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Areawide Models Comparing Synchronous Versus Asynchronous Treatments for Control of Dispersing Insect Pests

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ABSTRACT Integrated pest management (IPM) has the goal of combining several control methods that reduce populations of pest insects and their damage to tolerable levels and thereby reduce the use of costly pesticides that may harm the environment. Insect populations can be monitored during the season to determine when the densities exceed an economic threshold that requires treatment, often as an insecticide application. We developed a simulation model where insect populations varied in exponential growth in fields and dispersed to adjacent fields each day of a season. The first model monitored populations of individual fields in a grid of fields and treated any field with insecticide if it exceeded a threshold population (asynchronous model) as done in traditional IPM. The second model treated the entire grid of fields with insecticide when the average population of all fields exceeded the threshold (synchronous model). We found that the synchronous model at all growth and dispersal rates tested had average field populations during a season that were significantly lower and required fewer treatments than the asynchronous method. Parameters such as percentage of fallow fields, number of fields, and treatment threshold had little affect on relative differences between the two models. The simulations indicate that cooperation among growers in areawide monitoring of fields to obtain an average population estimate for use in treatment thresholds would result in significantly less insect damage and fewer insecticide treatments. The synchronous method is more efficient because population refugia are precluded from which dispersal could reintroduce insects.

KEY WORDS IPM, dispersal, modeling, treatment threshold, economic threshold

AGRICULTURAL CROPS ARE USUALLY grown as monocultures in fields that are mixed at larger scales as mosaics with other crop plant species. The fields usually are not contiguous for a particular crop but are more or less distributed randomly among relatively few other crop types (Brewster et al. 1999). Typically, agricultural managers monitor the pest insect population in each field so that when the population exceeds a predetermined density or damage level, termed the treatment threshold, action threshold, or economic threshold, then insecticide spray treatments are applied as needed (Rabb 1978, Knipling and Stadelbacher 1983, Johnson and Wilson 1995, Kogan 1995, Ellsworth and Martinez-Carrillo 2001). Such treatments of single fields at the threshold are a major part of IPM strategies that strive to use less insecticide than previously to reduce costs of application, environmental pollution, and health hazards (Graham and Knight 1965, Palm et al. 1969, Logan 1981, Dudley et al. 1989, Mols 1990, Barclay and Li 1991, Binns and Nyrop 1992, Kogan 1995, Dent 2000, Ellsworth and Martinez-Carrillo 2001).

In contrast to localized treatments, Knipling and Stadelbacher (1983) advanced the idea of areawide management of pest populations in control of early-season generations before they build up. The term "areawide" is increasingly used in research reports and usually means a cooperative management program applied to a regional area by using several complementary methodologies of IPM (Kogan 1995, Calkins 1998, Brewster et al. 1999). However, areawide programs using a single method have been conducted with pheromones to disrupt lepidopteran pests and to trap-out bark beetle pests on a large enough scale so that immigration into treated areas was insignificant (Bedard and Wood 1974, Huber et al. 1979, Bakke et al. 1983, Knipling and Stadelbacher 1983, Schneider 1989, Schneider et al. 1989, Hoffmann et al. 1991). In addition, areawide programs using the augmentation or release of natural enemies, insect pathogens, sterile males, insecticides, and early planting dates have been implemented for control of major pest species including codling moth, cotton bollworm, tobacco budworm, fruit flies, parasitic flies, boll weevil, corn rootworm, red imported fire ant, and silverleaf whitefly (Hammig et al. 1984, Carlson and Suguiyama 1985, Scholl et al. 1986, Bell and Hayes 1994, Kogan 1995, Enkerlin and Mumford 1997, Calkins 1998, Fuchs et al. 1998, Smith 1998, Tollefson 1998, Gray et al. 1999, Hardee et al. 1999, Ellsworth and Martinez-Carrillo 2001, Vargas et al. 2001, Hendrichs et al. 2002, Reichard 2002, Drees and Gold 2003, Siegfried et al. 2004, Vargas et al. 2004). A few models have addressed areawide crop- and pest-specific parameters of growth, dispersal, host resistance, and predation or parasitoids in attempts at predicting population and damage levels (Schneider 1989, Bessin et al. 1991, Legaspi et al. 1998). Implicit in the argument for areawide treatments is that sources of dispersing insects are suppressed to preclude reinoculation of previously treated areas (Nyambo 1991).

Although areawide management strategies are becoming common (Kogan 1995), the advantages of these programs are difficult to establish with scientific rigor because treatment and control areas are confounded by differences in temporal and spatial dimensions. For example, differences in time or place as well as the large scales required make it difficult to compare a method using traditional IPM thresholds and treatments of individual fields in a mosaic to a method using the same treatment threshold applied simultaneously over the entire mosaic of fields. However, comparisons may be done theoretically by computer simulation. Therefore, our objective was to simulate a mosaic of different crops infested by a polyphagous pest insect to investigate the interplay between pest population growth, dispersal, and control treatments termed "sprays." Randomly distributed populations of the pest insect in fields of a grid were allowed population growth and dispersal to occur each day from each field during a growing season. In the asynchronous model that is the traditional IPM practice, individual fields were monitored and sprayed if threshold population densities were exceeded. In the synchronous model, all fields were monitored for an average, but identical, population threshold that if exceeded elicited a synchronous treatment of all fields. The two treatment models were evaluated for performance based on the resulting average pest population, which is related to damage (Headley 1972, Williams et al. 1991), and the number of sprays needed during the season. The simulation parameters were varied widely to theoretically include many crop systems. The goal was a better understanding of the consequences of asynchronous versus synchronous control in areawide management.

Materials and Methods

In both the asynchronous and synchronous models, a large area was simulated consisting of various crops in fields of a row × column ($r \times c$) grid (usually 20 by 20 = 400 fields) infested early in the season by an insect pest. Initially, each field in the grid was assigned a growth rate g that was fixed during the season but varied among fields as a random variable with a normal probability function. This allowed different growth rates of the pest on different types of crops. The algorithm for selecting random numbers from a normal distribution about a specified *MEAN* and *SD* uses a uniform random number *RND* between 0 and 1 as given by Walker (1985):

$$MEAN + \sqrt{[-2 \cdot \ln(J)]} \cdot \cos(2 \cdot \pi \cdot RND) \cdot SD \qquad [1]$$

where $J = RND$ and $J > 0$. The population of each field grew successively each day based on its previous population added to the growth increment determined by multiplying g by the previous population. This is equal to an exponential growth function $Y = p\, e^{gx}$, where Y is the population on day x, and p is the initial population on day 0 (Ricklefs 1990).

Both the asynchronous and synchronous models in a comparison had identical input parameters during a season. These parameters were varied in different simulation runs, such as 1) $r \times c$ grid size to determine number of fields; 2) threshold population, T, eliciting spraying; 3) average growth rate g; 4) daily dispersal proportion; and 5) number of days in season. In some comparisons, variable numbers of fallow fields were introduced that were not entered by pests. Finally, a few simulations observed dispersal outward from the central field.

The simulations had the following steps:

(1) Set initial populations N at random in each field of $r \times c$ grid, $N(r,c)$, based on random numbers of a normal probability distribution (equation 1, $MEAN = 0.1T$ and $SD = 0.1T/3$). Set daily growth rate of each field, $g(r,c)$, at random from a normal probability distribution ($MEAN = g$ and $SD = g/3$). Choose locations of fallow fields, if any, at random.

(2) Add to the current population of each field in the grid the specific growth rate $g(r,c)$ multiplied by the current population [e.g., for top left field, $N(1,1) = N(1,1) + g(1,1)N(1,1)$].

(3) Disperse a proportion of the new population of insects from each infested field into the adjacent eight fields evenly unless any of these are fallow or outside the grid, in this case those subportions remain in the field. The dispersing insect numbers are placed in a temporary array so as not to increase field populations incorrectly because of the linear order of calculations.

(4) After all infested fields have dispersed insects, add the temporary array numbers to the appropriate field populations.

(5) In the asynchronous model, for all infested fields, if a population of a field is greater than or equal to the specified threshold T, then spray that field and reduce its population to at most a random number by using equation 1 with $MEAN = 0.01T$ and $SD = 0.01T/3$. Or in the synchronous model, if all infested fields have an average population greater than or equal to the threshold then spray all fields and reduce populations the same way. Record the number of fields sprayed in either model and represent fields in grayscale according to their population as a percentage of the threshold number for spraying.

(6) If there are more days left in the season, then repeat steps 2 through 6, otherwise calculate the average population per field per day during the season and shade fields. Also, report the average population per day for the grid area as well as the mean number of sprays per field during the season. For simplicity, it

was assumed that damage in a field over the season was directly related to the summation of the population per field per day over the season.

The above-mentioned model steps were coded in both QuickBASIC 4.5 (Microsoft, Redmond, WA) and Java 2.1 (Sun Microsystems Inc., Santa Clara, CA; Lemay and Perkins 1997, Vanhelsuwé et al. 1997, Cadenhead 1999) and are available from us. Adobe PostScript code (Adobe Systems, Mountain View, CA, Taft and Walden 1990) was integrated with QuickBASIC code to print results of simulations as shown in the figures. The Java code was compiled into an applet and integrated into HTML (Stanek 1996) and JavaScript code (Goodman 1996) for use on the Internet with a Web browser (http://www.wcrl.ars.usda.gov/cec/java2/spray.htm).

The dispersal behavior of insects in a 20 by 20 grid was modeled by releasing 400,000 from the center field and monitoring their diffusion over 200 d. A three-dimensional representation of the dispersal was done for comparison to previous dispersion patterns of correlated random walks (Byers 2000, 2001). The two models were compared visually by grayscale shades representing densities (i.e., populations per field) at various times during a 200-d simulated season. The two models also were compared for number of sprays in fields over the season and the average population per field per day for a range of growth rates g (0.025–0.3 in 0.025 steps) that randomly varied about g as described above at four simulations each, keeping dispersal proportion constant at 0.1. Similarly, a range of dispersal proportions was simulated at a mean growth rate ($g = 0.1$).

The effect of varying the treatment threshold and number of fields in the grid was simulated in both models. Also, the effect of random variation in a mean treatment threshold T ($SD = T/3$) among fields (but fixed during season) in the asynchronous model compared with a constant but identical T in the synchronous model was explored. Fallow fields at random locations within the grids were simulated in the two models at various proportions (0–50% of fields in steps of 5%) along with various dispersal and growth values under similar conditions. Linear and curvilinear least-

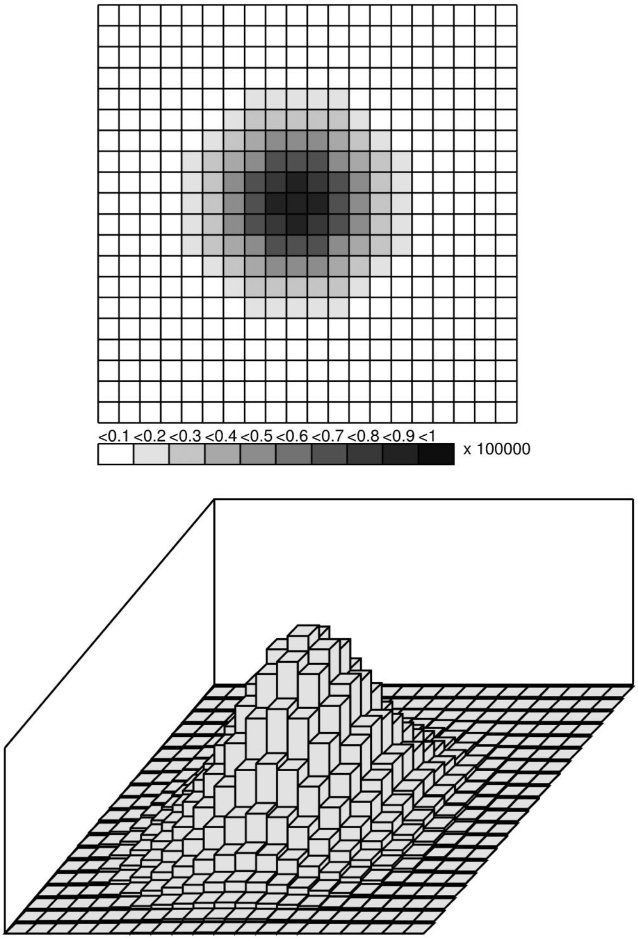


Fig. 1. Dispersal of 400,000 insects from field (10,10) in the synchronous model as shaded in 10 increments (top diagram) or represented in a three-dimensional bar graph (bottom diagram). Parameters were 0 for growth rate, 20 by 20 fields, 0.05 dispersal proportion, and 200-d season.

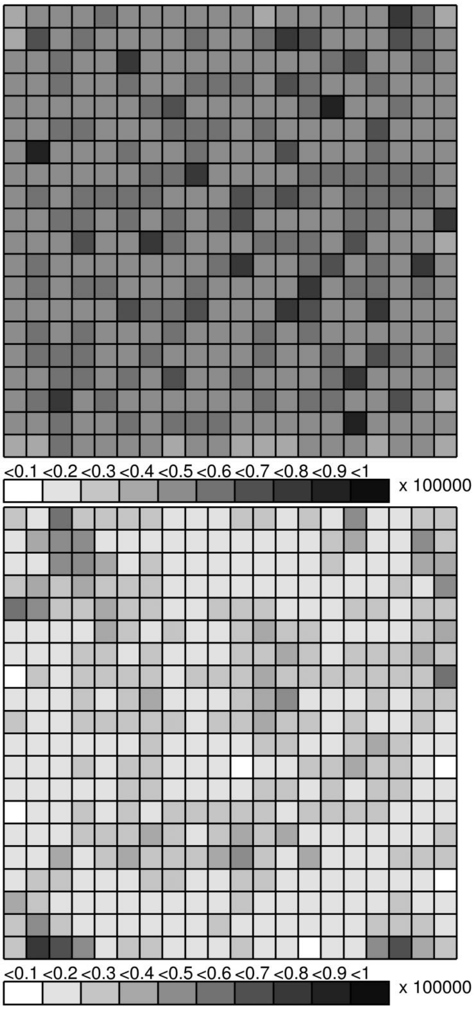


Fig. 2. Shading of average population per field per day over a 200-d season for the asynchronous model (top grid) compared with the synchronous model (bottom grid). Fields (400), average growth rate of 0.1 (*SD* = 0.1/3), dispersal proportion of 0.1, and spray threshold of 100,000 were identical in both models.

squares regression analyses were performed using methods found in Sokal and Rohlf (1995).

Results

The simulated dispersal of 400,000 insects placed initially in the center of a 20 by 20 grid of 400 fields over a 200-d period seems to fit a Gaussian distribution (Fig. 1). In all subsequent simulations, pest populations were introduced into all fields, and each field was allowed a fixed growth rate that varied among fields. In Fig. 2, both the asynchronous and synchronous models had the same parameters of growth, dispersal, and spraying threshold. However, the darker shading in the asynchronous model (top grid) indicates a higher damage level because of the greater average numbers per field per day over the 200-d period compared with the synchronous model (bottom grid). Specifically, both the overall average population per field per day (49,276 ± 7,433, ± SD) and the number of sprays per field (8.8 ± 3.1) were greater in the asynchronous model than in the synchronous model (21,656 ± 9,516 and 2 ± 0, respectively). Histograms of the numbers of fields with various numbers of sprays reveal a wider variation in sprays among fields in the asynchronous model (Fig. 3A), with most fields with more sprays than the four sprays per field in the synchronous model. The variation among fields in population numbers is similar between the two models, but the asynchronous model has greater populations than the synchronous model and there is little overlap (Fig. 3B).

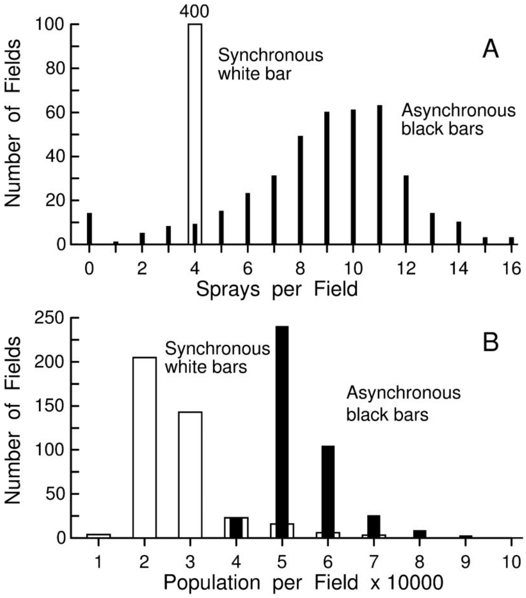
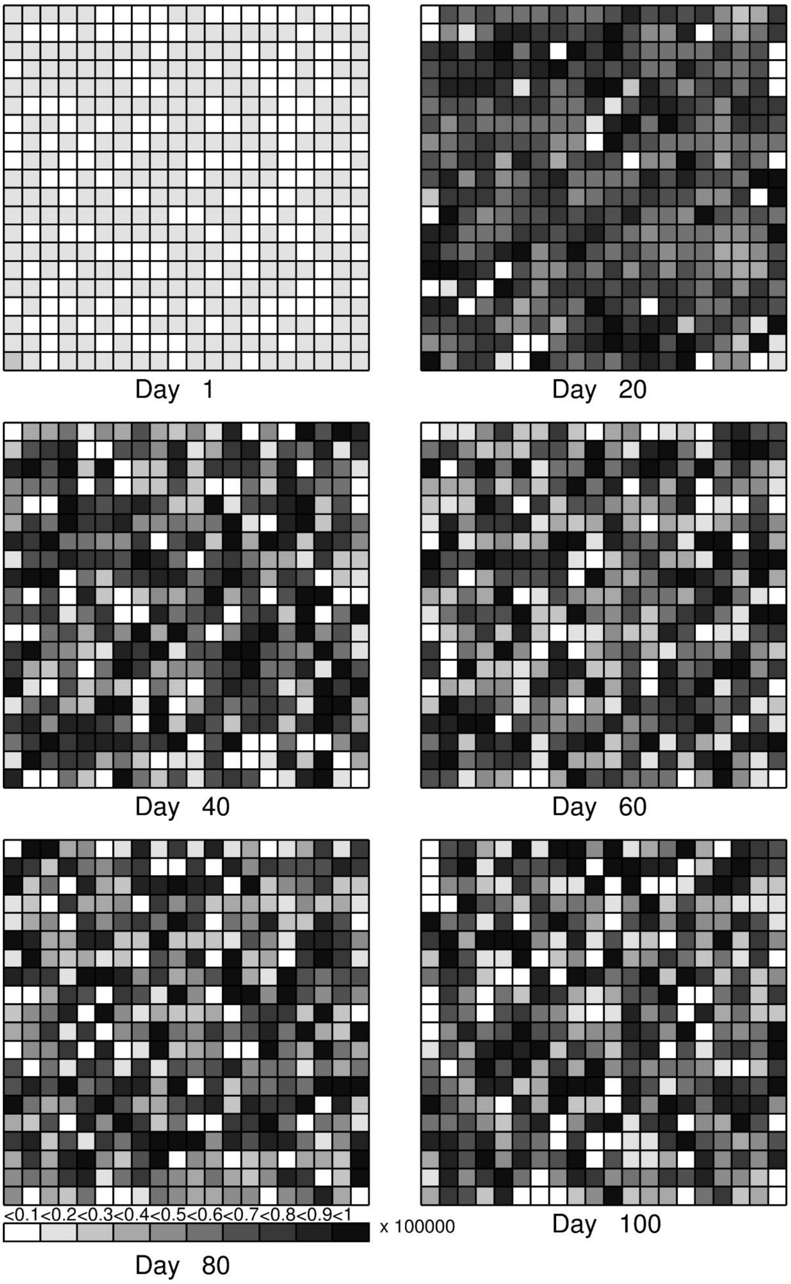


Fig. 3. (A) Histogram of number of fields in 400-field grid (data from Fig. 2) having various numbers of sprays during the season with the synchronous model and the asynchronous model. (B) Histogram of number of fields with various average population ranges (e.g., 0–10,000 = 1, 10,000–20,000 = 2) during the season with the synchronous and asynchronous models.

Initially on day 1, a low population in all fields was observed in the asynchronous model. By day 20, growth to high levels with increased variation among fields had occurred, by day 40 the field populations were highly variable with the darkest fields requiring sprays (resulting in white areas of low population), and by days 60, 80, and 100 considerable random variation in population densities among fields continued (Fig. 4). In the synchronous model, the variation in pest densities among fields was more uniform and cycled between low and threshold densities because of the nature of the simultaneous sprays (Fig. 5). Populations built up by day 20 until the average population of the entire area exceeded the threshold and was sprayed (after day 20 and before 40), then built


Day 1

Day 20

Day 40

Day 60

Day 80

Day 100

Fig. 4. Shading of field populations on indicated days of season for the asynchronous model with 400 fields, a mean growth g of 0.1 ($SD = g/3$), dispersal proportion of 0.1, and spray threshold of 100,000.

moderately by day 60, thereafter to be sprayed again (low populations by day 80) and built again to moderate populations by day 100. Decreasing the average growth rate slows the cycling of sprays. After a synchronous spray, there were no fields to provide sources of dispersing insects, so the field populations increased slowly as in the beginning of exponential growth.

The number of fields sprayed increased in a square-root relationship as the population growth rate increased at a constant dispersal rate (Fig. 6A, asynchronous: $Y = -4.7 + 42.9X^{0.5}$, $R^2 = 1$, $P < 0.001$, synchronous: $Y = -0.1/3 + 43X^{0.5}$, $R^2 = 0.99$, $P < 0.001$). The superiority of control by the synchronous model is evident at all growth rates because fewer sprays were necessary. Also, the synchronous model had lower average populations of insects at all growth rates compared with the asynchronous model (Fig. 6B). It seems that increases in growth rates have little affect on the average population density during the

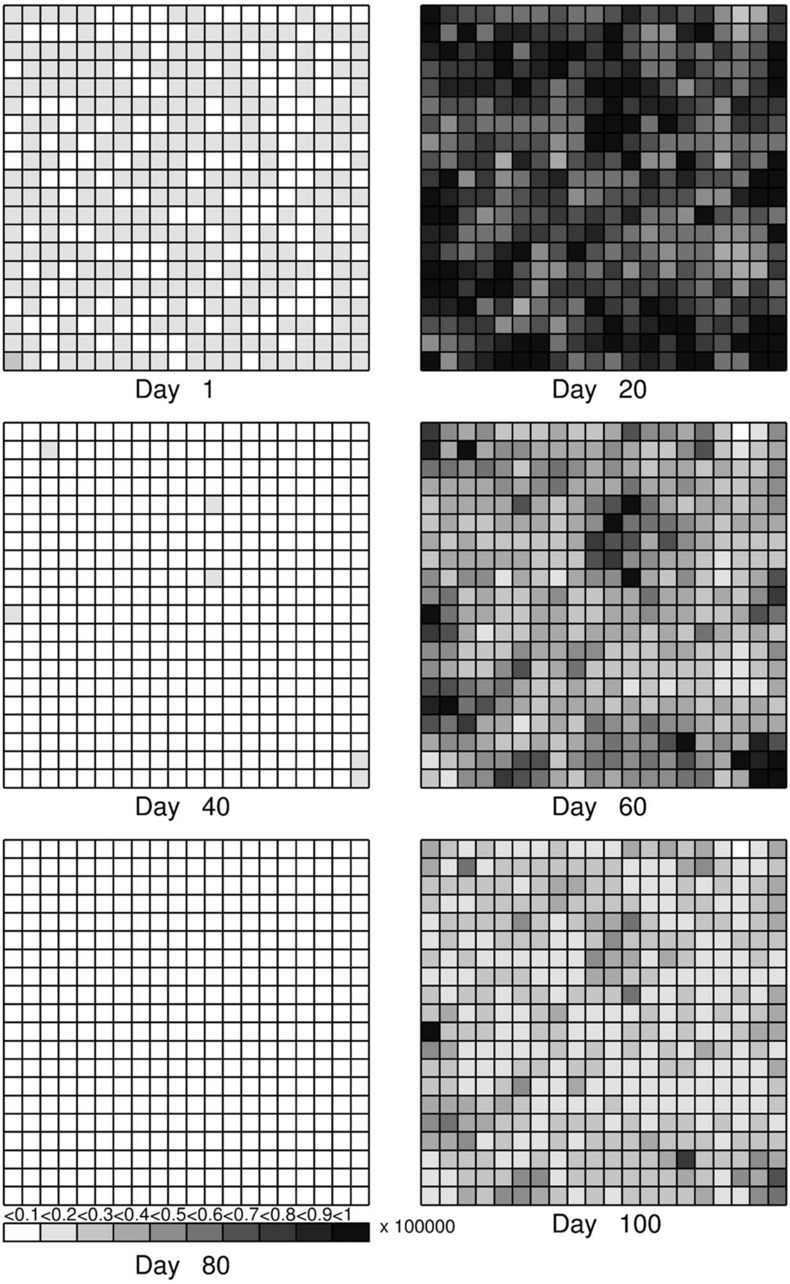


Fig. 5. Shading of field populations on indicated days of season for the synchronous model with 400 fields, a mean growth g of 0.1 ($SD = g/3$), dispersal proportion of 0.1, and spray threshold of 100,000.

season because of concomitant increases in sprays. Keeping the growth rate at 0.1 ($SD = 0.03$), an increase in dispersal rate caused sprays in the asynchronous model to increase as a power function ($Y = 16.3X^{0.26}$, $R^2 = 0.99$, $P < 0.001$) well above the sprays in the synchronous model, whereas the latter remained constant with no relationship with dispersal (Fig. 7A). The populations in the asynchronous model also increased as a power function with an increase in dispersal rate, and were much greater than the consistent populations of the synchronous model at all dispersal rates (Fig. 7B). Introducing an increasing number of fallow fields at random locations in the grid resulted in linear declines in average populations and number of sprays in the asynchronous model, and little if any affect on the synchronous model. However, the

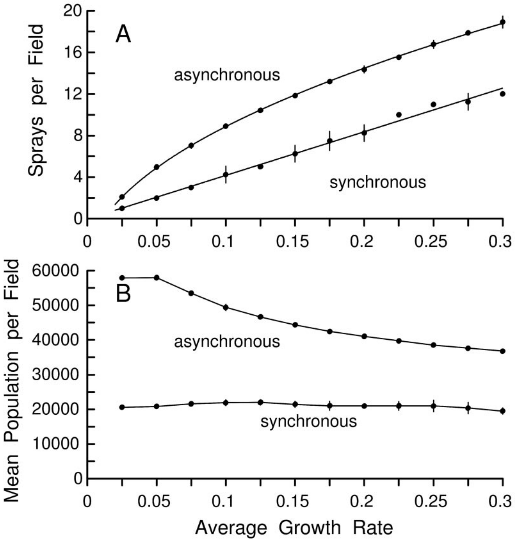


Fig. 6. Relationship between average population growth rate (*g* and *SD* = *g*/3) and the number of sprays during the season (A) and the average population per field per day (B) for the asynchronous and synchronous models. Simulations had 400 fields, a dispersal proportion of 0.1, and a threshold of 100,000 (error bars ± 95% CL, *N* = 4, may be hidden within point).

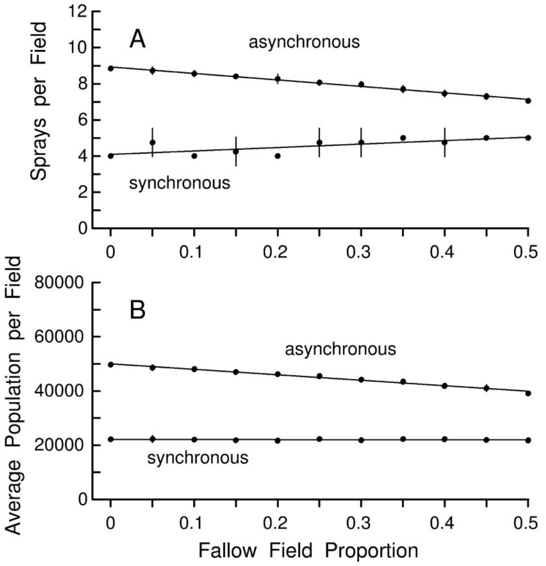


Fig. 8. Relationship between fallow field proportion and the number of sprays during the season (A) and the average population per field per day (B) for the asynchronous and synchronous models. Simulations had 400 fields, a mean growth rate of 0.1 (SD = 0.1/3), a dispersal proportion of 0.1, and a threshold of 100,000 (error bars ± 95% CL, *N* = 4, may be hidden within point).

synchronous model had significantly lower average population densities during the season as well as fewer required sprays (Fig. 8).

Differences in the number of fields in the grid had no significant affect on the differences between the two models. For example, given the same mean growth (0.1), dispersal proportion (0.1), days in season (200), and treatment threshold (100,000) in both models, a 20 by 20 grid of 400 fields in the asynchronous model required a mean of 8.93 ± 0.08 (±95% CL, *N* = 4) sprays per field per season and had a mean of 49,233 ± 168 insects per field during the season compared with the synchronous model with 2 ± 0 sprays per field and 22,072 ± 908 insects per field. The results were similar in a 100 by 100 grid of 10,000 fields with 9.07 ± 0.02 sprays per field 50,529 ± 88 insects per field in the asynchronous model, and 2 ± 0 sprays per field and 21,627 ± 281 insects per field in the synchronous model. Different treatment thresholds also did not alter the conclusion that the synchronous model results in fewer sprays and less insect damage. Raising or lowering the treatment threshold affected the mean population levels in both models but not the frequency of sprayings, whereas the proportions of mean populations and sprays between the models remained constant. For example, using the above-mentioned parameters a 400-field grid in the asynchronous model with a threshold of 1000 had 496 ± 3.8 insects per field (49.6% of threshold) and required 8.84 ± 0.23 sprays per field compared with the synchronous model with 215.5 ± 8 insects per field and 4 ± 0 sprays per field. Increasing the threshold to one million, the asynchronous model resulted in 495,306 ± 6,110 insects per field (49.5% of the larger threshold) with no effect on sprays per field (8.86 ± 0.17) compared with the synchronous method resulting in 218,693 ± 10,595 insects per field and 4.25 ± 0.8 sprays per field. Random

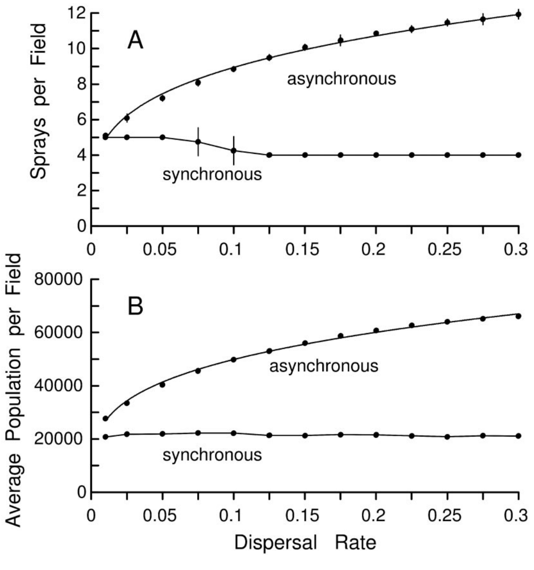


Fig. 7. Relationship between dispersal proportion and the number of sprays during the season (A) and the average population per field per day (B) for the asynchronous and synchronous models. Simulations had 400 fields, a mean growth rate of 0.1 (*SD* = 0.1/3), and a threshold of 100,000 (error bars ± 95% CL, *n* = 4, may be hidden within point).

variation in the treatment thresholds among fields about a mean of 100,000 in the asynchronous model (parameters in Fig. 2) had practically no effect on the population densities (48,826 ± 1,424 versus 49,669 ± 481 without variation) compared with about half that in the synchronous model (22,314 ± 715) with the same mean threshold. However, the number of sprays per field in the asynchronous (variable threshold) model increased (from 8.85 ± 0.09 to 11.04 ± 1.29; *t*-test, df = 3, 3; $P < 0.02$), which adds further support that the synchronous model (4.25 ± 0.8) is superior.

Discussion

Models are useful to define problems, organize thoughts, understand the system, identify areas to investigate, communicate understanding, make predictions, generate hypotheses, and act as standards for comparison (Worner 1991). The models presented here are helpful in understanding the effects of dispersal and growth parameters on pest damage and treatment needs when comparing asynchronous and synchronous spray treatments. The models do not make precise predictions about natural populations or costs of control because the models do not pertain to a specific pest species or crop. The nature of the "spray" treatment used in the models does not even need to be an insecticide but could be pheromone or other reproductive inhibitor (e.g., sterile release). The sprays reduced the populations and then had no further effect, so they are not comparable with reproducing pathogens with residual activities and dispersal potential.

The growth of insect populations in nature is exceedingly complex, being affected by weather, dispersal, physiological status of host plants, parasites and predators, and competing species (Rabb 1978, Knipling and Stadelbacher 1983, Schaalje and van der Vaart 1989, Schneider 1989, Mols 1990, Bessin et al. 1991, Legaspi et al. 1997, 1998). Thus, it is hardly surprising that many models are inadequate in predicting populations, their damage, and control costs (Wagner et al. 1996). In contrast, our model attempts to use the essential components of growth, dispersal, threshold-induced treatments, and spatial characteristics to determine whether areawide management on a synchronous basis is more efficient than for individual fields.

Growth of a population is exponential in theory when populations are in the initial growth phases such as after spraying or at the start of the season when density-dependent factors such as competition and damage-induced plant stress should have less influence (Ricklefs 1990, Turlings and Tumlinson 1992, Chamberlain et al. 2001). The daily stepwise population growth in a field was based on an exponential growth rate (Ricklefs 1990) that remained constant during the season. However, among fields in the grid the growth rate *g* could vary as selected from a normal probability distribution with three standard deviations either side of *g*. This was meant to simulate pest growth on different crops (e.g., cotton, melons, and alfalfa) in fields within the grid. However, an even larger range of simulated mean *g* values with the same proportion of variation did not affect the conclusion that synchronous treatments require fewer sprays and result in lower populations and associated damage in areawide programs (Fig. 6). The use of exponential growth was appropriate because spraying was done at a threshold of moderate populations (to avoid severe damage) where it was assumed that the population would not yet be limited. This is reasonable because treatment sprays reduce populations before they reach an inflection point in the logistic curve of population growth that is ultimately limited by the carrying capacity of the environment (Ricklefs 1990).

Another essential component of the models was the constant proportion of dispersal from any field to the surrounding eight fields. In actuality some insects might disperse into fields even further away, and only the vertically and horizontally adjacent cells would receive similar numbers, whereas the four diagonal adjacent cells would receive slightly less. However, these minor deviations were the same in both models. Simulating individual-based movement of insects would be the most realistic (Byers 1991, Turchin 1998) but is unlikely to provide additional insights for comparing the two models. In the test of dispersal from a point source (center field), the results exhibited an approximately Gaussian distribution as expected for population dispersal from a source as a correlated random walk (Fig. 1; Byers 2000, 2001).

Dispersal of insects was not allowed into fallow fields or outside the grid. Increases in the percentage of fallow fields up to 50% caused a gradual linear decline in average populations and in required sprays in the asynchronous model or little affect in the synchronous model, with the latter exhibiting lower populations and sprayings at all percentages (Fig. 7). The declines in the asynchronous model are apparently because of an effect of limiting the dispersal rate about certain fields surrounded to a variable extent by fallow fields acting as barriers. This can be considered as behavioral avoidance of nonhost areas with regard to fallow fields, or in the case of the grid periphery as either avoidance or that emigration is balanced by immigration with no net effect. In reality, weather and biotic factors could alter the dispersal and growth rates stochastically (McManus 1988), but choices over a large range of these parameters in the models did not alter the support for conducting synchronous treatments.

Varying the number of fields, days in a season, or treatment thresholds did not alter the conclusion that the synchronous model was more effective. However, too few days in a simulated season affects the number of sprays in discrete steps, especially in the synchronous model when the threshold may not be reached. The value of the treatment threshold also had virtually no impact on the outcome of the simulations. Thus, the threshold value is essentially arbitrary when the purpose is to compare the two models. The treatment threshold was varied in a few simulations to more closely simulate natural mosaics of different crops that would be expected to have different thresholds for the same pest. Interestingly, variation in the treatment thresholds among fields about a mean had little effect on insect densities but did increase the number of sprays in the asynchronous model (in the synchronous model any such variation is summarized in the mean threshold). In fact, the dimensions of a field were not specified because they would be related to the absolute thresholds and these had no affect on differences between the two models. However, it may be helpful in understanding the models to set either the field size or the threshold and adjust the other appropriately depending on the insect and crop species of interest. For example, a field might be 500 m on a side with a threshold of 2.5 million, or alternatively, a field might be 50 m on a side with the threshold set at 25,000.

As the treatment area is enlarged above an expected optimum, the synchronous method may become less efficient because of increased variation in topography and microclimates affecting growth rates. However, over large ranges of growth and dispersal levels, the simulations demonstrated the theoretical benefits of synchronous treatments using an average areawide threshold derived from many fields compared with the usual practice of monitoring the same fields individually for the same threshold and treating them independently. Thus, it seems advantageous to adopt the synchronous strategy because of lower populations and fewer required sprays. Lower populations should reduce the development of chemical resistance in the pest because of fewer chances of beneficial mutations, whereas less frequent sprays should lower the selection pressures from insecticide (Calkins 1998, Siegfried et al. 2004). Most importantly, synchronous methods may lower costs for treatments, increase crop yields, and require less augmentation with pest enemies (Johnson and Wilson 1995). Integration of complementary methods (e.g., pheromone, natural enemies, cultural, and resistance) in either an asynchronous or synchronous strategy increases the modeling complexity dramatically and might alter the conclusions here. Validation of the benefits of control programs in practice is difficult because of the biological complexity (Menke and Greene 1976, Welch et al. 1981, Boivin et al. 1991).

Implementation of a synchronous program requires coordination and cooperation of many growers sharing management costs (Hammig et al. 1984, Faust and Chandler 1998). However, this may be difficult because most growers have individual goals in a competitive market and may be reluctant to coordinate treatment strategies and share management costs with neighbors. The variation among fields in sprays and populations indicates growers would experience variable yields with regard to neighbors in either model, but the synchronous model provided nearly all growers with higher yields and fewer treatment expenses (Fig. 3). Adoption of a synchronous plan might be facilitated if growers not only agreed to share treatment costs but also to compensate those growers that suffered relatively higher damages. Although areawide control programs generally have used pheromones or biological agents in a synchronized way, treatment thresholds were not explicitly considered and results were not directly compared with single-field IPM. In the past, calendar spraying was a synchronous method whereby pest populations were sprayed on certain predetermined dates, but this assumes populations are historically consistent without considering particular areawide thresholds (AliNiazee 1981).

Experimenting with the simulation software should help managers better understand the synchronous benefits and provide the confidence necessary to initiate new cooperative ventures on an areawide basis. Another benefit of a synchronous treatment is the expected economic savings because of simultaneous application costs on larger scales (Graham and Knight 1965, Carlson and Suguiyama 1985, Calkins 1998) compared with unsynchronized, scattered treatments of fields. The models here are persuasive arguments for the synchronous approach using areawide population thresholds in many pest management situations.

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References Cited

AliNiazee, M. T. 1981. Improved control of the western cherry fruit fly, *Rhagoletis indifferens* (Dipt.: Tephritidae), based on area-wide monitoring. J. Entomol. Soc. Br. Columbia 78: 27–33.

Bakke, A., T. Saether, and T. Kvamme. 1983. Mass trapping of the spruce bark beetle *Ips typographus*. Pheromone and trap technology. Medd. Nor. Inst. Skogforsk. 38: 1–35.

Barclay, H.J.A., and C. Li. 1991. Combining methods of pest control minimizing cost during the control program. Theor. Popul. Biol. 40: 105–123.

Bedard, W. D., and D. L. Wood. 1974. Programs utilizing pheromones in survey and control: bark beetles–the western pine beetle, pp. 441–449. *In* M. C. Birch [ed.], Pheromones. North-Holland Publ. Co., Amsterdam, The Netherlands.

Bell, M. R., and J. L. Hayes. 1994. Area-wide management of cotton bollworm and tobacco budworm (Lepidoptera, Noctuidae) through application of a nuclear polyhedrosis virus on early-season alternate hosts. J. Econ. Entomol. 87: 53–57.

Bessin, R. T., R. E. Stinner, and T. E. Reagan. 1991. Modeling the area-wide impact of sugarcane varieties and predation on sugarcane borer (Lepidoptera: Pyralidae) populations in southern Louisiana. Environ. Entomol. 20: 252–257.

Binns, M.R.A., and J. P. Nyrop. 1992. Sampling insect populations for the purpose of IPM decision making. Annu. Rev. Entomol. 37: 427–454.

Boivin, G. A., B.J.P. R. Le, and J. A. Adams. 1991. Spatial dispersion and sequential sampling plan for the tarnished plant bug (Hemiptera: Miridae) on celery. J. Econ. Entomol. 84: 158–164.

Brewster, C. C., J. C. Allen, and D. D. Kopp. 1999. IPM from space: using satellite imagery to construct regional crop maps for studying crop-insect interaction. Am. Entomol. 45: 105–117.

Byers, J. A. 1991. Simulation of mate-finding behaviour of pine shoot beetles, *Tomicus piniperda.* Anim. Behav. 41: 649–660.

Byers, J. A. 2000. Wind-aided dispersal of simulated bark beetles flying through forests. Ecol. Model. 125: 231–243.

Byers, J. A. 2001. Correlated random walk equations of animal dispersal resolved by simulation. Ecology 82: 1680–1690.

Cadenhead, R. 1999. Sams teach yourself Java 2 in 24 hours. Sams Publishing, Indianapolis, IN.

Calkins, C. O. 1998. Review of the codling moth areawide suppression program in the western United States. J. Agric. Entomol. 15: 327–333.

Carlson, G. A., and L. Suguiyama. 1985. Economic evaluation of area-wide cotton insect management: boll weevils in the southeastern United States. NC Agric. Res. Ser. Bull. 473: 1–24.

Chamberlain, K., E. Guerrieri, F. Pennacchio, J. Pettersson, J. A. Pickett, G. M. Poppy, W. Powell, L. J. Wadhams, and C. M. Woodcock. 2001. Can aphid-induced plant signals be transmitted aerially and through the rhizosphere? Biochem. Syst. Ecol. 29: 1063–1074.

Dent, D. 2000. Insect pest management. CAB International, London, United Kingdom.

Drees, B. M., and R. E. Gold. 2003. Development of integrated pest management programs for the red imported fire ant (Hymenoptera: Formicidae). J. Entomol. Sci. 38: 170–180.

Dudley, N.J.A., R.A.E. Mueller, and J. A. Wightman. 1989. Application of dynamic programming for guiding IPM on groundnut leafminer in India. Crop Prot. 8: 349–357.

Ellsworth, P. C., and J. L. Martinez-Carrillo. 2001. IPM for *Bemisia tabaci:* a case study from North America. Crop Prot. 20: 853–869.

Enkerlin, W., and J. Mumford. 1997. Economic evaluation of three alternative methods for control of the Mediterranean fruit fly (Diptera: Tephritidae) in Israel, Palestinian Territories, and Jordan. J. Econ. Entomol. 90: 1066–1072.

Faust, R. M., and L. D. Chandler. 1998. Future programs in areawide pest management. J. Agric. Entomol. 15: 371–376.

Fuchs, T. W., D. R. Rummel, and E. P. III Boring. 1998. Delayed uniform planting for areawide boll weevil suppression. Southwest. Entomol. 23: 325–333.

Goodman, D. 1996. Danny Goodman's JavaScript handbook. IDG Books Worldwide, Inc., Foster City, CA.

Graham, S. A., and F. B. Knight. 1965. Principles of forest entomology. McGraw-Hill, New York.

Gray, E. W., P. H. Adler, A. C. Coscaron, S. Coscaron, and R. Noblet. 1999. Development of the first black fly (Diptera: Simuliidae) management program in Argentina and comparison with other programs. J. Amer. Mosq. Control Assoc. 15: 400–406.

Hammig, M. D., J. W. Jordon, and D. R. Griffin. 1984. An economic evaluation of a regional pest suppression program: boll weevil eradication in South Carolina. J. Agric. Entomol. 1: 219–226.

Hardee, D. D., M. R. Bell, and D. A. Streett. 1999. A review of area-wide management of *Helicoverpa* and *Heliothis* (Lepidoptera: Noctuidae) with pathogens (1987–1997). Southwest. Entomol. 24: 62–75.

Headley, J. C. 1972. Defining the economic threshold, pp. 100–108. *In* Pest control strategies for the future. National Academy of Science, Washington, DC.

Hendrichs, J., A. S. Robinson, J. P. Cayol, and W. Enkerlin. 2002. Medfly areawide sterile insect technique programmes for prevention, suppression or eradication: the importance of mating behavior studies. Fla. Entomol. 85: 1–13.

Hoffmann, M. P., L. T. Wilson, and F. G. Zalom. 1991. Area-wide pheromone trapping of *Helicoverpa zea* and *Heliothis phloxiphaga* (Lepidoptera: Noctuidae) in the Sacramento and San Joaquin valleys of California. J. Econ. Entomol. 84: 902–911.

Huber, R. T., L. Moore, and M. P. Hoffman. 1979. Feasibility study of area-wide pheromone trapping of male pink bollworm moths in a cotton insect pest management program. J. Econ. Entomol. 72: 222–227.

Johnson, M. W., and L. T. Wilson. 1995. Integrated pest management: contributions of biological control to its implementation, pp. 7–24. *In* J. R. Nechols, L. A. Andres, J.W. Beardsley, R. D. Goeden, and C. G. Jackson [eds.], Biological control in the western United States. Univ. Calif. Publ. 3361.

Knipling, E. F., and E. A. Stadelbacher. 1983. The rationale for area-wide management of *Heliothis* (Lepidoptera: Noctuidae) populations. Bull. Entomol. Soc. Am. 29: 29–37.

Kogan, M. 1995. Areawide management of major pests: is the concept applicable to the *Bemisia* complex?, pp. 643–657. *In* D. Gerling and R. T. Mayer [eds.], *Bemisia* 1995: taxonomy, biology, damage control and management. Intercept Ltd., Andover, United Kingdom.

Legaspi, B. C., Jr., J. C. Allen, C. C. Brewster, J. A. Morales-Ramos, and E. G. King. 1998. Area-wide management of the cotton boll weevil: use of a spatio-temporal model in augmentative biological control. Ecol. Model. 110: 151–164.

Legaspi, B. C., Jr., J. C. Legaspi, R. I. Carruthers, J. Goolsby, J. Hadman, W. Jones, D. Murden, and L. Wendel. 1997. Area-wide population dynamics of silverleaf whitefly (Homoptera: Aleyrodidae) and its parasitoids in the lower Rio Grande Valley of Texas. J. Entomol. Sci. 32: 445–459.

Lemay, L., and C. L. Perkins. 1997. Teach yourself Java 1.1 in 21 days, 2nd ed. Sams.net Publishing, Indianapolis, IN.

Logan, P. A. 1981. Estimating and projecting Colorado potato beetle *Leptinotarsa decemlineata* density and potato yield loss, pp. 105–118. *In* J. H. Lashomb and R. Casagrande [eds.], Advances in potato pest management. Proceedings of a Conference, 23–25 January 1980, New Brunswick, NJ. Ross Publishing Co., Stroudsburg, PA.

McManus, M.L.A. 1988. Weather behavior and insect dispersal. Mem. Entomol. Soc. Can. 146: 71–94.

Menke, W. W., and G. L. Greene. 1976. Experimental validation of a pest management model. Fla. Entomol. 59: 135–142.

Mols, P.J.M.A. 1990. Forecasting orchard pests for adequate timing of control measures, pp. 75–81. *In* M. J. Sommeijer and J. Van Der Blom [eds.], Proceedings of the Section of Experimental and Applied Entomology Netherlands Entomological Society Meeting, vol. 1. 15 December 15 1989. Utrecht, The Netherlands. Nederlandse Entomologische Vereniging, Amsterdam, The Netherlands.

Nyambo, B. T. 1991. The pest status of *Zonocerus elegans* (Thunberg) (Orthoptera: Acridoidea) in Kilosa district in Tanzania with some suggestions on control strategies. Insect Sci. Appl. 12: 231–236.

Palm, C. E., W. W. Dykstra, G. R. Ferguson, R. Hansberry, W. J. Hayes, Jr., L. W. Hazleton, J. G. Horsfall, E. F. Knipling, L. D. Leach, R. L. Lovvorn, et al. 1969. Insect pest management and control. Publ. 1695. National Academy of Science, Washington, DC.

Rabb, R. L. 1978. A sharp focus on insect populations and pest management from a wide-area view. Bull. Entomol. Soc. Am. 24: 55–61.

Reichard, R. E. 2002. Area-wide biological control of disease vectors and agents affecting wildlife. Rev. Sci. Tech. Off. Int. Epizoot. 21: 179–185.

Ricklefs, R. E. 1990. Ecology. W. H. Freeman & Company, New York.

Schaalje, G. B., and H. R. van der Vaart. 1989. Relationships among recent models for insect population dynamics with variable rates of development. J. Math. Biol. 27: 399–428.

Schneider, J. C. 1989. Role of movement in evaluation of area-wide insect pest management tactics. Environ. Entomol. 18: 868–874.

Schneider, J. C., R. T. Roush, W. F. Kitten, and M. L. Laster. 1989. Movement of *Heleothis virescens* (Lepidoptera: Noctuidae) in Mississippi in the spring: implications for area-wide management. Environ. Entomol. 18: 438–446.

Scholl, P. J., D. D. Colwell, J. Weintraub, and S. E. Kunz. 1986. Area-wide systemic insecticide treatment for control of cattle grubs, *Hypoderma* spp (Diptera: Oestridae): two approaches. J. Econ. Entomol. 79: 1558–1563.

Siegfried, B. D., L. J. Meinke, S. Parimi, M. E. Scharf, T. J. Nowatzki, X. Zhou, and L. D. Chandler. 2004. Monitoring western corn rootworm (Coleoptera: Chrysomelidae) susceptibility to carbaryl and cucurbitacin baits in the areawide management pilot program. J. Econ. Entomol. 97: 1726–1733.

Smith, J. W. 1998. Boll weevil eradication: area-wide pest management. Ann. Entomol. Soc. Am. 91: 239–247.

Sokal, R. R., and R. J. Rohlf. 1995. Biometry. W. H. Freeman & Company, New York.

Stanek, W. R. 1996. HTML, CGI, SGML, VRML, JAVA Web Publishing Unleashed. Sams.net Publishing, Indianapolis, IN.

Taft, E., and J. Walden. 1990. PostScript language reference manual. Addison-Wesley Publishing Company, Reading, MA.

Tollefson, J. J. 1998. Rootworm areawide management program in Iowa. J. Agric. Entomol. 15: 351–357.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, MA.

Turlings, T.C.J., and J. H. Tumlinson. 1992. Systemic release of chemical signals by herbivore-injured corn. Proc. Natl. Acad. Sci. U.S.A. 89: 8399–8402.

Vanhelsuwé, L., I. Phillips, G. T. Hsu, K. Sankar, E. Ries, P. Heller, J. McGloughlin, and J. Zukowski. 1997. Mastering Java 1.1, 2nd ed. SYBEX, San Francisco, CA.

Vargas, R. I., J. Long, N. W. Miller, K. Delate, C. G. Jackson, G. K. Uchida, R. C. Bautista, and E. J. Harris. 2004. Releases of *Psyttalia fletcheri* (Hymenoptera: Braconidae) and sterile flies to suppress melon fly (Diptera: Tephritidae) in Hawaii. J. Econ. Entomol. 97: 1531–1539.

Vargas, R. I., S. L. Peck, G. T. McQuate, C. G. Jackson, J. D. Stark, and J. W. Armstrong. 2001. Potential for areawide integrated management of Mediterranean fruit fly (Diptera: Tephritidae) with a braconid parasitoid and a novel bait spray. J. Econ. Entomol. 94: 817–825.

Wagner, T. L., R. L. Olson, J. L. Willers, and M. R. Williams. 1996. Modeling and computerized decision aids, pp. 205–249. *In* E. G. King, J. R. Phillips, and R. J. Coleman [eds.], Cotton insects and mites: characterization and management. Cotton Foundation Publ., Memphis, TN.

Walker, R. S. 1985. Understanding computer science, vol. II. Texas Instruments Inc., Dallas, TX.

Welch, S. M., B. A. Croft, and M. F. Michels. 1981. Validation of pest management models. Environ. Entomol. 10: 425–432.

Williams, D.W.A., R. W. Fuester, W. W. Metterhouse, R. J. Balaam, R. H. Bullock, and R. J. Chianese. 1991. Oak defoliation and population density relationships for the gypsy moth (Lepidoptera: Lymantriidae). J. Econ. Entomol. 84: 1508–1514.

Worner, S. P. 1991. Use of models in applied entomology: the need for perspective. Environ. Entomol. 20: 768–773.

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