FORUM

Estimating the Impact of *Lygus hesperus* on Cotton: The Insect, Plant, and Human Observer as Sources of Variability

JAY A. ROSENHEIM,[1] KIMBERLY STEINMANN, GAIL A. LANGELLOTTO, AND ANDREW G. ZINK

Department of Entomology, University of California, Davis, CA 95616

Environ. Entomol. 35(5): 1141–1153 (2006)

ABSTRACT Unexplained variation in the relationship between herbivore densities and the short-term appearance of crop damage is sometimes observed in pest management. Here we used a field survey of commercial cotton fields and a linked questionnaire for cooperating pest control advisors to document the existence of such unexplained variation in the impact of the western tarnished plant bug, *Lygus hesperus*, on upland cotton, *Gossypium hirsutum*. *L. hesperus* feeds preferentially on flower buds ("squares"), and the plant may respond to this damage with abscission of the square. We explored four classes of factors that might contribute to unexplained variation in square abscission. First, misperceptions by the human observer (i.e., sampling problems) may play a role, because commercial field scouts significantly underestimate densities of *L. hesperus* nymphs. Second, we found no support for the hypothesis that variable behavior expressed by *L. hesperus* contributes to unexplained variation in square abscission. *L. hesperus* seems to generate relatively predictable levels of square feeding damage; the variation that was observed was unrelated to grower categorization of fields as exhibiting normal versus unexpectedly high or low levels of square abscission. Third, variable plant responses to damage may instead be the key source of unexplained square abscission. Younger plants and plants with higher petiole phosphate concentrations expressed increased sensitivity to *L. hesperus* feeding; these correlations must, however, be tested experimentally before definitive conclusions are drawn. Fourth, another arthropod might be generating damage that was erroneously being attributed to *L. hesperus*. The omnivore *Geocoris pallens* was a candidate agent of cryptic damage to squares; however, an experiment showed that *G. pallens* generated only trivial square damage and no detectable increase in square abscission. Thus, this study has focused our attention away from the arthropod side of the interaction and toward the host plant as the primary source of greater than expected square abscission generated by *L. hesperus*.

KEY WORDS sampling error, variable insect behavior, variable plant responses, *Lygus hesperus*, *Gossypium hirsutum*

When viewed over a short time frame such as a small portion of a growing season, we generally expect to observe a monotonic, positive relationship between the density of an herbivorous arthropod and the amount of damage sustained by its host plant. Over the longer term, such as an entire growing season, plant compensation for herbivory can produce more complex patterns, including full or overcompensation for damage (Stowe et al. 2000). In some cases, however, unexplained variation is observed in the relationship between herbivore densities and the short-term appearance of crop damage (Orr et al. 2001). Herbivores that generate unpredictable impacts on their host plant can be an important impediment to integrated pest management (IPM). The uncertainty associated with such pests can cause risk-averse farmers to adopt highly conservative pest management practices (e.g., extremely low thresholds for applying insecticides) that preclude the establishment of more biologically based management.

Variation in the short-term production of crop damage that is not explained by estimates of herbivore densities can have at least four classes of potential explanatory factors. (1) First, misperceptions by the human observer may contribute. Problems with estimating either the density of the herbivore or the amount of crop damage fall under the category of "observational uncertainty" (Hilborn and Mangel 1997, Shea et al. 2002). There may also be underlying variability in the behavior expressed by (2) the herbivore or (3) the plant, in its response to herbivory. These sources of variability fall under the category of "process uncertainty," and may reflect stochastic variation in the environment or intrinsic aspects of the herbivore or the host plant. (4) Finally, there may be some other hidden factor that elicits plant responses that mimic the plant's response to the focal herbivore, and for which the focal herbivore erroneously re-

---

[1] Corresponding author, e-mail: jarosenheim@ucdavis.edu.

ceives the "blame." This is an example of what could be called "model uncertainty," where we are operating with a false underlying representation of the essential nature of the interaction we are studying.

The focus of this study is the impact of *Lygus hesperus* Knight on upland cotton, *Gossypium hirsutum*, in California. *L. hesperus* feeds on many parts of the cotton plant (Rosenheim et al. 2004); its economic damage, however, comes primarily from its feeding on developing flower buds (henceforth, "squares"; Leigh et al. 1988, Leigh and Goodell 1996). Plants respond to square damage by initiating an active physiological abscission response (Addicott 1982). In extreme cases, *L. hesperus* damage to squares can result in plants that set little or no fruit (Ellsworth 2000, Ellsworth and Barkley 2001, 2003; J.A.R., personal observation). The impact of *L. hesperus* on cotton has long been controversial (Scott and O'Keeffe 1976), primarily because of conflicting experimental results of season-long manipulations of *L. hesperus* density on cotton yield (Falcon et al. 1968, 1971, Sevacherian and Stern 1972b, Ellsworth 2000) and because of differing interpretations of cotton's ability to compensate for the loss of fruiting structures (Gutierrez et al. 1977). The question that we will focus on in this paper, however, concerns not the season-long response to *L. hesperus* damage, but rather the short-term square abscission response of plants to *L. hesperus* feeding. The short-term abscission response is important, because it is a key influence on whether or not farmers choose to apply insecticides. Farmers and pest control professionals have noted for many years that it is difficult to project the amount of short-term square abscission that will be observed in a field from the standard sweep-net density estimates of *L. hesperus* (Mauney and Henneberry 1979, 1984). Despite the long-standing nature of this question, researchers have never attempted to explore its basis. Indeed published studies have instead supported a highly deterministic relationship between *L. hesperus* density and square shed (Mauney and Henneberry 1984, Leigh et al. 1988). Nevertheless, the perceived uncertainty surrounding the impact of *L. hesperus* leads many growers to adopt spray thresholds that are substantially lower than the University of California recommendations. Because *L. hesperus* is primarily suppressed with foliar applications of broad-spectrum insecticides, treatments for *Lygus* are the prime cause of secondary outbreaks of other cotton pests (Leigh et al. 1966, Falcon et al. 1968, Eveleens et al. 1973, Stoltz and Stern 1978).

How plausible is each of the four classes of factors that might generate unexplained variation in *Lygus* impact on square abscission? Observational uncertainty is a perennial concern for any arthropod pest, but is a particularly acute problem for *L. hesperus* for several reasons. First, *L. hesperus* is highly damaging even at very low densities (the most widely used action threshold is just three *L. hesperus* per 50 sweeps when square abscission is high; University of California 1996). Actual densities are often quite low, and the variability of *L. hesperus* counts across replicate sweep samples is often high, including many zeroes, for fields that may still be approaching an action threshold. Second, whereas the universally used sweep net technique is quite successful in sampling the mobile adults, the nymphs are cryptic, often feed in protected locations, and may not be sampled as effectively (Byerly et al. 1978, Zink and Rosenheim 2004). Because the stage structure of *L. hesperus* populations has been shown to be highly variable, with some fields dominated by adults and other fields dominated by nymphs (Zink and Rosenheim 2004), an estimate of adult densities alone may not provide a good estimate of the total *L. hesperus* population density. Furthermore, like many herbivores, *L. hesperus* populations can also be highly patchy within a field (Sevacherian and Stern 1972a). Third, *L. hesperus* is mobile (Bancroft 2005, Carrière et al. 2006), and the possibility exists that "waves" of adults originating from habitats that have become unsuitable (e.g., recently mowed alfalfa fields or weedy fields that dry out during the summer) may move through cotton fields, generating damage but leaving the field before they are detected through routine sampling. Finally, although in principle it is straightforward to estimate square retention using plant mapping techniques (Kerby and Hake 1996, University of California 1996), this is labor intensive, and many field scouts rely instead on less formal observations of square retention or the appearance of "blasted squares" (squares that have abscised) in the sweep net. Thus, plant damage estimates may also be subject to substantial error. In sum, the potential exists for simple estimation errors of *L. hesperus* density or plant damage to produce the appearance of unexplained variation in square abscission when in fact none exists.

Variable feeding behavior of *L. hesperus* also seems plausible, given what we know of this insect's biology. First, *L. hesperus* is known to be an omnivore, feeding on the plant as an herbivore and on various soft-bodied arthropods as a predator (Naranjo and Hagler 1998, Wheeler 1976, 2001, Ehler 2004, Hagler et al. 2004, Rosenheim et al. 2004). Many omnivores are known to shift between herbivory and predation as the quality or quantity of different food resources changes (Agrawal et al. 1999, Agrawal and Klein 2000, McGregor et al. 2000, Limburg and Rosenheim 2001, Tillman and Mullinix 2003). Although field observations suggested that *L. hesperus* in California feeds almost exclusively as an herbivore (Rosenheim et al. 2004), the possibility remains that square feeding might vary as a function of the availability of other foods. Second, different *Lygus* developmental stages might have different propensities to feed on squares (Gutierrez et al. 1977, Mauney and Henneberry 1979, Ellsworth and Barkley 2003). Finally, a hypothesis discussed in the farming community, but as yet unexplored empirically, is that *L. hesperus* adults immigrating into cotton fields may come from a variety of previous host plants (weeds, crops, or native plant communities), and may therefore have different nutritional needs that are expressed as variable square feeding. In sum, there seem to be several factors that might modulate the per capita production of feeding injury by *L. hesperus*.

Of the possible explanations for variable *L. hesperus* impact, perhaps the least widely appreciated is the possible role of variable plant responses to herbivory. *L. hesperus* feeding is unlikely to kill cotton squares outright. Instead, *L. hesperus* feeding triggers a response by the plant to cease investing resources in the damaged square and instead to initiate abscission by forming a distinct abscission zone at the base of the square's peduncle (Strong and Kruitwagen 1968, Strong 1970, Addicott 1982, Patterson and Bleecker 2004). Thus, factors that influence the plant's resource allocation could modulate the plant's response to *L. hesperus* feeding damage. It has been shown, for example, that the fate of the reproductive structures located at the first and second positions on a fruiting branch are not independent: if the first position fruit is abscised, the plant is more likely to retain the second position fruit, and vice versa (Kerby and Buxton 1981). Furthermore, we know that plant source–sink relationships are important later in the season when the plant's load of developing fruits increases and abscission rates climb even in the absence of any square herbivory (Gutierrez et al. 1977, Kerby and Hake 1996, University of California 1996). Other ontogenetic effects could also be important; for example, it is unknown if the plant's propensity to retain undamaged squares varies early during the plant's shift from a purely vegetative growth mode (approximately nodes 0–6) to an increasingly reproductive mode. Finally, because *L. hesperus* may produce damage both mechanically and enzymatically, by injecting a cocktail of enzymes that continue to digest plant cells long after the feeding event is complete (Strong and Kruitwagen 1968, Agusti and Cohen 2000, Zeng and Cohen 2001), it is possible that variable plant defenses against digestive enzymes, such as polygalacturonase-inhibiting proteins, may also modulate the amount of tissue that is damaged by a given feeding event (L. R. Teuber, personal communication).

Finally, it is possible that, despite many years of intensive research in cotton entomology, some hidden factor is generating square shed for which *L. hesperus* is erroneously being blamed. In addition to *L. hesperus*, abiotic stress (heat, drought) and other insects [high densities of the thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter) (Hemiptera: Miridae), and several stinkbug species; University of California 1996] can also generate square shed, although these factors are generally directly observable in the field and as a result are mostly well understood. Perhaps the main candidates that have not yet been explored are common omnivores in the Order Hemiptera, including *Orius tristicolor* (White) (Hemiptera: Anthocoridae), *Geocoris* spp., and *Nabis* spp., which are generally viewed as biological control agents, but which also feed directly on the plant (Ridgway and Jones 1968, Coll 1998).

The goals of our study were to characterize the unexplained variation in *Lygus* impact on square abscission and to explore each of the four possible explanations for its appearance, including (1) sampling problems, (2) variable insect behavior, (3) variable plant responses to herbivory, and (4) hidden factors (other herbivores). Our intent was to conduct a study that would be both exploratory, generating testable hypotheses, as well as evaluative, providing definitive tests.

Materials and Methods

Survey of Commercial Fields. Our study needed to encompass both the plant–insect interaction and the human side of the pest management problem. Thus, the core of the study was a comparative survey of three classes of commercial cotton fields located in Merced, Fresno, and Tulare Counties: fields that were judged by the pest control advisor to exhibit (1) the expected amount of square shed, given the observed density of *L. hesperus* ($n = 8$), (2) more square shed than expected, given the observed density of *L. hesperus* ($n = 4$), and (3) less square shed than expected, given the observed density of *L. hesperus* ($n = 9$). Pest control advisors assigned their fields to one of the three categories in "real time"—that is, during the growing season, as they were sampling fields and monitoring plant growth. Fields with greater than expected square shed were particularly critical for our project, but were also the most difficult to obtain, in part because high square shed almost always triggered an immediate decision to treat the field, precluding our sampling. Cooperating pest control advisors were also asked to respond to a questionnaire exploring their methods of assessing *L. hesperus* density and crop damage, general agronomic information for the field, and their past estimates of *L. hesperus* density and crop damage (square retention) for the field.

We identified fields with higher or lower than expected levels of square abscission by soliciting collaborators from the community of pest control advisors working in the cotton industry in California's San Joaquin Valley. We explained the nature of our project at several meetings of farmers, pest control advisors, and cooperative extension specialists, in a private electronic newsletter ("MiteFAX"), in a University of California Cooperative Extension newsletter ("California Cotton Review"), and in weekly phone calls to the leading consultants working in cotton. The criteria for including a responding pest control advisor in our survey were (1) that they be able to provide us with permission to sample in at least one field that they judged to be exhibiting unexpectedly high or low levels of square abscission plus a field that they judged to be normal, (2) that the fields be free of foliar insecticide applications for at least the previous 3 wk and have no history of aldicarb use during the growing season (aldicarb is a persistent systemic insecticide), and (3) that the pest control advisor be willing to share data and respond to the questionnaire.

Field surveys were performed 12 June to 31 July 2003 during the early period of squaring and fruit set when the crop is sensitive to damage by *L. hesperus*, and as quickly as possible after the pest control advisor's notification. Mean plant size ranged from 9.4 to

18.6 mainstem nodes across the surveyed fields. We sampled the densities of *L. hesperus* and other larger arthropods (herbivores, omnivores, and predators) using the standard sweep net: a single sample consisted of 50 sweeps across the top of a single row of cotton plants with a 38-cm-diameter sweep net (University of California, 1996). *Lygus* spp. were counted, and all nymphs were collected and returned to the laboratory to identify them to instar. California cotton fields harbor primarily *L. hesperus,* but may also harbor smaller numbers of *L. elisus.* Four sweep net samples were taken at each of five locations around the periphery of the field, for a total of 20 samples (=1,000 sweeps total per field). At each of the five locations we also collected a sample of 10 mainstem leaves, taken from the fifth node from the terminal; these leaves were checked in the field to count aphids and thrips and to estimate the proportion of the lower leaf surface covered with active mite colonies. Different pest control advisors working in California cotton may use different numbers of sweeps (25 versus 50) to produce a *Lygus* density estimate. We emphasize that our sampling technique (50 sweeps per sample) and our choice of sampling locations were designed to approximate the sampling protocols that were used by the private consultants who monitored the fields that were included in our study (all of our cooperating consultants used 50 sweep samples). We did, however, spend considerably more time searching through the plant material collected in the net bag to find *L. hesperus* nymphs than is done commercially.

We also collected data on the condition of the cotton plants. For four plants at each of the five sampled locations per field (total $N = 20$), we recorded plant height and number of mainstem nodes, and "mapped" the plants, categorizing each mainstem node as a vegetative node, a vegetative branch, or a fruiting branch. The first position of each fruiting branch was examined to determine if the square had been retained or aborted. These data allowed us to calculate a standard metric of square retention: the proportion retention of first-position squares within the plant's top five nodes. First-position squares from the top five nodes were also dissected to quantify the percentage of developing anther sacs that were destroyed. Anther sac damage is a measure of feeding injury created by *L. hesperus* and reflects both the population density of *L. hesperus* and the per capita damage generated by *L. hesperus,* whereas square retention is a measure of the plant's response to that feeding damage.

Our estimate of mean anther damage is probably biased downward by the selective abortion of the most heavily damaged squares; aborted squares die and fall from the plant and thus cannot be dissected and scored. One outcome of this process is that the relationship between *L. hesperus* density and mean observed square damage might increase more slowly at higher bug densities. However, cotton plants are much less likely to shed older, more developed squares, even if they are heavily damaged (Strong 1970; A.G.Z., unpublished data), and thus the anther damage metric should still increase monotonically across the full range of *L. hesperus* densities.

Finally, at each of the five sampled locations per field, we measured plant density (number of plants per meter of cotton row; two counts made) and collected the petioles from 10 mainstem leaves at the fifth node for analysis of macronutrients, micronutrients, and potential toxins. Petioles were dried in an oven, ground and submitted for analysis to the Division of Agriculture and Natural Resources Analytical Laboratory.

Data were analyzed using simple bivariate linear regression, analysis of variance (ANOVA), and analysis of covariance (ANCOVA); in all cases "field category" (more abscission than expected; abscission as expected; less abscission than expected) was treated as an ordered variable. Forward stepwise multiple regression was used to identify variables for further exploration in ANOVA models (critical P value to enter the model = 0.10), interaction terms were only considered if both main effects were already present in the model, and higher-order interaction terms were not included in any models.

Impact of *Geocoris* on Square Retention. *Geocoris pallens* Ståhl (Hemiptera: Lygaeidae) was the only common arthropod present in our surveyed fields other than *L. hesperus* that could potentially feed on cotton squares and therefore contribute to higher than expected square shed. We therefore conducted a simple manipulative field experiment to test the hypothesis that *G. pallens* might be contributing to anther sac damage and square shed under conditions of low prey availability.

The experiment was performed 17 May to 1 June 2004 at the University of California West Side Research and Extension Center, Fresno County, CA, in an insecticide-free experimental plot of upland cotton, cultivar Maxxa. The experimental unit was a single cotton plant with 7.6 ± 0.1 mainstem nodes that was just beginning to produce squares (1–2 "pinhead" squares per plant). Plants were carefully searched to remove any motile *L. hesperus, G. pallens, O. tristicolor,* and any other predators (e.g., spiders); we made no attempt to remove the eggs of predators that oviposit into the plant (e.g., *O. tristicolor*). The only arthropod present that represented prey for *G. pallens* was the western flower thrips, *F. occidentalis.* We counted and removed all thrips present on the mainstem node leaves. Cages were enclosed in tapered polyester mesh plant sleeves (width at base, 20 cm; width at top, ≈36 cm; height, 48 cm). We assigned plants to one of two treatments, each replicated 18 times. Treatment 1 (control) received no other arthropods. Treatment 2 received a single adult female *G. pallens.* We collected *G. pallens* from the same cotton field not more than 1 h before their introduction into the experimental cages. Cages were sealed and left in the field for 15 d. We counted all stages of living *G. pallens* and motile *F. occidentalis* and recorded plant height, node number, and square retention at the first position of all fruiting branches. All squares were dissected to quantify damage to anther sacs. We also searched all plants for the

Table 1. Stepwise multiple regression analysis of the influences of different developmental stages of *L. hesperus* on anther sac damage and square retention

Step no.	Variable entered	Variable not entered	Estimate	df	Sum of squares	*F* ratio	*P*
Anther sac damage							
1	Adult density		0.0093	1	0.01563	13.4	0.0017
		Nymphs: first-third instar		1	0.00044	0.36	0.56
		Nymphs: fourth-fifth instar		1	0.00003	0.03	0.87
Square retention							
1	Adult density		−0.0216	1	0.0838	7.04	0.0157
		Nymphs: first-third instar		1	0.0049	0.40	0.54
		Nymphs: fourth-fifth instar		1	0.0100	0.84	0.37

presence of any other known square feeding arthropods.

Throughout the paper, values are presented as mean ± SE.

Results and Discussion

Sampling. By comparing our estimates of *L. hesperus* densities with those obtained for the same cotton fields by the commercial pest control advisors, we were able to assess whether or not sampling difficulties might contribute to unexplained variation in square abscission. We used only those fields for which the pest control advisor had taken a *L. hesperus* sample within the previous 7 d (on average, the pest control advisor's sample was taken 2.1 ± 0.6 d before our sample). For only 9 of the 21 sampled fields did the pest control advisors ($n = 4$) record separate counts for *L. hesperus* nymphs and adults. In these fields, pest control advisor estimates of nymphal *L. hesperus* densities (0.24 ± 0.17 nymphs/sweep sample) were lower than our estimates (1.49 ± 0.53; matched *t*-test: $t = 3.1$, df = 8, $P = 0.015$). Pest control advisor estimates of total nymph densities were lower than our estimates of the mean density of just the fourth- and fifth-instar nymphs (0.91 ± 0.38); these larger nymphs are captured in sweep nets with approximately the same efficiency as adults (Zink and Rosenheim 2004). Pest control advisor estimates of nymph density were, however, clearly correlated with our estimates ($r = 0.91$, df = 7, $P = 0.0072$), suggesting that pest control advisors are relatively consistent in their underestimation of nymph densities relative to our samples. Sweep nets do collect *L. hesperus* nymphs, but it is necessary to search carefully through the plant material that is collected in the sweep net to count *L. hesperus* nymphs (adult *L. hesperus,* in contrast, can be counted as they fly out of the sweep net). This labor-intensive step is rarely performed in commercial practice. The failure of pest control advisors to sample *L. hesperus* nymphs accurately underscores the potential for sampling problems to contribute to unexplained variation in square abscission; however, as discussed below, *L. hesperus* nymphs did not reach high densities in any of the fields we sampled, and nymphs did not generate significant effects on either anther sac damage or square retention. Thus, at least in the set of fields that we surveyed for this study, the potential for nymphal *L. hesperus* to generate unexplained variation in square abscission was not realized.

Pest control advisor estimates of *L. hesperus* adult densities (mean = 2.72 ± 0.93) were similar to ours (3.49 ± 0.81; matched *t*-test: $t = 1.82$, df = 8, $P = 0.11$). Pest control advisor estimates were also strongly correlated with ours ($r = 0.89$, df = 7, $P = 0.0012$). Finally, although the larger sample ($N = 17$) of pest control advisor estimates for the combined densities of *L. hesperus* nymphs and adults produced a lower mean (2.40 ± 0.62) than did our own sampling (4.62 ± 0.80), the two estimates were again strongly correlated ($r = 0.85$, df = 15, $P < 0.0001$). Thus, the sweep net seems to produce highly repeatable estimates of *L. hesperus* density, even across different observers. We conclude that sampling problems do not seem to underlie the difficulty of projecting the impact of at least the adult stage of *L. hesperus* on cotton.

Impact of *L. hesperus* on Anther Sac Damage and Square Abscission. We performed stepwise multiple regression analyses to determine which developmental stages of *L. hesperus* were generating observable levels of feeding damage (destroyed anther sacs within developing squares) and square abscission. In both cases, we detected significant effects for adults, but not for either small (first-third instars) or large (fourth-fifth instar) nymphs (Table 1). The results were qualitatively identical when we grouped all the nymphal stages into a single variable (data not shown). The absence of a significant role for *L. hesperus* nymphs is in marked contrast with recent work conducted in Arizona suggesting that nymphal stages have a strong impact on cotton yield (Ellsworth 2000, Ellsworth and Barkley 2001, 2003) and our own work suggesting that late-instar nymphs generate significant square abscission (Zink and Rosenheim 2005); in these cases, however, densities of nymphs were higher, and in many cases were substantially higher than densities of adults. Across all of our 21 sampled fields, mean densities of nymphs (1.41 ± 0.28) were much lower than densities of adults (4.03 ± 0.65; matched *t*-test: $t = 4.51$, df = 20, $P = 0.0002$). Thus, the failure to observe an effect for nymphal stages of *L. hesperus* may, at least in part, simply reflect their low abundances in our surveyed fields. In the analyses that follow, we use adult counts to reflect the damage potential of the *L. hesperus* population.

Characterizing Unexplained Variation in Square Abscission. The first question to ask about unexplained variation in square abscission is: is it a real phenomenon? That is, do our measurements suggest that fields judged by pest control advisors to exhibit higher or lower than expected levels of square abscission really deviate significantly from an underlying relationship between *L. hesperus* density and square retention? The answer appears to be "yes"—the pest control advisors are right. An ANCOVA showed both a significant effect for the covariate, *L. hesperus* adult density ($F_{1,17} = 11.4$, $P = 0.0036$), and for the main effect of field category ($F_{2,17} = 5.4$, $P = 0.016$). Pairwise contrasts confirmed the obvious trends in the data (Fig. 1A): fields identified as exhibiting more square abscission than would normally be expected, given the observed density of *L. hesperus,* did indeed fall below the square retention levels recorded for fields that were judged by pest control advisors to be normal ($F_{1,17} = 7.7$, $P = 0.013$) or fields that were judged to exhibit less square abscission than expected ($F_{1,17} = 9.0$, $P = 0.0081$). Fields that were judged to exhibit less square abscission than expected did not, however, deviate significantly from the normal fields ($F_{1,17} = 0.3$, $P = 0.60$). Therefore, at least that portion of the unexplained variation in square abscission that is most important from a pest management perspective (fields exhibiting more abscission than expected) seems to be a real phenomenon, instead of being merely a result of pest control advisor errors in assessing insect densities or crop damage. We obtained identical results when we repeated the analyses using total *L. hesperus* densities instead of just adult densities or when we included additional covariates for *L. hesperus* nymph densities (data not shown).

The next question to ask is: is unexplained variation in square abscission created by underlying variation in the feeding behavior of individual *L. hesperus* or by highly mobile *L. hesperus* populations that enter fields, create damage and square shed, and leave before being detected? We can address these questions by examining the relationship between observed adult *L. hesperus* density and the amount of feeding damage seen in developing anther sacs. If unexplained levels of square abscission are the result of either (1) *L. hesperus* in some fields feeding more avidly on cotton squares than in other fields or (2) mobile *L. hesperus* populations moving through fields, the class of fields identified as exhibiting more abscission than expected should also show more anther sac damage than expected. This was not the case; instead, an ANCOVA identified only an effect of *L. hesperus* adult density ($F_{1,17} = 10.0$, $P = 0.0057$) and no effect for field category ($F_{2,17} = 0.7$, $P = 0.52$) in explaining variation in anther sac damage (Fig. 1B). All pairwise contrasts between the three classes of fields were also nonsignificant ($P > 0.25$). Likewise, field category did not predict levels of anther damage on the older squares located at nodes 6–10 ($F_{2,16} = 0.8$, $P = 0.47$), suggesting that mobile *L. hesperus* populations had not been important for at least the previous month (new nodes are produced approximately every 3 d). Thus, *L. hesperus* produced a relatively predictable amount of feeding damage; neither variable *L. hesperus* feeding behavior nor mobile, transient populations of adult *L. hesperus* sweeping through the fields seemed to explain the higher or lower than expected levels of square abscission.

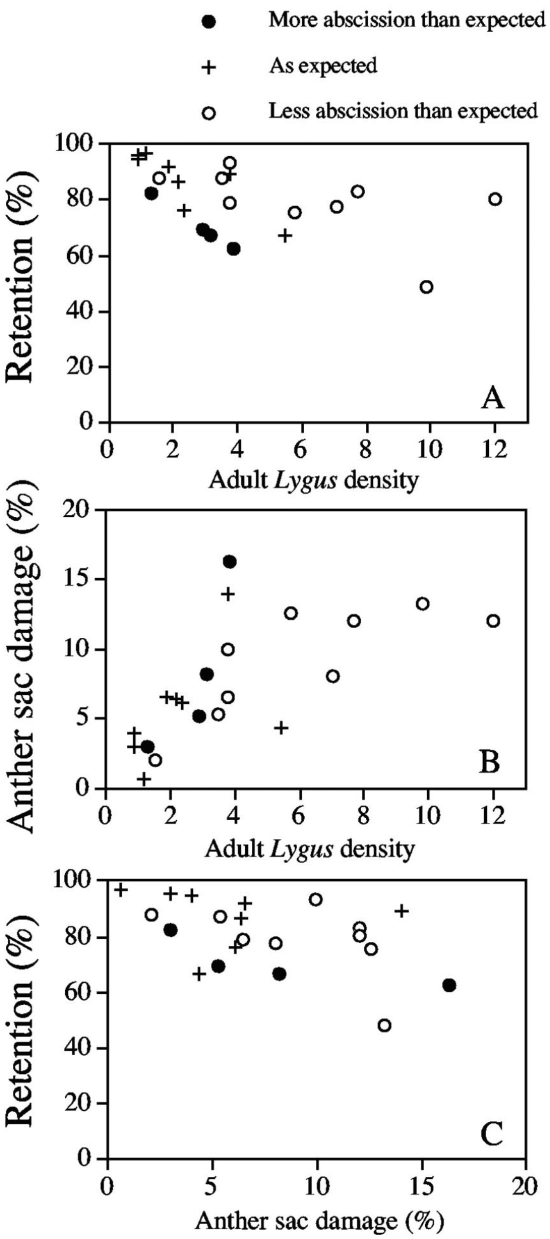

Fig. 1. Survey of commercial cotton fields judged by pest control advisors to be normal (square retention levels roughly as expected for the observed density of *L. hesperus*) versus exhibiting more square abscission than expected or less square abscission than expected. (A) Relationship between adult *L. hesperus* density, as estimated by sweep samples, and mean square retention at the first position of the top five fruiting branches. (B) Relationship between adult *L. hesperus* density and mean percent developing anther sacs killed in squares (first positions of top five mainstem nodes). (C) Relationship between anther sac damage and square retention.

Table 2. **Macronutrients and micronutrients in cotton petioles taken from fields where the impact of *L. hesperus* on square retention was considered to be normal (as expected), generating either less abscission than expected, or more abscission than expected, given the observed density of *L. hesperus* in the field**

Field type	NO_3-N ppm	NH_4-N ppm	K %	PO_4 ppm	S ppm	B ppm	Ca %	Mg %	Na ppm	Cl %	Zn ppm	Mn ppm	Fe ppm	Cu ppm
Less abscission than expected	11,439	540	5.04	1,479	2,060	30.9	2.07	0.70	2,035	1.73	18.4	19.8	34.0	4.48
	(1,370)	(151)	(0.47)	(110)	(213)	(0.9)	(0.10)	(0.06)	(297)	(0.11)	(1.4)	(1.6)	(3.1)	(0.32)
Normal	15,780	539	5.86	1,361	1,736	34.1	2.14	0.65	1,253	1.35	21.1	18.9	32.3	4.61
	(2,563)	(283)	(0.62)	(77)	(195)	(2.2)	(0.13)	(0.06)	(274)	(0.10)	(1.9)	(1.7)	(2.5)	(0.24)
More abscission than expected	17,065	720	6.59	1,905	2,200	35.5	2.29	0.62	666	1.13	22.5	20.3	36.5	5.18
	(3,635)	(413)	(0.32)	(204)	(278)	(2.1)	(0.23)	(0.05)	(146)	(0.23)	(3.0)	(3.0)	(3.9)	(0.38)
P	0.22	0.89	0.21	0.030	0.40	0.20	0.58	0.64	0.021	0.017	0.36	0.89	0.70	0.39

Values are means (SE).
P values represent the results of univariate ANOVAs examining the influence of field type on petiole nutrient content.

The third question is: is unexplained variation in square abscission a reflection of variable plant responses to herbivory? That is, might plants in some fields be more sensitive to a given amount of *L. hesperus* feeding damage, responding with a greater amount of square abscission, than plants in other fields? Here the data are less definitive, but provide at least a tentative suggestion that the answer is yes. An ANCOVA for square retention (dependent variable) revealed a marginally significant effect for the amount of anther damage ($F_{1,17} = 3.7, P = 0.070$). Although the main effect of field category was not significant ($F_{2,17} = 2.2$, $P = 0.14$), pairwise contrasts suggested that fields that exhibited more square abscission than expected also exhibited more square shed for a given amount of anther damage than did normal fields ($F_{1,17} = 4.4, P = 0.051$). Fields exhibiting less square abscission than expected did not differ significantly from the normal fields ($F_{1,17} = 0.6$, $P = 0.47$), confirming the suggestion that unexplained variation in square abscission was restricted to the high damage fields. These statistical results confirm the trends apparent from an inspection of the data (Fig. 1C): whereas the normal fields and the fields exhibiting less abscission than expected show similar abscission responses to anther damage, the fields exhibiting more abscission than expected tend to fall at the bottom of the scatter of points relating anther damage to square retention.

Plant-Based Factors: Nutrients. We recognized the theoretical possibility that plants might vary in their sensitivity to *L. hesperus* feeding damage. There are, however, no published or even informally discussed hypotheses suggesting what environmental factor(s) might modulate such an underlying variation in plant sensitivity. We therefore attempted to measure a broad range of possible factors related to plant macro- and micronutrients, as well as potential stressing agents, in the hopes that we might identify factors correlated with plant sensitivity. We emphasize that we view this as an exercise in generating hypotheses that can be tested with future experimentation, rather than an attempt to build a definitive argument for a causal role for any particular factor.

The results of the analyses exploring the possibility that nutrient or stressing agent concentrations might produce variation in square abscission are presented in Table 2. Although a MANOVA incorporating all 14 compounds measured failed to identify a significant effect of field type (Wilks' $\lambda = 0.096$, $P = 0.70$), univariate analyses did identify significant differences across field types for petiole phosphate (PO_4^{3-}), chloride (Cl^-), and sodium (Na^+) content. Fields in which plants exhibited more abscission than expected had higher levels of phosphate and lower levels of chloride and sodium. Given the large number of univariate analyses performed, these results clearly must be viewed very cautiously. To explore further the possible roles for these three compounds, we performed a multiple regression for factors shaping square retention, incorporating the observed role of adult *L. hesperus* density. These analyses identified a highly suggestive role for phosphate ($F_{1,18} = 11.6, P =$

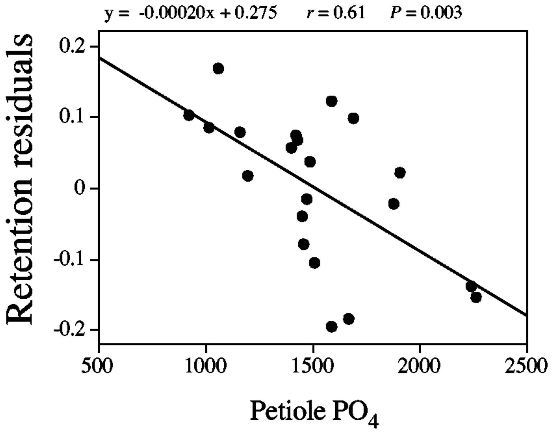

Fig. 2. Relationship between petiole phosphate content (parts per million) and the residuals from a linear regression of square retention on the density of adult *L. hesperus*. Cotton fields whose plants had higher phosphate contents exhibited square retention values that were lower than expected, given the observed density of adult *L. hesperus*.

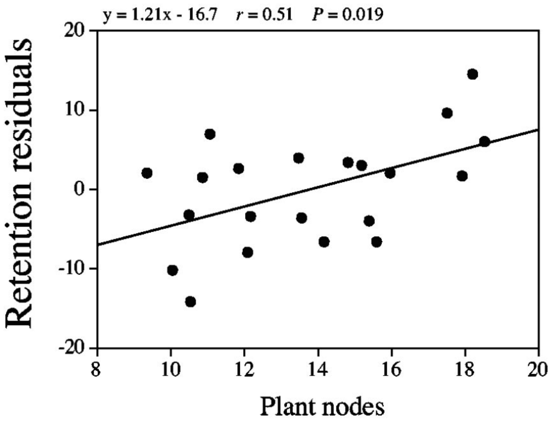

Fig. 3. Relationship between plant ontogeny (mean node number) and the residual variance in square retention. Residuals were obtained from a linear regression of square retention on the density of adult *L. hesperus*, petiole phosphate content, and the interaction of adult density × phosphate content. Cotton fields whose plants had more mainstem nodes exhibited square retention values that were higher than expected, given the observed density of adult *L. hesperus* and petiole phosphate levels.

0.0031; Fig. 2) and weaker suggestions for Cl^- ($F_{1,18}$ = 6.0, $P = 0.025$) and Na^+ ($F_{1,18}$ = 3.6, $P = 0.074$); plants with higher petiole phosphate concentrations seem to shed more squares. The significant effect for phosphate is still observed ($F_{1,17}$ = 11.1, $P = 0.0040$) even if "day of the year" is forced into the multiple regression first, showing that the result is not simply a reflection of underlying seasonal trends in square retention and phosphate levels. Finally, a multiple regression suggested that square retention was influenced by both main effects of *L. hesperus* adult density ($F_{1,17}$ = 29.8, $P < 0.0001$) and phosphate content ($F_{1,17}$ = 18.8, $P = 0.0005$) and by their interaction ($F_{1,17}$ = 7.5, $P = 0.014$), suggesting that phosphate is a candidate for a factor sensitizing plants to *L. hesperus* feeding damage.

Plant-Based Factors: Plant Ontogeny. There was an obvious shift during our survey in the types of fields identified for our sampling by cooperating pest control advisors. All four of the fields exhibiting more abscission than expected involved relatively young plants (mean node number range: 10.5–12.2), whereas the fields exhibiting normal levels of abscission and fields exhibiting less abscission than expected involved cotton plants at a broader range of growth stages (ranges: 9.4–17.9 and 10.9–18.6 nodes, respectively). Does plant sensitivity to *L. hesperus* feeding vary with plant development? We observed a significant effect for node number ($F_{1,19}$ = 6.6, $P = 0.019$; Fig. 3) in explaining residual variation in square retention after performing a multiple regression with the previously identified effects for adult *L. hesperus* density, phosphate content, and the *L. hesperus* x phosphate interaction. Younger plants had lower levels of square retention than did older plants. The interaction of node number × adult *L. hesperus* density was, however, not significant ($F_{1,15}$ = 2.1, $P = 0.17$).

Plant-Based Factors: Cultivar. We found no evidence to suggest that the different commercial cultivars of cotton that we sampled (Phytogen 72, $n = 9$; Sierra RR, $n = 5$; Riata RR, $n = 2$; OA 265, $n = 2$; others, $n = 3$) varied in their sensitivity to *L. hesperus* feeding. Cultivar did not explain a significant amount of the residual variance in square retention after removing the effect of *L. hesperus* adult density ($F_{4,16}$ = 0.5, $P = 0.71$). Similarly, the effect of cultivar was not significant ($P = 0.81$) in a multiple regression model including all previously identified significant influences on retention (data not shown). Given the small sample sizes, however, firm conclusions would be premature.

Full Statistical Model for Factors Influencing Square Retention. We performed a multifactor ANCOVA to examine how the influence of *Lygus* density on square shed is modulated by the other significant field- or plant-based variables identified above (Table 3). In the initial model, we withheld the anther damage variable, although even when it was included, it did not approach significance ($F_{1,\,12}$ = 0.3, $P = 0.61$). This analysis needs to be interpreted cautiously, because we are incorporating four main effects (*L. hesperus* adult density, phosphate content, node number, and field category) and two interactions to explain variance in a very small data set ($N = 21$). After accounting for variance explained by significant contributions for *L. hesperus* density, phosphate, and the *L. hesperus* density × phosphate interaction, and additional marginally significant contributions made by node number and node number × *L. hesperus* density interaction, there is still a significant effect for the field category variable. Thus, none of these factors completely accounts for the unexpected levels in square retention observed in some fields. However, the model explains a large proportion of the total observed

Table 3. Full ANCOVA model examining the influences of field category, *L. hesperus* adult density, plant growth stage (node no.), and petiole phosphate content on square retention levels

Source	df	Sum of squares	*F* ratio	*P*
Lygus adult density	1	0.1780	67.3	<0.0001
Phosphate	1	0.0256	9.7	0.0082
Field category	2	0.0254	4.8	0.028
Node no.	1	0.0099	3.7	0.076
Lygus adult density × phosphate	1	0.0309	11.7	0.0046
Lygus adult density × node no.	1	0.0115	4.3	0.058

Total model: $R^2 = 0.89$, $F_{7,13} = 14.9$, $P < 0.0001$.

variance in square retention ($R^2 = 0.89$), and if we remove the field category variable, we still have $R^2 = 0.81$. Thus, if future experimentation confirms the hypothesized roles of phosphate and plant ontogeny in modulating the impact of *L. hesperus* on square retention, the remaining unexplained variation in square abscission may be relegated to a very modest role (8% of the total variance in abscission values). Finally, none of the other plant-based factors measured in this study (any of the macro- or micronutrients; plant height:node ratios; plant density) or season effects (day of the year) came close to making a significant contribution toward explaining the residual variance from the model reported in Table 3 ($P > 0.15$ in all cases).

In theory, the significant variables identified in Table 3 might influence (1) how a given number of *Lygus* interact with the cotton plant to produce anther damage or (2) whether or not a given amount of anther damage elicits an abscission response from the plant. To explore these two transitions (*Lygus* to damage; damage to square shed), we conducted two stepwise multiple regressions. In the first, we examined variables correlated with the observed amount of anther damage (Table 4). This analysis identified a significant role for only adult *L. hesperus* density, and no effect of field category, node number, or phosphate. In the second, we examined variables correlated with square shed, including anther sac damage as an independent variable and withholding the *L. hesperus* density variable (Table 4). This analysis identified significant effects for the amount of anther sac damage and for phosphate, but no effects for node number or field category. If we force field category into the multiple regression at step 1 ($P = 0.067$), anther damage is added at step 2 ($P = 0.028$), phosphate content is added at step 3 ($P = 0.071$), and finally at step 4, the field category variable is deleted from the model, because it no longer makes a significant contribution ($P = 0.53$). Thus, the phosphate variable emerges in this analysis as a candidate explanation for fields exhibiting higher or lower than expected levels of square abscission (in contrast to the results reported in Table 3, where the field category variable was still significant even after phosphate was included). Phosphate concentration seems to be modulating the sensitivity of plants to damage.

Our experiences with trying to locate fields with higher or lower than expected levels of square abscission led us to suggest that such fields occur only infrequently. During several weeks of our study, we called many pest control advisors (often >30) who collectively manage hundreds of cotton fields, and could find no one who said that they had a cotton field exhibiting higher than expected square shed; no such fields were identified after the fourth week of our 8-wk survey. If ongoing experimental work confirms a role for petiole phosphate, we will be ready to conclude that most, if not all, of the previously unexplained variation in square abscission can be understood.

Hidden Factors. During our field surveys, we attempted to sample a broad array of herbivores and omnivores to see if any candidates emerged that might be responsible for a previously unrecognized impact on square retention. None of the other insects known to generate square damage, such as the cotton flea-

Table 4. Stepwise multiple regression of variables influencing anther sac damage and proportion of squares retained

Step no.	Variable entered	Variables not entered	Estimate	df	Sum of squares	*F* ratio	*P*
Anther sac damage							
1	*Lygus* adult density		0.0093	1	0.0156	13.4	0.0017
		Node no.		1	0.0000	0.00	0.99
		Phosphate		1	0.0001	0.06	0.81
		Field category (−1/0 vs 1)		1	0.0005	0.43	0.52
		Field category (−1 vs 0)		2	0.0016	0.68	0.52
Square retention							
1	Anther damage		−1.67	1	0.1006	11.0	0.0038
2	Phosphate		−0.00018	1	0.0749	8.2	0.0104
		Node no.		1	0.0160	1.83	0.19
		Field category (−1 vs 0/1)		1	0.0039	0.41	0.53
		Field category (0 vs 1)		1	0.0043	0.21	0.81
		Anther damage × phosphate		1	0.0091	1.00	0.33

Field category: −1, less retention than expected; 0, retention as expected; 1, more retention than expected.

hopper or stink bugs, were found in the surveyed fields. The dominant foliar herbivores were all present at exceptionally low mean densities; mean numbers per leaf across all 21 fields were 0.46 ± 0.20 for aphids and 0.82 ± 0.19 for thrips, and mite colonies occupied only 0.04 ± 0.04% of the undersurface of leaves. One omnivore, *Geocoris* spp., was common (mean count per sweep sample: 14.6 ± 1.6), especially in fields exhibiting higher than expected square abscission (20.0 ± 3.2 per sweep sample, more than five times as abundant as *L. hesperus* [3.7 ± 0.9/sweep sample] in the same fields). The density of *Geocoris* spp. was, however, not a significant predictor of variation in square retention when added to the model shown in Table 3 ($F_{1,12} = 1.4$, $P = 0.26$). Nevertheless, because *Geocoris* spp. are known to be omnivores, we felt that it would be prudent to assess the possibility that *Geocoris* spp. were generating anther damage and abscission.

Impact of *Geocoris* on Square Retention. We saw no aphids or spider mites at either the set-up or scoring of the experiment; thrips were present, with an average of 4.50 ± 0.65 thrips removed from each caged plant at set-up and 11.5 ± 1.1 total thrips on the mainstem leaves of each plant at scoring. At the close of the experiment, control treatment cages harbored no *G. pallens* adults, whereas the treatment cages to which *G. pallens* was added harbored an average of 0.56 ± 0.15 live adult female *G. pallens* ($F_{1,34} = 14.7$, $P = 0.0005$). There was, however, no significant effect of the *G. pallens* treatment on plant height (control, 31.6 ± 0.7 cm; +*G. pallens,* 31.9 ± 0.4; $F_{1,33} = 0.15$, $P = 0.70$), number of mainstem nodes (control, 11.2 ± 0.2 cm; +*G. pallens,* 11.3 ± 0.1; $F_{1,34} = 0.21$, $P = 0.65$), percent anther sac damage (control, 0.28 ± 0.22; +*G. pallens,* 1.47 ± 0.87; $F_{1,33} = 1.66$, $P = 0.21$), or percent square retention (control, 89.3 ± 3.2; +*G. pallens,* 88.3 ± 2.4; $F_{1,34} = 0.07$, $P = 0.79$). We found insects known to feed on cotton squares in two of our cages at the end of the experiment (one nymphal *L. hesperus* and one nymphal cotton fleahopper, *P. seriatus*). If we exclude these replicates from the analysis, the very small increase in damage to anther sacs observed in the +*G. pallens* treatment becomes just significant (one-tailed Kruskal-Wallis rank sum test, $\chi^2 = 2.7$, $P = 0.05$; Fig. 4A), but there continues to be no significant difference between treatments in square retention ($F_{1,32} = 0.64$, $P = 0.43$; Fig. 4B). Thus, we conclude that, although *G. pallens* may generate a little feeding damage to developing anther sacs under conditions of very low prey availability, the damage does not produce a detectable increase in square shed.

Geocoris pallens is a key biological control agent of *L. hesperus* (Leigh and Gonzales 1976; A.G.Z. unpublished data). Thus, any minor anther damage that it might generate is likely to be more than offset by its direct suppression of *L. hesperus.* Our findings parallel the experimental results reported for two other abundant omnivores in cotton, *Orius insidiosus* (Say) studied in Arizona (Mauney and Henneberry 1979) and *Nabis kinsbergii* studied in Australia (Wade 2004), which also have been shown not to elevate levels of square abscission.

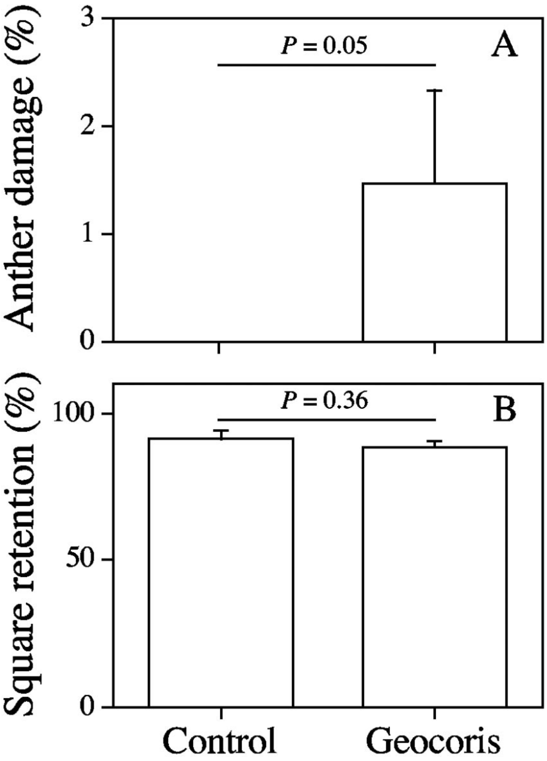

Fig. 4. Influence of *G. pallens* feeding on (A) mean percent of developing anther sacs within all first-position squares that are killed and (B) mean percent retention of squares at the first positions of all fruiting branches. Shown are means ± SE.

Variable Plant Behavior. Our analyses suggest that variable plant responses to herbivory may be the key cause of unexplained variation in square abscission. The role of phosphate was completely unanticipated. There is no suggestion of a role for phosphate in the literature on *Lygus*–cotton interactions or in the broader literature on the physiological ecology of abscission. Cotton growers do not add phosphorus as part of their standard fertilization program, and the between-field variation in petiole phosphate that we observed probably is a reflection of the variable crop rotation history of the field: cotton planted after vegetable crops that receive phosphorus fertilization is likely to exhibit higher petiole phosphate levels (R. Hutmacher, personal communication). This suggestion highlights the possibility that petiole phosphate levels could be correlated with any other aspect of the crop's biotic or abiotic environment that is influenced by the field's history of crop rotation. Our ongoing work is examining the possibilities that phosphorus has a direct, causal effect on cotton sensitivity as well as the possibility that it is simply a correlate of some other causal factor linked to crop rotation.

The role for mainstem node number was less surprising; we list here three complementary explanations for this result. First, square size (i.e., developmental stage) influences the probability of square abscission after damage. Squares develop over the course of ≈20–30 d to reach a final length of ≈40 mm (Mauney 1986). For plants that still have a favorable supply to demand ratio for photosynthate, small squares (≤5 mm long) that are mechanically damaged (a fixed number of insertions of a fine pin) are often shed, but larger squares (≥8 mm) are rarely shed (Strong 1970; A.G.Z., unpublished data). As plants grow, the size distribution of squares that they support must also change: plants in the earliest stages of reproductive growth (i.e., 6–8 mainstem nodes) will support almost exclusively the highly vulnerable, small squares, whereas plants nearing the end of the active period of fruit set (i.e., ≥18 nodes) will have some small, highly vulnerable squares but also many larger, less vulnerable squares. Thus, as plants mature, they support an increasing fraction of larger squares that are less sensitive to *Lygus* feeding damage. It is possible that this factor provides the primary, or even the full, explanation for the node number effect identified by our analyses.

Second, it is possible that plant sensitivity to *Lygus* feeding damage does not really decline as plants develop, but rather that the appearance of such a relationship is simply a spurious outcome of the influence of plant size on sweep net efficiency. Reanalysis of data collected during an earlier study suggests that sampling efficiency changes as plants grow, but the effect is the opposite of what would be needed to explain the decreased sensitivity of older plants to *L. hesperus.* Sweep nets captured a smaller fraction of the total *L. hesperus* population on larger cotton plants ($r = -0.65$, df $= 8$, $P = 0.04$; data from Zink and Rosenheim 2004).

Finally, it is possible that the plant changes its fundamental propensity to abort a damaged square as it develops through the seasonal window of fruit set. The pattern we observed here, higher retention in larger plants (Fig. 3), is the opposite of the general expectation that square retention declines seasonally as the plants accrue a heavier fruit load and the demand for photosynthates by developing fruits begins to outstrip the plant's photosynthate production (University of California 1996). It is perhaps possible that younger plants are more likely to abort damaged squares, because they still have ample time within the growing season to compensate for a lost square through adjustments in growth form or through compensatory increases in later square retention (Sadras 1998, Holman and Oosterhuis 1999, Stewart et al. 2001, Lei and Gaff 2003, Wilson et al. 2003).

Summary. The goal of our study was to evaluate longstanding claims from cotton growers that *L. hesperus* was imposing levels of square shed on cotton that could not be predicted from estimates of *L. hesperus* density. Our key results are as follows. First, we confirmed that cotton growers were correct in identifying a class of fields that exhibited abnormally high levels of square abscission, given the density of *L. hesperus* observed in the field (Fig. 1A). Thus, unexpected variation in square abscission seems to be real and is not solely an artifact of sampling problems. Fields with unexpectedly high levels of square abscission did not, however, have unexpectedly high levels of anther damage, suggesting that the unexpectedly high square abscission was not generated by variation in *L. hesperus* feeding behavior or by pulses of *L. hesperus* adults moving rapidly through fields, but rather by variation in the way the plant responds to that feeding damage. Second, the commercial pest control advisors who participated in our survey grossly underestimated the densities of *L. hesperus* nymphs relative to the adult stages. Thus, when abundant, nymphs might produce unexpectedly high levels of damage and square shed. Third, we were able to identify two novel correlates of square abscission: petiole phosphate concentration and plant growth stage (number of mainstem nodes); both were significant as main effects and in interactions with *L. hesperus* density, suggesting that they may reflect factors that sensitize cotton plants to *L. hesperus* herbivory (Table 3). We were only partially successful in determining whether these factors operated primarily by influencing the amount of damage *L. hesperus* generated (the *Lygus* to damage transition) or the way in which the cotton plant responded to that damage with abscission (the damage to abscission transition). Whereas *L. hesperus* adult density seemed to operate during the first transition (*Lygus* to damage), phosphate was identified as a correlate of the second transition (damage to abscission), and in doing so seemed to substitute for the effect of field type. How plant growth stage (node number) influences the impact of *L. hesperus* on square abscission was not resolved. Finally, the only viable candidate for a hidden factor, feeding by the omnivore *G. pallens*, was shown experimentally to be capable of only very minor amounts of anther damage, which produced no detectable elevation of square abscission. The work has, therefore, largely redirected our attention away from the herbivores and toward the plant and produced novel, testable hypotheses for factors that might modulate the sensitivity of cotton to *L. hesperus* herbivory.

Acknowledgments

We thank the pest control advisors who provided essential collaboration with us in the survey: G. Banuelos, J. Britton, L. Gallegos, U. Hernandez, G. Hiett, J. Ledford, B. Malm, and B. Vandenburg. We also thank P. Goodell, B. Hutmacher, the University of California Farm Advisors B. Marsh, D. Munk, B. Roberts, and R. Vargas, and S. Wright for helping to establish the key connections to the cotton PCA community and make the survey possible. We thank D. Smith and K. Spence for help in the field. This work was supported by the California State Support Board of Cotton Incorporated and the University of California Statewide Integrated Pest Management Project.

References Cited

Addicott, F. T. 1982. Abscission. University of California Press, Berkeley, CA.

Agrawal, A. A., and C. N. Klein. 2000. What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores. J. Anim. Ecol. 69: 525–535.

Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999. Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. Ecology 80: 518–523.

Agusti, N., and A. C. Cohen. 2000. *Lygus hesperus* and *Lygus lineolaris* (Hemiptera: Miridae), phytophages, zoophages, or omnivores: evidence of feeding adaptations suggested by the salivary and midgut digestive enzymes. J. Entomol. Sci. 35: 176–186.

Bancroft, J. S. 2005. Dispersal and abundance of *Lygus hesperus* in field crops. Environ. Entomol. 34: 1517–1523.

Byerly, K. F., A. P. Gutierrez, R. E. Jones, and R. F. Luck. 1978. A comparison of sampling methods for some arthropod populations in cotton. Hilgardia 46: 257–282.

Carrière, Y., P. C. Ellsworth, P. Dutilleul, C. Ellers-Kirk, V. Barkley, and L. Antilla. 2006. A GIS-based approach for areawide pest management: the scales of *Lygus hesperus* movements to cotton from alfalfa, weeds, and cotton. Entomol. Exp. Appl. 118: 203–210.

Coll, M. 1998. Living and feeding on plants in predatory Heteroptera, pp. 89–129. *In* M. Coll and J. R. Ruberson (eds.), Predatory Heteroptera: their ecology and use in biological control. Entomological Society of America, Lanham, MD.

Ehler, L. E. 2004. An evaluation of some natural enemies of *Spodoptera exigua* on sugarbeet in northern California. Biocontrol 49: 121–135.

Ellsworth, P. C. 2000. *Lygus* control decision aids for Arizona cotton, pp. 269–280. *In* J. C. Silvertooth (ed.), Cotton, a college of agriculture report. University of Arizona, College of Agriculture, Tucson, AZ.

Ellsworth, P. C., and V. Barkley. 2001. Cost-effective Lygus management in Arizona cotton, pp. 299–307. *In* J. C. Silvertooth (ed.), Cotton, a college of agriculture report. University of Arizona, College of Agriculture, Tucson, AZ.

Ellsworth, P. C., and V. Barkley. 2003. Making late season decisions to terminate insecticide use against Lygus, pp. 204–217. *In* J. C. Silvertooth (ed.), Cotton, a college of agriculture report. University of Arizona, College of Agriculture, Tucson, AZ.

Eveleens, K. G., R. van den Bosch, and L. E. Ehler. 1973. Secondary outbreak induction of beet armyworm by experimental insecticide applications in cotton in California. Environ. Entomol. 2: 497–503.

Falcon, L. A., R. van den Bosch, C. A. Ferris, L. K. Stromberg, L. K. Etzel, R. E. Stinner, and T. F. Leigh. 1968. A comparison of season-long cotton-pest-control programs in California during 1966. J. Econ. Entomol. 61: 633–642.

Falcon, L. A., R. van den Bosch, J. Gallagher, and A. Davidson. 1971. Investigation of the pest status of *Lygus hesperus* in cotton in central California. J. Econ. Entomol. 64: 56–61.

Gutierrez, A. P., T. F. Leigh, Y. Wang, and R. D. Cave. 1977. An analysis of cotton production in California: *Lygus hesperus* (Heteroptera: Miridae) injury—an evaluation. Can. Entomol. 109: 1375–1386.

Hagler, J. R., C. G. Jackson, R. Isaacs, and S. A. Machtley. 2004. Foraging behavior and prey interactions by a guild of predators on various lifestages of *Bemisia tabaci.* J. Insect Sci. 4: 1.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.

Holman, E. M., and D. M. Oosterhuis. 1999. Cotton photosynthesis and carbon partitioning in response to floral bud loss due to insect damage. Crop Sci. 39: 1347–1351.

Kerby, T. A., and D. R. Buxton. 1981. Competition between adjacent fruiting forms in cotton *Gossypium hirsutum.* Agron. J. 73: 867–871.

Kerby, T. A., and K. D. Hake. 1996. Monitoring cotton's growth, pp. 335–355. *In* S. J. Hake, T. A. Kerby, and K. D. Hake (eds.), Cotton production manual. University of California, Oakland, CA.

Lei, T. T., and N. Gaff. 2003. Recovery from terminal and fruit damage by dry season cotton crops in tropical Australia. J. Econ. Entomol. 96: 730–736.

Leigh, T. F., and D. Gonzales. 1976. Field cage evaluation of predators for control of *Lygus hesperus* Knight on cotton. Environ. Entomol. 5: 948–952.

Leigh, T. F., and P. B. Goodell. 1996. Insect management, pp. 260–293. *In* S. J. Hake, T. A. Kerby, and K. D. Hake (eds.), Cotton production manual. University of California, Oakland, CA.

Leigh T. F., H. Black, C. E. Jackson, and V. E. Burton. 1966. Insecticides and beneficial insects in cotton fields. Calif. Agric. 20: 4–6.

Leigh, T. F., T. A. Kerby, and P. F. Wynholds. 1988. Cotton square damage by the plant bug, *Lygus hesperus* (Hemiptera: Heteroptera: Miridae), and abscission rates. J. Econ. Entomol. 81: 1328–1337.

Limburg, D. D., and J. A. Rosenheim. 2001. Extrafloral nectar consumption and its influence on the survival and development of an omnivorous predator, larval *Chrysoperla carnea.* Environ. Entomol. 30: 595–604.

Mauney, J. R. 1986. Vegetative growth and development of fruiting sites, pp. 11–28. *In* J. R. Mauney and J. McD. Stewart (eds.), Cotton physiology. The Cotton Foundation, Memphis, TN.

Mauney, J. R., and T. J. Henneberry. 1979. Identification of damage symptoms and patterns of feeding of plant bugs in cotton. J. Econ. Entomol. 72: 496–501.

Mauney, J. R., and T. J. Henneberry. 1984. Causes of square abscission in cotton in Arizona. Crop Sci. 24: 1027–1030.

McGregor, R. R., D. R. Gillespie, C. G. Park, D.M.J. Quiring, and M.R.J. Foisy. 2000. Leaves or fruit? The potential for damage to tomato fruits by the omnivorous predator, *Dicyphus hesperus* Knight (Heteroptera: Miridae). Entomol. Exp. Appl. 95: 325–328.

Naranjo, S. E., and J. R. Hagler. 1998. Characterizing and estimating the effect of Heteropteran predation, pp. 171–197. *In* M. Coll and J. R. Ruberson (eds.), Predatory Heteroptera: their ecology and use in biological control. Entomological Society of America, Lanham, MD.

Orr, A., B. Mwale, and D. Saiti. 2001. What is an integrated pest management 'strategy'? Explorations in southern Malawi. Expl. Agric. 37: 473–494.

Patterson, S. E., and A. B. Bleecker. 2004. Ethylene-dependent and –independent processes associated with floral organ abscission in Arabidopsis. Plant Phys. 134: 194–203.

Ridgway, R. L., and S. L. Jones. 1968. Plant feeding by *Geocoris pallens* and *Nabis americoferus.* Ann. Entomol. Soc. Am. 61: 232–233.

Rosenheim, J. A., R. E. Goeriz, and E. F. Thacher. 2004. Omnivore or herbivore? Field observations of foraging by *Lygus hesperus.* Environ. Entomol. 33: 1362–1370.

Sadras, V. O. 1998. Herbivory tolerance of cotton expressing insecticidal proteins from *Bacillus thuringiensis:* responses to damage caused by *Helicoverpa* spp. and to manual bud removal. Field Crops Res. 56: 287–299.

Scott, D. R., and L. E. O'Keeffe (eds.). 1976. Lygus bug:host plant interactions. Proceedings of workshop at the XV

International Congress of Entomology, 19–28 August 1976, Washington, DC.

Sevacherian, V., and V. M. Stern. 1972a. Spatial distribution patterns of *Lygus* bugs in California cotton fields. Environ. Entomol. 1: 695–704.

Sevacherian, V., and V. M. Stern. 1972b. Sequential sampling plans for *Lygus* bugs in California cotton fields. Environ. Entomol. 1: 704–710.

Shea, K., H. P. Possingham, W. W. Murdoch, and R. Roush. 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning. Ecol. Appl. 12: 927–936.

Stewart, S. D., M. B. Layton, M. R. Williams, D. Ingram, and W. Maily. 2001. Response of cotton to prebloom square loss. J. Econ. Entomol. 94: 388–396.

Stoltz, R. L., and V. M. Stern. 1978. Cotton arthropod food chain disruptions by pesticides in the San-Joaquin Valley, California, USA. Environ. Entomol. 7: 703–707.

Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. Annu. Rev. Ecol. Syst. 31: 565–595.

Strong, F. E. 1970. Physiology of injury caused by *Lygus hesperus.* J. Econ. Entomol. 63: 808–814.

Strong, F. E., and C. Kruitwagen. 1968. Polygalacturonase in the salivary aparatus of *Lygus hesperus* (Hemiptera). J. Insect Physiol. 14: 1113–1119.

Tillman, P. G., and B. G. Mullinix, Jr. 2003. Effect of prey species on plant feeding behavior by the big-eyed bug *Geocoris punctipes* (Say) (Heteroptera: Geocoridae), on cotton. Environ. Entomol. 32: 1399–1403.

University of California. 1996. Integrated pest management for cotton, 2nd ed. University of California, Oakland, CA.

Wade, M. R. 2004. Behavioural ecology of the Pacific damsel bug, *Nabis kinbergii* Reuter (Hemiptera: Nabidae), in cotton farming systems: towards real IPM. PhD dissertation, University of Queensland, Queensland, Australia.

Wheeler, A. G., Jr. 1976. Lygus bugs as facultative predators. Proceedings of workshop at the XV International Congress of Entomology, 19–28 August 1976, Washington, DC.

Wheeler, A. G., Jr. 2001. Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists. Cornell University Press, Ithaca, NY.

Wilson, L. J., V. O. Sadras, S. C. Heimoana, and D. Gibb. 2003. How to succeed by doing nothing: cotton compensation after simulated early season pest damage. Crop Sci. 43: 2125–2134.

Zeng, F., and A. C. Cohen. 2001. Induction of elastase in zoophytophagous heteropteran, Lygus hesperus (Hemiptera: Miridae). Ann. Entomol. Soc. Am. 94: 146–151.

Zink, A. G., and J. A. Rosenheim. 2004. State-dependent sampling bias in insects: implications for monitoring western tarnished plant bugs. Entomol. Exp. Appl. 113: 117–123.

Zink, A. G., and J. A. Rosenheim. 2005. State-dependent feeding behavior by western tarnished plant bugs influences flower bud abscission in cotton. Entomol. Exp. Appl. 117: 235–242.

Received for publication 3 February 2005; accepted 15 June 2006.