Pink Bollworm Control in Southwestern Desert Cotton

I. A Field-Oriented Simulation Model

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II. A Strategic Management Model

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III. Strategies for Control: An Economic Simulation Study

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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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II. A Strategic Management Model

INTRODUCTION

THE HISTORY OF CONTROLLING pink bollworm, *Pectinophora gossypiella* (Saunders), in California's desert valleys is a case of experimentation outpacing understanding, resulting in chaotic pest control practices. Because of the pest's ability (without control) to decimate a cotton crop, *Gossypium hirsutum* L., in the late season (Henneberry, Bariola, and Russell 1978), and the insistence of farmers to grow long-season cotton, farmers resorted to using many questionable control practices to save their yields, hoping that research would eventually provide better answers. Thus, despite a general awareness that growing short-season cotton (i.e., terminating the crop early after the first fruiting cycle) and maintaining rigorous sanitation standards after harvest would virtually eliminate pink bollworm (PBW), growers clung to a near unilateral reliance on chemicals. With the synthesis of gossyplure, the true sex pheromone of PBW (Hummell et al. 1973), and its registration by the Environmental Protection Agency in 1978 for control of PBW (Brooks, Doane, and Staten 1979), a viable alternative to pesticide use appeared, and new control strategies proliferated (Shorey, Kaae, and Gaston 1974; Dean and Lingren 1982; Huber, Moore, and Hoffman 1979). Unfortunately, their efficacy for controlling PBW populations was not well documented.

What has been generally lacking is a solid biological basis upon which to found an integrated pest management program for PBW in cotton, using available control technology. A simulation model of the PBW and cotton interaction, coupled with extensive field data, lends itself well to providing that foundation. This paper describes a management model for PBW in cotton that facilitates the comparison of competing control strategies against PBW, and is an extension of the cotton and pink bollworm model (Stone and Gutierrez I., this series).

History of PBW Control

Pink bollworm invaded the desert cotton-growing valleys of southern California in 1965 and quickly became the key pest of cotton (Burrows et al. 1982). Before its arrival, the desert's long growing season had virtually guaranteed high cotton yields. Unfortunately, the same conditions proved favorable for the development of high populations of PBW, since effective natural controls in the area were virtually nonexistent. Before 1968, when research on PBW was begun at the University of California at Riverside, growers attempted to control PBW by relying on numerous applications of carbaryl during cotton's fruiting period, but generally discontinued applications in the latter part of the season. This control practice allowed PBW numbers to increase late in the season, typically leaving large overwintering populations which caused trouble in ensuing years (Burrows et al. 1982).

Pesticides in large doses are capable of controlling PBW (Werner, Moore, and Watson 1979), but they also eliminate cotton's beneficial insect complex, thereby allowing highly destructive secondary pest outbreaks of such species as cotton leaf perforator, *Bucculatrix thurberiella* (Busck); tobacco budworm, *Heliothis virescens*

(F.); and spider mites, *Tetranychus* spp. (Werner, Moore, and Watson 1979). This is similar to the situation in cotton in the San Joaquin Valley where several studies have shown that pesticides applied to control *Lygus hesperus* Knight suppress natural enemy complexes and allow secondary pest outbreaks of the beet armyworm, *Spodoptera exigua* (Hubner), and cabbage looper, *Trichoplusia ni* (Falcon et al. 1968; Falcon et al. 1971; Eveleens, van den Bosch, and Ehler 1974; Ehler, Eveleens, and van den Bosch 1974). As a result of these studies and further analysis (Gutierrez, Wang, and Regev 1979), use of pesticides to control moderate infestations of Lygus bug was often shown to be unnecesary.

In addition to the danger of inducing secondary pest outbreaks, three factors combined to reduce the use of pesticides against PBW in the early season. First, Butler and Henneberry (1976) and Westphal, Gutierrez, and Butler (1979) showed that although PBW infests squares, its feeding does not inhibit the squares from maturing and setting normal fruit. This meant that waiting to apply pesticides against PBW until there were significant numbers of susceptible bolls in the field would not significantly decrease cotton yields.

Second, increasing resistance of PBW to commonly used insecticides (Burrows et al. 1984) forced growers to use higher doses to achieve the same level of control. It simply became too expensive to spray for PBW throughout a season. The newer, more costly pyrethroid insecticides did not provide economic relief. Perhaps the greatest effect of this economic crisis was to change the perceptions of the growers, making them more receptive to alternative control stategies.

Third, commercial gossyplure, the true sex pheromone of PBW, became available in formulations which could inundate a field with the chemical and disrupt PBW mating (Brooks, Doane, and Staten 1979; Henneberry et al. 1981), thus providing a nontoxic alternative to pesticidal control of PBW. In the years since its introduction into the cotton ecosystem, gossyplure has become the best documented and tested sex pheromone for controlling an insect pest (Gaston et al. 1977; Boness 1975; Doane and Brooks 1980).

The Effects of Pheromone on Field PBW Populations

Because pheromones do not kill pests, their successful integration into pest management programs depends on proper manipulation in the field. This requires a thorough understanding of their effects on various aspects of the pest biology, particularly mating behavior. Unfortunately, the first tests of gossyplure gave inconsistent results because the relevant PBW mating biology was not well understood. These poor results called the use of pheromones as control agents into question (Smith, Flint, and Forey 1978).

Mating of PBW occurs via male moths' attraction to a sex pheromone emitted by the female and carried by the wind. Because of this behavior, it was thought that permeating cotton fields with synthetic pheromone (gossyplure) would confuse males and prevent them from orienting toward a female (Shorey 1976).

Confusion is not the only control strategy that employs sex pheromone. Gossyplure, for example, can be used in several ways to help control PBW population levels:

(1) It can be used to confuse and disorient males by saturating their environment with pheromone.

(2) It can be used to provide false trails for PBW males. It is thought that pheromone lowers PBW mating by leading males on a series of false trails of gossyplure; if the ratio of point sources to PBW females is high enough, mating would be disrupted.

(3) It can be used to kill males lured to pesticide-laced point sources of pheromone. Only a small amount of insecticide is used in each point source to minimize the kill of beneficial insects in the field. This is called the attracticide approach (Dean and Lingren 1982).

(4) It can act as a synergist when applied in combination with a full or reduced rate of insecticide. The pheromone is no longer expected to disrupt mating, but rather to stimulate male moth activity, increasing the frequency of encounters with the pesticide.

(5) It can be used to trap males en masse in pheromone traps to reduce or annihilate the male population in the early season. This strategy has been successful in areas with little PBW pressure (Graham et al. 1966; Huber, Moore, and Hoffman 1979).

Each of these strategies is based on assumptions about the behavior of PBW in the presence of gossyplure. The confusion technique assumes that the chemical communication between the two sexes of PBW is eliminated by disorienting the males in a virtual sea of pheromone. The false trail technique assumes males will follow a series of clear but fruitless plumes. Attracticide likewise relies on males' being able to orient toward the baited point sources. The dual application approach was formulated with only a vague notion of how the interaction of pesticide and pheromone affects male PBW mortality.

The work presented here examines the ability of gossyplure to disrupt PBW mating, with the intent to clarify the mode of action of gossyplure. Only once this is understood can the pheromone's efficacy as a control agent, bait, or synergist be properly examined.

THE MANAGEMENT MODEL

Both pesticide and pheromone applications have been incorporated into the PBW and cotton simulation model (Stone and Gutierrez I., this series). In the model, applications can be scheduled by calendar day, by degree-day, or can occur automatically based on some decision rule programmed into the simulation such as a threshold of PBW larvae per boll. The mathematical model will be presented first; field data follow in a later section.

Pesticide Submodel

The pesticide submodel assumes that a pesticide, at the time of application, achieves some maximum proportional kill, $K_{max} \epsilon [0,1]$, of adults and susceptible eggs of PBW. The rate of kill then decays with time (measured in degree-days) over a specified

interval, T_s. More extensive models for pesticide effectiveness have been proposed by Jones, Lloyd, and Stinner (1977). The equation for determining the effective kill rate (K) at time τ since the application is:

$$K(\tau) = \begin{cases} K_{max}e^{-\alpha\tau} & \text{for } \tau \leq T_s \\ 0 & \text{for } \tau > T_s \end{cases}$$

where α is sufficiently large to make $K(\tau)$ less than 0.0001 when τ equals T_s. Note that both τ and T_s are in degree-days.

Eggs laid on bolls are considered not susceptible to pesticide kill since they are generally laid within the bracts or under the calyx of the fruit (Henneberry and Clayton 1982). By contrast, eggs laid on vegetative parts of the plant are exposed to pesticide, either from direct pesticide cover, or indirectly when the eggs hatch and the first instar larvae search for a feeding site (Brazzel and Martin 1955, 1957). The relative proportion of eggs laid on the vegetative parts of cotton and on bolls changes during the season with cotton fruit phenology. Estimates of this proportion are taken from Henneberry and Clayton (1982) and egg mortality from pesticide is adjusted.

Bolls are considered susceptible to PBW attack when they are 200 to 400 degree-days old. This corresponds approximately to 14 to 28 days in the early season, and 10 to 21 days for most of the fruiting cycle later in the season when temperatures are higher. This physiological age window was chosen to be in close agreement with the standard definitions used in the field (Anon. 1982; Toscano, Sevacherian, and Van Steenwyk 1979).

Pheromone Submodel

The pheromone submodel is more complex since the reduction in PBW mating achieved is not strictly a dose-response relationship and because gossyplure is applied in discrete point sources, each emitting the pheromone at a characteristc rate (Brooks, Doane, and Staten 1979; Kydonieus et al. 1981). The submodel below is a general model for gossyplure applied in discrete point sources; however, the experiments used to validate the model were performed using the laminated plastic flake described by Kydonieus et al. (1981). The term "point source" refers to a generalized gossyplure-emitting device; the term "flake" refers specifically to the plastic flake used.

Field release of gossyplure from point sources

The number of point sources in the field at any time since application depends on the number of point sources applied per area, the loss rate of point sources from the plant, and the number of applied point sources that adhere to the foliage (application coverage). Point sources that do not adhere to the foliage do not contribute to disrupting PBW mating for three reasons (Dr. J. Gillespie, Herculite Products, Inc., personal communication):

(a) The exposed soil in a cotton field is very hot, and point sources landing on the ground very quickly lose their pheromone.

(b) The PBW male flight activity and mating occur usually at the top of the cotton canopy (Smith, Flint, and Forey 1978) so pheromone emitted at ground level may not affect mating success.

(c) Cultivation in cotton before the canopy closes buries point sources on the ground.

The loss rate of point sources from the plant is very difficult to quantify but such factors as cultivation, wind, rain, and diminishing effectiveness of the sticker applied to point sources during application affect the rate at which they fall from cotton leaves to the ground.

The number of point sources applied, H_0, is specified as an initial condition of the simulation. Application coverage is included as a scalar, $\phi(t) \epsilon [0,1]$, computed from a function of LAI, an output of the cotton model (Gutierrez et al. 1984). Thus, the initial number of effective point sources for a particular application is given by $H_0\phi(t-\tau)$ where τ is the time since application.

The simulation does not take cultural practices, wind, or rain into account; the decline in the number of the point sources from plants is handled strictly as a function of degree-days since application. The shape of the function describing this decay ($\psi(\tau)$) was derived empirically from qualitative observations of flake loss in the field and is shown in figure 1. In the model, $\psi(\tau)$ is generated numerically by an iterative algorithm.

The amount of pheromone release into the field at any time following an application can be calculated easily since the release rate of gossyplure from a point source can be measured over time and a functional relationship determined. Such a relationship has been quantified for gossyplure emitted from hollow fibres (Iyer et al. 1980). The
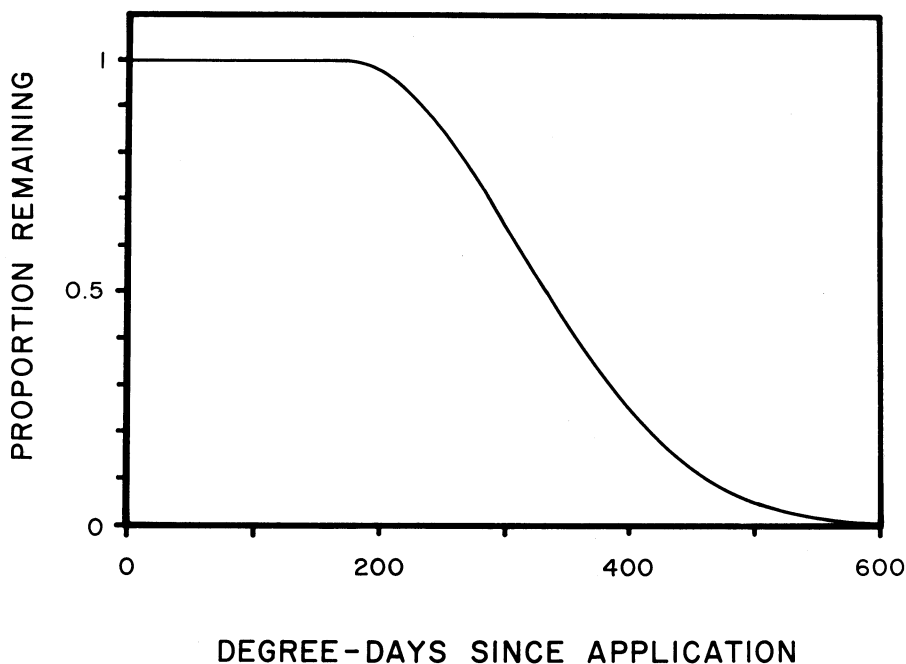

Fig. 1.   The proportion of pheromone point sources remaining on foliage as a function of degree-days since pheromone application.

release-rate function for flakes was estimated as part of this work and is described by the exponential decay model:

$$R(\tau) = R(0)\, e^{-b\tau}$$

where τ is time in degree-days since the application, $R(0)$ is the initial release rate from one flake, and b is a constant estimated from field data.

Thus, at any time (t), the amount of pheromone released per unit area (pheromone concentration = P) in a cotton field τ degree-days after application is given by:

$$P(t,\tau) = H_0 \phi(t-\tau)\psi(\tau)R(\tau)$$

and since pheromone applications are cumulative, the actual concentration of pheromone in the field is:

$$P(t) = P_1(t,\tau_1) + P_2(t,\tau_2) + \ldots + P_n(t,\tau_n)$$

where $\tau_1, \tau_2, \ldots, \tau_n$ represent the times since pheromone applications, P_1, P_2, P_n. In the model, only the two most recent applications are accounted for, since prior ones have usually decayed to an extent that they contribute little to the current concentration.

The effectiveness ($E(t)$) of this amount of pheromone in reducing mating is the last component of the pheromone model. It was assumed that there exists a lower threshold concentration of gossyplure in the field (P_T) above which no mating occurs via pheromonal communication between the two sexes. When the pheromone concentration falls below P_T the proportion of pheromone-mediated matings occurring is equal to the ratio $P(t):P_T$. Thus,

$$E(t) = \begin{cases} 1.0 & \text{if } P(t) \geq P_T \\ P(t)/P_T & \text{if } P(t) < P_T \end{cases}$$

Effects of pheromone on PBW mating success and fecundity

Gossyplure works by disrupting PBW mating but ultimately achieves its controlling influence by reducing the number of fertile eggs being laid ($\varsigma(t)$). In turn, $\varsigma(t)$ depends primarily on three factors:

(1) The number and age structure of PBW adults in the treatment area. This is simulated by the PBW population model (Stone and Gutierrez I., this series), and is denoted here by the array, $N(t)$, with elements $n_{a,h}(t)$, $a = 1,2,\ldots,n$. Here, h refers to the moth's larval host.

(2) The natural fecundity of the females. In the model, fecundity varies with (a) age and (h) larval history (Stone and Gutierrez I., this series), and is approximated by the rate array, F. A PBW female of age a, which fed as a larva on fruit class h (e.g., bolls), is assumed to lay $f_{a,h}\Delta t$ eggs during the time interval Δt. However, only if that female has mated will her eggs be fertile.

(3) The mating status of the females in the treatment area. Successful PBW mating under pheromone-treated and pheromone-free fields is examined below.

The natural pattern of PBW female mating has been studied by Lukefahr and Griffin (1957). They observed that under normal conditions (no artificial pheromone), approximately 60 percent of females mated the first night after emergence, and by the fifth night almost 95 percent of females were mated. This natural pattern of mating has been approximated from their data in the constant vector $M = [m_1, m_2, \ldots, m_n]$,

whose elements represent the proportion of females mated by age class (a) in an untreated cotton field. Under untreated conditions, therefore, the number of fertile eggs ($\zeta(t)$) produced by larval host (h) at time t is:

$$\zeta(t) = 0.5 \ \Sigma_h \ \Sigma_a \ n_{a,h}(t) \ f_{a,h} \ m_a$$

where 0.5 is a correction for sex ratio.

When pheromone is added to the system, two things happen: the frequency of PBW mating by pheromone communication is reduced by a factor E(t) as defined above, and male searching behavior becomes undirected. Smith, Flint, and Forey (1978) showed that PBW adults mate as frequently in small enclosures permeated with gossyplure as in untreated containers, and Lingren et al. (1980) observed that males exhibit random searching behavior in gossyplure-treated fields. It is thus highly likely that PBW males find females and mate successfully to some degree in gossyplure-permeated cotton fields.

When the concentration of pheromone in the field is above the threshold P_T, the model assumes that any mating occurring is due to random encounters of searching males (Q) with sedentary (calling) females. The function describing the proportion of females left unmated during a time interval (Δt) despite the males' random search is the zero term of a Poisson process:

$$X(t) = e^{-bQ(T)\Delta t}.$$

This equation is analogous to a Nicholson-Bailey (Nicholson and Bailey 1935) model where the constant b is the proportion of the universe searched by a male during time Δt.

The rate of mating in a pheromone-treated field can now be described mathematically. The proportion of unmated females remaining unmated at time, t, is E(t)X(t). The occurrence of random matings has the effect of diminishing the effectiveness of the pheromone. In the absence of pheromone, this becomes zero, in agreement with the assumption that random matings are a phenomenon induced by pheromone applications.

To estimate the number of fertile eggs produced in a pheromone-treated system, the model first determines the proportion of females mated in each age class over time (G(t), with elements $g_a(t)$, $a = 1,2,...,n$) (fig. 2). Before any pheromone is applied, this vector is identical to the constant vector, **M**, described above (i.e., G(0) = **M**), and is represented by the shaded bars in figure 2, day 0. The first day after a pheromone application, however, all the females already mated have aged 1 day (note that there is attrition in the aging process, but for convenience this is ignored for the moment) and are immune to the effects of pheromone. Because pheromone acts only on males, normal female mating behavior can be assumed (unshaded area of bars in figure 2). For example, only 60 percent of day-old females attempt to mate, hence pheromone affects the mating of only those 60 percent. For each age class, the corresponding proportion of affected females is given by the difference

$$\Delta g_a(t) = m_i - g_{a-1}(t - \Delta t)$$

where Δt is the width of each age class in degree-days and m_i is an element of vector **M**. The proportion of females in age class, a, mated at any time, t, can be written:

$$g_a(t) = g_{a-1}(t - \Delta t) + [1 - E(t)X(t)]\Delta g_a(t)$$
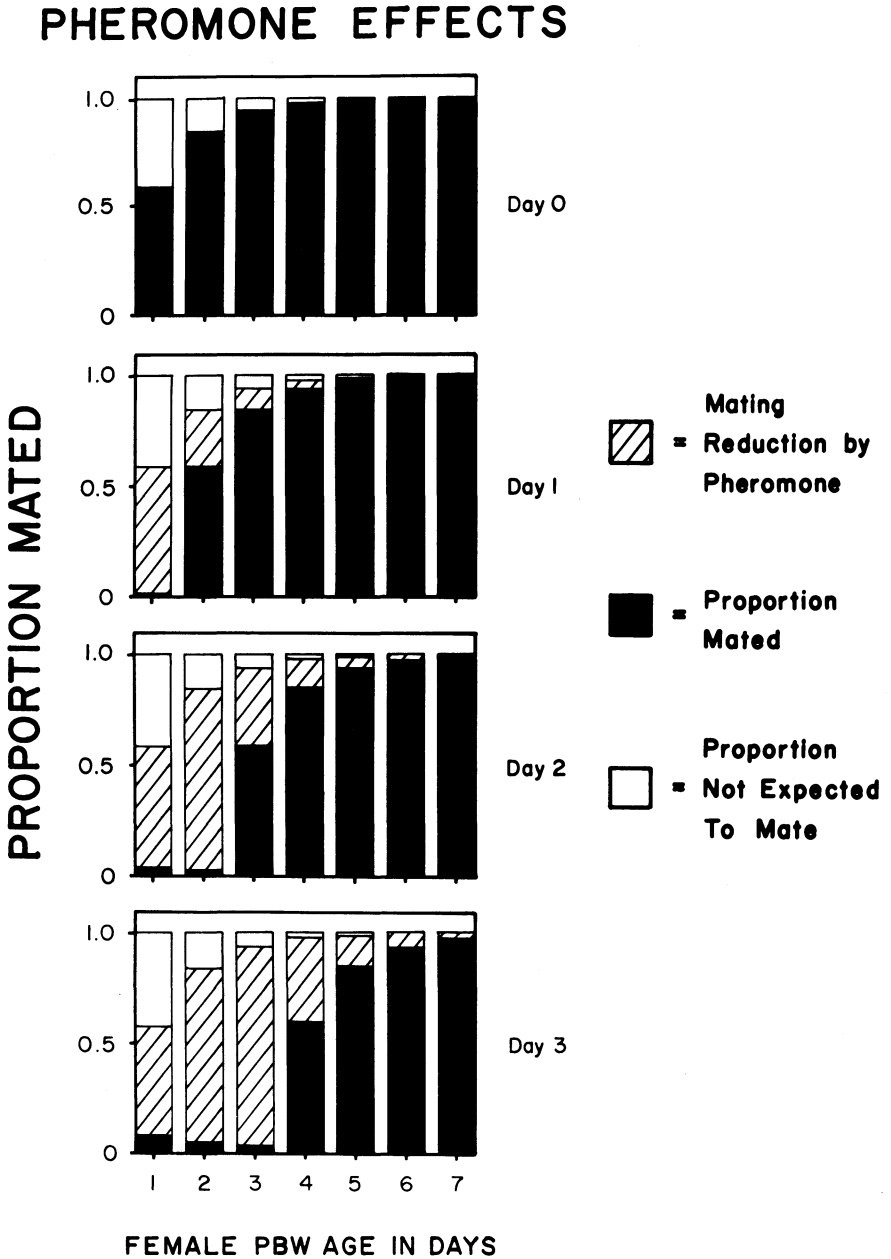
PHEROMONE EFFECTS

Fig. 2. The effectiveness of an application of artificial pheromone in reducing the proportion of female PBW moths mated in the field with time. This is a hypothetical example, ignoring attrition in the moths' aging process.

for all age classes a, where $g_0(t) = 0$ for all t. In this equation, $g_{a-1}(t-\triangle t)$ represents the females already mated that are simply aging into age class a; $\triangle g_a(t)$ represents the portion of the unmated moths aging into age class a that would normally be mated in the absence of pheromone, as described above; and $[1-E(t)X(t)]$ is the proportion of unmated moths that mate because pheromone concentration in the field is below threshold (P_T), or due to random mating.

The number of fertile eggs laid at time t in a pheromone system can now can be expressed:

$$\zeta(t) = 0.5 \, \Sigma_a \, \Sigma_h \, n_{a,h}(t) \, f_{a,h} \, g_a(t)$$

where all variables have been defined above.

To verify the PBW management submodel, each of the submodels was parameterized separately, and the total model then compared with field population dynamics data. The parameters for the pheromone release rate model were estimated from field experiments and the effects of pheromone and pesticide on adult population numbers and mating were compared with field data.

MATERIALS AND METHODS

Estimating Proportion Mating in PBW Females

During 1983, female PBW moths were collected in flight traps in two plots of cotton (Stone and Gutierrez I., this series). Each female was dissected in water under a dissecting microscope and its mating status determined by the number of spermatophores found in the bursa copulatrix. Females with at least one spermatophore in the bursa were considered mated. The two cotton plots were grown identically; only the insect control practices were different. The West plot, untreated until July 20, received just four insecticide treatments throughout the experiment. The East plot was treated exclusively with pheromone applied aerially at point source densities varying from 12,000 flakes/ha to 31,600 flakes/ha (last two applications) and gossyplure rates of 2.8 g/ha (four applications), 3.7 g/ha (four applications), and 7.4 g/ha (two applications). While no true check plot was available, the untreated West plot can be considered as such up to July 20.

Pheromone Release Rates

In a separate field, the release rate of gossyplure from flakes was monitored. In that experiment, 600 grams of flakes (approximately 108,000 flakes) were applied by air to a narrow strip of cotton (400 m × 15 m) on July 25. On five occasions at 3- to 4-day intervals, three samples of 64 flakes each were taken from the field and assayed for pheromone content in addition to three samples from the original pretreatment flakes. Each sample was wrapped tightly in aluminum foil and frozen until analyzed. Chemical analysis for gossyplure content was conducted by the Hercon Group (Herculite Products, Inc.).

RESULTS AND DISCUSSION

Release Rate of Phermone

Laboratory tests on the flake samples collected from the field measured the amount of gossyplure in mg still in each sample at the time of sampling. The gossyplure concentration ($Z(\tau)$) in milligrams per sample per degree-day can be approximately expressed by an exponential decay function,

$$Z(\tau) = 18.887 \ e^{-0.0032\tau}$$

where τ is time since pheromone application. The regression of the natural logarithm transformed data (n = 15) gave an R^2 value of .92. The amount of phermone released per flake per degree-day is given by the absolute value of the derivative of this function with time (τ) divided by 64, the number of flakes per sample:

$$R(\tau) = (0.0607/64)e^{-0.0032\tau}.$$

This release function tends to underestimate the initial release of gossyplure from the point sources, but since the total amount of gossyplure per acre at first is generally well above the threshold level P_T, this is not considered a significant problem. Perhaps a more accurate release function should be considered in future uses of this model.

Effects of Treatments on Adult PBW Populations

The influences of the insecticide and pheromone treatments on adult moth populations are shown in figure 3. *Because the flight traps used in sampling PBW moths do not provide estimates of absolute numbers of moths, only the timing and relative magnitude of population cycles are relevant.*

Insecticide treatment

In the insecticide treatment, simulation results matched field data very well (fig. 3A). The effect of each pesticide spray was dramatic but short-lived. This is especially evident for the two sprays in late July (fig. 3A, S_1, S_2) when PBW numbers were increasing rapidly. The pesticide killed most of the moths present on the day of application, but those adults were replaced almost immediately by new moths emerging from pupae isolated from the pesticide. Furthermore, the survival of the newly emerged moths was high due to the fast decay of the pesticide's effectiveness with time. The only spray that did not show this pattern was the last (S_4). But from the simulation of a check field (fig. 3C), it appears that this last application was made near the end of a population peak. Thus, the apparently longer effective period seen in the field data (days 245-260) may be fallacious. Since the overall pattern of adult numbers is dictated by the population pattern of the larvae pupating and emerging as adults, the true effectiveness of a pesticide application on adult numbers will be observed one generation after the spray.
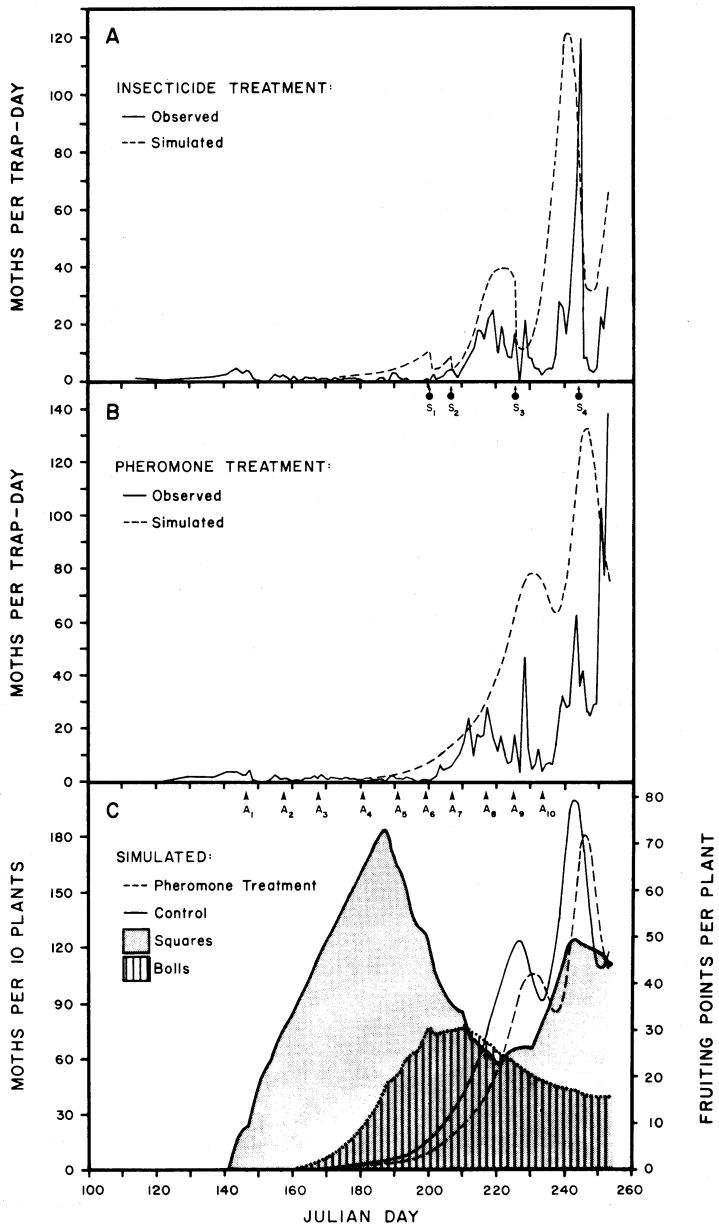
Fig. 3. Flight trap catches of PBW adults from 1983. Data are shown as the solid line. Simulation results are included for comparison, but not in scale, as the dashed line. Pesticide spray dates (*S*) and pheromone application dates (*A*) are indicated by arrows. A simulated cotton crop is included for reference.

Pheromone treatment

Adult numbers were not as well simulated in the pheromone treatment (fig. 3B). The major discrepancy was that the simulated peaks of adults were approximately 5 days late; however, the relative magnitude of these two peaks agreed well with the field data. The last explosive peak in the field was delayed enough in the simulation so that it does not appear in the figure. This problem in the simulation is probably due to an overestimation of the effectiveness of the pheromone in reducing midseason PBW mating. This is best illustrated by examining the pattern of PBW mating success.

Effects of Treatments on Mating Success of PBW Females

Insecticide treatment

Mating success was lowest during the early season (fig. 4A). This period covered the moths' spring emergence before the cotton plants in the study had begun squaring (fig. 3C). The relatively lower proportion of females mating in the field compared with the simulation was probably due to the fact that moths were at low densities, widely scattered outside of the field, resulting in lower than expected mating encounters throughout the early season. It suggests that a type III (c.f., Holling 1959) mating function by density might be more appropriate in the model.

When the cotton plants began producing squares (day 142), the proportion of mated females increased sharply in both the field and the simulation, although the model's predictions were still higher than observed. PBW males congregate in cotton only once fruiting forms are present (Kaae et al. 1977), and Butler et al. (1983) have shown that there is no difference between female and male movement in the early season. In the model, both males and females emerging in cotton emigrate if fruiting forms are not yet present. This keeps the age structure of females in the early season biased toward the youngest, least mated age groups. When suitable oviposition sites appear, older females that are much more likely to be mated remain in the field and therefore the simulated proportion of females mated increases.

In mid- to late season, the pattern of simulated proportion of females mated shows diminishing oscillations centered near 90 percent mated except after pesticide applications. The pattern in the field, while similar, was much more variable, with peaks well synchronized with those of the model. Pesticide applications caused the proportion of mated females to drop in both the field and the simulation. There is little doubt that insecticides interfere with adult PBW mating behavior to some degree, but the close agreement between the field data and the simulation results indicates that changes in the age structure of the PBW adult population following a pesticide application would more likely be responsible for the decrease in the proportion of females mated. In the days following a spray, relatively more of the moths in the field would be young and hence less likely to be mated.
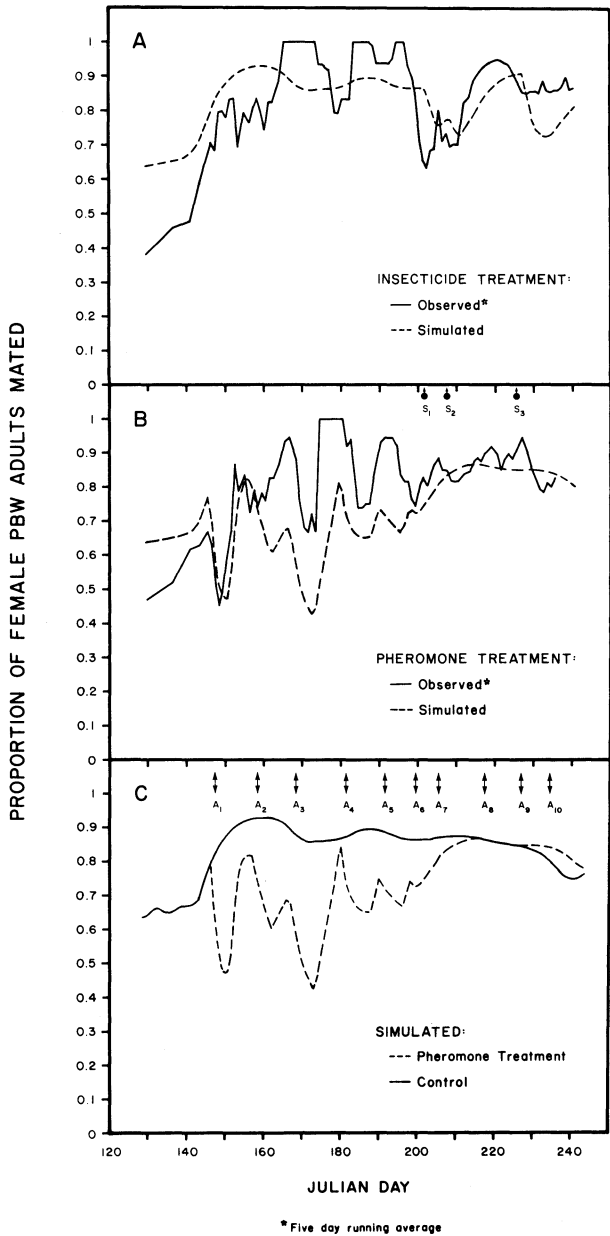
Fig. 4   Simulated and observed proportions of adult PBW females mated in 1983 for insecticide- and pheromone-treated plots. A simulated control plot is also included. Insecticide sprays (*S*) and pheromone applications (*A*) are marked by arrows.

Pheromone treatment

In the pheromone-treated plot (fig. 4*B*), the early season mating pattern was similar to that observed in the insecticide plot, but once pheromones were applied, the pattern changed abruptly. The proportion of females mated typically dropped after an application, reaching a minimum several days later before climbing again. Thus, the effectiveness of each pheromone application, if measured in the reduction of mated female moths, is highest several days after the pheromone is applied. This is because pheromone is effective only against unmated female populations, and the number of unmated females tends to increase for some time following a pheromone application (fig. 2). In the field, pheromone effectiveness has often been measured by its ability to reduce pheromone trap catches to zero immediately after application. This dramatic drop in trap catches reflects only the amount of gossyplure being emitted in the field. The actual proportion of mated females, and hence the number of fertile eggs being laid, is reduced much more gradually.

While the pattern of mating reduction remains about the same for each application (fig. 4*B*), the field data indicate a gradual diminution of the pheromone's ability to reduce mating as the season progresses. By August (day 212), despite three applications, there was no noticeable reduction in mating success. However, applications made before cotton fruiting forms are present may be ill advised. The PBW emerging before fruiting begins are scattered and are highly mobile, and many females may already be mated before entering fruiting cotton fields (Butler et al. 1983).

In the simulation, it is the density effect on random mating of PBW that causes the season-long reduction in pheromone effectiveness, and it is assumed here that the same process is at work in nature. The close fit of the model and the data (except at very low densities of PBW as discussed) does not indicate any need to postulate more complex biological mechanisms to explain the observed data. Therefore, because density seems to play so important a role in the effectiveness of pheromone applications, a prime goal of future research should be the development of monitoring techniques for adult populations in pheromone-treated fields.

Summary of pheromone effects

Because no true check field was available in the experiment after July 20, simulation was used here to examine the effects of gossyplure at high PBW densities. The overall effects of pheromone were compared to an untreated control, keeping all other factors in the two runs identical. The difference between the mating curves of the two treatments (fig. 4*C*) is a measure of pheromone effectiveness. The results here indicate that pheromone applications made through June show a substantial suppression of PBW mating. The results in July (days 181-212) are equivocal, while those of August indicate pheromone applications should have been discontinued. This pattern agrees well with current uses of pheromone in California, where applications are generally discontinued some time in July. Pheromone applications over the whole season obviously had a positive effect; however, it is just as obvious that by the end of June the effect was small and diminishing.

The effect of the pheromone on the population cycle of PBW adults, as simulated

(fig. 3*C*), shows that despite the pheromone's impotence in the late season, it both delayed and reduced the major population peaks of PBW that occurred in the uncontrolled field. The overall shape of the adult curve was not affected, suggesting that early season use of pheromone might delay the necessity for insecticide applications if those applications were based on a given level of adult activity.

Recall from figure 3*B* that the simulated population peaks in the pheromone treatment were 3 to 5 days later than observed. Since one of the effects of pheromone is to delay population peaks, it is reasonable to assume that the simulation was overestimating pheromone effectiveness. One factor contributing to this was that the model was designed to accommodate only a single application rate of pheromone throughout a season, but in the 1983 experiment, the appication rate (number of flakes per hectare) was increased through the season. For the simulation, all applications were made at 18,000 flakes per hectare, but as noted, field applications varied between 12,000 and 31,600 per hectare. The model needs to be corrected to account for these effects.

CONCLUSIONS

Control of PBW using pheromone to disrupt mating is an inversely density dependent phenomenon. As a result, early season pheromone use, when PBW populations are low, seems to be most efficacious. However, in the present study, PBW pressure was high, and pheromone suppression of mating became totally ineffective by early August. In situations where the PBW pressure is light, pheromone may adequately suppress PBW mating in mid- to late season.

Evaluating the effectiveness of a pheromone control program based only on pheromone trap catches can be misleading. Pheromone traps show maximal catch reduction immediately after pheromone applications. But because the maximum reduction in the proportion of mated females occurs several days after a pheromone application, and because the PBW population age structure significantly affects the success of pheromone in reducing the number of mated PBW females, neither the proportion nor the numbers of female PBW mated in the field follow the same pattern as catches of male PBW in pheromone traps. Furthermore, the reduction of pheromone trap catches even to zero does not mean that mating has ceased. Both the model and field data indicate that the percentage of mated females seldom drops below 50 percent.

Early season pheromone use may delay the necessity to spray insecticide to control PBW if sprays are made based on accurate measures of adult moth activity. Such use of pheromone would be beneficial to the natural enemy complex in cotton, reducing the risk of secondary pest outbreaks by reducing early insecticide use.

Further analysis of control strategies involving pheromone need to be conducted in fields under various levels of PBW pressure, as measured by the relative numbers of emergent PBW in spring. Stone et al. (III., this series) present a simulation-based analysis of PBW pest management.

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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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