Plant compensation, natural biological control, and herbivory by *Aphis gossypii* on pre-reproductive cotton: the anatomy of a non-pest

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Abstract

Crop plant compensation for herbivory and the population dynamics of herbivores are two key elements in defining an herbivore's pest status. We studied the dynamics of natural, unmanipulated populations of the aphid *Aphis gossypii* on seedling plantings of cotton, *Gossypium hirsutum* and *Gossypium barbadense*, over a 4-year period in California's Central Valley. Aphid populations colonized all plantings, but reached densities in excess of 0.5 aphids/leaf during only one year (1991), when outbreaks occurred. Outbreak populations were, however, ephemeral; predation and parasitism suppressed aphid populations prior to the initiation of flower bud production, when cotton plant growth may become photosynthate-limited. Effective natural biological control was observed despite the action of hyperparasitoids and the heavy mortality of immature parasitoids that occurred when predators consumed parasitized aphids.

We conducted manipulative experiments during 1991 and 1992 to quantify the ability of pre-reproductive *G. hirsutum* to compensate for aphid herbivory. In 1991 aphid populations in the high-damage treatment reached densities as high as any observed naturally during the past 37 years. Damage symptoms were severe: leaf area was reduced by up to 58% and total above-ground plant biomass was reduced by 45%. By the time of crop harvest, however, plants had compensated fully for the early damage in each of the three traits that define cotton's economic value: the timing of crop maturation, the yield of cotton fiber, and the quality of cotton fiber. Aphid feeding damage did, however, produce some changes in plant architecture that persisted throughout the growing season, including a decrease in the number of vegetative branches. In 1992 aphid populations and associated damage were much lighter, but the qualitative responses to herbivory were consistent with those observed in 1991. Plant compensation for early damage was complete for economically significant measures, and vegetative branch production was again suppressed in mature cotton plants. There was no evidence for a change in the suitability of *G. hirsutum* as a host plant for *A. gossypii* as a result of early damage ('induced resistance').

We conclude that pre-reproductive *G. hirsutum*, which has not yet begun strong allocations to reproductive structures or established architectural complexity, has retained effective means of compensating for herbivory. In contrast to other systems exhibiting strong compensation, *G. hirsutum* appears to compensate in part by enhancing apical dominance. The recognition of early-season *A. gossypii* as non-pests is critical to the sustainability of cotton production, because it will allow growers to forego pesticide applications that accelerate the evolution of pesticide-resistance and disrupt natural communities of predators and parasitoids.

Introduction

Plant responses to herbivory are fundamental to developing economic injury levels, which are a basic tenet of modern integrated pest management programs (Pedigo, 1989). Factors that suppress herbivore populations are also critical in defining the ability of herbivores to decrease crop yield, because suppressive factors may maintain herbivore damage below levels at which plant compensatory responses become ineffective.

The relative ability of plants to demonstrate partial, complete, or over-compensation for vertebrate or invertebrate herbivory is controversial (Belsky, 1986, 1987; Crawley, 1989; Maschinski & Whitham, 1989; Whitham et al., 1991; Belsky et al., 1993; Dyer et al., 1993; Rosenthal & Kotanen, 1994; Mathews, 1994; Paige, 1994; Aarssen, 1995). However, even advocates of the position that plants often compensate fully or overcompensate for herbivory support a 'biphasic response', in which increasingly severe herbivory eventually results in decreased plant growth or reproduction (Dyer et al., 1993; Lowenberg, 1994). There is also a broad consensus that plant compensation is influenced by environmental conditions, and in particular that plant compensation is likely to be enhanced by high availability of nutrients, water, and light and low levels of interspecific competition (Belsky, 1986; Whitham et al., 1991; Maschinski & Whitham, 1989; Belsky et al., 1993; Trumble et al., 1993; Aarssen, 1995). These are exactly the conditions that characterize many agroecosystems, leading to the suggestion that agricultural crops should demonstrate strong compensatory abilities (Belsky, 1986; Heinz & Parrella, 1992; Belsky et al., 1993; Aarssen, 1995). On the other hand, it has also been hypothesized that crop plants, as a result of agronomic selection for increased allocations to reproductive structures (e.g., Meredith & Wells, 1989) and decreased plasticity of growth form, have forfeited some of their ability to compensate for arthropod herbivory (Welter & Steggall, 1993; Rosenthal & Welter, 1995). In light of these divergent predictions, it is imperative that the ability of crop plants to compensate for damage be assessed experimentally to design management programs.

In this study, we document the population dynamics of early-season aphid populations, including the influence of natural populations of predators and parasitoids, to assess the likelihood that aphid populations colonizing pre-reproductive cotton will persist into reproductive stages of plant growth, which may be particularly sensitive to herbivory (Wilson, 1986; Brook et al., 1992c; Matthews, 1994). We then attempt to quantify the ability of pre-reproductive upland cotton, *Gossypium hirsutum* L., to compensate for herbivory by the cotton aphid, *Aphis gossypii* Glover. We conclude that highly effective natural biological control, coupled with a strong compensatory response of pre-reproductive cotton, renders early-season cotton aphids non-pests. Therefore, current control practices for this aphid on pre-reproductive cotton, based largely on prophylactic insecticide treatments, are likely to be counterproductive and should be abandoned.

Materials and methods

Population dynamics of early-season aphids. We studied the population dynamics of cotton aphids developing naturally on seedling cotton in insecticide-free but otherwise conventionally managed cotton. Study sites were as follows: 'Shafter', the University of California (UC) Shafter Research Station, Kern County; 'Kearney', the UC Kearney Agricultural Center, Fresno County; 'West Side', the UC West Side Research and Extension Center, Fresno County; and 'Davis', the UC Davis Student Experimental Farm, Yolo County. Upland cotton, *Gossypium hirsutum* L., cultivar GC510 was planted in 1991 and 1992, cultivar 'Maxxa' was planted during 1993 and 1994, and one plot of pima cotton, *Gossypium barbadense* L., cultivar S-7 was planted in 1994. Cotton seed was not treated with systemic insecticides.

Aphids were sampled approximately weekly in each study site by collecting 40–100 leaves into 70% ethanol. Cotyledons were collected until the first true leaf was present. The oldest true leaf was collected until the plants reached the 5-node stage, at which time we began collecting the mainstem leaf at the fifth node down from the terminal, where the first node is defined as one with an unfurled leaf >2.5 cm wide. Aphids and other arthropods were rinsed off the leaves manually in the laboratory over a fine sieve (78.7 mesh per cm), collected into 70% ethanol, and counted with a stereomicroscope. We counted aphids and aphid 'mummies' formed by the development of the primary parasitoids, and categorized mummies as follows: (1) 'intact', i.e., without emergence holes or signs of predation; (2) 'emerged', i.e., with a smooth, circular emergence hole left by an emerged primary parasitoid; (3) 'hyperparasitized', i.e., with a rough-edged approximately circular emergence hole left by an emerged hyperpara-

site, either *Alloxysta bakeri* (Kieffer) (Hymenoptera: Cynipidae) or *Pachyneuron siphonophorae* (Ashmead) (Hymenoptera: Pteromalidae); or (4) 'predated', i.e., with a large, irregular hole, usually on the dorsal side, indicating an attack by one of the two dominant coccinellid beetles present in cotton during the early season, *Hippodamia convergens* Guérin-Méneville and *Coccinella novemnotata franciscana* Casey. Counts of predated aphid mummies provided us with a measure of the intensity of predation on aphids; because some attacked mummies are dislodged from the plant (R. Colfer, pers. comm.), this measure is likely to underestimate the true impact of predation. Preliminary studies suggested that adult *H. convergens* do not have clear preferences for non-mummified aphids versus mummified aphids (R. Colfer, pers. comm.).

During 1991 we also collected weekly samples of up to 100 mummified aphids, with not more than five mummies collected from a single plant. Mummies were held in a paper bag in a cooler and transported to the laboratory where they were placed individually in gelatin capsules for rearing.

Plant growth was monitored approximately weekly by counting the number of mainstem nodes above the cotyledons and measuring plant height (from the cotyledons to the top node) for 10-20 plants per sample.

1991 herbivore impact experiment. We manipulated the densities of cotton aphid populations in small, replicated field plots of cotton during the seedling and early vegetative growth periods (from 27 April to 28 May), and then maintained the plots relatively aphid-free for the remainder of the field season. We monitored plant growth, the timing of crop maturation, cotton yield, and cotton fiber quality to quantify the impact of herbivory and the cotton plant's ability to compensate for early damage.

Upland cotton, *G. hirsutum* L. Acala cultivar GC-510, was grown in the field at Shafter under standard commercial practices except that no insecticides (seed or foliar treatments) were used other than as specified below. Weeds were suppressed effectively with a pre-plant application of herbicides (Treflan, Caperol) on 28 January and by mechanical cultivation and hand-hoeing during the growing season. The field was planted on 12 April in rows separated by 1.02 m, and was furrow irrigated. The field received 145.7 kg of N/ha on 3 June to maintain recommended levels of plant nutrition. Plant growth regulators were not applied.

Plots, each comprising six 3.05 m-long rows of cotton, were arranged in ten blocks of four plots each. The blocks ran perpendicular to the furrows. Plots were separated by 2 m of bare ground along the length of rows and by two bare plant rows. The outer two rows of each plot were not sampled during the experiment, and were used to minimize potential edge effects. Seedling stands were thinned on 6 May to achieve a relatively uniform spacing of plants; each plot (the central four rows only) had a total of 101–120 seedlings after thinning.

We initially planned to apply four different treatments, each associated with a different density of aphids (control, low, medium, and high); however aphid populations crashed before the low and medium treatments were differentiated. Thus, the final treatments were: control, with as few aphids as possible; medium-1; medium-2; and high, with as many aphids as possible. To suppress aphids in the control plots, a selective aphicide (pirimicarb; 0.60 g Pirimor 50W/liter water) was applied until runoff to the undersides of leaves with a Hudson sprayer on 6, 13, and 20 May. The first two of these applications killed essentially all resident aphids; however, the third application was largely ineffective. To increase aphid densities in the high density plots, we augmented natural aphid densities in two ways. First, cotton aphids from a laboratory colony were outplanted in the high density plots on 27 April; although exact counts of aphids released per plant were not made, we were able to approximately double the number of aphids on the seedlings. Second, all predators (primarily coccinellid beetle eggs, larvae, and adults, and syrphid fly eggs and larvae) were manually removed from all plants in the high-density plots on 13 and 20 May. Because natural predator densities in the field were high and predators moved readily between plots, it was difficult to prevent predators from re-entering high density plots after manual removals. We therefore applied a low rate of carbaryl (5.94 ml of Sevin 27% flowable formulation per liter of water, applied at a rate of 445 ml/ha) to the entire field (all treatments). Pilot experiments conducted outside the main experimental area demonstrated that this low rate killed predators, but did not have a detectable direct effect on the aphids. We did not directly manipulate the aphid densities in the medium-1 and medium-2 treatments.

Aphid densities began to increase during late August and early September; on 10 September we therefore applied bifenthrin (2.22 ml Capture 2E per liter water applied at 210 l per hectare), which sup-

pressed aphids effectively until the cotton was chemically defoliated on 23 September. Plots were hand harvested on 4–5 October.

Aphid densities were sampled weekly beginning on 6 May, when the first true leaves appeared. From 6–28 May we sampled the oldest true leaf present on the plants; beginning 3 June (when most plants had >5 mainstem nodes) we sampled the mainstem leaf at the fifth node from the plant terminal. Ten leaves were sampled per plot and stored in a plastic bag with a small quantity of 70% ethanol to preserve the arthropods. Aphids and other arthropods were recovered from the leaves as described above. The area of the lower surface of each leaf was measured using a LICOR LI-3000 leaf area meter with a motorized belt so that aphid densities could be expressed as numbers per square centimeter of lower leaf surface.

To document plant responses to herbivory, we sampled ten plants per plot at four times during the experiment. To prevent our weekly leaf sampling from potentially altering the growth characteristics of these samples, we flagged these plants at the beginning of the season, choosing every third plant, and did not sample any leaves from them. On 27 April, before applying the experimental treatments, we sampled plants at the cotyledon stage by cutting plants at the soil level. Samples were dried in an oven at 60–65 °C to a constant weight and then weighed to measure total above-ground dry mass. On 3 June (post-treatment) plant node counts were taken and plant height measured (from the cotyledon scar to the point where the petiole of the newest mainstem leaf [width >2.5 cm] attached to the mainstem). Plants were then cut at the cotyledon scars and dried in an oven at 60–65 °C and weighed to estimate total above-ground dry mass. For the last two samples (at mid-season, 6 August, and just prior to defoliation, 19–21 September), we gathered detailed data on plant structure and biomass allocation for each of the ten plants sampled (Kerby & Hake, in press). Plant height and node number were measured as before. Every mainstem node for each plant was categorized as follows: if a fruiting branch was present, we recorded the first position of the fruiting branch as containing either a square (i.e., a flower bud), a white flower (1-day old), a young boll (beginning with 2-day old flowers and including bolls that had not grown beyond the tips of the boll bracts), a mature boll, an open boll, or an aborted position (no reproductive structure present); if no fruiting branch was present, we recorded the presence or absence of a vegetative branch. Plants were then divided into leaf, stem plus petiole,

and fruiting structures, and each part separately dried in an oven at 60–65 °C to a constant weight and then weighed. Although our plant sampling reduced plant density within the experimental plots somewhat, final plant densities were still well within the normal range used in commercial California production.

To measure the timing of crop maturation, we gathered two types of data. First, for each of the ten plants sampled and mapped on 19–21 September, we counted all open bolls and mature bolls that had not yet opened. Second, we counted the total number of bolls per plot that had not opened by 8 October (after harvest was completed).

Samples of ginned cotton lint were tested for a large number of quality-related parameters at the Texas Tech University International Center for Textile Research and Development (Lubbock, Texas, USA). This center operates a Motion Control Model 4000 HVI system equipped with a Shirley Developments Limited FMT 3 Fiber/Maturity Tester. Cotton lint samples were also tested for total reducing sugar content (potassium ferricyanide method) and stickiness (minicard test) at the USDA Cotton Quality Research Station, Clemson, South Carolina, USA (Perkins, 1993).

1992 herbivore impact experiment. The design and methodology for the 1992 experiment were as described above for the 1991 experiment with the following modifications. Cotton was planted on 3 April. Plots were separated by 3.05 m of bare ground along the length of rows. The density of plants was lower than in 1991; plant counts made at the end of the season showed an average of 62.8 ± 1.4 (SE) plants per plot (four central rows only).

We initially planned to apply four different treatments, each associated with a different density of aphids (control, low, medium, and high); however aphid populations crashed before the control and low density treatments were differentiated. Thus, the final treatments were: control (2 plots per block), with as few aphids as possible; medium; and high, with as many aphids as possible. Densities of naturally colonizing aphids were extremely low; thus, no manipulations were needed to maintain the control plots free of aphids. To increase aphid densities in the medium and high density plots, we augmented natural aphid densities in three ways. First, cotton aphids from a laboratory colony were outplanted in the medium density plots on 15 and 30 April and in the high density plots on 15 and 22 April. Second, all predators and mummified aphids were manually removed from all plants in the

high-density plots on 22 and 30 April and on 7 May. Third, we twice applied carbaryl at a low rate that had no detectable effect on aphids across the entire experimental field (all treatments) to kill predators and parasitoids that were reinvading the high density aphid plots (18 April: 0.16 kg/ha AI; 23 April: 0.11 kg/ha).

Aphid densities in all treatments crashed by 7 May. Aphid densities remained very low until late June, when populations increased and remained at low to moderate densities through July and August, decreasing to very low levels by early September. No insecticides were applied for these or any other mid- or late-season pests.

Aphid densities were sampled on 15 and 22 April by counting all aphids on a single cotyledon of each of ten plants per plot in the field. On 30 April and 7 May the oldest true leaf present on ten plants was sampled and processed in alcohol. Additional samples were made on 8 and 14 July and on 8 September by sampling the mainstem leaf at the fifth node. Leaf areas were measured for all true leaves sampled.

Whole plants were sampled at three times during the experiment to document responses to herbivory; some of these plants may have had a few leaves removed during the leaf sampling to measure aphid densities. A representative sample of plants was obtained by taking plants at regular intervals (e.g., every tenth plant) within each plot. A pre-treatment plant biomass sample (10 plants per plot) was collected on 15 April. On 13 May we sampled 20 plants per plot for the post-treatment sample. The final biomass sample for full plant mapping (10 plants per plot) was taken on 9–10 September. To estimate the timing of crop maturation, we again estimated the proportion of bolls that had opened on each of the ten plants sampled for mapping.

Statistical analysis. The herbivore impact experiments were analyzed using 2-way ANOVA, with main effects for block and treatment. Pairwise contrasts were used to compare each aphid density treatment with the control. Because we did not know *a priori* which of a large number of mid- and late-season plant traits might respond to aphid feeding on pre-reproductive cotton, we analyzed many traits. To avoid drawing erroneous conclusions from a potential proliferation of Type I error, we only interpret results that were supported by very low P values (i.e., P values that would still be significant after correcting for multiple comparisons using Bonferroni's inequality) or results that were observed at P < 0.05 in both the 1991 and 1992

experiments. To examine the functional relationship between the intensity of herbivory and plant response, we conducted regression analyses. The intensity of early-season aphid herbivory within each experimental plot was quantified using the weekly samples to calculate cumulative aphid-days (aphid numbers multiplied by the number of days present) from the time of plant emergence (1991: 21 April; 1992: 15 April) until the time when early-season aphid populations crashed (1991: 28 May; 1992: 7 May). In 1991 for the control plots only, we included aphid density estimates of zero for the days after the first two applications of pirimicarb, which were very effective. To test the hypothesis that early herbivory induced plant resistance to subsequent aphid populations, we regressed early-season cumulative aphid-days on: (i) for 1991, the cumulative aphid-days for the aphid populations that appeared during the remainder of the growing season (28 May to 19 September); and (ii) for 1992, the mean number of aphids present per fifth main stem leaf on 8 and 14 July.

Results

Population dynamics of early-season aphids. *Aphis gossypii* colonized pre-reproductive cotton during all four years of the study, but reached densities in excess of 0.5 aphids per leaf only during 1991 (Figures 1–4). Aphid populations on seedling cotton in 1991 were as high or higher than any observed during the past 37 years (T. F. Leigh & P. Wynholds, pers. comm.). Densities at the Shafter site peaked at over 60 aphids per leaf on plants at the 2-node stage and declined rapidly over the next 2 weeks (Figures 1A,B). Predation appeared to be the dominant factor responsible for the aphid population decline. Mummified aphids, mostly formed by *Lysiphlebus testaceipes* (Cresson) (Table 1), were never abundant relative to unmummified aphids, and most of the mummies were predated by coccinellid beetles prior to parasitoid emergence (Figure 1C). The hyperparasitoid *A. bakeri* was present, but was never abundant (Table 1). By May 28 aphid populations had declined below levels of detection, and all of the remaining aphid mummies had been destroyed by coccinellid beetles. Densities at the Kearney site peaked at or before the 1-node stage, and mummified aphids were common (Figure 1D,E,F). Two hyperparasitoids were common: *A. bakeri* and *P. siphonophorae* (Table 1). Once again, however, most aphid mummies were predated prior to the emergence of parasitoid or hyperparasitoid progeny (Figure 1F), suggesting a sig-
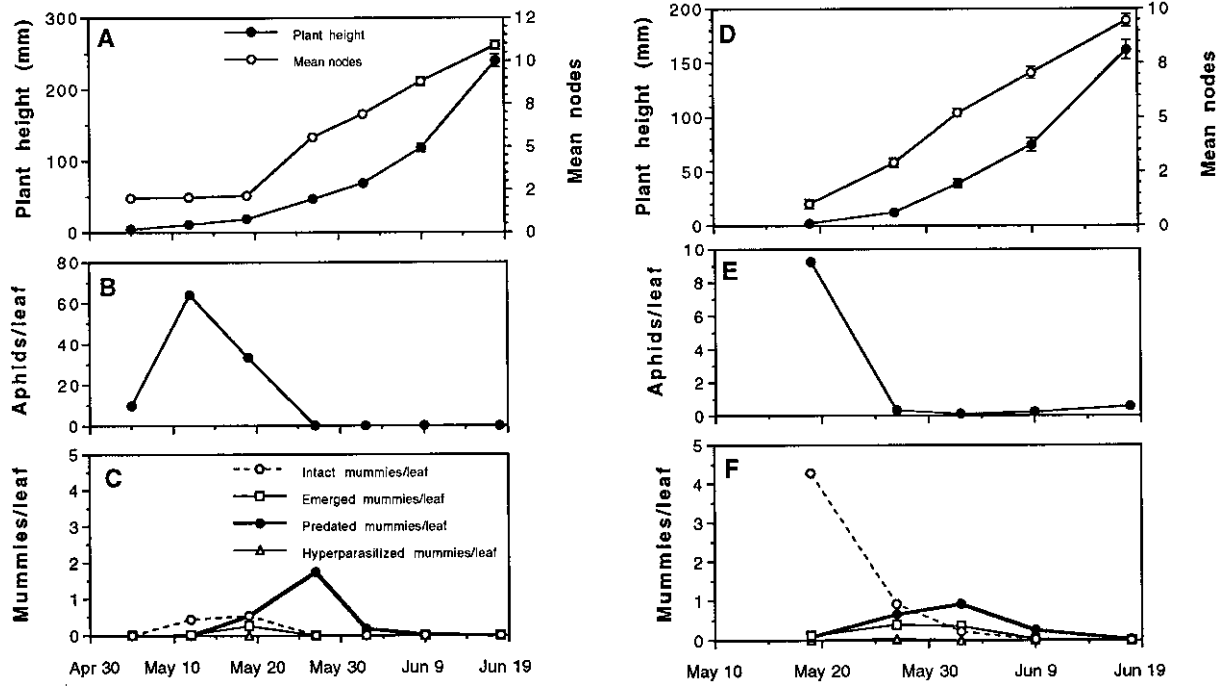
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Figure 1. Early-season aphid population dynamics 1991. Shafter site: (A) mean (±1 SE) plant height and number of mainstem nodes, (B) aphid densities, and (C) impact of parasitoids and predators. Kearney site: Idem (D)–(F).
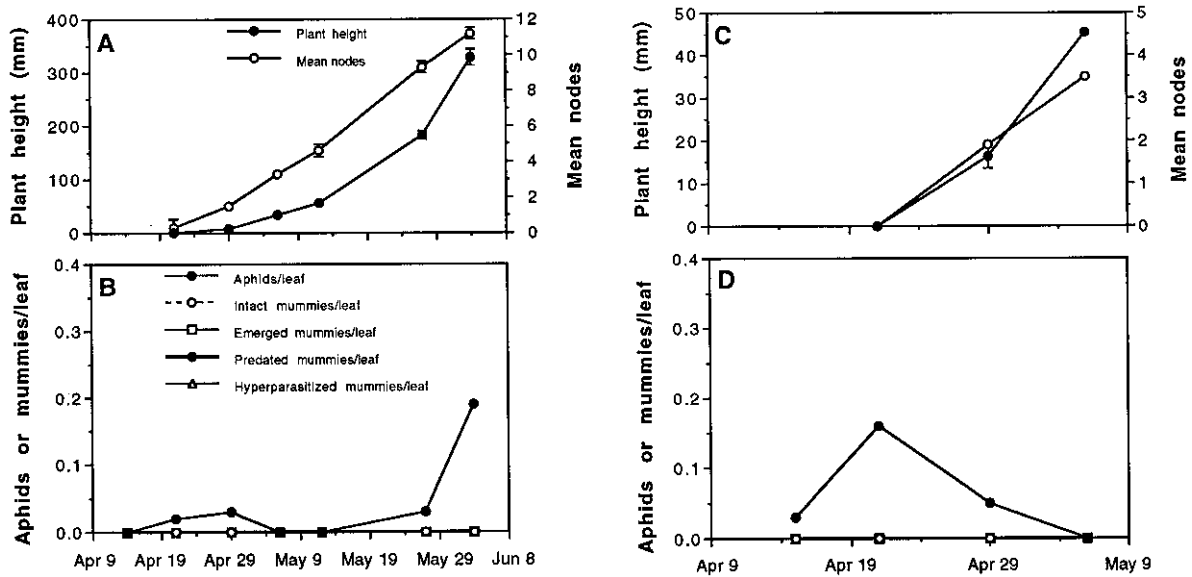

Figure 2. Early-season aphid population dynamics 1992. Shafter site: (A) mean (±1 SE) plant height and number of mainstem nodes, (B) aphid densities and impact of parasitoids and predators. West Side site: Idem (C), (D).

nificant role for predation in suppressing aphid populations. Although these correlative observations can provide only circumstantial evidence that predators suppressed aphids, the predation hypothesis is sup-

ported more definitively by manipulative experiments (Colfer & Rosenheim, 1995; see Discussion).

Aphid densities were generally too low on seedling cotton 1992–1994 to assess sources of mortality accur-

Table 1. Number of primary parasitoids and hyperparasitoids reared from mummified *A. gossypii* collected on seedling cotton in 1991

(A) Shafter

Parasitoid	6 May	13 May	20 May
Primary parasitoid species			
Lysiphlebus testaceipes (Cresson)	3	82	77
Aphidius sp.	0	4	1
Hyperparasitoid species			
Alloxysta bakeri (Kieffer)	0	10	18

(B) Kearney

Parasitoid	21 May	28 May	3 June	10 June
Primary parasitoid species				
Lysiphlebus testaceipes (Cresson)	67	4	2	0
Diaeretiella rapae (MacIntosh)	1	0	0	0
Hyperparasitoid species				
Alloxysta bakeri (Kieffer)	30	19	0	0
Pachyneuron siphonophorae (Ashmead)	0	18	10	1

ately, but the action of aphid parasitoids was detected at three sites (Figures 3F, 4B,C), and at two of these sites predator activity was indicated by aphid mummies found with holes left after predator attack.

1991 herbivore impact experiment. Cotton seedlings in the experimental plots were colonized by alate aphids within a week of emergence, and aphid densities increased rapidly over the ensuing four weeks (Figure 5). Our experimental manipulations succeeded in generating a wide range of cumulative aphid-days/cm^2 leaf across the plots (range: 47–481; mean±SE for control plots = 118 ± 19; medium-1 = 162 ± 10; medium-2 = 176 ± 26; high = 364 ± 38; Kruskal-Wallis test, d.f. = 3, $\chi^2 = 17.1$, P < 0.001). Aphid populations in the high density treatment peaked on 20 May at densities of 25.6 ± 2.4 (SE) aphids per cm^2 of leaf, or 154 ± 20 (SE) aphids per average-sized leaf. Despite our attempts to sustain these high aphid densities by excluding natural enemies with insecticides and manual removal, predators (primarily *H. convergens* and *C. novemnotata franciscana*) and parasitoids (almost exclusively *L. testaceipes*) became extremely numerous by the end of May, and between 20 May and 28 May the aphid populations crashed. We were unable to find a single living aphid anywhere in our experimental field on 28 May. Aphids were the only significant arthropod populations present on seedling cotton or at any subsequent time during the growing

season; natural control of other potential pests (including spider mites, *Tetranychus* spp., and *Lygus* spp.) was excellent.

Damage symptoms from aphid feeding on cotton seedlings were severe. Aphids caused leaves to cup, crinkle, and fail to expand normally (Figures 6 and 7), and some leaf abscission was observed. The upper surfaces of leaves became covered with honeydew and aphid exuvia, and 'shadows' of honeydew-soaked soil were evident beneath each plant. Plant growth was stunted, as measured on 3 June by either plant height or total above-ground plant dry weight (Table 2, Figure 8A). Treatments with intermediate densities of aphids showed a significantly increased number of main-stem nodes following the period of damage compared to either the control or the high density aphid treatment (Table 2), which may have been a response to abscission of damaged leaves.

Measurements of plant growth and structure taken during the growing season revealed a pattern of complete compensation for early aphid damage. Differences in mean leaf area disappeared by 9 July, approximately 6 weeks after aphid populations crashed (Figure 6B). By 6 August, the large differences in total above-ground dry plant mass had also disappeared (Table 2, Figure 8B), and allocation of biomass to leaf, stem, and fruit production did not differ across treatments. The three parameters most closely tied to the value of the cotton crop, the timing of crop maturation

Table 2. Herbivore impact experiment 1991. Influence of different intensities of herbivory on cotton growth and biomass allocation. Traits are defined on a per plant basis; each plot contributed one value representing the mean of 10 individually measured plants. Shown are means ± SE. Two-way ANOVA was conducted with main effects for block and treatment; P values are reported for the main effect for treatment. Asterisks indicate means that are signficantly different from the control; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Plant trait	Control	Medium 1	Medium 2	High	P
April 27 (pre-treatment)					
Total dry weight (g)	0.0666 ± 0.0001	0.0644 ± 0.002	0.0640 ± 0.001	0.0645 ± 0.002	0.57
June 3					
Total dry weight (g)	1.38 ± 0.10	1.13 ± 0.07*	1.10 ± 0.03**	0.76 ± 0.04***	<0.0001
Mainstem nodes	6.79 ± 0.16	7.38 ± 0.14**	7.53 ± 0.05***	6.94 ± 0.19	0.002
Height (cm)	8.59 ± 0.45	7.21 ± 0.38**	6.74 ± 0.15***	5.16 ± 0.22***	<0.0001
August 6					
Total dry weight (g)	80.3 ± 3.7	85.6 ± 5.3	89.1 ± 3.2	79.7 ± 3.7	0.28
Leaf dry weight (g)	21.2 ± 0.9	21.9 ± 1.1	22.1 ± 0.8	21.4 ± 0.9	0.89
Stem dry weight (g)	23.7 ± 1.4	23.2 ± 1.7	23.1 ± 1.2	22.0 ± 1.0	0.86
Fruit dry weight (g)	36.0 ± 1.8	40.4 ± 2.6	43.7 ± 1.2**	36.3 ± 2.1	0.018
Height (cm)	33.0 ± 0.6	32.5 ± 0.8	32.2 ± 0.6	32.1 ± 0.5	0.75
Mainstem nodes	19.51 ± 0.18	20.21 ± 0.19**	20.12 ± 0.17*	20.07 ± 0.11*	0.022
Vigor index	0.778 ± 0.017	0.723 ± 0.010**	0.721 ± 0.011**	0.722 ± 0.012**	0.008
Nodes to 1st fruiting branch	6.86 ± 0.12	6.72 ± 0.12	6.57 ± 0.13	6.68 ± 0.10	0.36
Fruiting branches	13.65 ± 0.22	14.49 ± 0.18***	14.55 ± 0.06***	14.39 ± 0.14**	0.0006
Vegetative branches	0.08 ± 0.02	0.04 ± 0.02	0.04 ± 0.02	0.04 ± 0.03	0.46
Retention top 5 fruit (%)	52.2 ± 1.0	55.6 ± 4.4	56.2 ± 2.8	61.8 ± 3.4	0.23
Retention bottom 5 fruit (%)	79.2 ± 2.1	74.4 ± 2.0	77.2 ± 1.7	74.0 ± 1.6	0.20
Squares	0.8 ± 0.1	1.0 ± 0.2	1.0 ± 0.1	1.3 ± 0.2**	0.038
September 20					
Total dry weight (g)	138.2 ± 9.7	146.3 ± 3.3	134.5 ± 5.9	139.8 ± 6.2	0.65
Leaf dry weight (g)	15.3 ± 1.3	16.3 ± 0.8	16.2 ± 1.0	14.1 ± 1.0	0.37
Stem dry weight (g)	27.7 ± 1.8	26.6 ± 1.0	24.6 ± 0.7	24.2 ± 1.1	0.12
Fruit dry weight (g)	94.8 ± 7.4	103.4 ± 2.7	93.7 ± 4.7	101.5 ± 4.7	0.47
Height (cm)	85.4 ± 1.9	83.6 ± 1.4	82.1 ± 1.3	82.3 ± 1.3	0.34
Mainstem nodes	20.30 ± 0.10	21.06 ± 0.24**	21.12 ± 0.30**	20.96 ± 0.21*	0.017
Vigor index	1.89 ± 0.05	1.75 ± 0.03*	1.72 ± 0.05**	1.73 ± 0.03**	0.017
Nodes to 1st fruiting branch	5.97 ± 0.13	6.13 ± 0.16	6.20 ± 0.18	6.30 ± 0.17	0.62
Fruiting branches	15.33 ± 0.13	15.93 ± 0.25	15.92 ± 0.31	15.66 ± 0.17	0.13
Vegetative branches	0.54 ± 0.08	0.27 ± 0.06**	0.17 ± 0.03***	0.12 ± 0.05***	0.0001
Retention top 5 fruit (%)	18.8 ± 2.3	13.0 ± 1.5*	10.4 ± 1.1**	14.4 ± 1.8	0.012
Retention bottom 5 fruit (%)	78.4 ± 1.2	76.4 ± 2.3	71.8 ± 2.6	74.6 ± 2.6	0.18
Mature bolls	12.5 ± 9.0	13.3 ± 4.4	12.0 ± 6.2	13.0 ± 5.4	0.38
Mature bolls open (%)	72.7 ± 1.7	75.8 ± 1.4	74.4 ± 1.5	72.1 ± 0.6	0.29

as measured by the proportion of all mature bolls that had opened prior to crop defoliation (Table 2, Figure 9), cotton yield (Table 3, Figure 10), and cotton fiber quality (Table 3) did not vary across treatments. Different measurements of cotton fiber maturity produced different and contradictory results (Table 3). Micronaire, the most widely used measure of fiber maturity, showed no trend across treatments. Lint fraction and gin turnout, which decrease with increasing boll maturity, suggested that aphid feeding accelerated fruit maturation. The 'fiber fineness' test suggested that early aphid feeding led to coarser, more mature fibers. Finally, the 'percent maturity' test suggested that maturity was depressed by aphid feeding. Perhaps most importantly, fiber maturity was extremely high across all of the experimental treatments.

Table 3. Herbivore impact experiment 1991. Influence of different levels of early-season aphid populations on final cotton yield and fiber quality. Shown are means ± SE. 2–way ANOVA was conducted with main effects for block and treatment; P values are reported for the main effect for treatment. Asterisks indicate means that are significantly different from the control; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Crop measure	Control	Medium 1	Medium 2	High	P
Yield					
Bolls not open 10/8	8.00 ± 0.92	7.80 ± 1.30	7.40 ± 1.36	7.20 ± 1.32	0.97
Seed cotton yield (g)	6735 ± 230	6555 ± 151	6722 ± 138	6496 ± 99	0.53
Cotton lint yield (g)	2596 ± 91	2533 ± 60	2595 ± 54	2488 ± 42	0.44
Cotton seed yield (g)	3910 ± 136	3811 ± 90	3906 ± 79	3805 ± 54	0.70
Gin loss (%)	3.43 ± 0.10	3.24 ± 0.09	3.29 ± 0.08	3.13 ± 0.05	0.11
Lint fraction	0.3822 ± 0.0008	0.3832 ± 0.0010	0.3831 ± 0.0014	0.3793 ± 0.0011*	0.02
Gin turnout (%)	38.53 ± 0.07	38.64 ± 0.10	38.61 ± 0.13	38.29 ± 0.11	0.039
Lint quality					
Micronaire	4.56 ± 0.03	4.57 ± 0.03	4.58 ± 0.03	4.54 ± 0.03	0.77
Fiber length (cm)	2.908 ± 0.047	2.906 ± 0.025	2.918 ± 0.044	2.911 ± 0.044	0.92
Uniformity ratio (%)	83.81 ± 0.32	84.20 ± 0.24	84.40 ± 0.27	84.41 ± 0.29	0.43
Fiber strength	31.67 ± 0.57	30.90 ± 0.37	30.90 ± 0.39	31.02 ± 0.31	0.54
Elongation (%)	6.74 ± 0.05	6.67 ± 0.03	6.71 ± 0.07	6.72 ± 0.02	0.74
Leaf index	2.60 ± 0.43	2.60 ± 0.43	2.30 ± 0.30	2.30 ± 0.21	0.88
RD (a color measure)	80.78 ± 0.22	80.91 ± 0.17	81.25 ± 0.25	81.17 ± 0.18	0.42
+b (a color measure)	8.74 ± 0.07	8.67 ± 0.06	8.63 ± 0.08	8.82 ± 0.04	0.20
Maturity (%)	95.7 ± 1.25	91.9 ± 1.10*	94.1 ± 1.55	89.7 ± 0.73***	0.0048
Fiber fineness	158.0 ± 2.9	166.6 ± 2.0*	162.7 ± 2.9	169.9 ± 1.9**	0.0093
Minicard stickiness test	0.10 ± 0.11	0.20 ± 0.14	0.10 ± 0.11	0.20 ± 0.14	0.89
Sugar content (%)	0.44 ± 0.03	0.40 ± 0.02	0.41 ± 0.02	0.39 ± 0.02	0.29

Aphid feeding damage did, however, produce some changes in plant architecture that persisted throughout the growing season (Table 2). The primary changes were an increase in the number of fruiting branches (6 August sample) and a suppression of the production of vegetative branches late in the growing season (20 September sample).

Aphid populations were very low throughout the mid-season, and began to increase in late August and early September (Figure 5B). To test the possibility that early aphid feeding produced long-lasting changes in plant suitability for aphids ('induced resistance'), we regressed cumulative mid- and late-season aphid-days ('y'; 28 May to 19 September) on cumulative early-season aphid-days ('x'). The test produced no support for the induced resistance hypothesis ($y = 1.38 + 0.0014x$; $r = 0.29$, $n = 40$, $P = 0.07$).

1992 herbivore impact experiment. Few aphids colonized seedling cotton in our experimental plots during 1992, and densities remained low (Figure 11, and see below). Aphids were barely detectable in plots where we did not augment populations with greenhouse-reared aphids. Our experimental manipulations generated a relatively small range of cumulative aphid-days/leaf across the plots (range: 0–124.5; mean ± SE for control plots = 0.4 ± 0.1; medium = 5.4 ± 1.7; high = 61.1 ± 10.4; Kruskal-Wallis test, d.f. = 3, $\chi^2 = 30.4$, P < 0.0001). Aphid predators (*H. convergens* and *C. novemnotata franciscana*) and parasitoids (*L. testaceipes*) were still abundant, however, and were observed moving out of nearby barley fields which were drying down and being harvested at the same time that cotton was emerging. On 17–18 April we observed that most of the outplanted aphids were consumed by coccinellid larvae and adults, and adult parasitoids were observed in the field ovipositing into outplanted aphids on 22 April within minutes of aphid release into the field. As in 1991, we were unable to protect outplanted aphids from predator and parasitoid attack, and by 7 May aphid populations had crashed.

In 1992 damage symptoms were generally modest. Leaves on which aphid colonies developed in the high density treatments were cupped and crinkled, and
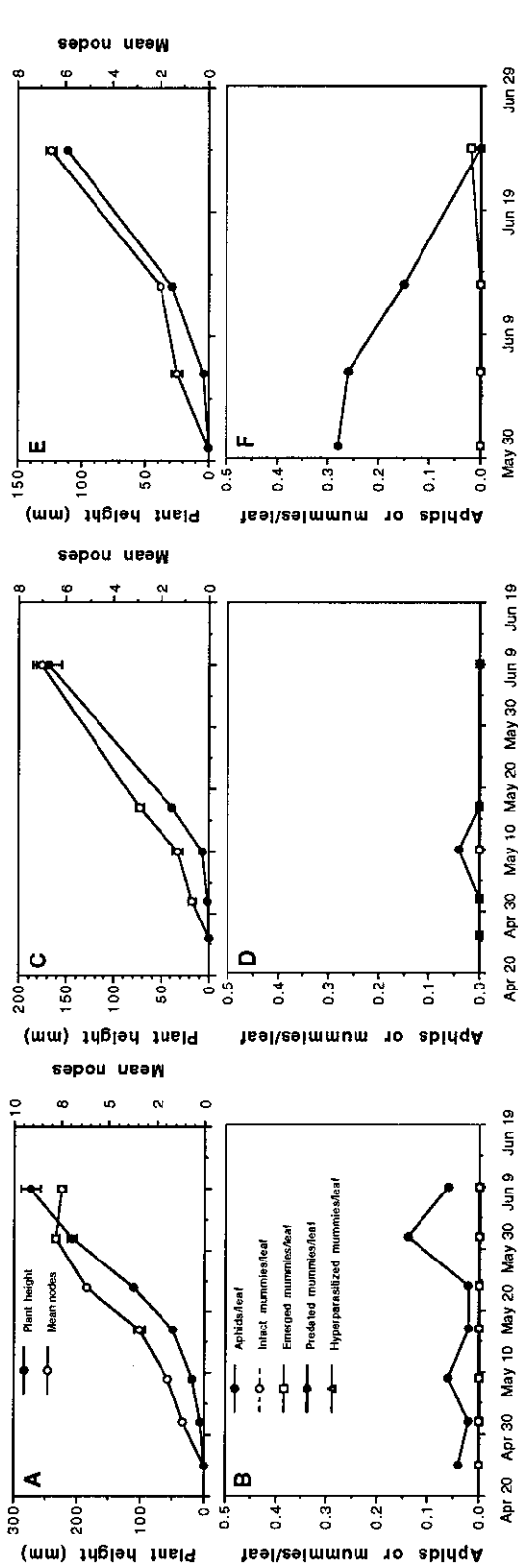
Figure 4. Early-season aphid population dynamics 1994. Shafter, (A) *G. hirsutum* field 1; (B) *G. hirsutum* field 2; (C) *G. barbadense*.

Figure 3. Early-season aphid population dynamics 1993. Shafter site: (A) mean (±1 SE) plant height and number of mainstem nodes, (B) aphid densities and impact of parasitoids and predators. West Side site: Idem (C), (D); Davis site, Idem (E), (F).
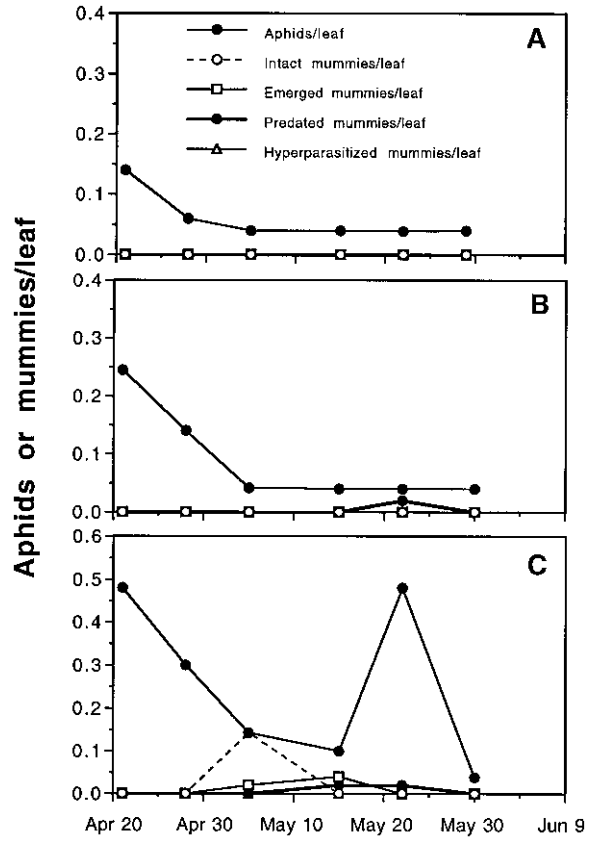
some leaf abscission was observed. Although these effects were not sufficiently consistent to generate significant omnibus F-tests for treatment effects on mean leaf area (30 April, $F_{2,28} = 2.4$, P = 0.11; 7 May, $F_{2,28} = 0.5$, P = 0.62), the one pairwise comparison that might be expected to produce a sensitive test for damage based upon observed aphid densities (Figure 7) was significant (mean leaf area 30 April, control plots = 5.21 ± 0.31 cm^2; high density plots = $4.51 \pm 0.0.31$ cm^2; $t = 2.2$, P = 0.04). Neither total plant biomass nor plant height were significantly influenced by the modest densities of aphids; however, as was observed in the medium aphid density treatments in 1991, aphid feeding caused an increase in the mean number of mainstem nodes (Table 4), which may have been a response to leaf abscission.

Complete compensation was again observed during 1992 for early-season aphid damage. Leaf area showed no significant differences across treatments on 8 July, 14 July, or 8 September (data not shown, P > 0.50).

Table 4. Herbivore impact experiment 1992. Influence of different intensities of herbivory on cotton growth and biomass allocation. Traits are defined on a per plant basis; each plot contributed one value representing the mean of 10–20 individually measured plants. Shown are means ± SE. Two-way ANOVA was conducted with main effects for block and treatment; P values are reported for the main effect for treatment. Asterisks indicate means that are signficantly different from the control; *P < 0.05; **P < 0.01

Plant trait	Control	Medium	High	P
April 15 (pre-treatment)				
Total dry weight (g)	0.0629 ± 0.0011	0.0648 ± 0.0010	0.0618 ± 0.0010	0.12
May 13				
Total dry weight (g)	0.748 ± 0.053	0.799 ± 0.065	0.713 ± 0.039	0.44
Mainstem nodes	4.48 ± 0.14	4.65 ± 0.17	4.93 ± 0.12**	0.03
Height (cm)	54.6 ± 2.5	57.0 ± 2.9	57.3 ± 2.1	0.52
September 9				
Total dry weight (g)	203.9 ± 12.9	180.4 ± 17.8	195.4 ± 17.0	0.47
Leaf dry weight (g)	28.9 ± 1.9	26.3 ± 2.8	28.6 ± 2.7	0.63
Stem dry weight (g)	48.6 ± 2.8	42.4 ± 3.9	44.8 ± 3.6	0.29
Fruit dry weight (g)	126.4 ± 8.5	111.8 ± 11.5	121.9 ± 10.9	0.51
Height (cm)	80.3 ± 2.1	78.4 ± 2.9	79.7 ± 2.2	0.84
Mainstem nodes	20.69 ± 0.29	20.58 ± 0.46	21.20 ± 0.40	0.50
Vigor index	1.72 ± 0.02	1.70 ± 0.05	1.65 ± 0.04	0.15
Nodes to 1st fruiting branch	7.11 ± 0.11	6.94 ± 0.15	6.92 ± 0.16	0.47
Fruiting branches	14.38 ± 0.31	14.47 ± 0.44	15.10 ± 0.43	0.36
Vegetative branches	3.54 ± 0.15	3.56 ± 0.14	2.98 ± 0.14*	0.027
Retention top 5 fruit (%)	5.5 ± 0.9	5.7 ± 1.4	5.2 ± 1.4	0.96
Retention bottom 5 fruit (%)	63.0 ± 2.6	61.4 ± 3.7	57.3 ± 3.9	0.39
Mature bolls	16.6 ± 11.2	14.6 ± 14.4	16.0 ± 13.1	0.49
Mature bolls open (%)	0.853 ± 0.024	0.887 ± 0.034	0.855 ± 0.030	0.52

No differences were observed in total above-ground dry plant weight, or in biomass allocations to leaf, stem, or fruit (Table 4). As in 1991, the three parameters of greatest economic significance, the timing of crop maturation as measured by the proportion of bolls opened on 9 September (Table 4), cotton yield, and cotton fiber quality (Table 5), did not vary significantly across treatments.

The modest level of aphid feeding damage did produce one effect on plant architecture that persisted to the mature plant stage: the production of vegetative branches was suppressed in the high aphid density treatment (Table 4), as was observed in 1991.

We tested for induced resistance to aphids by regressing the mean density of aphids per leaf on 8 and 14 July (dependent variable) on the cumulative early-season aphid days per plot (independent variable); the test revealed no effect of early aphid feeding ($y = 25.1 - 0.047x$; $r = -0.13$, $n = 40$, $P = 0.42$).

Discussion

Natural, unmanipulated populations of the aphid *A. gossypii* colonized seedling cotton plants during all four years of the study, but became abundant during only one year (1991). The high density populations observed in 1991 were ephemeral, disappearing before the plants reached the six-node stage (when the production of flower buds begins; Kerby and Hake, in press). Aphid population declines were associated with strong suppressive effects of predation and, to a lesser extent, parasitism. In manipulative studies, aphid feeding resulted in an immediate decrease in leaf area (Figures 6 and 7), plant height (Table 2), and total above-ground biomass (Figure 8, Table 2). Cotton plants consistently showed complete compensation for early damage in the three parameters that define the monetary value of the crop: the timing of crop maturation (Figure 9, Tables 2–4), cotton fiber yield (Figure 10, Tables 3 and 5), and cotton fiber quality (Tables 3 and 5). Aphid feeding on

Table 5. Herbivore impact experiment 1992. Influence of different levels of early-season aphid populations on final cotton yield and fiber quality. Shown are means ± SE. Two-way ANOVA was conducted with main effects for block and treatment; P values are reported for the main effect for treatment. Asterisks indicate means that are signficantly different (P < 0.05) from the control

Crop measure	Control	Medium	High	P
Yield				
Seed cotton yield (g)	6260 ± 167	6295 ± 316	6472 ± 323	0.80
Cotton lint yield (g)	2371 ± 63	2401 ± 122	2470 ± 124	0.74
Cotton seed yield (g)	3626 ± 98	3618 ± 179	3739 ± 187	0.81
Gin loss (%)	4.29 ± 0.10	4.38 ± 0.14	4.09 ± 0.11	0.24
Lint fraction	0.3770 ± 0.0011	0.3803 ± 0.0008*	0.3806 ± 0.0010*	0.04
Gin turnout (%)	37.88 ± 0.08	38.14 ± 0.08*	38.16 ± 0.10*	0.04
Lint quality				
Micronaire	3.81 ± 0.04	3.80 ± 0.06	3.84 ± 0.05	0.84
Fiber length (cm)	1.104 ± 0.005	1.093 ± 0.005	1.099 ± 0.006	0.36
Uniformity ratio (%)	81.76 ± 0.23	81.19 ± 0.40	81.49 ± 0.21	0.39
Fiber strength	34.09 ± 0.32	34.63 ± 0.78	34.67 ± 0.65	0.63
Elongation (%)	5.87 ± 0.03	5.82 ± 0.03	5.84 ± 0.04	0.62
Leaf index	2.05 ± 0.05	2.80 ± 0.56	2.50 ± 0.42	0.18
RD (a color measure)	81.67 ± 0.14	81.84 ± 0.25	81.06 ± 0.49	0.19
+b (a color measure)	9.13 ± 0.04	9.16 ± 0.06	8.99 ± 0.16	0.38
Maturity (%)	82.9 ± 5.8	84.3 ± 8.8	89.9 ± 0.7	0.73
Fiber fineness	132.2 ± 2.1	130.3 ± 3.2	138.1 ± 1.9	0.11

seedlings did, however, have effects on plant architecture that persisted until harvest: plants sustaining early damage produced fewer vegetative branches (Tables 2 and 4). There was no evidence to support the hypothesis that early-season aphid feeding induced changes in cotton plant quality that influenced mid- or late-season aphid populations.

Population dynamics. Our observational studies conducted 1991–1994 suggest that high densities of cotton aphids develop only sporadically on pre-reproductive cotton. This observation is consistent with less formal observations made from 1959–1990 in the San Joaquin Valley (T. F. Leigh & P. Wynholds, pers. comm.) and in 1995–1996, although a small fraction of the cotton acreage planted on the eastern side of the valley appears to experience high densities of aphids on seedling cotton more frequently (L. D. Godfrey & S. Wright, pers. comm.). Aphid populations on seedling cotton were ephemeral. Our inference that aphids were suppressed primarily by natural enemies rather than some other factor (e.g., a decrease in plant suitability or seasonal increases in temperature) is based upon two lines of evidence. The first, and weaker, evidence is the synchrony of the declines in aphid populations and the

appearance of large numbers of predated aphid mummies. In the most dramatic case, 100% of the mummies were attacked at the same time that the aphid population crashed (Figure 1C), suggesting very intense predation. Casual observations made in this field site at the time of aphid population collapse revealed extensive cannibalism among dense populations of coccinellid larvae that had completely consumed all herbivores present in the field (J. A. Rosenheim, pers. obs.). The second, and stronger, evidence comes from manipulative field experiments demonstrating that aphid populations caged on seedling cotton to exclude natural enemies continued to increase rapidly as cotton plants grew and matured (Colfer & Rosenheim, 1995). In contrast, aphid populations were suppressed in cages with openings that permitted entry by either parasitoids alone or combinations of parasitoids and predators. Effective suppression of aphid populations by natural enemies appears to occur despite a high incidence of predator attack on parasitoid offspring developing within mummified aphids ('intraguild predation', Rosenheim et al., 1995) and the action of hyperparasites.
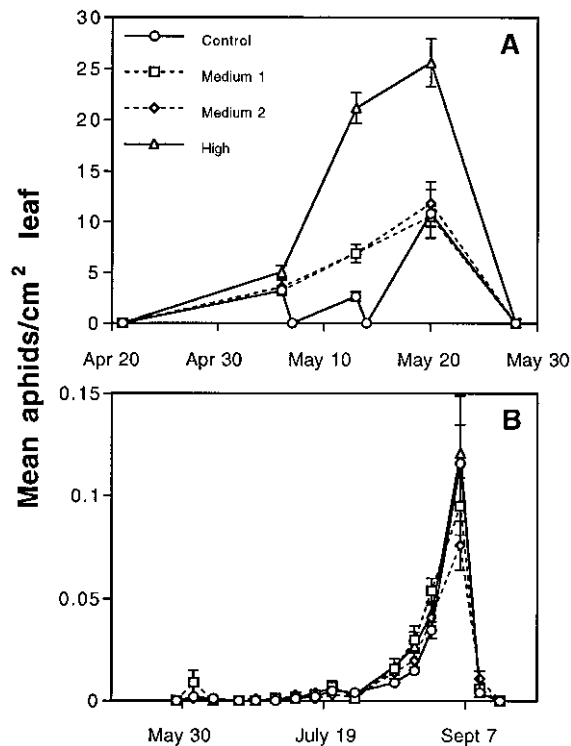
Figure 5. Herbivore impact experiment 1991. Mean (±SE) density of aphids per cm^2 of lower leaf surface. (A) Aphid densities on seedling cotton over the period when the different treatments were applied. The majority of plants had germinated by 21 April. The control plot was sprayed with pirimicarb on 6, 13, and 20 May. (B) Aphid densities for the remainder of the season; note the different y-axis scale. Bifenthrin was applied to all plots on 10 September.

Figure 6. Herbivore impact experiment 1991. Impact of aphid feeding on the area of the undersurface of mainstem leaves. (A) First true leaf, showing the impact of aphid feeding on leaf expansion. (B) Leaves sampled from the fifth mainstem node below the terminal. Results of 2–way ANOVA: $^*P < 0.05$; $^{***}P < 0.001$.
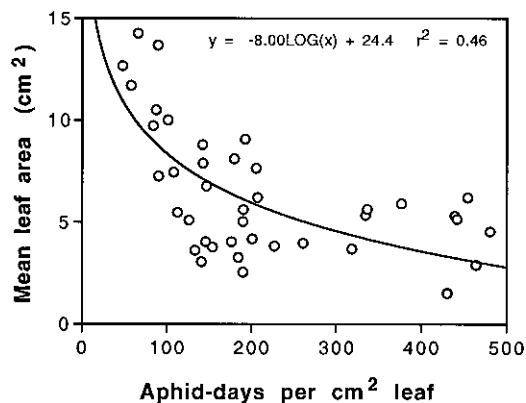

Figure 7. Herbivore impact experiment 1991. Influence of early-season aphid feeding (total aphid days accumulated between 21 April and 28 May) on the mean area of the fifth mainstem node leaf for each of the 40 experimental plots sampled on 3 June (immediately following the crash of the early-season aphid populations).
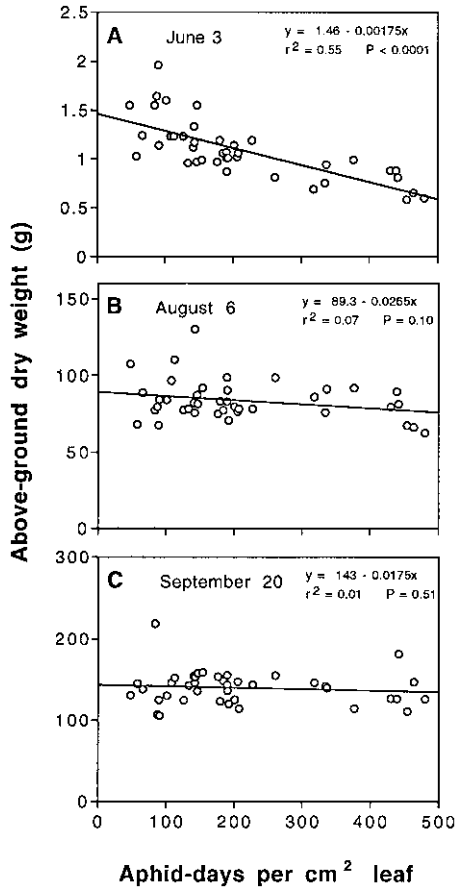
Plant compensation. Our study has demonstrated that cotton can compensate fully for aphid herbivory sustained during the pre-reproductive stages of plant growth. This result is consistent with observations of the impact of *A. gossypii* on pre-reproductive cotton in Texas (see the 1990 trial reported by Parker & Huffman, 1991) and Israel (Drishpon, 1992) and a large body of research documenting cotton's ability to compensate for at least some forms of natural and artificial herbivory (primarily defoliation and damage to reproductive structures), especially during early growth stages (Wilson, 1986; Kerby & Keeley, 1987; Brook et al., 1992a–c; Terry, 1992; Kerby et al., 1992; Dyer et al., 1993; Matthews, 1994).

Brook *et al.* (1992c) demonstrated that the ability of cotton to compensate for fruit damage was a function of overall yield levels: high-yielding plants undercompensated for damage, whereas low-yielding plants overcompensated. In this regard, it is noteworthy

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Figure 8. Herbivore impact experiment 1991. Influence of early-season aphid feeding (total aphid days accumulated between 21 April and 28 May) on the mean above-ground plant dry weight for each of the 40 experimental plots. (A) 3 June, immediately after the crash of the early-season aphids; (B) 6 August; and (C) 20 September.
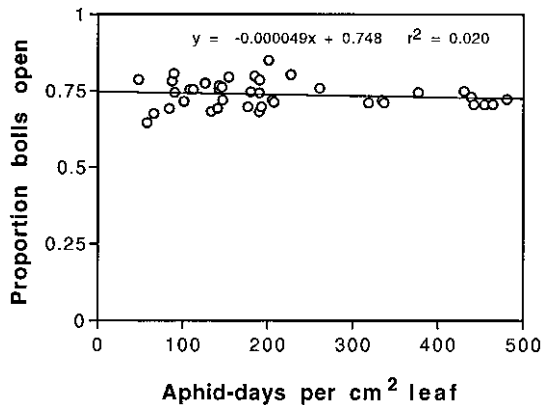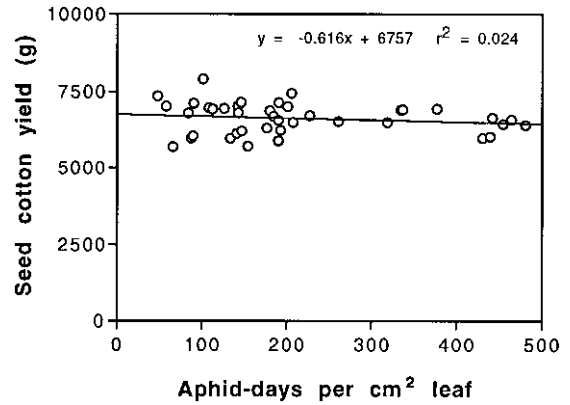

Figure 9. Herbivore impact experiment 1991. Influence of early-season aphid feeding (total aphid days accumulated between 21 April and 28 May) on the mean proportion of mature bolls that opened prior to defoliation (19–21 September) for each of the 40 experimental plots.

Figure 10. Herbivore impact experiment 1991. Influence of early-season aphid feeding (total aphid days accumulated between 21 April and 28 May) on the mean seed cotton weight for each of the 40 experimental plots.
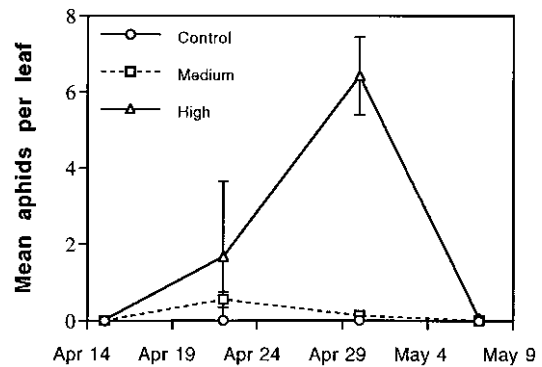

Figure 11. Herbivore impact experiment 1992. Mean density of aphids per leaf on seedling cotton over the period when the different treatments were applied.

that the yields obtained in the control plots of our aphid impact studies were high (equivalent to 2095 kg of cotton lint per hectare in 1991 and 1915 kg/ha in 1992), approximately 150% of recent average yields in the San Joaquin Valley, but still well within the range of yields commonly observed in California (Kerby & Goodell, 1993). Thus, our studies suggest that even under conditions of high yield, seedling cotton can compensate effectively for aphid damage.

The physiological mechanism by which compensation for aphid damage occurs is unknown. However, plants whose growth is constrained by the availability of sinks for photosynthate may generally have stronger abilities to compensate for herbivory than plants whose growth is limited by sources of photosynthate (Trumble et al., 1993). Kerby & Keeley (1987) and Kerby et al. (1992) have suggested that upland cotton grown under

California conditions is largely sink limited until 7 mainstem nodes have been produced, when the plants begin to produce squares (flower buds). Furthermore, because photosynthate for developing bolls is produced primarily by nearby leaves located on the same fruiting branch or the mainstem leaf located at the same node (Kerby & Hake, in press), damage to leaves on mainstem nodes located below the first fruiting branch may have little impact on subsequent boll development. Aphid populations colonizing seedling cotton in the San Joaquin Valley are usually transient due to the action of natural enemies, and all of the populations that we monitored were controlled before cotton reached nodes 6–7, when the first fruiting branches were produced (Figures 1–4, Tables 2 and 4). Thus, our experiments may be an example of strong compensation by a plant that is primarily sink-limited, and therefore less influenced by the loss of photosynthate to phloem-feeding aphids and the impairment of leaf function due to aphid damage.

Changes in plant structure in response to aphid feeding may also contribute to compensation. An important mechanism by which plants are thought to overcompensate for herbivory is through the release of apical dominance and the associated increase in growth from nonapical meristems (Trumble et al., 1993; Aarssen, 1995; Watson, 1995). And yet, in this study, it appears that compensation occurs at least partially through the reverse effect: the suppression of vegetative growth at nonapical meristems. Aphid feeding in both 1991 and 1992 suppressed the production of vegetative branches. Vegetative branches are produced low on the cotton plant (mean ± SE nodes from cotyledon to vegetative branches during 1991, 6.18 ± 0.18; 1992, 4.80 ± 0.06), and differentiation of the first floral buds occurs when the plants have 2–3 true leaves (Mauney, 1986; Kerby & Hake, in press). Thus aphids feeding on seedling cotton may damage meristems destined to develop into vegetative branches, or influence the developmental fate of these meristems in other indirect ways. While vegetative branches can make small contributions to total yield, they can only do so by producing their own fruiting branches, which occurs at a much slower rate than on the mainstem (Kerby & Hake, in press). Fruit retention rates and boll size are also smaller on vegetative branches than on the mainstem (Kerby & Hake, in press). Thus, early aphid feeding, by suppressing the production of vegetative branches, shifts cotton from a more vegetative to a more reproductive growth form and may thereby contribute to yield compensation. Cotton is a peren-

nial plant grown as an annual crop in California; it is thus possible that damaged cotton would under-yield undamaged cotton during the second or subsequent years of reproduction due to its smaller investment in structures that can eventually bear large numbers of fruiting branches (e.g., Foggo, 1996).

Cotton appears to have undergone domestication while retaining substantial abilities to compensate for early-season herbivory. The damage generated by aphid feeding during April and May occurs, however, at a time when the plant is not yet reproductive, and it may be primarily during the period of fruit production that domesticated plants are particularly sensitive to herbivory. Similarly, the possibility that domesticated plants have reduced tolerance for herbivory because of their more determinate and less plastic architectures may have less immediate bearing on the ability of seedling crops to tolerate herbivory, because seedlings often have not developed the architectural complexity that characterizes the mature plant.

In summary, our findings of strong compensation in seedling cotton are consistent with several previous studies, and may reflect seedling cotton growth being limited by sinks rather than sources of photosynthate. Early aphid feeding suppressed the production of vegetative branches late during the growing season, thereby producing a less vegetative and more reproductive growth form. While mature crop plants have been hypothesized to be more sensitive to herbivory because of selection for increased yield or architectural simplicity, these effects of domestication may be less important for the early, pre-reproductive stages of crops.

Induced resistance. Experimental studies conducted by Karban and his colleagues have demonstrated that cotton seedlings respond to artificial or natural herbivory with changes in subsequent resistance to herbivores; plants whose cotyledons or first true leaves were fed upon by spider mites, *Tetranychus* spp., were subsequently less suitable hosts for the growth of spider mites (Karban & Carey, 1984; Karban, 1986; Karban et al., 1989), the beet armyworm, *Spodoptera exigua* (Hübner) (Karban, 1988), and a pathogenic vascular wilt fungus *Verticillium dahliae* Kleb. (Karban et al., 1987, 1989). This 'induced resistance' is in contrast to the 'induced susceptibility' to spider mites caused by removing the apical bud from small cotton seedlings (Karban and Niiho, 1995). Thus, different types of herbivory appear to induce different changes in plant suitability, and altered plant suitability may influence

a taxonomically broad array of herbivores. Wool & Hales (1996) obtained mixed results in initial laboratory investigations of the possibility that *A. gossypii* might induce resistance in cotton seedlings.

To test the hypothesis that early feeding by cotton aphids induces changes in plant suitability for aphids, we examined the relationship between the density of early-season aphid populations and the density of aphid populations that developed subsequently in the same plots during the mid- and late-season. For both the 1991 and 1992 experiments we found no evidence for any effect of early-season herbivory. The 1991 experiment might have failed to detect an induced resistance response, even if one had been present, for two reasons. First, even the seedlings in the control treatments experienced moderate aphid feeding damage, and the induced resistance response may reach a maximum with only small levels of herbivore damage (Karban & English-Loeb, 1988). Second, aphid populations did not reappear until late August, long after the initial damage, and it is unclear if induced resistance persists in the field until the late season (Karban, 1986). However, both of these potential problems were eliminated in the 1992 study, and we still observed no evidence for induced changes in plant suitability. Although more carefully controlled studies would be valuable, we conclude from these initial field explorations that aphid feeding on cotton seedlings does not appear to produce major changes in the expected density of aphid populations developing on later plant growth stages.

Implications for an aphid management strategy. Insecticides are widely used on seedling cotton in the San Joaquin Valley. The severe damage symptoms produced by the heavy aphid populations during 1991 (Figures 6–8) elicited the application of broad-spectrum materials across much of the growing region. The cost of these applications also has contributed to the wider adoption of prophylactic use of insecticides, either as seed treatments (using acephate) or as applications of granular aldicarb or phorate at planting. Although aldicarb is also used to suppress root-knot nematodes and early-season spider mite populations, applications of aldicarb are justified in part by their ability to suppress aphid populations. Foliar insecticides, seed treatments, and aldicarb provide protection for no more than six weeks (L. D. Godfrey, pers. comm.), and thus suppress insects only during the pre-reproductive stage of cotton growth, when plant compensation appears to be strong. Thus, costly insecticides are widely deployed to control populations

of an herbivore that appears from our results to be a non-pest.

Might this early-season insecticide use be costly in ways other than the direct costs of purchasing and applying the chemicals? We feel that the answer is 'yes' for two reasons. First, integrated pest management in California cotton is founded on the tenet of maximizing natural biological control of a suite of herbivores, including *A. gossypii*, *Lygus* spp., *Tetranychus* spp., *Helicoverpa zea* (Boddie), and *Spodoptera* spp., that have the potential to become economic pests. Early-season insecticide use may delay the establishment of the community of predators and parasitoids that contribute to the suppression of these arthropod populations, both by directly poisoning these natural enemies and by eliminating the host/prey populations that support natural enemy population growth (Wilson et al., 1991; Zhang & Chen, 1991; Rosenheim & Wilhoit 1993; Wilson et al., 1996). The small-plot experiments reported in our study do not reveal the effects of early-season aphid populations on predator community establishment, because the plots are so small that predators readily move between treatments. However, on the spatial scale of commercial cotton fields, the presence of prey for predators during the early season may be important. Consistent with this thesis is the observation that in comparison to untreated cotton, cotton fields planted with acephate-treated seed develop larger populations of aphids during the early squaring period of plant growth (L. D. Godfrey, pers. comm.), when aphid feeding can suppress yield (Fuson et al., 1995; see also Parker and Huffman, 1991). (This rebound of aphid populations does not, however, occur after imidicloprid seed treatments or applications of granular aldicarb.) Second, an increasingly acute problem in cotton pest management is the appearance of insecticide resistance in key arthropod pests (including aphids, mites, and whitefly; Grafton-Cardwell, 1991; Hardee & Ainsworth, 1993; Leclant & Deguine, 1994). The single most important means of slowing the evolution of resistance is to minimize selection pressures exerted by pesticide applications (Denholm & Rowland, 1992). Thus, insecticide use should be reserved for periods when pest suppression is critical for crop protection. Applications targeted for non-damaging populations, such as aphid populations on seedlings, promote resistance in aphids and other herbivore populations that are incidentally exposed to the pesticide. This decreases our subsequent ability to control these pests at times when

their feeding has a significant impact on yield or crop quality (Hardee & Ainsworth, 1993).

In what growing areas and under what conditions is our conclusion that pre-reproductive cotton can compensate fully for aphid damage appropriate? First, our observations of the transient nature of aphid populations on seedling cotton appear to be representative of conditions throughout California's Central Valley with the exception of an area of cultivation located along the eastern side of Tulare County, where early aphid populations occur more frequently and often persist into cotton's reproductive growth stages (L. D. Godfrey & S. Wright, pers. comm.). Further work is needed to quantify cotton's ability to compensate for damage generated by these more persistent aphid populations, but it is clear that sufficiently dense mid-season populations will depress yields (Fuson et al., 1995). Second, we can speculate that cotton's ability to compensate for early aphid damage might be reduced by subsequent stress from herbivory or other factors. In both of our manipulative experiments, cotton sustained very little mid- and late-season herbivore pressure. However, we feel that the most sensible course of action is to manage later sources of plant stress if and when they appear, rather than anticipating what effects they might have if left unchecked. Finally, can growers planting *G. hirsutum* cultivars different from the one tested here (GC-510) rely on our results? Recent field experimentation conducted in the San Joaquin Valley with the cultivar Maxxa, which has emerged as the predominant cotton cultivar in California, has shown that it too appears to compensate fully for aphid feeding damage on pre-reproductive growth stages (L. D. Godfrey, pers. comm.). It is impossible to extrapolate with confidence to cultivars that have not been tested. However, we note that although early-season pesticide applications may seem like a conservative, prudent management strategy, we suggest that just the converse is often true: early-season pesticide use may inflate the subsequent risk that damaging herbivore populations will develop. The massive and devastating region-wide outbreaks of aphid and spider mite populations witnessed in California in 1995 show just how destructive a management strategy based upon early, aggressive use of insecticides can be (pers. obs.).

In conclusion, because pre-reproductive *G. hirsutum* has retained effective means of compensating for herbivory, subject to the caveats discussed above early-season *A. gossypii* should be recognized as non-pests. Use of insecticides to control aphids on seedling cotton is therefore generally unnecessary, and probably threatens the sustainability of cotton production by accelerating the evolution of pesticide-resistance and disrupting communities of natural enemies.

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