. Ferreira (1980) observed nine species of VBC parasitoids from samplings made at four different locations; *Microcharops bimaculata* was the most common, followed by *Euplectrus pluteri* and *Patelloa similis*. Predators of VBC are normally polyphagous, and the major part of predation occurs during egg or early larval instars. Species composition varied according to year, geographic location, time of planting, historic of the area, etc., but most common predators were spiders, hemipterous

(*Tropiconabis* spp., *Geocoris* spp., *Orius* spp., *Podisus* spp.) and beetles (*Calosoma granulatum*, *Callida* spp. and *Lebia concinna*), according to Turnipseed (1972) and Ferreira (1980).

Insect diseases are caused by fungi, bacteria and viruses, which normally kill the infected specimens. The VBC is naturally infected by the fungi *Nomuraea rileyi* (Farlow) Swanson, *Entomophthora* spp. and *Beauveria bassiana*. The fungus *N. rileyi* is considered the most important natural enemy of the VBC; it causes dead larvae to appear white, and therefore is commonly known as 'white disease'. During sporulation of the fungus, dead larvae appear green. The epizootics of this fungus are highly dependent upon climatic conditions, specially relative humidity inside the soybean canopy. In years with adequate weather conditions, an epizootic of *N. rileyi* decimates the population of the VBC, maintaining it at low density levels up to the end of the soybean cycle. Natural occurrence of *Baculovirus anticarsia* (Carner & Turnipseed, 1977; Corso et al., 1977) is not as important as epizootic of *N. rileyi*; however, since not depending on climatic condition, its use as a biological insecticide has replaced part of the chemical insecticide used to control VBC on soybeans planted in the southern most Brazilian states (Gazzoni, 1994).

Developing this simulation model had the following objectives: a) synthesize available information about the pest and its interfaces; b) fill gaps in the state of art of scientific knowledge; c) identify need for future research to fully implement the system; d) make numeric experimentation to test consistency of the model; and e) identify the necessity of developing a predictive model.

The simulation model

The model describes the evolution of the population of *A. gemmatilis* in any given soybean area, but for calculation purposes a surface area of one hectare was used. Initially the model had been written in CSMP III (Continuous System Modeling Program), a mainframe computer language especially developed for simulation models; later it was also translated to Fortran IV for adaptation to microcomputers.

Descriptions of formulas had been done using conventional mathematical notation, exception made for expressions such as "N=N+1" whose sense is only computational. Besides literal notation, block diagram is used to explain parts of the model. The symbols of parameters are normally composed of initials of their Portuguese names.

The complete model comprises seven sub-models and their interactions, as shown in Fig. 1. The main sub-model is the pest model (A); some interactions were not considered in spite of their clear importance, such environment x soybean, because this was not an objective of the model.

The planting date was considered as day 1 for all model calculations. Simulation starts at emergence of soybean occurring 5-7 physiological days after planting. The sequence of events is explained on the block diagram shown in Fig. 2, where each block represents a set of calculations to obtain variable values on parameters to be passed to other blocks.

Sub-model A: *A. gemmatalis*

Stages of development

The metabolism of insects and consequently their life cycle is highly dependent on temperature, and several studies have related insect growth to "heat units". In this model the physiological day (PD) concept was adopted (Waddill et al., 1976; Bernhardt & Shepard, 1978). Through this concept, at 27°C one physiological day is equal to one chronological

day (PD=CD); at lower temperatures PD>CD and above 27°C PD<CD, calculated through mathematical formulas. Having established relationships between the target insect biology and temperature, the PD concept by-passes temperature considerations directly upon the insect. Table 1 shows the life cycle of the VBC adjusted to the PD concept. Population of VBC at the end of day t was represented by $X_{1,t}, X_{2,t}, \dots, X_{44,t}$, where each $X_{i,t}$ meant the total number of insects with PD=i, at the end of day t (t=1,2,...,44). Notation of population at the beginning of each day is represented by $Y_{i,t}$, using the same concepts of the end of the day. The physiological day equation was proposed by Waddill et al. (1976), as follows:
 $PD = 1/24 \{ [0.55(TMAX - TMIN) + TMIN] - THT + [0.15(TMAX - TMIN) + TMIN] - THT \}$
 where:

- TMAX = daily maximum temperature;
- TMIN = daily minimum temperature;
- THT = insect developmental threshold.

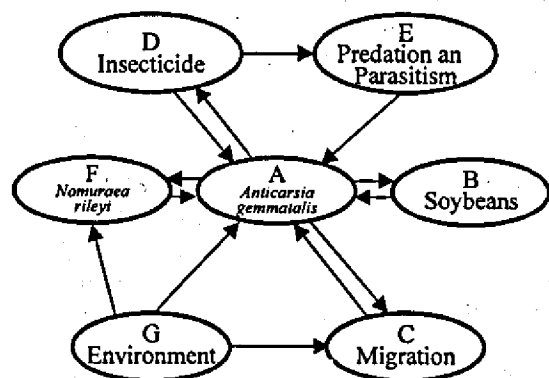


FIG. 1. Structure of the model and relationships among its sub-models.

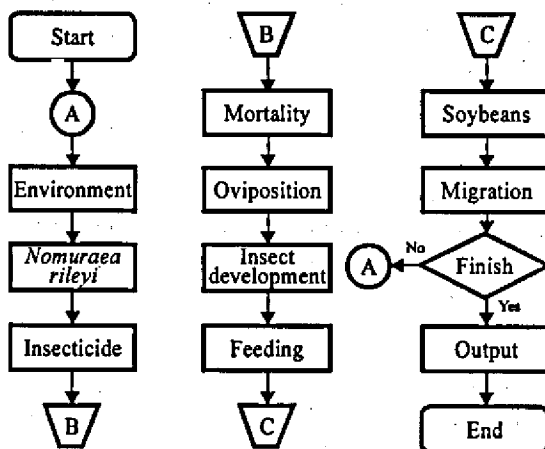


FIG. 2. Logical fluxogram of the model.

TABLE 1. Life cycle of *A. gemmatalis*, measured in physiological days.

| Type | Egg | | Larvae | | | | | Pupa | Moth | Total |
|-------------|-----|---|--------|----|----|----|----|------|------|-------|
| | 1 | 2 | 2 | 2 | 2 | 2 | 2 | | | |
| Single | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 10 | 19 | 44 |
| Accumulated | 5 | 7 | 9 | 11 | 13 | 15 | 25 | 44 | 44 | |

Source: Moscardi (1979).

In this model, THT=15°C derived from the experience of the authors and from similar values adopted in other models. Bernhardt & Shepard (1978) also used THT = 15°C for validating the PD equation, using the Mexican bean beetle (*Epilachna varivestis*) as an example.

Oviposition

Oviposition is one of the inputs of the model, jointly with migration of moths at the beginning of the soybean cycle. Age of moths, measured in PD, and temperature are the most important parameters influencing daily rate of oviposition. Total number of eggs laid on a given day is expressed by:

$$NOVOS_t = FF * AT * \sum_{i=26}^{44} F_i X_{i,t} \quad (1)$$

where:

- NOVOS_t = number of eggs laid on day t;
- FF = the sexual ratio of moths in the simulation area;
- AT = tabulated adjusting factor depending on daily mean temperature;
- F_i = fecundity of females with i days (eggs*female⁻¹*day⁻¹).

Result of the expression was stored daily in X_{i,t}, meaning the number of eggs with PD=1. Table 2 presents values of F_i at fixed 27°C. For moths with non-tabulated ages, fecundity was obtained by interpolation with the function AFGEN of CSMP. Values of correction factors of fecundity, according to temperature (AT) are shown on Table 3, and non-tabulated values were obtained by interpolation.

Mortality

The factors affecting survival of insects in the model are a) natural mortality; b) predation and parasitism; c) entomopathogens; d) low availability of food; f) insecticide and e) aging. Considering Y_{i,t} the initial population of day t, the model calculated final population according to the expression:

$$X_{i,t} = INT (\lambda_{i,t} Y_{i,t}) \quad (2)$$

where:

INT = a function returning the integer of the argument;

λ_{i,t} = overall survival rate for day t and for insects with i physiological days;

Y_{i,t} = initial population of day t.

The value of λ_{i,t} was calculated through the expression:

$$\lambda_{i,t} = (1-\mu_{i,t}^a)(1-\mu_{i,t}^b)(1-\mu_{i,t}^c)(1-\mu_{i,t}^d)(1-\mu_{i,t}^e)(1-\mu_{i,t}^f) \quad (3)$$

where:

μ^j_{i,t} = mortality rates (j=a, b, c,f).

When larval population is too high, a leaf area shortage may occur, reducing availability of food. In the case of the plant leaf area index (LAI) being equal to zero, all larvae on instars 1 to 4 died, as well as 70% of the 5th and 40% of 6th instars. The surviving insects finished the larval stage and became pupae. Natural mortality can occur in all stages of insect development except the moths, as the aging curve included all mortality factors. For eggs and pupae, natural mortality was a component of hatching rates, whereas natural mortality of larvae is shown on Table 4. These data reflect the experience of the authors exclusively and do not constitute experimental results.

TABLE 2. Fecundity of *A. gemmatalis* at fixed 27°C, by female and by day.

| Stage | Age in physiological days | | | | | | | | |
|-------|---------------------------|----|----|-----|-----|-----|----|----|----|
| | 26 | 28 | 29 | 30 | 31 | 32 | 37 | 42 | 44 |
| Eggs | 0 | 0 | 50 | 250 | 200 | 150 | 40 | 20 | 2 |

Source: Moscardi (1979).

TABLE 3. Coefficients for correcting oviposition of *A. gemmatalis*.

| Coefficient | Temperature (°C) | | | |
|-------------|------------------|-----|-----|-----|
| | 13 | 20 | 27 | 32 |
| AT | 0 | 0.8 | 1.0 | 1.0 |

Source: Leppla et al. (1977).

TABLE 4. Natural mortality (μ^a_{i,t} (%)) of larvae of *A. gemmatalis*.

| Factor | Instar | | | | | |
|--|--------|-----|-----|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Age ¹ | 4-5 | 6-7 | 8-9 | 10-11 | 12-13 | 14-15 |
| μ ^a _{i,t} (%) ² | 4 | 3 | 2 | 1 | 0 | 0 |

¹ Physiological days.

² Rate of mortality of the correspondent age, in the same column.

Feeding

Intensity of larval consumption of soybean leaves depended on larval instar and temperature. In order to match larval consumption and LAI, the first was calculated in ha*day⁻¹, by the following expression:

$$CON_t = 10^{-3} PD_t \sum_{i=4}^{15} CF_i X_{i,t} \quad (4)$$

where:

- CON_t = leaf area consumption (ha*day⁻¹);
- PD = physiological day;
- CF_i = individual consumption of larvae with i PD.

Values of individual consumption (CF) are shown on Table 5. The variation of consumption capacity according to temperature is implicit on the weighing of CON_t by PD_t.

Development

Insect development was processed by the model in a complex way. When a PD is completed, insects with 44 days left the system; those with 43 days changed to 44 days and so on up to NOVOS_t that changed to X_{1,t}. To determine the moment to trigger the changing, the model used two variables. The first one was called ULDF (last record of physiological day) and started the process with 1 and its values are only integers (1,... 44). The second variable was called DFA and represented physiological time accumulated and started the process with value = 0. When DFA => ULDF, a physiological day had been completed and equations which implement the insect development were processed. At the same time, ULDF was incremented by one. If one chronological day was completed, but physiological time was not enough to increment one PD, age structure of the insects was not changed, excepting NOVOS,

TABLE 5. Daily consumption (CON) of soybean leaf area by *A. gemmatalis*, in cm².

| Factor | Instar | | | | | |
|------------------|--------|-----|-----|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Age ¹ | 4-5 | 6-7 | 8-9 | 10-11 | 12-13 | 14-15 |
| CON | 0.2 | 0.4 | 1.5 | 4.0 | 12.30 | 29.00 |

¹ Physiological days.

Source: Adapted from Reid (1975).

which received the addition of new eggs laid during the chronological day. Block diagram on Fig. 3 help understanding the overall process.

Being X_{i,t} the number of insects with i PD at the end of day t, the number of insects on each PD of next day (t+1) was calculated to obtain Y_{i,t+1} for i=1,...44, depending on value of DFA. If a new PD has not been completed, initial population of the next day was calculated as follows:

$$Y_{i,t} = X_{i,t-1}, \quad i=2,3,\dots,44 \quad (5)$$

$$Y_{1,t} = X_{1,t-1} + NOVOS_{t-1}$$

When a PD had been completed, initial population of the following day was calculated by the expressions:

$$X_{3,t+1} = \rho_{lag} X_{3,t}$$

$$X_{27,t+1} = \rho_{mar} X_{26,t}$$

$$Y_{i,t} = X_{i-1,t-1} \quad (i=44,\dots,2)$$

$$Y_{1,t} = NOVOS_{t-1}$$

where:

ρ_{lag} = rate of hatching of larvae;

ρ_{mar} = rate of emergence of moths.

The last two equations describe development of insects as a whole, while the first two equations implemented conditions for hatching of larvae and moth emergence, which depended on mean temperature. In Table 6, values of ρ_{lag} and ρ_{mar} and values for non-tabulated temperatures obtained by interpolation are presented.

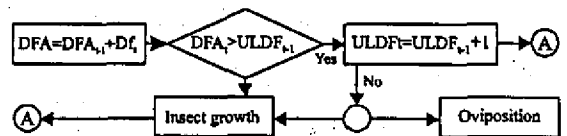


FIG. 3. Logic fluxogram of the growing process.

TABLE 6. Rate of hatching of larvae (ρ_{lag} (%)) and moths (ρ_{mar} (%)) of *A. gemmatalis*.

| Rate of | Mean temperature (°C) | | | | | | | | |
|----------------------|-----------------------|----|----|----|----|----|----|----|----|
| | 18 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 32 |
| hatching | 18 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 32 |
| ρ _{lag} (%) | 0 | 2 | 10 | 30 | 50 | 70 | 80 | 85 | 85 |
| ρ _{mar} (%) | 20 | 29 | | | | | | 63 | 45 |

Source: Adapted from Leppla et al. (1977).

Sub-model B: soybeans

For the purposes of this simulation model, soybean is conveniently represented by its leaf area index (LAI). This index is a non-dimensional function of time and, when multiplied by the soil surface area, furnished the available leaf area at any time. In this model soybean was considered to be cv. Paraná planted in the middle of the recommended period (ca. November 15) with 50 cm between rows and 20 plants per meter of row. Emergence was considered to occur at the 7th day after planting and bloom on the 45th day after planting. Values of LAI for soybean under these conditions were previously estimated by the authors as presented in Table 7. Gazzoni & Moscardi (1998) had developed a cubic exponential function to describe relationships between days after planting and LAI, allowing more precise calculation of leaf area corresponding to a given day, as follows:

$$LAI_t = 0.012 * e^{(0.24D - 2.97E-03 D^2 + 9.6 E-06 D^3)} \quad (7)$$

where:

e = natural (neperian) logarithm base;

D = days after planting.

All coefficients of the equation were statistically significant at p=0.05, and the most recent version of the model use the calculated LAI data instead of former tabulated data. The rate of variation (TEN) of soybean leaf area (AF) can be positive or negative, and trend was calculated as follows:

$$TEN_t = AF_t - AF_{t-1} \quad (8)$$

When leaf area consumption is high, forcing a deviation from the normal LAI curve, the soybean plant reacted, according to its stage of development, opening new leaves to recover, at least partially, the leaf area eaten by the larvae. This recovery process hypothesis was largely based on data obtained by Gazzoni (1974), but it is deeply complex and not totally clear even after the investigation of Gazzoni

& Moscardi (1998), whose mathematical equations are presented on Table 8. Some of the equations (V3 - 100% and R2 - 100%) presented negative intercept, but its values were so close to zero, that it was considered not necessary to recalculate them, because these equations are used by the model only when defoliation surpass 5%. In this case, the output of the equation will be always positive. Initially the recovery process reflected the opinion of the authors and considered that recovery on day t (RECUP) was an important component of effective leaf area, calculated as follows:

$$AFE_t = AFE_{t-1} + TEN_t + RECUP_t - CON_t \quad (9)$$

where:

AFE_t = effective leaf area of soybeans on day t;

RECUP_t = recovery of soybean leaf area on day t, following a defoliation that occurred previously;

CON_t = leaf area consumption as calculated on (4).

Comparison between AFE with leaf area expected for the same day t gave the loss of leaf area (PAF), used as an indicator for insecticide spraying, and was calculated through the expression:

$$PAF_t = 1 - AFE_t / AF_t \quad (10)$$

The recovery of leaf area did not occur as an immediate reaction to leaf area loss. Following a defoliation, supposed mechanism of leaf area recovery is flagged and became effective with the opening of new leaves some days after, or delaying the falling of elderly leaves during reproductive

TABLE 7. Leaf area indexes (LAI) for soybean cv. Paraná.

| Factor | Days after planting | | | | | | | | |
|--------|---------------------|---|------|------|------|------|------|-----|-----|
| | 1 | 7 | 20 | 32 | 41 | 58 | 84 | 102 | 115 |
| LAI | 0 | 0 | 0.39 | 1.07 | 1.84 | 2.81 | 1.74 | 0 | 0 |

Source: Gazzoni & Moscardi (1998).

TABLE 8. Mathematical equations describing the relationship between soybean defoliation and leaf area recovery, by growth stage and intensity of defoliation.

| Stage | Defoliation | Equation ¹ | r ² |
|----------------|-------------|---|----------------|
| V ₁ | 33% | Y = 0.6 - 0.062X + 0.01X ² | 1.00 |
| V ₁ | 67% | Y = 0.29 - 0.025X + 0.0067X ² | 1.00 |
| V ₁ | 100% | Y = -0.04 + 0.04X | 1.00 |
| V ₂ | 33% | Y = 2.16 + 0.24X - 0.00595X ² | 1.00 |
| V ₂ | 67% | Y = 0.95 + 0.28X - 0.076X ² | 1.00 |
| V ₂ | 100% | Y = 0.009 + 0.089X + 0.0028X ² | 1.00 |
| R ₁ | 33% | Y = 2.89 + 0.11X - 0.043X ² | 1.00 |
| R ₁ | 67% | Y = 1.41 + 0.14X - 0.053X ² | 0.97 |
| R ₁ | 100% | Y = -0.097 - 0.0017X + 0.0045X ² | 1.00 |
| R ₂ | 33% | Y = 1.66 - 0.165X + 0.007X ² | 1.00 |
| R ₂ | 67% | Y = -0.79 - 0.045X + 0.001X ² | 1.00 |
| R ₂ | 100% | Y = -0.09 + 0.0075X + 0.00036X ² | 1.00 |

¹ All parameters of the equations were statistically significant for p=0.05.

Source: Gazzoni & Moscardi (1998).

stage. The triggering of the process was made when the conditions $PAF_{t-1} > 5\%$ and $CON_t > 10^{-5}$ were fulfilled for the first time. Variable FLAG is set to 1, indicating the recovery process was activated. A transitory variable (AUX) stored 10% of the difference between AF_{t-1} and AFE_{t-1} , to be used as the recovery base value on day $t+2$. If conditions to start the recovery mechanism persisted, the process continued. In the case of $PAF_{t-1} < 5\%$ or $CON_{t-1} < 10^{-5}$ for any $t' > t$, FLAG was reset to indicate the end of the process, and 30% of the difference between AF_{t-1} and AFE_{t-1} was used for recovering leaf area on day $t'+2$. The variables RECUP0, RECUP1, RECUP2,...RECUPN presented on Fig. 4 are also reset.

Sub-model C: Migration

This routine controlled input and output of moths on the simulation area. The process of migration included the concept of local overwintering of VBC forms, and also alternative hosts, which are still largely unclear. Information used in the model represented primarily the opinion of the authors. The whole process was warped by two working hypotheses: a) At any time, the available soybean

leaf area determined the maximum capacity of support of moths, in the sense that leaf area would condition the survival rate of moth offspring, and the number of moths migrating into the area. When the number of moths exceeded that maximum, a part of them left the model, while migration into the model was accepted only up to this limit. For initial migration, the maximum capacity of the model is this limit, but as larvae fed on leaf area and reduced effective LAI, the maximum number of moths was reduced and provoked migration out of the model. As a matter of fact, the natural process should include other compensation mechanisms such as reduced egg laying and reduced larval consumption in order for a given population to survive on an established soybean leaf area. Meanwhile, for purposes of the model at this step of development, the concept of limit of environmental support would have an effect similar to more complex natural interactions that are still obscure. b) Induction of migration would be governed by the need to find adequate environmental conditions for the offspring of the moths, and as the act of flying medium or long distances requires energy, competing with the reproduction process itself, migration would occur on a negative exponential relation to its age, managed by the model through the parameter ULMIG, meaning the highest age at which the model allows a moth to migrate. Support capacity of moths (CS) was exponentially correlated to effective leaf area, being expressed by:

$$CS_t = MAXMAR (1 - e^{-\alpha_1 AFE_t}) \tag{11}$$

where:
 CS_t = capacity of support of moths on day t ;
 $MAXMAR$ = maximum capacity of support of moths;
 α_1 = adjust factor (constant=3).

The constant factor α_1 was obtained by repeatedly exercising the model for adjusting this parameter, with 3 being the value which yielded the most adequate results. The maximum value for MAXMAR was arbitrarily defined by the authors as 80,000, based on their own observations and did not constitute experimental data. If the number of moths (TM) in a given moment t is lower than CS_t , a fraction of the difference between CS_t and TM_t entered the area of the model, and this fraction was calculated considering the prognosis of availability

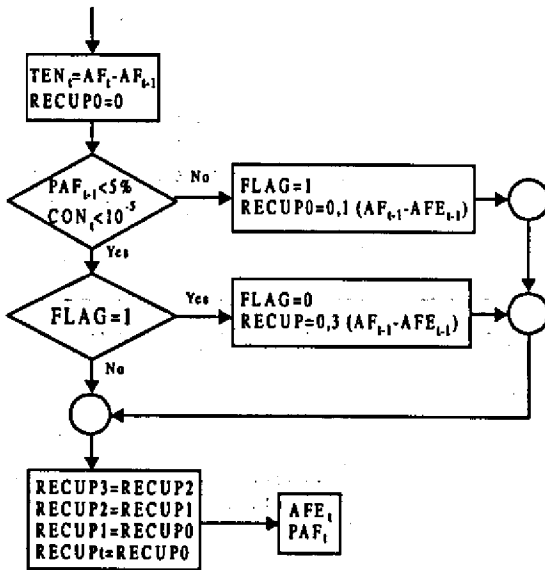


FIG. 4. Logic fluxogram of the mechanism of recovery of soybean leaf area.

of leaf area in the near future. The higher the estimated leaf area (AFEST) the closer to 1 would be the fraction. The target for the near future was considered to be 8 physiological days, based on time necessary for eggs laid on day t to enter 3rd instar, where leaf consumption effectively increases. Another factor conditioning migration did not interfere with calculation up to a given date (ULMIG), when a correction factor is applied to a previous calculation of migration. The number of moths entering the area was calculated as:

$$\alpha_3 = \text{STEP}(\text{FIMIG}) ((50 * (\text{TIME} - \text{FIMIG}) + (105 - \text{FIMIG}))$$

$$\text{IMIG} = (\text{CS} - \text{TM}) * (1 - e^{-\alpha_2 \text{AFEST}}) * e^{-\alpha_3} \quad (12)$$

where:

FIMIG = end of migration process;

IMIG = day of first moths migrating into the model;

α_2 = adjust factor (constant = 5E-03);

AFEST = estimated leaf area.

The constant factor α_2 was also obtained by repeatedly exercising the model. The adjustment of the model yielded 5E-03 as the best value for this constant, under the present model conditions. This value may vary if other conditions are changed. STEP is a CSMP function returning zero if TIME is lower than FIMIG and one in the reverse case. Age distribution of the migrating moths follows the same pattern of the ones existing previously in the simulation area. In the case where the number of moths is larger than CS, a fraction of the moths between 1 and ULMIG physiological days left the model, supposedly migrating to an area with best food and reproductive conditions. Number of moths leaving the area was calculated through the expression:

$$\text{EMIG} = \text{MAR} * e^{-\alpha_4 \text{AFEST}} \quad (13)$$

where:

EMIG = number of moths leaving the model;

MAR = number of moths with 1 to ULMIG physiological days;

α_4 = adjusting factor (constant=5E-02).

The constant factor α_4 was obtained through a sequence of simulations, changing its value. The best results were obtained when 5E-03 was used as a constant. This value may vary if other conditions in the model, like life or time parameters are changed.

Sub-model D: Insecticide

Application of insecticide was made when: a) number of days from planting to day t was lower than 95; b) number of larvae from instars 4th to 6th was greater than 400,000 of PAF > 30%, before day 45 or PAF > 15% after day 45 (Gazzoni et al., 1981).

The insecticide is characterized by: a) number of days of effectiveness of control; b) daily mortality of VBC larvae from the day of application to the end of its effectiveness; c) daily mortality of predators and parasitoids of VBC. Insecticide considered was endosulfan, chosen because it was the standard on CNPSO evaluation tests (Oliveira et al., 1988), having an active range of 20 days. Table 9 presents the rate of mortality of VBC larvae caused by the insecticide (μ^a), measured as mortality over surviving (t-1) individuals. The impact over biological control ($\Delta\mu^b$) was represented as a correction factor over the mortality caused by predation and parasitism (μ^b). It was assumed that the effect of insecticide over any larval instar was the same, and had no effect upon eggs, pupae and moths, and that the number of applications of the

TABLE 9. Larval mortality (μ^a (%)) of *A. gemmatilis* and impact on its natural enemies ($\Delta\mu^b$ (%)), caused by an application of endosulfan.

| Mortality index | Days after application | | | | | | | | | | | | | | | | | | | |
|-------------------|------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|-----|-----|-----|-----|-----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| μ^a (%) | 85 | 50 | 35 | 30 | 23 | 19 | 15 | 12 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 | 0 |
| $\Delta\mu^b$ (%) | 90 | 90 | 90 | 90 | 90 | 90 | 90 | 90 | 90 | 91 | 92 | 93 | 95 | 98 | 100 | 100 | 100 | 100 | 100 | 100 |

insecticide was defined by fulfillment of application conditions, even within the 20 day period of action of the insecticide.

Sub-model E: Predation and parasitism

Approach to this routine was made upon an overall rate (μ^b), instead of discriminating between each specie of natural enemy; also mortality caused by them is differentiated only in relation to the stages of insect development, whose values are shown in Table 10. These values represent only the experience of the authors and are not supported by experimental data.

Sub-model F: *Nomuraea rileyi*

Among the entomopathogens that might affect VBC population, the white disease, caused by *N. rileyi* was selected to be used in the model, as it causes by far the largest natural mortality of VBC larvae under field conditions. According to Allen et al. (1971), field epizootics occurred given a) mean temperature $\geq 23.5^\circ\text{C}$; b) relative humidity $\geq 75\%$ and c) larval density $\geq 5.m^{-2}$. The model assumed that once the epizootic was triggered, environmental conditions would help the natural spreading of the fungus on VBC populations; rates of mortality were applied over a 20-day period, during which almost all the population would have been decimated.

TABLE 10. Rate of mortality (μ^b (%)) caused by predation and parasitism of *A. gemmatilis*.

| Rate | Egg | | Larvae | | | | | |
|-------------|-----|----|--------|---|---|---|---|--|
| | 1 | 2 | 3 | 4 | 5 | 6 | 6 | |
| μ^b (%) | 5 | 20 | 15 | 5 | 2 | 1 | 1 | |

Nevertheless, once the above mentioned conditions were detected again after the completion of the epizootic process, it began again. The rate of mortality caused by *N. rileyi* on VBC larvae is presented in Table 11 and exclusively reflects the opinion of the authors, as no experimental data was found on the subject.

Sub-model G: Environment

The environment for soybean and insect development is represented by tabulated data containing maximum (TMAX) and minimum (TMIN) temperatures. From this data the model calculated the expressions of daytime temperature (TD), nighttime temperature (TN), mean temperature (MT) and physiological day (PD). The duration of the day (CD) was also calculated in terms of numbers of hours between sunrise and sunset. Expressions are:

$$A_1 = (-0.14354442 + (6.805337E-02 * \text{latitude}));$$

$$A_2 = \sin(1.81784862 + (1.668753E-02 * \text{julian}));$$

$$A_3 = (12.0888429 + (1.94507E-03 * \text{latitude}));$$

$$CD_t = A_1 + A_2 + A_3; \tag{14}$$

$$TD_t = 0.55 (TMAX_t - TMIN_t) + TMIN_t; \tag{15}$$

$$TN_t = 0.15 (TMAX_t - TMIN_t) + TMIN_t; \tag{16}$$

$$TM_t = ((TD_t * CD) + (TN_t * (24 - CD))) / 24, \tag{17}$$

where:
 latitude = latitude for Londrina - PR (Brazil) 23.3°S ;
 julian = is the number of the chronological day t (1 = Jan. 1st, 365 = Dec. 31st).

The coefficients of the expression were repeatedly calculated through a data set of astronomical hours of sunrise and sunset, extracted from astronomical tables.

Fig. 5 presents a standard population of *A. gemmatilis*, as simulated by the mathematical model, that fit well with results obtained through effective survey made in the same ecological region by CNPSO scientists, demonstrating that the model does not yield unrealistic data.

TABLE 11. Larval mortality (μ^c (%)) of *A. gemmatilis* caused by the fungus *Nomuraea rileyi*.

| Rate | Days after application | | | | | | | | | | | | | | | | | | | |
|-------------|------------------------|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| μ^c (%) | 1 | 2 | 2 | 3 | 5 | 7 | 10 | 15 | 22 | 30 | 40 | 55 | 75 | 90 | 91 | 92 | 93 | 93 | 93 | 93 |

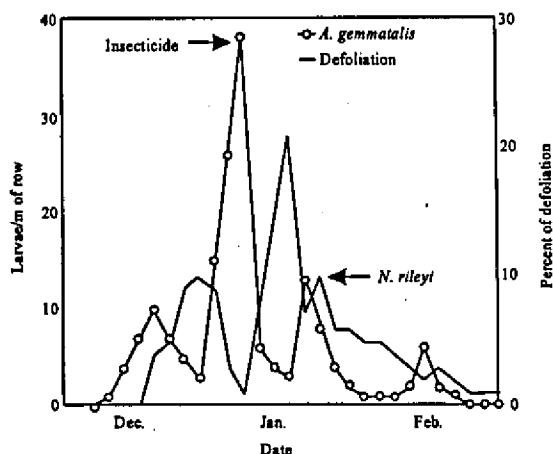


FIG. 5. Number of larvae of *A. gemmatalis* per meter of row of soybean and percent of defoliation of leaf area, as simulated by the model.

CONCLUSIONS

1. Information on *Anticarsia gemmatalis* biology and ecology is enough to simulate its life cycle and feeding habits on a realistic basis.
2. Information is lacking especially in regard to the migration process and to tritrophic interactions among plant, pest and natural enemies.
3. The internal consistency of the model allows for further development of predictive models for the same insect.

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