Spatial Distribution of Preimaginal *Bemisia tabaci* (Homoptera: Aleyrodidae) in Cotton and Development of Fixed-Precision Sequential Sampling Plans

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ABSTRACT Studies were conducted to examine distributional patterns of *Bemisia tabaci* (Gennadius) eggs and nymphs on two cultivars of upland cotton, *Gossypium hirsutum* L., and one American Pima cotton, *G. barbadense* L., and to develop efficient sampling plans for estimating densities of immatures. On a per square centimeter basis, both eggs and nymphs were equally distributed among the four leaf sectors delineated by the major leaf veins. This pattern was independent of the nodal location of the leaf, cultivar, or sampling date. However, based on counts on 3.88-cm^2 disks near the petiole of the leaf, both egg and nymphal were aggregated at the proximal end of each sector. The relationship between disk and whole leaf counts varied with nodal position and cultivar. The greatest number of eggs and nymphs were found on mainstem leaves from nodes 2–4 and 4–7 (mainstem terminal = node 1), respectively. This pattern changed slightly with time but was similar among the three cultivars. The lowest coefficients of variation were associated with leaf counts from nodes 4–5 and 5–6 for eggs and nymphs, respectively. Based on variance partitioning and sampling cost analysis, a single 3.88-cm^2 disk from the base of the second sector of the fifth mainstem node leaf was determined to be the most efficient sample unit for estimating egg and nymphal densities. Sequential sampling stop lines were calculated for this sample unit using Green's (1970) method. Sample plan validation using Monte Carlo simulation indicated that actual levels of precision (SEM/mean) were poorer than those specified at low densities of immatures and better than specified at high densities. Further simulations indicated that stop lines for specified precisions of 0.20, 0.25, or 0.30 would maintain an average precision of 0.25 when egg or nymphal densities are <10, between 10 and 100, or >100 per leaf disk, respectively. These sampling plans allow efficient monitoring for pest management application and will aid the study of *B. tabaci* population dynamics in cotton.

KEY WORDS sweetpotato whitefly, spatial distribution, sequential sampling plan

THE SWEETPOTATO WHITEFLY, *Bemisia tabaci* (Gennadius) has been present in Arizona and California since the 1920s (Russell 1975), but it has only been in the past decade that population outbreaks of this insect have created significant problems (Duffus & Flock 1982, Butler & Henneberry 1984, Natwick & Zalom 1984). *B. tabaci* is currently recognized as one of the most significant pests of cotton and several spring and fall vegetables in Arizona and southern California (USDA 1992). The underlying causes of these recent outbreaks are not completely understood but are related in part to the emergence of a new biotype which, among other things, causes squash silverleaf, appears to have a broader host-plant range, produces greater amounts of honeydew, and is more fecund (Byrne & Miller 1990, Bethke et al. 1991, Costa & Brown 1991).

Management of *B. tabaci* presents a significant challenge because of its intercrop movement, high reproductive potential, broad host range, resistance to insecticides, and its habitation of the underside of foliage. The development of reliable and cost-effective sampling methods is essential to basic study of the population dynamics of *B. tabaci* and to the establishment of decision criteria for implementing control programs. Precision and efficiency are two of the most important considerations of any sampling program. Efficiency of effort is particularly critical for *B. tabaci* because of its small size and potential for high population densities. Sampling efficiency must balance cost considerations against the quality of the information provided by the sampling program.

The development of sampling plans, including the size of the sample unit, the number of samples to take, and the allocation of samples within the sample universe, depends on an understanding of the underlying spatial distribution of the

target insect (Morris 1960, Southwood 1978). A number of sampling methods have been developed to estimate population densities of immature *B. tabaci* in various crops (Butler et al. 1986, Ekbom & Rumei 1990). As a result of the preference of ovipositing females for young foliage and the sedentary nature of the immature stages (Gerling et al. 1980), eggs and nymphs are distributed vertically on the plant with eggs and early instar nymphs on younger foliage near terminal growing points and older instars on progressively older leaves (Ohnesorge et al. 1980, Melamed-Madjar et al. 1982, von Arx et al. 1984, Ohnesorge & Rapp 1986, Bellows & Arakawa 1988, Abisgold & Fishpool 1990, Rao et al. 1991, Lynch & Simmons 1993). Several studies have shown that sampling effort can be reduced by counting or rating the densities of immatures on smaller sections of entire leaves and by selecting leaves from specific nodes containing the highest densities of the desired stage (Melamed-Madjar et al. 1982, von Arx et al. 1984, Ohnesorge & Rapp 1986, Abisgold & Fishpool 1990, Lynch & Simmons 1993). Von Arx et al. (1984) developed sequential sampling plans for red-eyed nymphs based on counting insects on a distal sector of an individual mainstem leaf, the nodal position of which changes as the plant develops.

Here, we report on the spatial distribution of eggs and nymphs of *B. tabaci* within leaves, within plants, and within fields of cotton in the southwestern desert of the United States. Based on this detailed spatial analysis we determined optimal sample units and developed and tested sequential sampling plans for estimating densities of eggs and nymphs with fixed levels of statistical precision.

Materials and Methods

Within-Leaf and Within-Plant Distributions. We examined within-leaf and within-plant distributions of *B. tabaci* eggs and nymphs from mid-June to late-August at the University of Arizona, Maricopa Agricultural Center (MAC), Maricopa, AZ, in 1992. Samples were collected from two early-season upland cottons, *Gossypium hirsutum* L., "Deltapine 50" (DP-50) and "Stoneville 506" (ST-506) and one American Pima cotton, *G. barbedense* L. (PS-7). The two upland cottons were arranged in a split-plot design as part of an experiment to examine the effect of irrigation scheduling and cultivar on *B. tabaci* and pink bollworm, *Pectinophora gossypiella* (Saunders), populations (Flint et al., unpublished data). Twenty-four individual plots, ≈0.1 ha each, were arranged contiguously in a 2.4-ha area. In addition, a 0.2-ha plot of PS-7 was established nearby (0.3 km) for the purpose of examining *B. tabaci* distributions. Plant densities averaged 80,000 plants per ha with 1.02-m row widths and no insecticides were used. On 17 June two whole plants were randomly collected from each of the 24 separate upland plots (24 plants per cultivar). Approximately every other week thereafter until 25 August, two plants were randomly collected from 9–10 individual upland plots (9–10 plants per cultivar) and ≈10 plants were randomly collected from the PS-7 plot. All plants were taken to the laboratory and the single mainstem leaf from each of the first seven nodes below the mainstem terminal (considered node one) were removed. These individual leaves were then subdivided into four sectors delineated by the three main leaf veins (Fig. 1). Additionally, a 3.88-cm^2 circular disk (No. 14 cork-borer with a 2.22-cm diameter) was taken from the proximal portion of each sector such that it just fit within the major leaf veins. The sectors, and disks contained within, were numbered consecutively from left to right with the underside of the leaf facing up. Eggs and nymphs were counted separately for each disk and sector under a binocular dissecting microscope. Nymphs included every stage from crawlers through terminal stage nymphs (pupae). On the first sampling date (17 June) we subdivided leaves from all nodes and made counts, but on the next three sampling dates (16 and 29 July, 10 August), only leaves from nodes 2, 5, and 8 were subdivided and counted. On the remaining nodes we made only whole-leaf counts of eggs and nymphs. On the final sample date (25 August), insects were counted only on disks from the second leaf sector. These changes in protocol were made necessary by the dramatic increase in the number of eggs and nymphs as the season progressed. Leaves that could not be counted on the day of collection were stored in plastic bags at 4°C. In

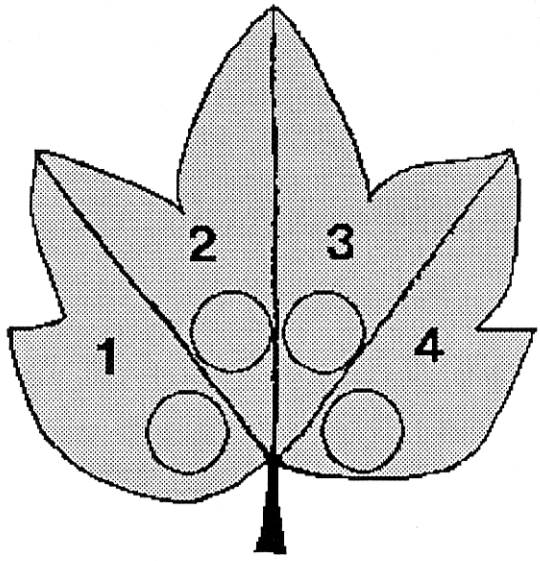

Fig. 1. Location of various sample units on a cotton leaf with under-surface facing up.

general, all counts were completed within 1 wk of sample collection. Sector and total leaf areas were determined for 10 leaves per node for each cultivar on 16 July and 10 August with an image analysis system (Decagon Devices, Pullman, WA). We also recorded the time it took to count individual leaf disks for a total of 20 disks on these two dates.

We converted counts of eggs and nymphs to numbers of insects per cm^2 of leaf area for each leaf subunit (sector or disk) to examine the distribution of eggs and nymphs within individual leaves. Analysis of variance (ANOVA) (SAS 1985) was used to test for differences in abundance relative to the leaf subunits for each cultivar. In our design dates were whole plots, and nodes and leaf subunits were subplots and sub-subplots, respectively. The element plants-within-dates was entered as a random factor. We used only data from nodes 2, 5, and 8 from the first four sampling dates for this analysis and all counts were transformed by $\ln(x + 1)$. Only leaves with at least five eggs or nymphs were included in the analyses. We performed similar analyses to test for differences in distributional patterns of eggs and nymphs along the mainstem relative to cultivar and sample date by adding cultivar as a main plot factor. In this instance we used whole-leaf counts transformed by $\ln(x + 1)$ and plants without eggs or nymphs were eliminated from the analyses. We regressed the nodal position of the most infested leaf (eggs or nymphs) on degree-days (12.8 and 30°C lower and upper thresholds, respectively, using the method of Allen [1976]) from planting to test for changes in the central tendency of insect distributions along the mainstem over the season. Analysis of covariance was performed to test for heterogeneity in regression parameters across cultivars.

Within-Field Distributions. We collected additional leaf samples in 15 commercial upland and Pima cotton fields in Maricopa and Pinal Counties, AZ, from 20 August to 22 September to further examine within-field distributions of eggs and nymphs. In each field, 50 leaves from fifth mainstem nodes (see discussion of optimal sample unit below) were collected at 10 sites along a diagonal transect with an arbitrarily selected starting point that was at least 10 m from the edge of each field. Leaves were collected from five consecutive plants at each site within a field before moving over 10 rows and up ≈20 m. Leaves were individually bagged and returned to the laboratory where eggs and nymphs were counted on 3.88-cm^2 disks taken from the second sector of each leaf. The times required to collect five consecutive leaves and to move between sampling sites within a field were estimated in three fields ranging from 16 to 32 ha in size.

Sample Plan Development. The total variances of counts of eggs and nymphs taken at the MAC were partitioned into cultivar, plant, node and leaf subunit (sectors or disks) components using a nested-design ANOVA (SAS 1985). We used the general relationship for two and three-stage sampling:

$$n_2 = (S_2^2/S_1^2)^{1/2}(C_1/C_2)^{1/2} \quad (1)$$

given by Cochran (1977; pp. 281, 288) to estimate the optimal number of disks or sectors to sample per leaf and the optimal number of leaves to sample per plant. Here, $S^2{}_i$ are variance components and C_i are cost estimates for various sample units. Costs were estimated from the time required to collect and count individual samples. A nested ANOVA was also used to partition the total variance of counts on leaf disks in commercial fields into within and between site components. We used equation 1 for two-stage sampling to determine the optimal number of disks to sample for eggs and nymphs at each site within a field.

We used Taylor's power law (TPL) (Taylor 1961, 1984), $S^2 = am^b$, where S^2 is variance, m is mean density, and a and b are fitted parameters, to further examine the efficiency of various sample units for estimating egg and nymphal densities. We regressed $\ln(S^2)$ on $\ln(m)$ for data sets from the MAC to compare the relative efficiency of whole leaves, leaf sectors and leaf disks. Following Cochran's (1977, p. 77) formula for sample size (n) and substituting am^b for S^2 from TPL, we calculated the density-dependent minimum sample sizes required to estimate density with a precision of D = (SEM/mean) as:

$$n \geq am^{b-2}/D^2 \quad (2)$$

We then estimated the density-dependent cost of each sample unit by multiplying n by C_i, where C_i is the cost per sample unit i. The 15 commercial field data sets were combined with the 14 data sets from the MAC to estimate the parameters a and b of TPL by regressing $\ln(S^2)$ on $\ln(m)$. Using Green's (1970) modification of Kuno's (1969) method for fixed-precision sequential sampling we constructed separate sequential sampling plans for eggs and nymphs. The critical cumulative count, T_n, as a function of sample size is given by:

$$T_n \geq (an^{1-b}/D^2)^{1/(2-b)} \quad (3)$$

Sample Plan Validation. We evaluated the performance of our sequential plan stop lines through Monte Carlo simulation (Nyrop & Binns 1991). For mean (m) values ranging from 0.5 to 1000, the simulation used TPL to estimate variances (S^2) and then used these values of m and S^2 to calculate density-dependent values of k ($= m^2/[S^2 - m^2]$) to parameterize negative binomial distributions. The influence of errors in TPL regressions were also considered in the simulation based on the assumption that $\ln(S^2)$ for a given $\ln(m)$ were normally distributed

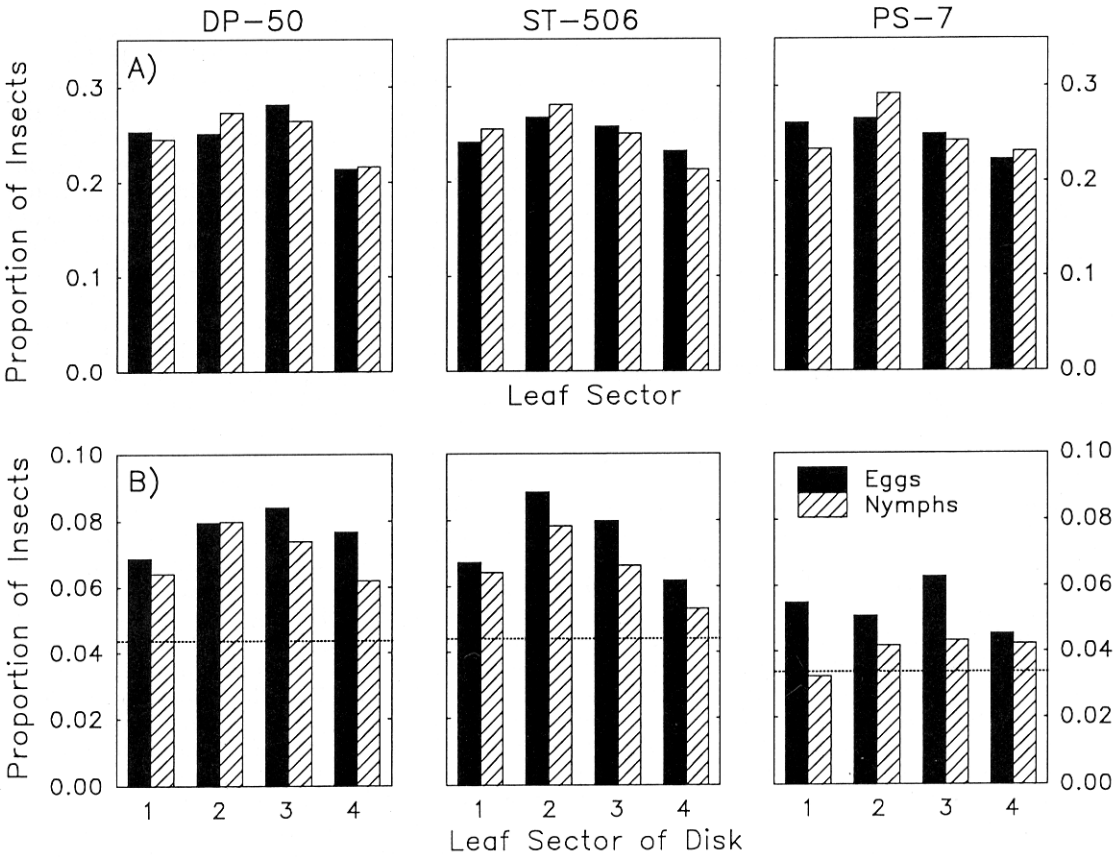

Fig. 2. (A) Distribution of *B. tabaci* eggs and nymphs on the four sectors of whole cotton leaves taken from the second, fifth, and eighth mainstem nodes of three cotton cultivars. (B) Distribution of *B. tabaci* eggs and nymphs on 3.88-cm^2 disks from each of the four sectors of a fifth mainstem node leaf for three cottons. The dotted lines indicate the average proportion of whole leaf area subsumed by the disk. Distributions in A and B are based on total insect counts from four dates.

about the regression line (Nyrop & Binns 1991). The simulation generated random sample points from the negative binomial distribution and accumulated counts until the sequential stop lines terminated sampling. The actual level of precision (SEM/mean) and the number of samples taken were calculated at each iteration. We performed 500 iterations of the simulation and recorded mean values of precision and sample size for each mean tested. After establishing relationships of average precisions and sample sizes with mean density, we then used simulation to estimate the requisite levels of precision that would be necessary to generate stop lines that resulted in actual desired levels of precision. In all analyses the minimum sample size was fixed at 10.

Insect Identity. The DNA pattern of a sample of the sweetpotato whiteflies examined in this study was confirmed by a RAPD-PCR (randomly amplified polymorphic DNA–polymerase chain reaction) assay (Gawel & Bartlett 1993) to be typical of that displayed by Strain B *B. tabaci*.

Results

Within-Leaf and Within-Plant Distributions. The total area of upland cotton (DP-50 and ST-506) leaves was divided approximately equally among the four sectors delineated by the major leaf veins (Fig. 1). The percentage of area subsumed by each sector was (mean ± SEM; $n = 10$) 25.7 ± 0.5, 23.6 ± 0.4, 24.4 ± 0.2, 26.3 ± 0.5% for sectors 1 to 4, respectively. Leaves of PS-7 were larger than upland leaves at the same node and the center two sectors subsumed ≈56% of total leaf area (22.3 ± 0.8, 28.3 ± 0.5, 27.5 ± 0.6, 21.9 ± 0.7%, sectors 1–4, respectively). In general, *B. tabaci* eggs and nymphs were distributed in direct proportion to leaf sector areas (Fig. 2A). The number of eggs per cm^2 did not differ significantly among leaf sectors for any cultivar ($F < 1.38$; df = 3, 181; $P > 0.25$), indicating that eggs are evenly distributed at this scale of resolution. In addition, although egg densities changed with time ($F > 71.47$; df = 3, 26; $P < 0.01$) and across

nodes of the mainstem ($F > 4.16$; df = 2, 29; $P < 0.026$) there were no significant date × sector, node × sector, or node × date × sector interactions ($P > 0.18$). Thus, patterns of oviposition on individual leaves remained constant across the mainstem nodes examined, and over time. Likewise, nymphal densities changed with time ($F > 37.25$; df = 3, 17; $P < 0.01$) and across nodes of the mainstem ($F > 4.04$; df = 2, 20; $P < 0.034$), but the number of nymphs per cm^2 did not differ between sectors of DP-50 and PS-7 leaves ($P > 0.17$), and there were no date × sector, node × sector, or node × date × sector interactions ($P > 0.13$) for these two cultivars. The number of nymphs per cm^2 differed significantly among sectors of ST-506 ($F = 5.37$; df = 3, 140; $P = 0.002$) and the date × sector interaction was also significant ($F = 2.97$; df = 6, 140; $P = 0.01$) indicating that distributions among sectors varied over time for this cultivar. In general, it would be reasonable to extrapolate densities per cm^2 for whole leaves from estimates per cm^2 on individual leaf sectors.

Egg and nymphal counts on leaf disks from each of the four sectors did not vary significantly from one another for any cultivar ($P > 0.14$) and there were no significant two-way or three-way interactions ($P > 0.09$) with date of sample collection or leaf node. The basal portions of the leaf were more densely populated with eggs and nymphs than the remainder of the leaf for all cultivars (Fig. 2B). For example, in DP-50 and ST-506 the 3.88 cm^2 disk subsumed ≈4.5% of the area of a fifth mainstem node leaf, but contained between 6.7 to 8.8% of the eggs and 5.3 to 7.9% of the nymphs on the whole leaf. For the larger Pima PS-7 leaves, the disk subsumed only 3.4% of the area of fifth node leaves and contained 4.5 to 6.3% of the eggs and 3.3 to 4.3% of the nymphs on the whole leaf (Fig. 2B). Pooling counts from all four disks, the density of eggs per cm^2 was significantly greater on disks than the whole leaf for the three cultivars ($F > 9.65$; df = 1, 63; $P < 0.003$). Date interactions ($F > 17.98$; df = 3, 63; $P < 0.0001$) were significant for all cultivars, and node interactions ($F > 14.95$; df = 2, 63; $P < 0.0001$) were significant for the upland cottons. No three-way interactions were significant ($P > 0.22$) for any cultivar. Thus in general, the relationship between the number of eggs per cm^2 on disks and on whole leaves varied over time and also varied by the location of the leaf along the mainstem branch. These effects are probably related to changes in insect density over sample dates and to the changing proportion of area subsumed by disks on larger leaves from nodes further removed from the terminal.

The same general patterns were evident for nymphal distributions. Significantly more nymphs per cm^2 were found on disks than on whole leaves in the upland cottons ($F > 24.56$; df = 2, 48; $P < 0.0001$) and, as with eggs, interactions with both date and node were significant ($F > 4.80$; df = 2, 48; $P < 0.013$). On PS-7 no significant differences were found between disks and whole leaves ($P > 0.08$) and none of the interaction terms were significant ($P > 0.12$).

Significant errors would be incurred if numbers of insects per square centimeter estimated on disks were extrapolated to whole leaves based solely on leaf area, especially for upland cottons. To permit estimation of whole leaf numbers from counts on leaf subunits, we calculated regression equations for various nodes of PS-7 and combined upland cottons (Table 1). Because we had found date to be a significant factor, we used a stepwise procedure (SAS 1985) to determine the best independent variables to include in the regressions. Also, we found that counts from the second or third sector (whole sector or disks) were consistently more highly correlated with whole leaf counts and, therefore, we used leaf subunits from the second sector in our regression analysis. In almost all cases, date, entered as degree-days after planting, did not significantly contribute to the regression models ($P > 0.30$). In the majority of cases, sector or disk counts alone accounted for ≥90% of the variation in whole leaf counts. In only one instance (nymphs on Pima PS-7 leaves from the second node) was the regression nonsignificant ($P = 0.19$). This was due mainly to the low density and inconsistent presence of nymphs on leaves from this node. Also, with few exceptions intercept terms were not significantly different from zero ($P > 0.05$), indicating that in most instances whole leaf counts were directly proportional to sector or disk counts.

As expected, eggs and nymphs of *B. tabaci* exhibited definite differences in density among leaves of the mainstem (Fig. 3). Pooling insect counts over five sample dates, leaves from the third node consistently had the greatest number of eggs regardless of cultivar. This difference was most distinct for DP-50, whereas in ST-506 and PS-7 relatively large numbers of eggs were also found on leaves from nodes two and four. Nymphs occupied leaves further down the mainstem. Overall, the largest number of nymphs were on leaves from the fifth node for all cultivars; however, a relatively large number of nymphs were found on leaves from nodes four, six and seven. Interestingly, the corresponding coefficients of variation (CV = 100%[SD/mean]) were inversely related to insect density (Fig. 3, hatched bars). Counts of eggs from the fourth and fifth nodes had the lowest CVs as did nymphal counts from the fifth and sixth nodes. Pooling cultivars, the third and fifth nodes contained the greatest number of eggs and nymphs, respectively, but the lowest CVs were associated with counts of both stages on leaves from the fifth mainstem node (eggs 170.6%, nymphs 182.1%). Counts on fifth node leaves accounted for over

Table 1. Linear regressions relating densities of *B. tabaci* eggs and nymphs on various leaf subunits to whole leaves, and total densities on mainstem leaves two–eight to fifth node leaves

Cotton	Leaf node	x	Eggs				Nymphs			
			$b \pm$ SEM	a	r^2	n	$b \pm$ SEM	a	r^2	n
			Whole leaf[b] = $a + bx$							
Upland[a]	2	Sector 2	3.32 ± 0.09	65.87*	0.96	64	3.36 ± 0.14	0.64*	0.94	39
		Disk 2	9.51 ± 0.25	48.41*	0.96	64	8.54 ± 0.56	3.67*	0.86	39
	5	Sector 2	4.19 ± 0.15	−30.64*	0.91	77	2.92 ± 0.13	26.66	0.89	64
		Disk 2	10.82 ± 0.43	30.59*	0.89	77	8.22 ± 0.50	42.21	0.82	64
	8	Sector 2	2.69 ± 0.11	46.12	0.91	55	3.81 ± 0.05	0.56*	0.99	58
		Disk 2	7.72 ± 0.29	21.44*	0.96	55	13.16 ± 1.17	4.09*	0.84	58
Pima PS-7	2	Sector 2	4.10 ± 0.18	−14.97*	0.96	21	2.24 ± 0.14	7.17	0.96	14
		Disk 2	17.85 ± 2.00	51.98*	0.81	21	14.24 ± 10.36*	21.15*	0.14	14
	5	Sector 2	3.32 ± 0.14	29.77*	0.97	22	3.59 ± 0.28	−9.79*	0.90	19
		Disk 2	14.39 ± 1.45	24.99*	0.83	22	21.18 ± 2.82	33.56*	0.77	19
	8	Sector 2	3.32 ± 0.24	231.43*	0.90	23	3.18 ± 0.19	24.12*	0.94	22
		Disk 2	16.85 ± 1.32	255.90*	0.89	23	14.67 ± 1.66	56.26*	0.80	22
			Mainstem leaves[c] = $a + bx$							
Upland	5	Leaf	4.02 ± 0.18	169.17	0.86	88	2.86 ± 0.15	47.22	0.81	85
Pima PS-7	5	Leaf	2.80 ± 0.26	299.42	0.84	24	3.26 ± 0.30	48.96*	0.84	24

Asterisks indicate that regression parameters were not significantly greater than zero (t-tests; $P > 0.05$).
[a] DP-50 and ST-506 combined.
[b] Whole leaf counts <1 were excluded from the analyses.
[c] Sum of whole leaf counts from mainstem nodes 2–8. Total mainstem counts <1 were excluded from the analyses.

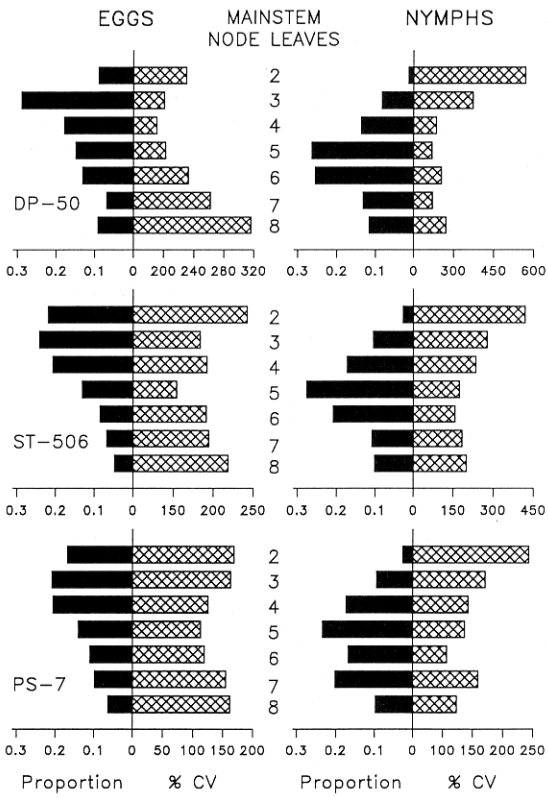

Fig. 3. Distributions of eggs and nymphs of *B. tabaci* on mainstem node leaves and associated coefficients of variance (% CV = SD/mean x 100%) on three cotton cultivars. Distributions are based on total insect counts over five dates.

84% of the variation in total egg and nymphal counts on whole leaves from the second through the eighth nodes (Table 1).

Analysis of variance indicated that distributions of eggs and nymphs along the mainstem were similar among cultivars, but that overall distributions changed with time. Cultivar × node interactions were not significant ($P > 0.08$), but cultivar × node × date interactions were highly significant (eggs: $F = 4.16$; df = 66, 935; $P < 0.01$, nymphs: $F = 7.49$; df = 66, 931; $P < 0.01$). Changes in the distribution of immature *B. tabaci* along the mainstem were primarily associated with overall shifts of eggs and nymphs towards nodes higher on the plant at progressively later sample dates (Fig. 4). Analysis of covariance indicated that neither the slopes ($P > 0.07$) nor the intercepts ($P > 0.07$) of regressions of the nodal position of the most infested leaf on degree-days after planting varied significantly across cultivars. The regression of nodal position of the most infested leaf on degree-days for all cultivars combined was significant for eggs ($F = 5.05$, df = 2, 120; $r^2 = 0.04$; $P = 0.03$) and nymphs ($F = 17.65$, df = 1, 117; $r^2 = 0.13$; $P < 0.01$). Over the course of sampling from mid-June to late-August the average position of the most infested node varied less than one node for eggs and just over one node for nymphs. Plant measurements from the same plots (Flint et al., unpublished data) indicated that the mean (±SEM; $n = 12$) number of mainstem nodes per upland cotton plant increased from 13.9 ± 0.7 in late-June to 21.5 ± 2.3 in mid-August. Similar data are not available for PS-7.

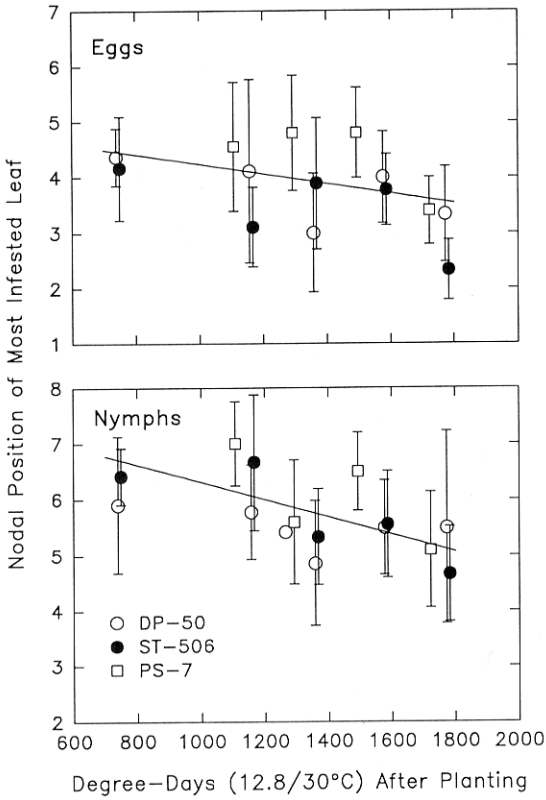

Fig. 4. Relationship between the nodal position of the most infested mainstem leaf and accumulated degree-days for eggs and nymphs of *B. tabaci* on three cottons. Regressions were calculated using all data points, but for clarity only means with 95% confidence limits are plotted.

Variance Partitioning and Optimal Sample Unit. Analysis of variance of sampling data from the MAC indicated that between plant variation was the largest variance component for both egg (>80%) and nymphal (>54%) counts regardless of whether we considered sectors or disks as whole leaf subunits (Table 2). For eggs, progressively smaller variance components were contributed by between-cultivar, between-node, and within-leaf factors. The same was generally true for nymphal counts, with the exception that the between-node component contributed over one-third of the total variation.

The time required to count 3.88-cm^2 leaf disks increased in direct proportion with density and averaged (±SD) 1.7 ± 0.8 min for eggs and 1.2 ± 0.9 min for nymphs for densities from 30–650 eggs and 20–560 nymphs per disk. Based on the distribution of immatures on whole fifth mainstem node leaves (Fig. 2) we estimated the average time to count an individual sector and a whole leaf to be 6.3 and 22.3 min for eggs, and 4.2 and 16.3 min for nymphs. From timed studies of sample collection in commercial fields, it took an average of 0.3 ± 0.1 min to collect a single fifth node leaf and 0.7 ± 0.3 min to move to a new sampling site within a field.

From equation 1, we used estimates of variance components along with these estimates of sampling costs to determine the optimal sample unit for egg and nymphal counts. First, examining whole leaves within-plants, we determined that a single leaf per plant would be the optimal sample unit for either eggs or nymphs. This follows directly from the relatively high cost (time) of sampling whole leaves and the large between-plant variance. Next, considering leaf sectors as whole leaf subunits, our calculations indicated that the most efficient sample unit would be a single sector for both eggs and nymphs. Likewise, considering disks as whole leaf subunits, we calculated the optimal sample unit to be a single disk per leaf for both eggs and nymphs. Given that the lowest CVs were associated with fifth mainstem node, it would be most efficient to take whole leaf, or sector or disk subsamples from leaves at this node.

To examine the relative efficiencies of whole leafs, sectors and disks, we pooled cultivars and used TPL to estimate separate mean variance

Table 2. Analysis of variance of *B. tabaci* counts made at the Maricopa Agricultural Center, Maricopa, AZ, 1993

Source	df	Sector subunits			Disk subunits		
		MS	Variance component	% Total variance	MS	Variance component	% Total variance
Eggs							
Between cultivars	2	355.50	0.64	10.26	189.22	0.32	7.72
Between plants	123	58.75	5.07	80.48	39.60	3.40	80.73
Between nodes	229	1.70	0.37	5.94	1.38	0.30	7.06
Within leaves	1065	0.21	0.21	3.32	0.19	0.19	4.49
Total	1419	6.03	6.30	100.00	4.06	4.21	100.00
Nymphs							
Between cultivars	2	121.43	0.21	6.12	25.54	0.03	1.52
Between plants	123	25.92	1.88	55.50	13.11	0.94	54.39
Between nodes	229	4.72	1.14	33.63	2.57	0.60	35.07
Within leaves	1065	0.16	0.16	4.75	0.16	0.16	9.02
Total	1419	3.30	3.39	100.00	1.70	1.72	100.00

Table 3. Parameters of Taylor's power law for eggs and nymphs of *B. tabaci* estimated for different sample unit sizes

Sample unit[a]	ln[a] ± SEM (ln[a])	b ± SEM (b)	r^2	n
		Plot data set[b]		
Eggs				
Disk	1.158 ± 0.273	1.617 ± 0.061	0.983	14
Sector	1.000 ± 0.290	1.666 ± 0.066	0.985	11
Whole leaf	−0.196 ± 0.464	1.901 ± 0.084	0.981	11
Nymphs				
Disk	0.856 ± 0.204	1.556 ± 0.057	0.984	14
Sector	0.704 ± 0.235	1.575 ± 0.065	0.986	11
Whole leaf	−0.600 ± 0.339	1.889 ± 0.073	0.987	11
		Combined data set[c]		
Eggs	1.094 ± 0.328	1.766 ± 0.064	0.965	29
Nymphs	0.931 ± 0.248	1.688 ± 0.058	0.968	29

TPL parameters were estimated by linearizing $S^2 = am^b$, where m is mean density and S^2 is the variance.
[a] All sample units taken from the fifth mainstem node down from the terminal. Leaf subunits taken from the second sector.
[b] Plot samples from the Maricopa Agriculture Center, Maricopa, AZ.
[c] Plot samples plus commercial field samples (disks only) from Maricopa and Pinal counties, AZ.

relationships for whole leaves, second sector, and second sector disk subunits (see Fig. 1) from the fifth mainstem node. Parameters are given in Table 3. Too few data points were available to calculate separate regressions for each cultivar; however, examination of scatter plots (not shown) suggested no obvious departure of any one cultivar from a single overall regression. Using equation 2 we then calculated the density-dependent minimum sample size that would be required for each sample unit to estimate mean densities with a precision of 0.25 (Fig. 5). Based strictly on the size of the sample, whole leaf counts were most efficient at egg or nymphal densities up to ≈1,000 per leaf, followed by sector and disk counts, respectively. However, this pattern was essentially reversed when sampling costs were considered. Summing the time re-

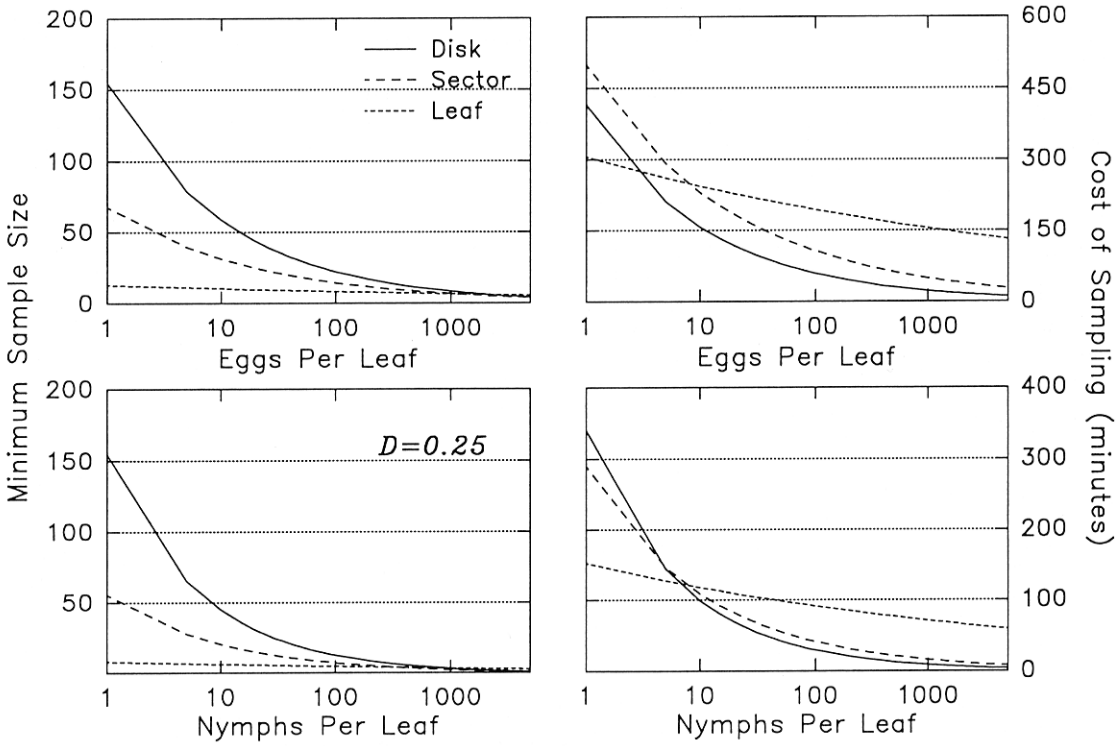

Fig. 5. Density-dependent minimum sample sizes and costs required to estimate densities of *B. tabaci* eggs and nymphs with a precision of 0.25 (SEM/mean) using three different sample units (one leaf, one sector, or one disk per plant). The cost of single disk, sector, and whole leaf counts were 2.7, 7.4, and 23.3 min for eggs and 2.2, 5.2, and 17.3 min for nymphs. These costs include the time required to collect and count samples.

Table 4. Analysis of variance of *B. tabaci* counts in commercial fields, Maricopa and Pinal counties, AZ

Source[a]	df	Eggs			Nymphs		
		MS	Variance component	% Total variance	MS	Variance component	% Total variance
Between fields	14	36.35	0.67	31.00	82.73	1.61	59.38
Between sites	135	2.79	0.32	14.98	2.21	0.28	10.22
Within sites	600	1.17	1.17	54.01	0.82	0.82	30.40
Total	749	2.12	2.17	100.00	2.61	2.71	100.00

[a]Based on 3.88-cm^2 disks taken from the proximal portion of the second sector of the fifth mainstem node leaf.

quired to collect samples from the field and to count them in the laboratory, disks, sectors and whole leaves required a mean of 2.7, 7.4, and 23.3 min to process for eggs and 2.2, 5.2, and 17.3 min for nymphs. Whole leaves are more cost efficient at extremely low densities (<10 eggs or nymphs per leaf); however, leaf disks are most cost efficient at all higher densities (Fig. 5). The cost of using sector counts was only slightly higher than disks for nymphs at densities >10 nymphs per leaf. Based on the analyses presented in this section we concluded that a single leaf disk from the second sector of a fifth mainstem node leaf would be the optimal sample unit per plant for estimating the density of both eggs and nymphs.

Within-Field Distribution. Using a single disk from the fifth leaf, we then examined within-field distributions of *B. tabaci* eggs and nymphs in commercial production fields. Analysis of variance for eggs revealed that the largest variance component was associated with variation among the disks taken from five consecutive plants at each sample site within a field (54%), and the smallest component was associated with between site (within a field) variability (15%) (Table 4). Similarly, between-site variability was the smallest component for nymphs (10%), but the greatest variability was associated with the between-field component (60%). From equation 1, we determined that a single disk per site within a field would be the most efficient sample unit for both eggs and nymphs. This resulted from the relatively high cost of counting a disk in relation to the low cost of moving to a new sampling site within the field.

Sequential Sampling Plan. In total, 29 field-date data points from plot studies at the MAC and the 15 commercial fields sampled were used to estimate TPL relationships for eggs and nymphs based on second sector leaf disks from the fifth mainstem node. *B. tabaci* populations at the MAC increased in an exponential fashion from 17 June to 25 August (mean ± SEM per disk, n = 10–24) (DP-50: eggs, 0.6 ± 0.4 to 997.7 ± 256.7; nymphs, 0.1 ± 0.1 to 475.7 ± 84.7; ST-506: eggs, 0.04 ± 0.06 to 746.7 ± 85.9; nymphs, 0.04 ± 0.06 to 332.2 ± 31.5; PS-7: eggs, 0.6 ± 0.4 to 913.5 ± 120.2; nymphs, 0.4 ± 0.2 to 281.4 ± 51.0). Population densities in the commercial fields ranged from 67.2 ± 13.0 to 1438.6 ± 374.7 per disk for eggs and from 23.7 ± 7.3 to 781.7 ± 170.3 for nymphs. Our TPL regressions were based on a range of densities spanning five orders of magnitude.

Coefficients of determination for TPL regressions exceeded 96% (Table 3, bottom). Initially, we calculated separate ln-ln regressions for the MAC plot and commercial field data sets; however, a test for heterogeneity of regression lines indicated that neither the slopes (=Taylor's b) ($P > 0.08$) nor the intercepts ($P > 0.08$) were significantly different from one another for either immature stage. Following Green's (1970) method (equation 3) we calculated sequential sampling stop lines for both immature stages as functions of sample size for fixed-precisions of 0.1 and 0.25 (Fig. 6). Stop lines for alternative precision values could be easily calculated from equation 3 and parameters a and b presented in Table 3. In general, a smaller sampling effort would be needed to estimate nymphal densities in comparison with eggs, particularly at higher levels of precision. For instance, a sample of ≈20

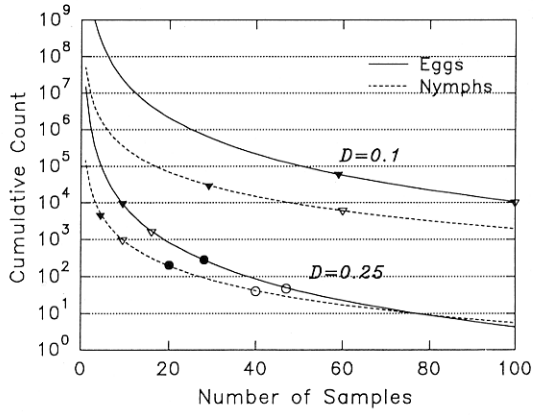

Fig. 6. Sequential sampling stop lines for estimating densities of *B. tabaci* eggs and nymphs at fixed precisions of 0.1 and 0.25 (Kuno 1969) using Taylor's power law to represent the mean–variance relationship (Green 1970). The sample unit is a 3.88-cm^2 disk from the basal portion of the second sector of the fifth mainstem node leaf (see Fig. 1). Open circles, solid circles, open triangles, and solid triangles denote mean densities of 1, 10, 100, and 1,000, respectively.

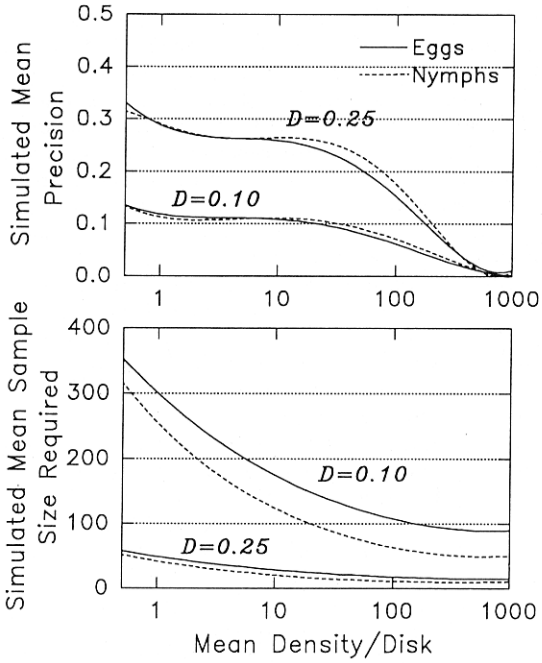

Fig. 7. Mean precision levels and mean sample sizes necessary to obtain specified levels of precision from Monte Carlo simulations using sequential sampling plans for eggs and nymphs of *B. tabaci* over a range of mean densities typical of field populations. Simulations assumed an underlying negative binomial distribution with a density-dependent *k* parameter and incorporated variability in the TPL mean-variance regression. Results are based on 500 iterations per mean value and fixed precisions (D) of 0.10 and 0.25. Minimum sample size was 10.

leaf disks would be required to estimate mean nymphal densities of 10 per disk with a precision of 0.25, but a sample size of 28 would be required to estimate the same mean density of eggs (Fig. 6, solid circles). This is largely a function of the lower levels of aggregation for nymphs as indicated by the smaller value of Taylor's *b*.

Sample Plan Validation. Monte Carlo simulations revealed that actual levels of sampling precision only approximate those specified, with actual levels deviating considerably from specified levels at high population densities (Fig. 7). Based on a mean of 500 simulations, precision was poorer than a specified 0.25 at densities <7 per disk. Conversely, actual mean precision was better than 0.25 at densities greater than about 20 per disk and was <0.01 at densities over 700–800 per disk. This pattern was similar for a specified precision of 0.1, although actual precision remained near 0.1 over a wider range of densities. At densities ≤1 insect per disk average sample sizes of >40 were required for a precision of 0.25. Fewer than 15 leaf disks were required at densities >200 per disk. At a specified precision of 0.1, an average sample size >300 would be required to estimate densities ≤1 and >50 or 90 leaf disks would be required on average to estimate nymphal and egg densities, respectively, >500 per disk.

Because actual and specified levels of precision differed over a wide range of densities, we performed further simulations to calculate the levels of precision that would need to be specified to generate stop lines with the desired average behavior over a range of densities (Table 5). For example, at mean densities of <1 and a desired precision of 0.25, stop lines should be generated with a precision of 0.2, but a specified precision of 0.3 would be sufficient to generate stop lines for densities >50. Only at relatively moderate densities (20–40 per disk) were the specified and desired level of precision the same (Table 5).

Discussion

We showed that *B. tabaci* eggs and nymphs had definitive, and fairly predictable distributional patterns within individual cotton plants in the deserts of south-central Arizona. Leaves from mainstem nodes 2–4 (from the terminal) consistently had the greatest number of eggs, and although there was considerable plant to plant variation in the location of the most infested leaf, the mean position of this leaf shifted only one node over a 2-mo period from mid-June to late-August. This coincided with an increase in the mean number of mainstem nodes from about

Table 5. Simulation analysis to estimate requisite levels of precision to generate sequential sampling stop lines with an actual level of precision near 0.25 for different density classes of *B. tabaci* eggs and nymphs. Results are based on 500 iterations per mean value and a minimum sample size of 10 disks

Mean/disk	Eggs			Nymphs		
	Specified precision	Mean actual precision[a]	Mean sample size[a]	Specified precision	Mean actual precision[a]	Mean sample size[a]
0.5–09	0.20	0.26–0.24	87–78	0.20	0.26–0.24	80–67
1–10	0.22	0.26–0.23	63–37	0.225	0.25–0.24	52–25
20–40	0.25	0.25–0.22	25–21	0.25	0.26–0.24	17–14
50–100	0.30	0.24–0.18	14–12	0.30	0.25–0.19	10
>100	0.40	0.20	10	0.30	0.19	10

[a] Range of means associated with specified range of mean densities.

14 to 22 during roughly the same time interval. Leaves from nodes 4–7 contained the most nymphs and again the mean position of the most infested leaf only declined one node over two months. Ohnesorge & Rapp (1986) concluded that sampling for third and fourth instars should be confined to mainstem nodes 3–7, and they also found a slight shift in the position of the most infested leaf up the plant over time. In contrast, Gerling et al. (1980) reported that the mean position of the most infested leaf for pupae shifted from the sixth node in July down to the eleventh node in August, and Melamed-Madjar et al. (1982) reported a similar shift for nymphs (all instars) from the fifth-sixth node in June to the seventh-eighth node in July. These differences are probably related in part to different cultivars and weather conditions that change the relationship between insect development and plant growth. Similar to other studies (e.g., Melamed-Madjar et al. 1982, Ohnesorge & Rapp 1986), we choose to define the position of the most infested leaf from the terminal down. This accelerates the collection of leaves for sampling and avoids the problem of miscounting nodes from the ground when older mainstem leaves have abscised.

Most published sampling studies have focused on defining the position of the most infested leaf. However, from a sampling perspective, more important than the location of this leaf is the location of the least variable leaf. We found a consistent negative relationship between immature densities and CVs (SD/mean) on leaves from given mainstem nodes, with counts from the most infested leaf generally having the lowest CV. This same property was reported for sampling of *B. tabaci* pupae (von Arx et al. 1984). Although counting immatures on the most infested leaf may be more time-consuming, the lower variation of counts from these leaves would require fewer samples to obtain density estimates with the same precision. We found that the location of the most infested leaf for eggs was the third node, however, the lowest CVs were estimated from nodes 4–5. This finding, along with the fact that simultaneous counts of eggs and nymphs from the same disk were faster than individual counts for each stage, was the main reason for selecting fifth mainstem node leaves as the location of the sample unit for our sample plans.

Within individual leaves, *B. tabaci* immatures were evenly distributed between sectors on the basis of leaf area. A similar conclusion was reported for leaf sectors by von Arx et al. (1984) for *B. tabaci* pupae on two cultivars of cotton in Sudan. In contrast, Ohnesorge and Rapp (1986) determined that third and fourth instar nymphs were found in disproportionately higher numbers on the distal (sectors 2 and 3) sectors of an upland cotton in comparison with the proximal sectors and Rao et al. (1991) reported that nymphs were more abundant on the left half of the leaf (sectors 1 and 2) and generally more abundant on proximal sectors. However, Rao et al. (1991) did not report sector areas or account for differences in sector area in their analysis. We found that immatures were nonrandomly distributed on whole cotton leaves with eggs and nymphs aggregated near the petiole. As a result, counts on disks from the base of the leaf, in contrast to counts on leaf sectors, cannot be directly converted to counts per whole leaf simply on the basis of area. However, disk counts were highly correlated with whole leaf counts and regression analysis revealed that >82 and 77% of the variation in fifth node whole leaf counts could be explained by second sector disk counts from upland and pima cottons, respectively. In turn, >81% of the variation in immature counts from the first eight mainstem nodes combined was explained by whole leaf counts from the fifth node. Because we did not count eggs and nymphs on the whole plant, relationships between the various sample unit counts and absolute population densities currently cannot be determined. However, several studies have indicated that mainstem leaves harbor a large fraction of the insects on whole cotton plants. Ohnesorge & Rapp (1986) found that ≈26% of all late instar nymphs inhabited leaves on mainstem nodes 3–7 and von Arx et al. (1984) reported that ≈50% of *B. tabaci* pupae on a plant are found on mainstem leaves. Counts from mainstem leaves are probably indicative of whole plant populations. Although our sample plan may not be adequate for detailed population studies (e.g., life tables), they should be useful in comparative studies of population dynamics and in assessing relative densities for pest management application.

The merits of using whole leaf, sector, or disk counts for estimating immature densities depends on the variance properties and costs associated with each sample unit. Taking sample cost into consideration, variance partitioning revealed that only one leaf, sector, or disk should be selected per plant. This resulted mainly from high plant to plant variation. Likewise, Ohnesorge & Rapp (1986) concluded that a single sample per plant was best for estimating the densities of third and fourth instars. Further analysis using Taylor's mean–variance relationship suggested that leaf disks were the most efficient sample unit over a broad range of densities for eggs and nymphs. Also, we have found that accuracy between counters is better when using smaller sample units such as leaf disks. Finally, our results of calculating TPL coefficients for whole leaves and leaf subunits supports the conclusion of recent simulation analyses that the magnitude of Taylor's b appears to be sample unit size dependent (Sawyer 1989). Thus, it

would be important to maintain a consistent sample unit if Taylor's *b* was being used as an index of aggregation for comparative studies of *B. tabaci* distributional patterns.

Simulation analyses reinforced the fact that sample size requirements and true levels of precision for any one sampling effort may depart significantly from those specified by the plan (Hutchison et al. 1988, Nyrop & Binns 1991). This stochastic feature derives from inherent properties of the sequential sampling procedure and the error associated with TPL regressions relating variances to means (Hutchison et al. 1988). To provide a preliminary validation of our sampling plans we used a simulation procedure that included stochastic variation in our TPL regression model and drew random samples from populations with negative binomial distributions incorporating a density-dependent *k* value. Our analyses demonstrated that specified levels of precision may be realized over only a fairly restricted range of densities. For example, at densities of eggs or nymphs <10 our plan would require too few samples to achieve the desired precision, but at densities >100 more samples than necessary would be specified. This general pattern of poorer than expected and better than expected precision at low and high densities, respectively, has been demonstrated using the same validation procedure for other sampling plans (Trumble et al. 1989). Further, this deviation can be acerbated by the inclusion of variation in the TPL regression, particularly at low densities. Nyrop & Binns (1991) point out that the density-dependent *k* parameter of the negative binomial may vary abnormally at low densities when the variance is calculated as a stochastic function based on the TPL regression. Thus, the poorer mean precision calculated by simulation may not accurately reflect the performance of the sampling plan at low densities. Nonetheless, until our sampling plan can be tested against actual field data we feel that a more conservative approach may be warranted at low population densities. Thus, to achieve, for example, a nominal precision of 0.25 we recommend that sequential plan stop lines be generated with specified precisions of 0.20–0.22 at low densities. The better than expected precisions at higher densities is partly the result of the imposition of a minimum sample size of 10. Regardless, adjustments in the specified level of precision are less important at higher densities because sample size requirements change relatively little at densities >50 per disk (see Table 5 and Fig. 7).

Our simulation analyses should not be considered a rigorous validation of the sample plan. Recent analyses (Trumble et al. 1989) suggest that temporal and spatial variability in the underlying mean–variance relationship may limit the development of robust sequential sampling plans that are applicable from year to year and from one geographic locale to the next. Our sequential plans are based on sample data collected during a fairly restricted period and within a relatively small geographical area. Further testing, with actual field data collected over a wider geographic area will be necessary to adequately test the performance and operating characteristics of our sample plans. Once we have a better understanding of the relationship between *B. tabaci* abundance and crop damage, sampling research for pest management application should emphasize the development of decision rules that integrate estimates of density with economic thresholds for pest control (Binns & Nyrop 1992). For such applications it may be most efficient to develop and evaluate binomial sampling plans that use presence–absence or densities above a specified tally threshold to determine whether a sample unit is infested. This approach would further reduce sampling effort but still provide the necessary precision for pest control decision-making.

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