

Pink Bollworm Control in Southwestern Desert Cotton

I. A Field-Oriented Simulation Model N. D. Stone and A. P. Gutierrez

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ABSTRACT

I. A Field-Oriented Simulation Model

A simulation model for pink bollworm (PBW) and cotton was developed, field validated, and incorporated into an industry sponsored regional PBW management program for southwestern desert cotton. The PBW model differs from earlier versions in its incorporation of stochastic development, the expansion of the concept of physiological time to include nutritional influences of the cotton host on larval development, and its ability to simulate the kinds of data typically collected by pest control advisors when monitoring cotton for pink bollworm.

II. A Strategic Management Model

A simulation model of pink bollworm populations, as affected by insecticide and pheromone applications in cotton, is described. The simulation results compared favorably to field data. The study indicates that use of sex pheromone for control of pink bollworm by mating disruption inversely depends on density and therefore is most effective in the early season when populations are low. Compared to untreated fields, pheromone-treated fields show delayed population peaks and reduced overall infestation. Pheromone applications in the early season delay but do not obviate the need to spray insecticide to limit infestation levels.

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Pink Bollworm Control in Southwestern Desert Cotton¹

I. A Field-Oriented Simulation Model

INTRODUCTION

SIMULATION MODELS of economically important pest species and their host crops have long been recognized as potentially important tools in production agriculture (Watt 1961), but few have been delivered in useful form to the field. This paper presents a case study in which a simulation model describing the interaction of pink bollworm, *Pectinophora gossypiella* (Saunders), and cotton, *Gossypium birsutum* L., was developed with the specific goal of field implementation. The model has since been used as part of an industry supported regional pink bollworm (PBW) management program in Arizona and in the Palo Verde and Imperial valleys of California (Gillespie, Stone, and Kydoneus 1985).

The biologies of cotton and pink bollworm have been extensively reviewed (see Gutierrez et al. 1975; Noble 1969; Gutierrez et al. 1977); relevant PBW biology is discussed below.

Biology of the Pink Bollworm

Pink bollworm adults are small nocturnal moths whose larvae feed within the fruiting structures of their host plants. Mating occurs in early morning hours, peaking at 3:30 a.m., when females climb near the terminals of cotton plants and emit a calling pheromone (Lukefahr and Griffin 1957). Females may mate multiply, but a single insemination suffices for the female to produce a full complement of fertile eggs (Lukefahr and Griffin 1957; Butler et al. 1983). This pheromone-mediated mating is explored in detail in Stone and Gutierrez (II. this series).

Eggs are laid on all parts of the cotton plant, but once cotton fruits (bolls) are present, eggs are placed preferentially on them (Henneberry and Clayton 1982). Even though larvae can and do complete development on the maturing cotton flower buds (squares), they are not favored (Henneberry and Clayton 1982). Upon hatching, larvae on bolls generally bore directly into the fruit, while larvae from eggs laid on nonfruiting structures must search for a suitable feeding site (Brazzel and Martin 1955). Generally, only one larva survives in a square, but several can develop within a single boll (Brazzel and Martin 1955). In either case, larval development occurs in a single fruit. Pupation occurs in the soil near the soil surface (Noble 1969) or in the lint of the bolls (Lukefahr and Griffin 1962). Natural mortality to the pupal stage can be high, especially under extreme temperatures (Pinter and Jackson 1976); cultural practices and soil moisture also affect pupation success (Clayton and Henneberry 1982). The PBW overwinter as diapausing final instar larvae. Diapause is induced primarily by short photoperiod and

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low nighttime temperatures (Gutierrez, Butler, and Ellis 1981), but is also influenced by nutritive quality of its food source and moisture (Adkisson 1961; Adkisson, Bell, and Wellso 1963).

Pink Bollworm Damage and Control

Infested squares flower and set fruit normally, despite larval feeding (Westphal, Gutierrez, and Butler 1979). In the bolls, however, larvae feed on the seeds and lint, causing economic losses due to reduced yields and lowered lint quality (Brazzel and Gaines 1956; Henneberry, Bariola, and Russell 1978). Furthermore, larvae that exit through the boll wall leave a small hole (about 2 mm diameter) which precipitates additional damage from invading saprophytic microorganisms.

Because of the burrowing habits of PBW larvae, control with insecticides is effective primarily against the egg and adult stages (Burrows et al. 1982); once bolls are present, even the eggs are protected, since a large proportion are laid within the bracts of the fruit or between the boll and the calyx (Henneberry and Clayton 1982). Only the adults are fully exposed to aerially applied inscricides.

Monitoring PBW populations is also hindered by the life history of the pest and relies principally on three sampling methods:

- (1) Dissecting 14- to 21-day-old (susceptible) bolls looking for evidence of larval entry or presence. This method is commonly called "boll cracking" (Toscano, Sevacherian, and Van Steenwyck 1979).
- (2) Trapping adult males in flight traps baited with artificial PBW sex pheromone (Hummell et al. 1973; Flint and Merkle 1983; Huber and Hoffmann 1979; Lingren et al. 1980).
- (3) Examining flowers on the day of blooming for presence of PBW larvae. The larvae spin webs which often tie together the developing petals and prevent proper blooming. The result is an easily noticed rosetted bloom (Noble and Robertson 1964).

No method is completely satisfactory. Boll cracking discovers young larvae, but control practices must be undertaken against adults whose population cycles precede larval cycles. Using boll-cracking data to time insecticide applications against adult PBW therefore incorporates a time lag into the decision-making process. Pheromonebaited trap catches monitor adults, but they have been shown to be highly variable (Beasley, Henneberry, and Adams 1984). Rosetted bloom counts are reliable only before substantial numbers of bolls are present.

EXPERIMENTAL STUDIES

Cotton Growth and Development

Plant-growth data were collected during the summers of 1983 and 1984 in California's Palo Verde Valley. Plants in 1983 were sampled in two small (about 1 hectare) plots grown identically and in accordance with the region's standard commercial practices. In 1984, plants were sampled in five commercial fields (16 to 32 hectares each). Five whole plants were taken from each field two times per week, and the plant parts mapped according to age and position on the plant; percent leaf area damaged was also recorded (Gutierrez et al. 1975; Westphal, Gutierrez, and Butler 1979). Each plant from 1983 was then dissected into leaves, stems and roots, and fruit parts, dried in a convection oven at 45° C for 1 week, and weighed to determine dry matter accumulation. The plant stand in each field was determined at or just before first bloom by averaging five counts of plant numbers in 40 m of row; spacing between rows was approximately 1 m (1.016 m).

Individual flowers and squares were surveyed over time to determine average developmental times between pin-square and flower, and between flower and mature boll. Square development was defined to begin when a leaf in the terminal whorl supporting the axillary square was approximately 7 to 8 mm long and could be separated from the terminal to expose the square. Flowering rates were sampled three times weekly by counting the number of white blooms per 40 m of row.

Note: In 1983 the cotton suffered severe water stress due to cultural practices beyond experimental control, causing much uneven, stunted growth.

Pink Bollworm Population Dynamics

The 1983 small plots mentioned above were used to follow PBW infestation patterns under controlled conditions. The single-hectare plots (E=East and W=West in figure 1*a*), were bordered to the north by alfalfa, and to the south and west by fallow ground. The west plot (W) had alfalfa to the east; the east plot (E) had wheat followed by bermudagrass to the east. The plots were planted April 6 with a resulting stand density of 7.2 plants per meter-row. Cotton had been planted in the same fields the previous year.

Plot W was treated four times during the season with the insecticide Permethrin, applied in oil for the first three, and Azadrin for the last. Plot E was treated 10 times with pheromone only. Pheromone was applied at rates of 2.8 g/ha (four applications), 3.7 g/ha (four applications), and 7.4 g/ha (last two applications) active ingredient in three-layer plastic laminate flakes (Kydoneus et al. 1981). All applications were made by air according to the area's standard practices.

Adult populations were monitored using modified malaise (flight) traps (Butler 1966; Butler et al. 1983). Six traps were placed in and around each plot in the pattern shown in figure 1*b*. Traps were emptied daily from 6 to 7 a.m. Moths were collected in clear glass jars containing a small square (2.5 cm^2) of Shell No-Pest Strip. Fresh squares were substituted at least once each month throughout the study. Moths collected from the malaise traps were removed to the laboratory, counted, and sexed under a dissecting microscope.

Larvae feeding on cotton squares were sampled by rosetted bloom surveys; larvae infesting bolls were counted by cracking bolls. During the blooming period from June 10 to August 29, surveys of 40 m of row were made every 1 to 4 days. Counts were made of the number of white (less than 1-day-old) flowers, and the number and instar of any PBW larvae found within the blooms.

Boll cracking was impossible at times because bolls of an appropriate age were not consistently available due partly to the fruiting pattern of cotton and partly to the a)



b)



Fig. 1. Experimental cotton plots from 1983 showing relative position and proximity to other crops (a) and flight trap placement (b).

fact that the plants had suffered the severe water stress mentioned earlier. When susceptible bolls were present, 50 to 60 of the 14- to 21-day-old bolls were taken from the field at 2- to 4-day intervals through early August. They were removed to the laboratory, opened along the natural sutures between the locules, and examined for the presence of PBW larvae. Larval numbers and approximate instar were recorded.

THE MATHEMATICAL MODEL

A simulation of the pest management of PBW necessarily involves three interconnected elements: a crop model, a pest model, and a management model. The bases for the first two elements presented here, are the Gutierrez cotton model (Gutierrez et al. 1975, 1984; Wang et al. 1977), and the PBW submodel (Gutierrez et al. 1977, Gutierrez, Butler, and Ellis 1981; Westphal, Gutierrez, and Butler 1979). Modeling the pest management of PBW is discussed in Stone and Gutierrez (II. this series). The cotton model has been field tested with good results in Brazil (Gutierrez et al. 1984), the Sudan (von Arx, Baumgaertner, and Delucchi 1983), as well as in the United States in California and Arizona (Gutierez et al. 1975, 1977). It is included here with some modifications. The structure of the PBW model has been greatly altered.

Cotton

The cotton model is a plant-canopy model, simulating a cotton field under the assumption that all plants are growing identically. The pattern of development of the average plan is in part determined by weather and initial planting density. Spacing of cotton plants determines the extent to which branches and roots of neighboring plants intermingle and thereby compete for resources. Thus, planting density is an index of interplant competition, and all growth rates are functions of density.

Plant parts are treated as populations and linked by energy flow. Aging and attrition within each subpopulation are modeled by a distributed delay algorithm (Manetsch 1976; Vansickle 1977). This algorithm deterministically distributes aging rates in an age-specific population vector according to Gamma probability density functions describing the mean and variance of biological developmental times.

The delay process for a fruit subpopulation (e.g., bud, flower, boll) is described below in terms of the storage of biomass, numbers, or energy (W^j) in each substage. Note that the substages within each subpopulation (W_i^j) are of equal width in terms of physiological time.

$$\frac{dW^{j}_{1}(t)}{dt} = x^{j}(t) - r^{j}_{1}(t)$$

$$\frac{dW^{j}_{2}(t)}{dt} = r^{j}_{1}(t) - r^{j}_{2}(t)$$

$$\vdots$$

$$\frac{dW^{j}_{k}(t)}{dt} = r^{j}_{k-1}(t) - y^{j}(t)$$

where, $W^{j}(t) = \Sigma_{i=0}^{k} W_{i}^{j}(t)$ is the storage within the subpopulation (e.g., number of squares), $x^{j}(t) = r_{0}^{j}(t)$ is the birth rate into the subpopulation (e.g., rate of squaring), $r_{k}^{i}(t) = y^{j}(t)$ is the rate of flow out of the subpopulation (e.g., rate of blooming). The number of substages used (k) and the mean transit time in physiological units for a subpopulation (T^j) determine the flow rates as:

$$r_i^j(t) = \frac{k}{T^j} W_i^j(t), i = 1, 2, \dots, k.$$

The above storage equations can be altered to include net attrition (Vansickle 1977). In the following, μ includes net immigration and total mortality and is thus bounded: $\mu \in [-\infty, 1]$.

$$\begin{split} \frac{dW_1^{i}(t)}{dt} &= x^{j}(t) - r_1^{i}(t) - \mu_1^{j}(t)W_1^{i}(t) \\ \frac{dW_2^{j}(t)}{dt} &= r_1^{j}(t) - r_2^{j}(t) - \mu_2^{j}(t)W_2^{j}(t) \\ &\vdots \\ \frac{dW_k^{j}(t)}{dt} &= r_{k-1}^{j}(t) - y^{j}(t) - \mu_k^{j}(t)W_k^{j}(t) \end{split}$$

The birth and aging to the next age group of new plant parts occurs via x^{j} and y^{j} , respectively; net growth of existing plant parts is modified by μ_{i}^{j} . All variables x^{i} , y^{j} , and μ^{j} are linear functions of the appropriate photosynthate supply-demand ratio (S/D).

All plant part subpopulation models are linked through the metabolic pool model for photosynthate allocation (see Gutierrez et al. 1975, 1984). The daily photosynthetic rate and a fraction of reserves are allocated from the metabolic pool according to the priority scheme reported by Gutierrez et al. (1975). Photosynthate goes first to meet the respiration requirement, then to fruit growth, then to vegetative growth, and last to reserves.

Weather effects combine with population density effects to drive the cotton model. Photosynthesis is a function of leaf mass and the amount of solar radiation received by the plant, while the nutrient demand rates of the plant subpopulations are density and temperature dependent. The S/D ratio thus provides an index of density dependent effects as influenced by weather. It is used as a measure of physiological stress to adjust plant growth and fruiting rates over time. Other meteorological influences have been ignored, as have irrigation, fertilization, and cultural practices, primarily because suitable models for them are not available. Despite these simplifications the model's predictions have been extremely accurate.

Pink Bollworm

In its 1981 form, the PBW model contained three separate elements: a diapause emergence model, a diapause induction model, and a development model. The first two of these have been included here without revision. The reader should refer to Gutierrez et al. (1977), Gutierrez, Butler, and Ellis (1981), and Westphal, Gutierrez, and Butler (1979) for a full description. This paper deals with the last portion of the PBW model, the development of PBW and the influence of the plant on that development.

The basic population dynamics equations for PBW are similar in form to those representing the subpopulations of plant parts in the cotton model. Ignoring the distributed delay process for convenience, and letting N(t,a) be the number of PBW of age, a, at time, t; $\mu_N(\bullet)$ be a complex net mortality function which depends on time, age, density, temperature, etc.; and i(t) be the net gain rate due to migration (see Gutierrez et al. 1977); the population equation for PBW becomes a von Foerster (1959) equation:

$$\partial N / \partial t + \partial N / \partial a (da/dt) = -\mu_N(\bullet) N(t,a) + i(t)$$

In the model, the aging process has been modified to incorporate developmental variability as described above for cotton.

The PBW adult population is further divided into those that overwintered as diapausing larvae, N_d ; those that developed as larvae in squares, N_s , and those that developed as larvae in bolls, N_b . The corresponding fecundity rates, f_b , f_s , and f_d , of these adult classes differ and satisfy the relationship, $f_b > f_s > f_d$.

Eggs laid by PBW adults develop through four larval instars, a pupal stage, and a final adult stage. Mean developmental rates with a given variance govern aging. Values for mean developmental times, as well as age-specific mortalities and fecundities, are reported in Gutierrez et al. (1977).

Modeling Plant Effects on PBW Oviposition and Survivorship

The phenology of the cotton crop affects PBW development by influencing not only the moth's fecundity and availability of food, but also PBW survivorship and developmental rate.

Egg survivorship depends largely on where they are laid. In the early season, when cotton plants are small and without bolls, PBW females oviposit randomly on vegetative parts of the plant that are relatively exposed to predators and pesticides: terminals, leaves, and crevices (Henneberry and Clayton 1982; Brazzel and Martin 1957). In the model, 90 percent of eggs are potential victims of pesticides and predation. Later in the season, PBW females oviposit preferentially on bolls. Brazzel and Martin (1957) report 34 to 55 percent of eggs were laid on bolls after there were four bolls per plant. Henneberry and Clayton (1982) and Westphal, Gutierrez, and Butler (1979) give similar figures for ovipositional preference once bolls are present. Accordingly, in the PBW model fewer eggs (65 percent) are considered potential targets for insecticide and predators once bolls are present. Furthermore, the survivorship of larvae infesting fruit of different ages varies linearly with the fruit's age as shown by Westphal, Gutierrez, and Butler (1979).

The age of the fruit in which a PBW larva feeds dramatically affects the aging rate of that larva and, hence, the timing of population peaks and cycles (Lukefahr and Griffin 1962). This nutritional influence of the plant on the development of PBW is discussed in Gutierrez et al. (1977) and is revised here, modeled as the continuous function, $\Omega(D(t))$, where D(t) is the age in degree-days of the host fruit, and $\Omega(D)$ is

a scaling multiplier for the developmental rate of the infesting larva. When $\Omega(D) = 1.0$, the developmental rate of a larva feeding on a host fruit of age D is aging at a rate exactly equal to that achieved on standard lab diet (see Appendix).

The PBW larvae are represented in a two dimensional population matrix, V (for a graphical representation of V see *Summary of PBW Development* below). This array incorporates PBW age structure in one dimension and the age of the fruit infested in the other. The number of larvae of age i infesting fruit of age j at time t is held in entry (i,j) of V. When $\Omega(D(t))$ is discretized into an array of nutritional ratios, Ω_j , the aging process through any entry of V can be described mathematically. Two processes are involved. First, fruit ages at a rate governed by a complex aging function, $f(\bullet)$, which incorporates the distributed delay process described above. Some larvae of age i but in fruit of age j-1 will move into entry (i,j) when the fruit they are in matures to age j. Similarly, some larvae in (i,j) will age out to (i,j+1) because the fruit they infest has matured to the next age class. The second aging process is similar to that just described. The overall change in any entry of array, V, can be written:

$$v_{i,i}(t+1) = v_{i,i}(t) + f(\bullet)[v_{i,i-1}(t) - v_{i,i}(t)] + g(\bullet)[\Omega_{i-1}v_{i-1,i}(t) - \Omega_i v_{i,i}(t)]$$

Aging along the i-dimension represents accumulation of physiological age by a PBW larva and occurs at different rates with time depending on the age of the host (i.e., the nutritional ratio or scalar involved), the accumulated degree-days in the time step, and the mean and variance characteristics of the distributed time-delay function. Aging in the j-dimension depends only on the development of the plant; recall that PBW infestation in fruit is not thought to alter significantly the growth of the fruiting forms.

The two-dimensional aging process was completed by determining at what physiological age PBW larvae molt. The larval stage consists of four and sometimes five instars within the fruit (Watson and Johnson 1974) as well as a brief prepupal, nonfeeding stage (Lukefahr and Griffin 1962). For the purposes of this model it was assumed that all larvae go through just four instars within the fruit. Developmental times of the different instars (table 1) were determined experimentally by Dr. W.

Temperature (C°)	Number per instar	Developmental time (days)*								
		$1st \pm SD$		$2nd \pm SD$		$3rd \pm SD$		$4th \pm SD$		
17.5	30	203.2	13.7	199.8	54.3	215.0	62.8	533.2	81.3	
19.0	30	176.8	39.1	152.5	78.2	96.6	32.4	203.6	67.5	
25.0	30	72.7	6.1	70.2	36.6	54.1	24.9	133.5	37.0	
27.5	24	98.3	37.8	76.8	46.3	51.9	16.8	125.8	26.7	
30.0	30	50.4	9.7	67.1	29.1	48.6	7.6	131.8	22.6	
34.0	30	70.4	15.4	68.6	25.0	59.0	25.7	116.6	29.2	
35.0	14	72.0	23.1	61.4	26.0	71.6	33.9	126.4	37.9	
Pooled	188	109.4	61.6 a	103.5	69.4 a	87.5	66.6b	204.0	153.9c	

 TABLE 1.
 MEAN DEVELOPMENTAL TIMES OF PBW LARVAE, BY INSTAR,

 REARED AT CONSTANT TEMPERATURE

*Pooled means for instars not followed by the same letter are significantly different by multiple comparisons using Bonferroni's test (procedurewise error rate ≤ 0.05).

Hutchinson and Dr. G. D. Butler, Jr. of the Western Cotton Research Lab of USDA in Phoenix, Arizona as part of an ongoing experiment (W. Hutchinson, personal communication).

The mean developmental times over all temperatures show that the fourth instar took the longest and the third instar the shortest amount of time to complete development, while the first and second instars were statistically indistinguishable. When developmental times were converted to proportions (table 2), the instars' proportional developmental times over all temperatures are approximately constant.

Summary of PBW Development

The total aging process described above is summarized in figure 2. Larvae accumulate physiological age from left (just hatched larva) to right (larva ready to pupate); the fruiting forms of cotton age physiologically from top (pin-square) to bottom (mature boll). The aging process is shown as a series of paths through time.

The influence of the nutritional function is easily seen by examining the shape of the developmental paths. For example, a larva entering a very young square (no. 1) shows a nearly vertical path, indicating that it ages very slowly due to the low nutritional value of the young square. Only after the young square ages does its nutritional content rise, increasing the horizontal aging component of the larva so that it moves diagonally to point A, where it molts to become a second instar. The larva then continues to grow and molt until its path reaches the rightmost edge of the figure (point B), where it completes its feeding, cuts an exit hole from the square, drops to the ground, and pupates. Notice that only a small percentage of larvae actually complete their development (paths intersect the right edge of the figure) before the square has become a flower, bloomed, and dried. Field bloom surveys of white flowers revealed PBW-damaged flowers usually contained larvae, but flowers with exit holes cut in the petals and no larvae remaining were also occasionally found.

Following most of the paths to completion in the squares shows that despite a rather wide range of entry points in time, larvae in mature squares tend to be in or near

Temperature Number per		Proportional developmental time							
(C°)	instar	1st	2nd	3rd	4th	Sum*			
17.5	30	0.177	0.174	0.187	0.463	1.001			
19.0	30	0.282	0.239	0.156	0.324	1.001			
25.0	30	0.223	0.208	0.166	0.404	1.001			
27.5	24	0.276	0.207	0.150	0.366	0.999			
30.0	30	0.172	0.220	0.166	0.443	1.000			
34.0	30	0.225	0.220	0.187	0.369	1.001			
35.0	14	0.221	0.190	0.214	0.375	1.000			
Pooled	188	0.217	0.205	0.173	0.404	0.999			

 TABLE 2.
 PROPORTIONS OF TOTAL PBW LARVAL DEVELOPMENT SPENT IN EACH LARVAL INSTAR, DETERMINED AT CONSTANT TEMPERATURES

*Total proportional development may differ from unity due to rounding error.





progress of individual PBW larvae that hatch and enter fruit of various ages (extreme left). PBW aging rates vary, depending on the nutritional value of the fruit host at any particular time. Completion of development occurs when paths reach the rightmost edge of the figure; (a) shows develop-Summary of PBW development in fruit. Fruit age vertically downward and larvae age horizontally to right. The paths shown follow the ment in squares; (b) shows development in bolls. Fig. 2.

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their fourth instar. In bolls, most PBW complete their development before bolls mature, because the nutritional value of bolls is higher initially than that of squares. Thus, exit holes in bolls due to PBW infestation are much more common in the field and larvae do not bunch up as they do in squares.

The greatest value of the two-dimensional structure shown in figure 3 is that it gives the model the ability to simulate PBW infestation in particular age categories of the cotton fruit. Of course, this assumes that the cotton fruiting model is reasonably accurate. Given this, two obvious applications of the model are: to simulate numbers of PBW larvae in flowers and numbers of PBW larvae in bolls considered susceptible. Each is calculated at any time, t, by the expression,

$$\begin{array}{ccc} t_2 & b \\ \Sigma & \Sigma & v_{i,j} \\ j = t_1 & i = a \end{array}$$

where the age interval t_1 to t_2 defines the stage of cotton fruit in question, and a and b are the relevant larval instars of PBW, a,b ϵ { 1,2,3,4 }.

EXPERIMENTAL RESULTS

To allow the comparison of simulated and observed PBW larval populations, the pest control measures undertaken in the two experimental plots in 1983 were modeled and included in some of the simulations below. The management model used is described in detail in Stone and Gutierrez (II. this series).

The accuracy of the cotton model in reproducing field data is demonstrated in figures 3 and 4. The simulated results are plotted as the lines through the data. The simulation of water-stressed cotton was accomplished by adjusting the normal growth parameters for Delta Pine cotton by factors suggested by extensive field sampling (Stone 1984). Figure 3*A* also shows the comparison between the stressed cotton fruiting pattern and the expected pattern for unstressed cotton. Note that the model predicts the correct phenology and abundance of squares, flowers, and bolls, although the simulation of stressed cotton tended somewhat to overestimate flower numbers after day 185 (fig. 3*B*).

A discrepancy is that the model predicted a small amount of flowering 10 days earlier than measurable in the field. This occurred because the distributed delay model produces continuous values for plant population counts instead of using integer values. The aging process initially produces small real number values like $F_p = 0.01$ flowers per plant, which in turn are multiplied by the number of plants per unit area to determine the simulated number of flowers per unit area. If the plant stand were D = 70,000 plants/ha, this would produce a simulated value of $F_T = 700$ flowers/ha. Realistically, the likelihood of any plant having a flower in a field in which the average plant is only 1/100th of the way toward producing a flower is much closer to zero. What is missing from the model is the probability (P_i) of a plant having i flowers, given F_p , where $i = \{0, 1, 2, ...\}$. If P_i were known, F_T could be calculated as $F_T = D\Sigma_i(iP_i)$. Because the problem is significant only for short times and because very small numbers are involved, the model was not altered. However, as shown below, this caused a small problem in the PBW simulations.



Fig. 3. The fruiting and flowering patterns for a water-stressed field of Delta Pine 90 cotton from 1983. Square and boll numbers (A) and flower counts (B) are plotted and compared to simulated data. Two simulations are included in A: the dashed lines show the output for unstressed cotton, and the solid lines show output with corrections for stress. Only the stressed cotton simulation is included in B as the solid line.



Fruit Points / Plant

PBW Population Dynamics

Recall that in 1983 the East plot was treated exclusively with pheromone and the West only with pesticide. Consequently, where convenient below, the plots are designated by relative location and/or treatment.

Spring emergence of adult diapause moths

The observed spring emergence of PBW adults from diapause, as measured by malaise trap catches, was nearly identical in the two plots (fig. 5). Peak emergence occurred around May 23 (day 143), and the overall pattern was unimodal, with a single depression shortly after peak (May 30 = day 152), corresponding to a period of low nighttime temperatures. The simulated emergence, shown as the dashed line in figure 5, follows nearly the same pattern, including a reduced emergence near day 152. Note that malaise trap counts are relative estimates; hence, only the relative timing and magnitude of the simulated and observed data in figure 5, not the absolute numbers, should be compared.



Fig. 5. Observed PBW spring emergence from diapause as measured by the relative abundance of adult PBW moths caught in flight traps in the two experimental plots in the early spring of 1983. The dashed line superimposed on the data is the pattern of emergence produced by the PBW model. Because the observed data are only relative measures, the simulated pattern is included without a vertical scale.

Within-season PBW adult populations

In all the PBW adult trap data taken, there was a large amount of daily fluctuation, at times obscuring long-term patterns of population growth. These daily fluctuations have been attributed to highly variable local weather conditions (Beasley, Henneberry, and Adams 1984). In comparing such field data with simulation results, we will focus on the smoother underlying trends in the data, regarding a population cycle as a rise and fall of population which may encompass several radical daily fluctuations.

The simulated adult population curve in the insecticide treatment (fig. 6A) resembles well the malaise trap data, considering that the simulation was for a field not treated with pesticide or pheromone. It represents the pattern expected in a check field. The pattern of malaise trap catches in the pheromone treatment (fig. 6B) was similar to that found in the pesticide plot and approximated by the check field simulation. This was expected since the malaise traps did not compete with applied pheromone to lure and catch PBW moths, and thus should not have experienced any diminution of trapping efficiency in the pheromone plot.

PBW larval infestation

Because a specific number of fruits or length of row was sampled to estimate larval infestations, the field data provided a measure of absolute larval densities. This allowed the model's results to be compared directly to observed values. The absolute larval densities predicted by the model depend to some degree on the number of PBW adults emerging from diapause entered as an initial condition of the simulation. Because overwintering densities of diapause larvae and their survival were not measured, the parameter of initial PBW infestation was adjusted until the peak magnitude of the simulated larval densities was within 10 percent of the highest observed density in the pheromone treated field (day 241). This small adjustment did not significantly alter the pattern of PBW larval infestation produced by the simulation.

Larvae in blooms. The percent of blooms infested by third and fourth instar PBW larvae measured in both plots showed very low infestations from the time of first flower (day 168) until around day 230 (fig. 7*A*, *B*). After this time, the percent infestation increased dramatically in the pheromone plot, but less quickly in the pesticide plot. The observed increase was due to both increasing PBW larval numbers and a decrease in the number of flowers in the field.

The simulations and the data show similar patterns of percent infestation, a notable exception being the time just before the first flowers were seen in the field (day 168). The simulation shows larval infestation at this time even though the number of flowers is nearly zero. As discussed above, this inaccuracy is due to the fact that the distributed delay process produces small real-valued numbers of flowers and larvae in its calculations. Between days 156 and 168, fractional numbers of flowers and larvae infesting those flowers are output from the model, but at levels so low that finding a flower on even a single plant in the field would be highly unlikely. Thus, an infestation percentage is produced in the apparent absence of flowers or larvae.

Larvae in bolls. Figure 8 shows both the simulated and observed numbers of larvae per boll for both the pesticide and pheromone plots. Bolls were sampled intensively until early August, when susceptible bolls in the stressed fields became scarce. Because



Fig. 6. Population cycles of PBW adults in (A) the insecticide (West) plot and (B) the pheromone (East) plot in 1983. Adult numbers represent the average daily catch of the five samples collected in flight traps in and around the field. The simulated pattern as shown represents the model's output in the absence of any control measures. Flight trap data are relative, so only the timing and relative magnitude of peaks should be used for comparison with the simulated data.



Fig. 7. PBW larval infestation in (A) the insecticide (West) plot and (B) the pheromone (East) plot, calculated as the percent of third and fourth instar larvae found (solid line) and simulated (dashed line) in white cotton blooms (blooms less than 1 day old).

the model did not require a minimum sample size to produce an estimate of larval infestation, simulation results are presented throughout August.

In the pheromone plot, infestation increased steadily through the sampling period. The simulated infestation (dashed line) showed the same pattern although it underestimated larval infestation in late July and early August and was higher than observed on August 22. Nevertheless, the overall trends were well predicted.

In the pesticide plot, larvae per boll remained low through August 4, when sampling was temporarily discontinued. However, one final sample taken August 29 showed greatly increased larval infestation. The simulation results are consistent with the observed data, although the peak shown at August 18 cannot be verified.

The agreement between the simulations and the data suggest that the relatively lower infestations of larvae in bolls in the pesticide plot in July and early August can be attributed to the difference in the pest control treatments between the two plots.

1984 Fields

As part of the Hercon Group's PBW pest management program for southwestern desert cotton in 1984, several fields in the Palo Verde and Imperial valleys of California, as well as select fields in Arizona, were simulated using the cotton and PBW model.



Fig. 8. Observed and simulated PBW larval infestations of bolls. All larval instars found were combined and divided by the total number of bolls sampled from each plot. Bolls sampled were considered susceptible by touch. Not enough susceptible bolls could be collected in the insecticide plot during the interval denoted by an asterisk to make a reasonable sample.

The model was used to predict squaring and flowering patterns (first appearance and peak production) as well as the timing of PBW generations (F1 and F2 generations) infesting early season cotton. These predictions were used to recommend timing of pheromone and insecticide recommendations.

CONCLUSIONS

The PBW and cotton model as presented here assembles much of our knowledge of the plant-pest interaction in a way such that the model's assumptions can be tested in the field (i.e., validated). The model has shown how generation cycles of PBW adults are influenced by cotton fruit phenology and weather. Furthermore, it has reproduced patterns of PBW infestations in the field as measured by typical sampling methods.

This model, combined with subroutines that simulate PBW control practices, can be very useful in evaluating the problem of PBW management in southwestern cotton. Even in its elementary form, this model has been successfully integrated into a commercial pest management program, providing improved predictive ability to pest management decision makers, and helping to explain the pattern of within-season PBW infestation in the Southwest.

APPENDIX

Development of the Continuous Nutritional Function

Lukefahr and Griffin (1962) took newly hatched first instar PBW larvae and placed them on fruit of known ages. They covered the fruit with plastic screen bags and monitored them daily, measuring how long each larva took to cease feeding, pupate, and finally emerge. They concluded that development was faster in squares than in bolls, and that speed of development increased with the age of the fruit initially infested.

Gutierrez et al. (1977) used Lukefahr and Griffin's data to produce scalars of PBW developmental rates. These scalars were average correction factors for total larval development, based on what age fruit a larva infested. Scalars for squares and bolls were implemented separately, but similarly so only PBW's relationship to squares is discussed here. In the Gutierrez et al. model, the developmental rate of all the larvae in squares at each time step was multiplied by a weighted average (D_s) of the developmental scalars (d_s) for all squares infested with PBW larvae:

$$D_{s} = \left[\sum_{j=1}^{S} (d_{s}(j) \sum_{i=1}^{L} N_{j}(t,i))\right] / \sum_{m=1}^{S} \sum_{k=1}^{L} N_{m}(t,k)$$

where S and L are the number of age classes of squares and larvae respectively, $N_i(t,a)$ is the number of PBW aged a infesting fruit aged i, and $d_s(i)$ is the developmental scalar for a square of age i. This provided a good approximation, but because of the vital nature of the nutritional link between the cotton plant and PBW developmental rates, the relationship was reexamined.

Instead of incorporating nutrition as a correction factor for the aging process, the

concept of physiological time was expanded to include the quality of the food source. Clearly, a given amount of time spent feeding on an inferior food source would not advance an organism the same amount physiologically as would the same amount of time feeding on a superior food source. A nutritional scalar, Ω , that varies as a function of fruit age (D) was created to represent the relative developmental rate of PBW larvae feeding in the fruit compared with the developmental rate of larvae feeding on lab diet. Given such a function, the time in degree-days for a larva to complete its development (ΔD_L) will always satisfy the equation:

$$\int_{D_0}^{D_0 + \Delta D_L} \Omega(x) \, dx = K$$

where D_0 is the age of the fruit when first infested, $D_0 + \Delta D_L$ is the fruit age when the larva completes feeding, $\Omega(x)$ is the nutritional value of the food source as a function of the fruit age, x is a variable of integration, and K is the total developmental time of the larval period when grown on lab medium. Age, in this context, is in degree-days, D(t), defined as follows. If T(t) is the temperature at time t, and T_0 is the lower thermal threshold for development, then let

$$\Gamma(t) = \begin{cases} 0 & \text{if } T(t) \leq T_0 \\ \\ T(t) - T_0 & \text{if } T(t) > T_0. \end{cases}$$

Then degree-days accumulated between times t₁ and t₂ is given by:

$$D(t) = \int_{t_1}^{t_2} \Gamma(\tau) \, \mathrm{d}\tau$$

where τ is a variable of integration.

The nutritional function, $\Omega(D(t))$, is a dimensionless ratio of nutritional worth incorporating all nutritional influences of the plant on PBW development. Graphically, larval development will be complete when the area under the $\Omega(D(t))$ curve, from the moment of the larva's entry into the fruit to its exit from the fruit, is equal to K. As shown in figure A-1b, $\Omega(D(t))$ for lab diet is always 1.0, and thus a PBW larva beginning development at time t_0 will always complete development at time $(t_0 + K)$. However, when $\Omega(D(t))$ varies with time as it does for cotton fruiting structures, the amount of time in degree-days for a feeding larva to complete development can vary tremendously. For example, if a just-hatched first instar PBW enters a young square of low nutritional value (figure A-1a), the area accumulated during its initial tenure in the fruit will be minimal; thus, it will take the larva much longer to mature $(\Delta D_L = A)$ than a larvae that entered an older square of higher nutritional value $(\Delta D_L = B)$. The difference between the developmental times of two such larvae can be over a week in the field (Lukefahr and Griffin 1962).

The nutritional function currently used in the PBW simulation was derived from assumptions that the nutritional value of a square is zero in both a newly formed



Fig. A-1. Influence of the nutritional worth of food source, $\Omega(t)$, on pink bollworm larval developmental times in (a) squares, and (b) artificial diet. Time is in degree-days. The nutritional value 1.0 is assigned to the artificial diet in (b) to facilitate comparisons of development in the lab and in the field. A and B represent the average times in degree-days a larva would take to complete development if it began feeding at the time indicated by the solid and dashed upward arrows, respectively.

square (pin-square) and a dry flower, and that nutritional value increases in a nonlinear fashion described by the beta function:

$$\Omega(D) = c[(D/A_s)^a (1 - (D/A_s))^b]$$

where A_s is the age of a mature, zero-valued flower; a and b are parameters, fitted to data, which determine the shape of the curve; and c is a constant, fitted to determine the height of the curve. For squares, b was assumed equal to one. This causes the curve to fall to zero while approaching a negative slope between zero and infinity. The shape of the curve is determined only by a. The parameters a and c for squares, and a, b, and c for bolls were determined by a computer program which minimized the least-squared difference between Lukefahr and Griffin's data and simulated data using the nutrition curve. The fits for squares and bolls are shown in figure A-2.

Not only does the simulation appear to reproduce the field data, but it also shows the intuitively appealing extrapolations on either side of the data. For example, there are some squares and bolls too old to support a developing larvae to pupation because they lose their nutritional worth before the larvae complete developing. In figure A-2, the mean developmental period for larvae entering squares increases explosively to infinity for squares of age over 430 degree-days at the time of entry. On the other hand, larvae entering very young squares achieve virtually no physiological development for their feeding efforts. Thus, a larva entering a very young square ought to develop in a time that is almost 10 degree-days longer than a larvae that entered a square 10 degree-days older. In the simulation, the slope of the modeled development curve approaches negative one near squares of age zero, showing the expected behavior.



Fig. A-2. Pink bollworm larval developmental time in squares and bolls as a function of fruit age at the time of infestation. Data are from Lukefahr and Griffin (1962) converted to degreedays. The curves represent the model's output based on the nutritional value function, $\Omega(t)$, as described in the text.

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III. Strategies for Control: An Economic Simulation Study

The cotton-pink bollworm model and the management model developed by Stone and Gutierrez (I and II of this series) are used to evaluate different strategies for controlling pink bollworm in the southwestern desert. Pesticide sprays based on an ultraconservative economic threshold of 2 percent infested bolls are found to be the most profitable in the absence of penalties for heavy insecticide use. Insecticide sprayed on thresholds over 8 percent infested bolls did not control pink bollworm.

Pheromone in combination with insecticide greatly enhanced profits and was the best workable strategy tested since a 2 percent threshold is probably too difficult to sample accurately in the field. The efficacy of using early season insecticide applications at and before the first hostable squares are present is discussed, as is the possible impact of early season insecticide applications on beneficial insect populations.

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