Midseason Pest Status of the Cotton Aphid (Homoptera: Aphididae) in California Cotton: Is Nitrogen a Key Factor?

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ABSTRACT   Field experiments were conducted from 1996 to 1998 to assess the effects of nitrogen fertilization rates and planting dates on the population dynamics of the cotton aphid, *Aphis gossypii* Glover, during the midgrowing season of California cotton. Cotton aphids reached higher densities in high nitrogen fertilized plants (227 kg N/ha, rate currently used by cotton growers) than in low nitrogen fertilized plants (57 kg N/ha). In addition, late-planted cotton (May–June), which had more nitrogen content, also harbored higher aphid populations than early plantings (April). Overall, aphid abundance was positively correlated with plant nitrogen content. In a moderate aphid pressure year (1996), planting the cotton early (April) was effective in keeping the aphid population below the midseason economic threshold. However, in a high aphid pressure year (1997), it was necessary to drastically reduce the nitrogen fertilization to 57 kg N/ha to maintain the aphid density under this threshold. Recent cultural practices in California cotton include higher rates of nitrogen fertilization, which increases nitrogen content of plants. The current data suggest that this practice (i.e., high fertilization) is an important factor contributing to the increased severity of the cotton aphid as a pest of California cotton during the midseason.

KEY WORDS   nitrogen, planting date, fertilizer, population dynamics

THE PEST STATUS of the cotton aphid, *Aphis gossypii* Glover, has changed in the last decade in the cotton production areas of California. Its importance has escalated from an occasional pest in California's San Joaquin Valley in the early 1980s to one of the key midseason pests of Acala cotton (*Gossypium hirsutum* L.) in the 1990s. The following five hypotheses have been suggested to explain why cotton aphid populations in California cotton have increased over the last 10 yr: (1) the use of synthetic pyrethroids which are known to have a detrimental effect on natural enemy populations, (2) the commercial introduction of Pima cotton (*Gossypium barbadense* L.) beginning in 1989, (3) changes in the agro-ecosystem landscape in the San Joaquin Valley, (4) the use of new varieties of Acala cotton, and (5) an increase in nitrogen and irrigation inputs. Some of these hypotheses have been previously discussed (Godfrey and Rosenheim 1996, Kidd et al. 1996). The current study experimentally tested the hypothesis that increased nitrogen fertilization contributed to increasing aphid populations.

Cotton aphid populations can be present at any time of the cotton-growing season. Outbreaks of this insect during the early season (prereproductive stage of cotton) are not, however, of economical importance because of the strong compensatory capacity of the plant at this phenological stage and the efficient biological control exerted by parasitoids and coccinellids (Rosenheim et al. 1995a 1997).

Conversely, aphid infestations during the midseason (squaring and boll filling period) can directly affect the yield by reducing fruit retention and decreasing boll weight (Fuchs and Minzenmayer 1995, Fuson et al. 1995, Godfrey et al. 1997). In addition, late-season (following boll opening) aphid outbreaks may cause contamination of the lint of open bolls with honeydew, thereby reducing the quality and value of the lint (Rosenheim et al. 1995a).

The natural enemy community present during the mid- and late cotton growing season, a complex of green lacewings and several hemipteran predators, usually do not exert adequate biological control of aphids (Rosenheim et al. 1993, 1995b, Rosenheim and Cisneros 1994). This inadequate biological control may be a result of a combination of two factors. First, these natural enemies feed on each other, thereby reducing the overall intensity of predation pressure on aphid populations (Rosenheim et al. 1995b; Cisneros 1997; Cisneros and Rosenheim 1997, 1998). Second, the cotton aphid shows high phenotypic plasticity in its fecundity and developmental time (Rosenheim et al. 1994, Godfrey et al. 2000), increasing its population growth rate when favorable conditions exist. This increase in the rate of population growth may allow the cotton aphid to escape from biological control exerted by less effective natural enemies.

Phenotypic plasticity has also been documented in the cotton aphid morphology (Mittler 1973; Miyazaki 1989a, 1989b; Rosenheim et al. 1994; Wool and Hales 1996, 1997). Some of the key factors that affect the aphid morphology and fecundity are plant nutrient status, temperature, photoperiod, and host plant spe-

cies (Mittler 1973; Akey and Butler 1989; Miyazaki 1989a; Wilhoit and Rosenheim 1993; Rosenheim et al. 1994; Wool and Hales 1996, 1997). More recently, it has been demonstrated that this pest also shows phenotypic plasticity in its response to insecticides when the nutrient status within the host plant is modified (Fuson and Godfrey 1994, Fuson et al. 1995, McKenzie et al. 1995, Cisneros and Godfrey 1998, Cisneros 1999) or when the aphids feed on different host plants (Cisneros 1999).

Nutrient status, an indicator of host plant quality, has been shown to play an important role in the population dynamics of many herbivores. Nevertheless, the published literature on this topic contains conflicting information. Many studies have shown a positive effect on herbivore density or performance (fecundity, development growth, and survivorship) when plant nutrient status is enhanced through fertilization. However, a substantial number of studies have also found negative effects or no effects (see reviews of Scriber and Slansky 1981; Scriber 1984a, 1984b; Waring and Cobb 1992). Thus, a definitive pattern on the response of herbivores to host quality cannot be concluded for all species. In the majority of the studies examining herbivore response to host quality, one major determinant of plant quality for phytophagous insects has been nitrogen. Nitrogen, fundamental for amino acid and protein synthesis in any biological system, constitutes around 0.5–5% of plant tissue and 10% of animal tissue (Mattson 1980), and is considered to be frequently limiting for both plants and their consumers (McNeill and Southwood 1978, Mattson 1980, Strong et al. 1984).

In highly nitrogen fertilized agro-ecosystems, nitrogen may not be a limiting nutrient for herbivores. In these agricultural settings, phytophagous arthropods that respond positively to plant nitrogen content may be more likely to reach pest status after a certain nitrogen concentration within the host plant is reached. Under laboratory conditions, cotton aphids showed a higher fecundity and a shorter developmental time when fed on cotton seedlings that were fertilized with nitrogen (Rosenheim et al. 1994). In field experiments with dryland cotton in the Rolling Plains of Texas, Slosser and collaborators (1992, 1998) demonstrated that planting date had a significant effect on the population dynamics of cotton aphids, with late plantings (late June) having more aphids than earlier plantings (late April and May). In addition, they found a positive correlation between nitrogen levels within the plant and aphid abundance in one of the planting dates (late May) (Slosser et al. 1997). The maximum nitrogen application rate in these studies was, however, about 100 kg/ha, which is less than half of the amount currently used in California cotton.

The cotton production practices in the San Joaquin Valley of California have shifted to a higher use of nitrogen and irrigation inputs in the last two decades. Records from the past 20 yr show that the average rate of nitrogen fertilizer used by California growers has significantly increased from approximately 110 kg N/ha in the early 1980s to about 200 kg N/ha in the
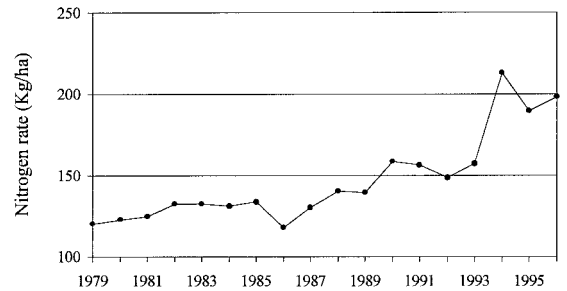

Fig. 1. Nitrogen application rates used in California cotton since 1979. Data were obtained from the USDA Economics and Statistics System database (1998).

mid-1990s (Fig. 1). Part of these changes appears to be linked to the commercial introduction of mepiquat chloride, a cotton plant growth regulator, in 1981 (Kerby et al. 1986) and the development of new cotton varieties with a more determinate growth pattern.

Before the 1980s, traditional management practices relied on irrigation or nitrogen fertilization stress during the early vegetative development of the plant to reduce vegetative growth and to encourage fruiting. With mepiquat chloride, growers have been able to avoid excessive vegetative growth without the use of potentially yield-limiting cultural stresses. Thus, with the increase of nitrogen and irrigation inputs by growers, cotton plants probably have higher nutrient contents than they had a decade ago. The cotton aphid may have exploited these changes in cotton production practices, resulting in a change in its pest status.

In the current study, the direct effects of planting date and different levels of fertilization on the population dynamics of the cotton aphid were investigated over a 3-yr period. We hypothesized that these cultural practices increase nitrogen contents within the plant, which may increase the likelihood of aphid outbreaks when other conditions for the insect are optimal. Our study also tested the hypothesis that the current pest status of the cotton aphid in California during the midseason is a result of an increase over the years of nitrogen fertilization inputs in cotton.

Materials and Methods

The population dynamics of naturally occurring cotton aphids developing on Acala cotton 'Maxxa', grown under different cultural practices, were studied from 1996 to 1998. All experiments were conducted in field plots located at the University of California Cotton Research and Extension Center near Shafter, Kern County. To test the hypothesis that agronomic factors that increase nitrogen content within the plant may also increase the population densities of the cotton aphid, two experiments were designed. In one experiment, cotton was planted at different planting dates, but the other cultural practices, such as irrigation, plant density, and fertility rate, were kept constant among treatments. In the second experiment, the planting date was kept constant in all treatments and

the nitrogen fertilization rate was modified. Thus, both experimental designs were expected to change the plant nitrogen content. In all experiments, the plant density was 10–13 seeds/m, the row width was 1 m, and the amount of water used in each growing season was 82–92 cm/ha. Herbicides (Caparol 4 liter [Ciba, Greensboro, NC] and Treflan 5 [DowElanco, Indianapolis, IN,] mixed at 2.5 and 1 pints, respectively) were applied preemergence each year. On 3 June 1996 and 30 May 1997, an acaricide (Zephyr 0.15 EC [Merck, Rahway, NJ] at 0.005 kg [AI]/ha) was sprayed to control the buildup of spider mites in the plots. No plant growth-regulators were used.

Planting Date Experiment. Cotton was planted on three to four planting dates: 16 April, 7 May, 28 May, and 18 June in 1996; 4 April, 2 May, and 30 May in 1997; and 23 April, 11 May, and 29 May in 1998. The plot size in 1996 and 1997 was four rows by 91 m in length, and in 1998 it was four rows by 45.5 m. In each year, there were four replicates for each planting date arranged in a randomized complete block design. Plots were fertilized with nitrogen when plants reached the 8-node stage. Nitrogen rates were adjusted based on preplant residual soil nitrogen to reach 227 kg N/ha, which is currently the standard nitrogen rate for cotton in the San Joaquin Valley. The planting dates, chosen for these experiments, were within the common range of planting dates used by cotton growers in this area. Currently, the earliest legal planting date for cotton in the San Joaquin Valley starts on 10 March, and most plantings are done by the end of April, weather permitting.

Cotton aphids were sampled at approximately weekly intervals from 7 July to 7 August 1996, from 16 June to 20 August 1997, and from 7 July to 1 October 1998. From each plot, 20 main-stem leaves located at the fifth node down from the terminal were collected in paper bags and transported to a laboratory where aphids were counted. Dark and light phenotypes were counted separately. In 1997 and 1998, petiole samples were also taken at weekly intervals to measure the plant nitrate concentrations via petiole analysis. This analysis quantified total nitrates by using a 2% acetic acid extraction method (Johnson and Ulrich 1959) followed by zinc reduction and conductimetric analysis (Carlson 1978). Each petiole sample consisted of 20 petioles from fifth main-stem node leaves. Sampling started on 9 July 1997 and 22 July of 1998, and ended on 20 August and 1 October, respectively. In 1996, petiole samples were taken only on 1 August.

Nitrogen Experiment. In 1997, cotton was planted on 4 April and plots were fertilized when plants reached the 8-node stage with two nitrogen fertility levels: 57 and 227 kg N/ha (adjusted based on residual soil nitrogen). Plots of cotton planted on 22 April 1998 were fertilized with three nitrogen levels: 57, 136, and 227 kg N/ha. In both years, plots (four rows by 91 m) were arranged in a randomized complete block design with four and three replicates, respectively. Irrigation schedule and plant density was kept constant in all treatments.

Cotton aphids were sampled at approximately weekly intervals from 16 June to 20 August 1997 and from 7 July to 1 October 1998 as described above. The petioles of these leaves, starting on 9 July 1997 and 22 July 1998 were also collected to measure plant nitrate content through petiole analysis.

Data Analysis. Peak densities of aphids (light + dark phenotypes), peak densities of dark phenotypes, and petiole nitrate contents in each experiment were compared using a two-way analysis of variance (ANOVA). The least significant differences least significant difference (LSD) method at $\alpha = 0.05$ was used to separate means when significant differences were detected ($P < 0.05$) by ANOVA. Regression analysis was used to test for linear relationships between peak aphid abundance and petiole nitrate contents in each experiment. For each regression analysis, replication data were used (Gomez and Gomez 1984). Because the nitrate contents may affect the generation time and fecundity of aphids, it was expected that peak aphid populations would lag behind nitrate levels by approximately one generation (1–2 wk). Therefore, nitrate contents for the regression analysis are based on samples taken 2 wk before the aphid peak, except for the experiment of 1996 in which petiole samples were only taken the same day of the peak aphid density.

Results

Planting Date Experiment. During 2 of the 3 yr of the study, aphid densities during the midseason reached damaging levels. In 1996, the cotton aphid peak density in all treatments was reached on 1 August with a maximum density higher than the midseason economic threshold (e.g., >50–100 aphids/leaf) (Fig. 2a). The earliest planting date (16 April) had a significantly lower number of aphids than the other planting dates (Table 1). There was a trend for more dark-phenotype aphids in the latest planting date (18 June) compared with the other planting dates (Fig. 3a); however, the difference was not statistically significant (Table 1). In addition, petiole nitrogen contents were significantly different among planting dates with the earliest planting date treatment having the lowest amount of nitrates (Table 1). A positive linear relationship was found between the aphid peak densities and the plant nitrate contents ($F = 11.98$; df = 1,14; $P < 0.01$; Fig. 4a).

In 1997, the aphid pressure was the highest of the 3 yr of the study, with aphid densities exceeding 1,800 individuals per leaf in some plots. The cotton aphid peak density in all planting dates occurred on 22 July (Fig. 2b). Aphid abundance in the latest planting (30 May) was the highest, with four times more aphids than in the earliest planting (Table 2); however, the aphid densities in all treatments exceeded the economic threshold (Fig. 2b). There were also more dark-phenotype aphids in the latest planting date (30 May) compared with the earliest date (4 April) (Fig. 3b; Table 1). The nitrate contents within the plants were also significantly different among the treatments, with
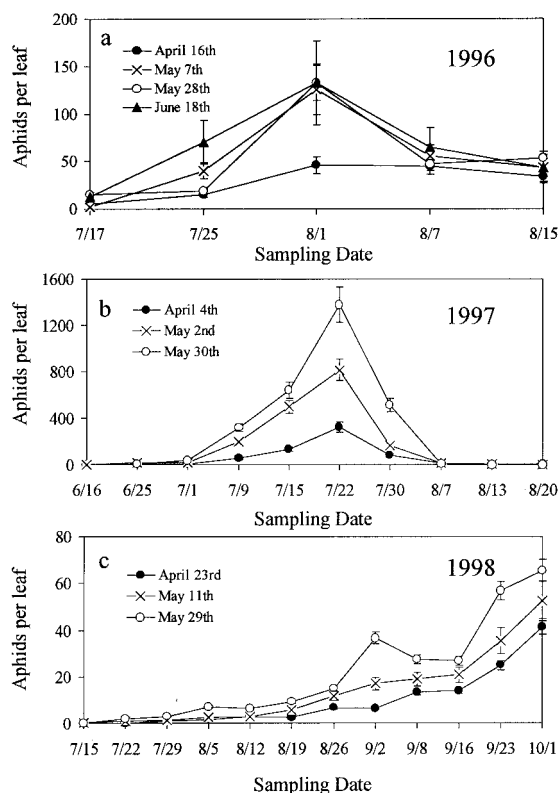
Fig. 2. Effects of cotton planting date on the population dynamics of the cotton aphid. Shown are the total number of aphids per leaf (mean ± SE) in the planting date experiments of (a) 1996, (b) 1997, and (c) 1998.

Fig. 3. Effects of cotton planting date on the population dynamics of the cotton aphid. Shown are the number of dark aphids per leaf (mean ± SE) in the planting date experiments of (a) 1996, (b) 1997, and (c) 1998.

early plantings showing lower concentration of petiole nitrates than the later plantings (Table 1). Additionally, there was a positive relationship between aphid abundance and nitrogen levels within the plants ($F = 40.09$; df = 1, 10; $P < 0.0001$; Fig. 4b).

In 1998, cotton aphid densities were lower during the midseason than in 1996 and 1997, and they did not exceed the midseason economic threshold in any of
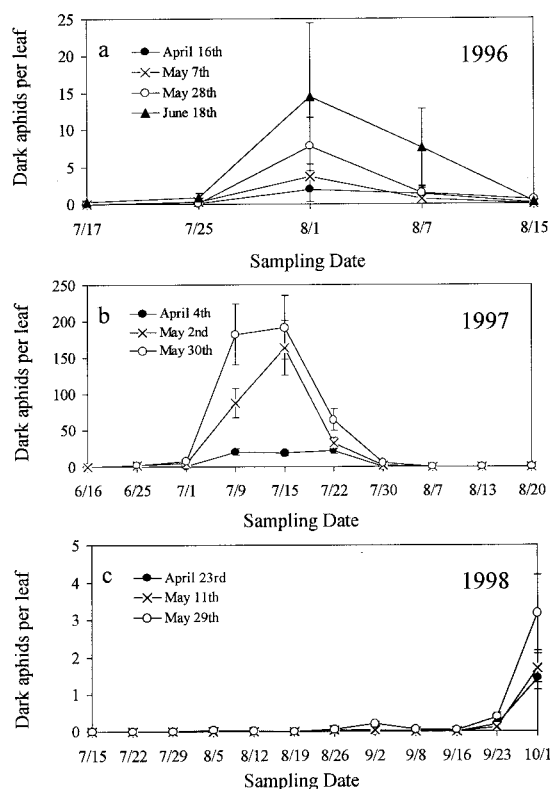
the planting dates. The peak density observed for this year occurred later in the season on 1 October. Peak densities in all treatments exceeded the late-season economic threshold (e.g., 15 aphids per leaf) (Fig. 2c). As in previous years, aphid peak density in the latest planting (29 May) was significantly higher than the density in the early planting date treatment (23 April). Dark-phenotype aphid abundance (Fig. 3c), which increased later in the season, was not significantly different among planting dates (Table 3). The petiole analysis showed that the nitrate contents were higher in the late planting date (29 May) compared with the two other plantings (Table 3). The aphid abundance at their peak was positively correlated to the petiole nitrate contents present 2 wk before this peak ($F = 17.76$; df = 1, 10; $P < 0.01$; Fig. 4c).

Nitrogen Experiment. During the 2 yr of this experiment, the aphid densities reached midseason pest status only in 1997. In 1997, cotton aphid peak densities in all plots occurred on 22 July (Fig. 5a), with aphid densities in the high nitrogen treatment (227 kg N/ha) three times larger than in the low nitrogen treatment (57 kg N/ha) (Table 4). Dark-phenotype aphids were also significantly more abundant in the high nitrogen plots than in the low nitrogen plots (Fig. 6a; Table 4). Plants in the high nitrogen plots had three times the amount of nitrates than the ones in the low nitrogen
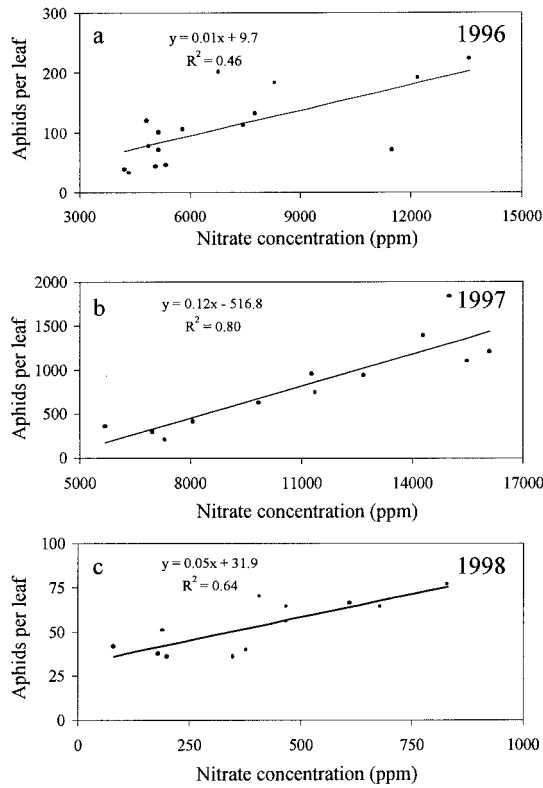
Table 1. Planting date experiment 1996 showing the average number of aphids per leaf (mean ± SE) at peak density (1 August) and the average number of dark phenotypes per leaf (mean ± SE) also at peak density (1 August)

Planting date treatments	Avg no. of aphids per leaf[a]	Avg no. of dark aphids per leaf[a]	Petiole nitrate content (ppm)[a]
16 April	46.2 ± 8.9a	1.9 ± 1.6a	4,680 ± 241.8a
7 May	126.13 ± 26.6b	3.7 ± 1.7a	5,570 ± 465.0ab
28 May	132.15 ± 18.3b	7.8 ± 3.9a	7,160 ± 710.2b
18 June	132.88 ± 44.0b	14.45 ± 9.9a	10,660 ± 1826.3c
F	5.35	1.81	12.18
df	3, 9	3, 9	3, 9
P	<0.05	0.215	<0.01

Petiole nitrogen contents (parts per million of nitrates) correspond to samples taken at six weeks from the last planting (1 August).

[a] Values within columns followed by the same letter are not significantly different (LSD at the 0.05 level).

Fig. 4. Relationship between the total number of cotton aphids per leaf at their peak density and petiole nitrate concentrations in the planting date experiments of (a) 1996, (b) 1997, and (c) 1998.

plots (Table 4). There was a positive relationship between aphid abundance at the peak density and petiole nitrate contents ($F = 26.38$; df = 1, 6; $P < 0.01$; Fig. 7a).

In 1998, the aphid population build-up appeared later in the season, reaching the highest numbers in the last sampling date (sampling was stopped because the plots were sprayed with a defoliant). In all nitrogen treatments aphid numbers were higher than the

Table 2. Planting date experiment 1997 showing the average number of aphids per leaf (mean ± SE) at peak density (22 July) and the average number of dark phenotypes per leaf (mean ± SE) also at peak density (16 July)

Planting date treatments	Avg. no. of aphids per leaf[a]	Avg. no. of dark aphids per leaf[a]	Petiole nitrate content (ppm)[a]
4 April	322.6 ± 44.4a	19.6 ± 4.0a	6,047.5 ± 333.5a
2 May	815.3 ± 77.9b	163.5 ± 37.3ab	10,275.0 ± 118.1b
30 May	1379.2 ± 161.7c	287.8 ± 66.4b	15,600.0 ± 402.1c
F	21.41	8.89	338.17
df	2, 6	2, 6	2, 6
P	<0.01	<0.05	<0.001

Petiole nitrogen contents (parts per million of nitrates) correspond to samples taken at six weeks from the last planting (15 July).

[a] Values within columns followed by the same letter are not significantly different (LSD at the 0.05 level).

Table 3. Planting date experiment 1998 showing the average number of aphids per leaf (mean ± SE) at peak density (1 October) and the average number of dark phenotypes per leaf (mean ± SE) also at peak density (1 October)

Planting date treatments	Avg. no. of aphids per leaf[a]	Avg. no. of dark aphids per leaf[a]	Petiole nitrate content (ppm)[a]
23 April	41.5 ± 3.2a	1.4 ± 0.3a	11,233.3 ± 284.8a
11 May	52.4 ± 8.5ab	1.7 ± 0.4a	14,175.0 ± 970.7b
29 May	65.5 ± 4.3b	3.8 ± 1.2a	18,875.0 ± 428.9c
F	6.37	2.42	22.69
df	2, 6	2, 6	2, 6
P	<0.05	0.17	<0.01

Petiole nitrogen contents (parts per million of nitrates) correspond to samples taken at six weeks from the last planting (15 July).

[a] Values within columns followed by the same letter are not significantly different (LSD at the 0.05 level).

late-season economic threshold of 15 aphids per leaf (Fig. 5b). The peak density occurred on 1 October with higher aphid numbers in the 227 kg N/ha plots compared with the other two treatments (Table 5). No significant differences were found in dark phenotype aphids among treatments (Fig. 6b; Table 5). Plants that were fertilized with 227 kg N/ha showed higher levels of nitrates in their petioles compared with plants in the low nitrogen treatment (Table 5). A positive relationship was also found between aphid abundance and nitrate contents within the plant ($F = 18.38$; df = 1, 7; $P < 0.01$; Fig. 7b).

Discussion

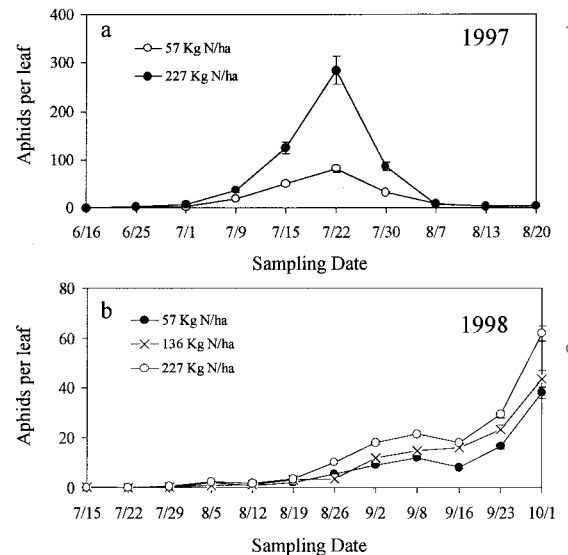The current data indicate that both the planting date and the level of nitrogen fertilization modify the

Fig. 5. Effects of nitrogen fertilization on the population dynamics of the cotton aphid. Shown are the total number of aphids per leaf (mean ± SE) in the nitrogen experiments of (a) 1997 and (b) 1998.

Table 4. Nitrogen experiment 1997 showing the average number of aphids per leaf (mean ± SE) at peak density (22 July) and the average number of dark phenotypes per leaf (mean ± SE) also at peak density (22 July)

Nitrogen treatments	Avg no. of aphids per leaf	Avg no. of dark aphids per leaf	Petiole nitrate content (ppm)
57 kg N/ha	81.2 ± 6.8	2.8 ± 1.4	5,097.5 ± 765.9
227 kg N/ha	284.6 ± 28.3	10.3 ± 1.6	11,825.0 ± 259.4
F	39.26	49.08	80.93
df	1, 3	1, 3	1, 3
P	<0.01	<0.01	<0.01

Petiole nitrogen contents (parts per million of nitrates) correspond to samples taken at three months from the planting date (9 July).

plant nitrogen content, and this factor influences the abundance of the cotton aphid. Plants that were planted later or were fertilized with more nitrogen showed higher levels of nitrogen in their tissue than plants that were planted earlier or fertilized with less nitrogen. In addition, plants with higher levels of nitrogen content, regardless of the experiment, also harbored more aphids. Thus, the occurrence of the aphid peak density may be affected by factors extrinsic to the plant (e.g., environmental factors) as suggested by Slosser and collaborators (1992, 1997, and 1998), the level of this peak seems to be influenced by the plant nitrogen content.

In years with moderate aphid pressure (1996), planting the cotton early (16 April) prevented aphids from surpassing the economic threshold. However, in a year with high aphid pressure (1997), changing the planting date to an earlier date (4 April) was not enough to keep the aphid densities below the eco-
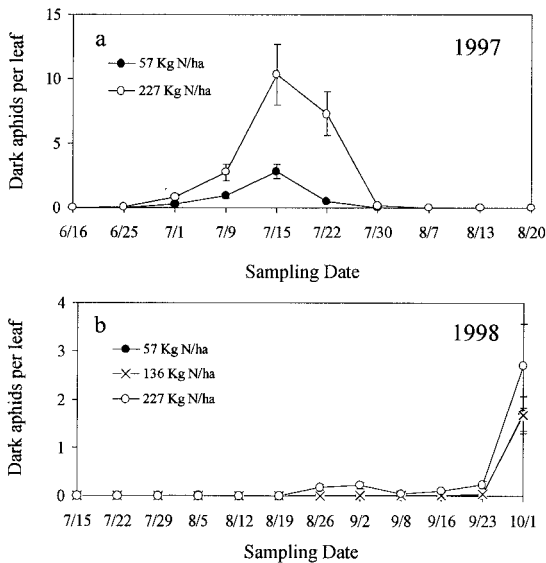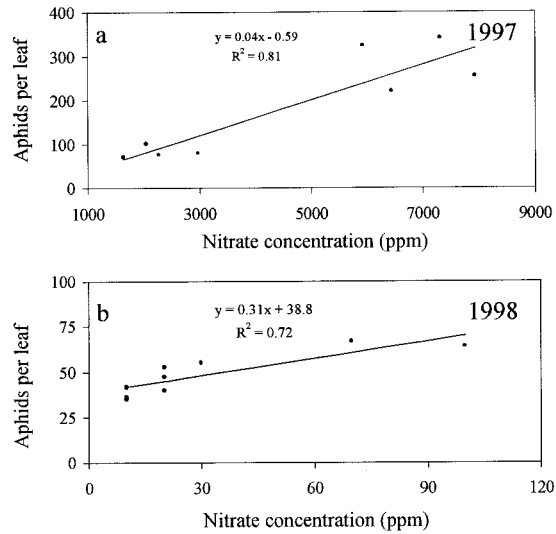

Fig. 7. Linear relationship between the total number of cotton aphids per leaf at their peak density and petiole nitrate concentrations in the nitrogen experiments of (a) 1997 and (b) 1998.

nomic threshold. In this year, aphid populations were prevented from reaching the economic threshold only when the amount of fertilizer applied to the plants was drastically reduced.

In 1998, there were no midseason aphid outbreaks in any of the treatments. Despite the presence of optimal environmental conditions (i.e., cool temperatures) for the pest in June (average maximum and minimum temperatures: 29.2 and 13.9°C, respectively), aphids were practically absent until mid-July when the temperatures increased (average maximum and minimum: 35.6 and 17.5°C, respectively). The weather patterns (El Niño phenomenon) observed in this year (i.e., cool and wet spring conditions) are suspected to be responsible for the low number of aphids during the midgrowing season. Thus, unfavorable spring conditions in 1998 not only delayed cotton planting in the San Joaquin Valley but also did not

Fig. 6. Effects of nitrogen fertilization on the population dynamics of the cotton aphid. Shown are the number of dark aphids per leaf (mean ± SE) in the nitrogen experiments of (a) 1997 and (b) 1998.

Table 5. Nitrogen experiment 1998 showing the average number of aphids per leaf (mean ± SE) at peak density (1 October) and the average number of dark phenotypes per leaf (mean ± SE) also at peak density (1 October)

Nitrogen treatments	Avg no. of aphids per leaf[a]	Avg no. of dark aphids per leaf[a]	Petiole nitrate content (ppm)[a]
57 kg N/ha	37.9 ± 2.1a	1.7 ± 0.4a	3566.7 ± 256.2a
136 kg N/ha	46.7 ± 3.7a	1.7 ± 0.1a	5213.3 ± 471.0ab
227 kg N/ha	61.9 ± 3.4b	2.7 ± 0.3a	7693.3 ± 1206.0b
F	27.61	3.35	7.76
df	2, 4	2, 4	2, 4
P	<0.01	0.139	<0.05

Petiole nitrogen contents (parts per million of nitrates) correspond to samples taken at three months from the planting date (22 July).
[a] Values within columns followed by the same letter are not significantly different (LSD at the 0.05 level).
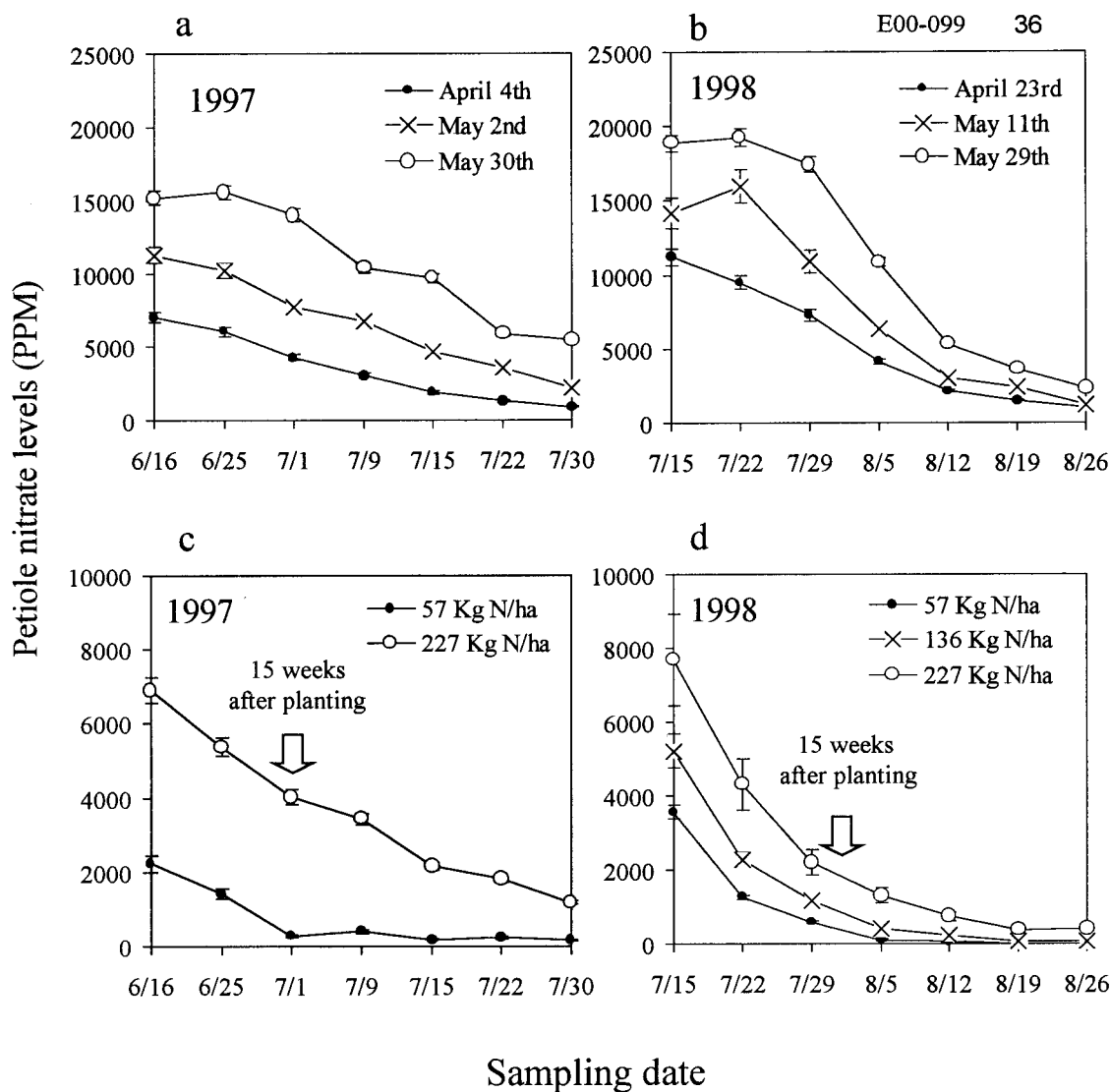
Fig. 8. Petiole nitrate concentrations (mean ± SE) over the growing season in the planting date experiments of (a) 1997 and (b) 1998, and in the nitrogen experiments of (c) 1997 and (d) 1998.

allow the planting of spring crops, such as melons. Melons are an alternate host for the cotton aphid when coming from its overwintering hosts. Thus, melons may be an important reservoir of cotton aphids to infest other crops later in the season. The absence of this crop in 1998 may have contributed to a generally low numbers of cotton aphids in spring and early summer of 1998.

The cool and wet spring conditions of 1998 were also unfavorable for cotton development. Root development was poor and probably reduced the plant's ability to absorb nutrients deeper in the soil profile. In fact, nitrogen levels within the plants in the nitrogen experiment declined faster than the previous year (Fig. 8). This translated into low nitrogen contents within the plants during the time the aphids were

present (they became detectable in late July) and probably slowed the aphid population growth. Although aphids were not abundant during the midseason, their numbers slowly built up later in the season to densities beyond the late-season economic threshold (15 aphids per leaf). This increase in aphid numbers may have been triggered by the change of environmental conditions (e.g., the onset of fall conditions) that are more favorable to aphid reproduction.

The positive trends found in the current study between cotton aphid abundance and the plant nitrogen levels are not restricted to this species. In many other systems (both agricultural and nonagricultural) diverse herbivore species have been shown to respond positively to increases in nitrogen content of the host

plant (see reviews of Scriber 1984a, 1984b; Waring and Cobb 1992). Positive responses to nitrogen have been observed in insect fecundity, survivorship, weight gain, and oviposition preference. In the case of the cotton aphid, laboratory (Rosenheim et al. 1994) and field (Godfrey et al. 2000) experiments with cotton have indicated that increases in plant nitrogen content can augment the fecundity of the aphid and at the same time shorten its generation time. Thus, the growth rate of the aphid population can increase dramatically in a relatively short period of time (i.e., a few weeks) when aphids are growing under favorable conditions (i.e., high host quality combined with optimal temperature and photoperiod).

In field experiments in the Rolling Plains of Texas, Slosser and collaborators (1998) showed that cotton aphid population dynamics are influenced not only by the nitrogen content of the plant but also by leaf moisture, temperature, and solar radiation, among other factors. It is important to notice that in their study the highest amount of nitrogen fertilizer used was about 100 kg/ha, which is less than half of the average nitrogen rate used by California cotton growers, and that the fertilizer was applied just before each planting rather than as a side-dress, postemergence application as in our study

California cotton growing conditions are quite different from those of the Rolling Plains of Texas (dryland cotton). Besides different nitrogen rates used in both cotton production areas, there are also dissimilarities in cotton varieties, irrigation practices (i.e., CA, cotton is furrow irrigated), and yield expectations by growers. In addition, there are variations in pest problems, natural enemy complexes, and cotton aphid genotypes (the San Joaquin Valley is geographically isolated from other cotton growing areas in the United States). Despite these differences, similar results were obtained in these two systems in that aphids were more abundant in late cotton plantings and on plants with higher levels of nitrogen. The higher aphid levels recorded during our experiments, compared with the densities observed by Slosser and colleagues in Texas cotton, may have been attributed to the higher levels of nitrogen used.

A consistency of the timing of the peak aphid densities among treatments within and between experiments each year was found in the current study, indicating that factors not related to the plant (i.e., environmental factors) may influence the timing of the aphid peak densities. Slosser and collaborators (1998) found that the timing of peak densities of aphids was regulated by high and low (<20°C) temperatures, and to a lesser degree by nitrogen availability within the plant. They also found that the aphid population decline was regulated by biotic factors such as predator density per leaf, peak number of aphids per leaf, and by percentage leaf nitrogen and moisture, with the predator numbers being the most important factor.

The decline of the aphid populations observed in 1996 and 1997 after reaching their peak densities during the midseason, seemed to be regulated by unfavorable environmental conditions (i.e., hotter temperatures) rather than the action of natural enemies. In California, the natural enemies present during the mid- and late season usually fail to regulate the aphid populations. Predator-predator interactions among the aphid natural enemies (lacewings and hemipteran predators) seem to be the culprit of the disruption of the aphid biological control (Rosenheim et al. 1993, 1995; Rosenheim and Cisneros 1994, Cisneros 1997; Cisneros and Rosenheim 1997, 1998). In addition, parasitoids and entomopathogens are practically absent at this time of the year in California.

This study has also provided some support for the hypothesis that the current midseason pest status of the cotton aphid in California cotton may be a result, at least in part, of an increase in nitrogen inputs by growers over the years. Thus, cotton aphid pressure on cotton has increased in the last decade paralleling the changes in California cotton nitrogen inputs. In a companion study, we found that the same agronomic practices that influence the aphid population dynamics also affect the susceptibility of this aphid to insecticides. In that study, aphids that fed on plants with higher levels of nitrogen were less susceptible to several insecticides tested than aphids from plants with lower nitrogen levels (Cisneros and Godfrey 1998). Reducing the rate of nitrogen fertilizer may seem to be an obvious solution. However, cotton production practices (particularly nitrogen fertilization and irrigation inputs), in which the emphasis is placed on maximum yield, have evolved to a point that most growers would not want to compromise their yield. Conversely, the use of high amounts of nitrogen fertilizers on crops in the San Joaquin Valley has provoked a public concern over ground water contamination. Furthermore, nitrogen needs and application rates on cotton are currently being reevaluated showing that the amount of nitrogen that growers currently use may be higher than needed to maximize yield (Hutmacher et al. 1998). Therefore, a future research priority is to determine a balance between nitrogen need of the crop and maximum yield production with a level of fertilizer that mitigates the aphid population increase. Nitrogen content reductions in plant tissue may be achieved by planting the cotton early, reducing the amount of nitrogen fertilizer, and potentially by splitting total nitrogen application into smaller quantities. Because aphids consume amino acids and nitrates from the plant phloem, it may be possible to convert the nitrogen into forms that the aphids will not be able to use, such as proteins. This could be achieved by adding potash and phosphate fertilizers (these two nutrients play an important role in the synthesis of proteins) when nitrogen fertilizer is applied.

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