# Population Dynamics and Within-Plant Distribution of the Mite *Calacarus flagelliseta* (Acari: Eriophyidae) on Papaya in Hawaii

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J. Econ. Entomol. 97(5): 1563–1569 (2004)

**ABSTRACT** An important element in developing a management strategy for a new pest is the study of its seasonal dynamics and within-plant distribution. Here, we studied the mite *Calacarus flagelliseta* Fletchmann, De Moraes & Barbosa on papaya, *Papaya carica* L. (Caricaceae), in Hawaii to quantify 1) patterns of seasonal abundance, 2) its distribution across different vertical strata of the papaya canopy, and 3) shifts in its use of the upper versus the lower surfaces of papaya leaves. Nondestructive sampling conducted in two papaya plantings revealed that 1) populations of *C. flagelliseta* peak during the summer; 2) mites are most abundant in the middle and lower strata of the plant canopy, and least abundant on the youngest leaves found in the upper canopy; and 3) mites are found more predominantly on the upper leaf surfaces when overall population density peaks, suggesting that individuals move from the lower to the upper leaf surfaces when food resources on the lower leaf surface have been exploited by conspecifics. These results have significant implications for the development of sampling plans for *C. flagelliseta* in papaya.

**KEY WORDS** herbivorous mite, papaya, sampling technique, within-plant distribution

MITES IN THE SUPERFAMILY Eriophyoidea are important pests in agricultural systems (Jeppson et al. 1975, Lindquist et al. 1996). The minute size of these sucking herbivores makes it difficult to quantify their within-plant distribution and seasonal patterns of abundance, but these aspects of their biology are critical to devising sampling plans and formulating management recommendations (Perring et al. 1996).

Despite the fact that most eriophyid mites have limited ability to walk across the plant surface and are dispersed passively on air currents (Sabelis and Bruin 1996), most studies have shown that the spatial distribution of these mites on their host plants tends to be nonrandom. For instance, Muraleedharan et al. (1988) examined the distribution of three eriophyoids on tea and found that two species were concentrated on the upper or middle canopies of the bushes, whereas the third species was distributed more evenly across the different plant strata. Pena and Baranowski (1990) demonstrated that the middle canopy of lime trees harbored higher densities of the citrus rust mite, *Phyllocoptruta oleivora* (Ashmead), than the leaves from the upper or lower canopies.

We examined the within-plant distribution of *Calacarus flagelliseta* Fletchmann, De Moraes & Barbosa (Acari: Eriophyidae), a mite attacking papaya, *Papaya carica* L. (Caricaceae), foliage in Hawaii, United States, and Brazil (Hamasaki and Heu 1991, Fletchmann et al. 2001) and believed to be host-specific (J. Amrine, personal communication). Adults are 220–246 $\mu$m in length, fusiform, and grayish brown with white longitudinal wax bands (Fletchmann et al. 2001). It was first reported in Hawaii in the early 1990s (Hamasaki and Heu 1991) and mistakenly identified as *Calacarus brionesae* Keifer (J. Amrine, personal communication). Today, *C. flagelliseta* is a key pest of papaya in Hawaii. It punctures the first layer of epidermal cells of papaya leaves with its cheliceral stylet-like mouthparts and sucks out the cell contents, eventually producing discolored areas on the leaf (Jeppson et al. 1975). High populations of this mite can cause papaya leaf margins to roll into tubes (Fournier et al. 2003). *C. flagelliseta* accelerates leaf senescence and reduces fruit yield by 30% (V.F. et al., unpublished data). No natural enemies of *C. flagelliseta* have been found in Hawaii (V.F., personal observation). The basic biology and ecology of *C. flagelliseta* remain poorly studied. Papaya growers routinely apply pesticides, usually sulfur, to prevent *C. flagelliseta* outbreaks (V.F., personal observation).

In this study, we investigated the seasonal dynamics and within-plant distribution of *C. flagelliseta.* We first developed a sampling technique that allowed us to

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0022-0493/04/1563–1569$04.00/0 

quantify mite density nondestructively in the field. We then used this technique in two experimental papaya plantings to address three objectives: 1) to quantify the seasonal abundance of *C. flagelliseta*, 2) to determine whether mite density varies across different vertical strata of the papaya canopy, and 3) to examine seasonal shifts in the use of the upper versus the lower surfaces of papaya leaves.

## Materials and Methods

**Host Plant.** *P. carica* is a short-lived perennial, native to Central America (Storey 1976) and introduced into Hawaii some 200 yr ago (Yee et al. 1970). It is a fast-growing herbaceous plant that starts producing fruit within the first year after planting and yields fruit year-round. Papaya trees in commercial orchards typically consist of a single erect stem up to 4 m in height with a terminal crown of ≈20–40 large, palmately lobed leaves. Trees are usually grown for 3 yr, after which they become too tall to be efficiently harvested. New papaya leaves are produced year-round, emerging from the growing tip of the trunk. Thus, young leaves are located in the upper canopy, and old leaves are found in the lower canopy. The life span of a papaya leaf can reach 6 mo when herbivorous mites and other pests, such as powdery mildew, are suppressed (V.F. et al., unpublished data).

**Sampling Technique.** Obtaining a rapid and accurate estimate of eriophyid abundance can be challenging (Hall et al. 1991, 1994; Rogers et al. 1994; Perring et al. 1996). Because *C. flagelliseta* can reach densities as high as 290,000 individuals on a single leaf (unpublished data), we needed to develop a subsampling technique to accurately estimate its abundance on individual leaves. Moreover, our aim was to count the mites in the field, without removing foliage. As a sampling unit, we used a 2.54 by 2.54-cm grid mounted to a hand lens (4× collapsible magnifier, Bioquip Products Inc., Gardena CA). For each leaf, we randomly selected the location of five samples (one sample was equal to one grid) on the upper leaf surface, and five on the lower leaf surface (total of 10 samples per leaf). We counted all motile individuals (nymphs and adults) within the grid. When densities were high (≥100 individuals within the grid), we counted mites in only one-quarter (location randomly chosen) of the grid and multiplied by four to estimate the population within the full grid.

To characterize the subsampling technique, we compared counts obtained with this method to counts obtained in the laboratory. We selected 16 papaya leaves that seemed to harbor a wide range of rust mite densities. For each of these leaves, we first applied our subsampling procedure in the field as described above. We then put each leaf in an individual plastic bag and transported the bags in a cooler to the laboratory, where we measured the length of each leaf's midrib. To collect the rust mites off each leaf, we placed the leaf in a 1-liter jar filled with water and five drops of domestic bleach (2.25% sodium hypochlorite). The jar was shaken for 2 min and poured over a sieve (400 meshes per centimeter). Leaves were also hand rinsed over the sieve under a gentle trickle of water. Finally, the sieve contents were collected into vials and stored in 70% ethanol. We used a subsampling procedure to count all motile stages of rust mites in the alcohol samples. The contents of each vial were poured into a larger container, and water was added to obtain a known total volume (20–60 ml). The sample was then placed on a stir plate, and the contents were stirred gently with a small stir bar. One percent of the total volume was then removed with a micropipetter, and mites were counted under a dissecting microscope. For each vial, we repeated this step, i.e., counting the rust mites in 1% of the total volume, three times, and the mean was taken. Density on the whole leaf was estimated by multiplying by 100 the mean number of mites.

We used the observed relationship between the midrib length of a papaya leaf and its total surface area (area $-1{,}584.6 + 88.1$ [midrib length in centimeters]; $R^2 = 0.87$; $F_{1,74} = 506$; $P < 0.0001$) to estimate the surface area of each sampled leaf. We obtained this relationship by measuring the midribs of 75 leaves and measuring their total area using a leaf area meter (LI-3000, LI-COR, Lincoln, NE).

**Within-Plant Distribution over Time.** Our research was carried out at the University of Hawaii Poamoho Experimental Station on Oahu, HI. We repeated the same descriptive study twice (years 1 and 2) in pesticide-free papaya plots.

*Year 1.* In June 2000, we selected 10 plants (9 mo old, 2 m in height, Solo variety, 'X77′) from a papaya field, and these same 10 plants were periodically sampled over an 8-mo period (sample dates: 11 June, 26 July, 22 August, 22 September, 22 November 2000, and 22 January 2001). Counts were performed nondestructively in the field. For each plant, rust mite densities were estimated on every third leaf, beginning from the oldest (but not fully senescent leaf; a leaf was considered "fully senescent" when its entire surface was yellow) and ending with the newest leaf whose midrib length was ≥12 cm (fully expanded leaves generally have midribs ≥30 cm in length). Papaya plants in our experimental plot had on average 15–24 leaves (midrib length ≥12 cm), so that a total of five to eight leaves per plant were sampled for *C. flagelliseta.* These leaves were later assigned to the lower (1–3 oldest sampled leaves), the mid- (2–3 mid-age sampled leaves), or the upper (two youngest sampled leaves) canopy. Mite density per leaf was estimated using the subsampling technique described above.

*Year 2.* The design and methodology for the second year were as described above for year 1 with the following modifications. In April 2001, we selected 12 papaya plants (5 mo-old, 1 m in height, Solo variety, 'X-77′), and these same 12 plants were resampled once a month across 13 mo (4 April 2001–4 April 2002).

**Statistical Analysis.** We analyzed each year separately. We compared mite populations (cumulative mite-days as dependent variable) across the different canopy strata using repeated measures multiple analysis of variance (MANOVA) (SAS Institute 2000),

with canopy stratum (three strata) as the main effect; $\alpha$ level = 0.05. We calculated mite-days by using the formula $(X_{i+1} - X_i)\ (Y_i + Y_{i+1})/2$, where $X_i$ and $X_{i+1}$ are consecutive sampling dates and $Y_i$ and $Y_{i+1}$ are the corresponding estimates of mite density (Ruppel 1983), and we summed mite-days across the duration of our sampling period to obtain a measure of time-cumulative population size. We compared cumulative mite-days in the lower, mid-, and upper canopy by using Tukey–Kramer tests (SAS Institute 2000).

We performed time series analyses (STATA 2003) to test whether the proportion of all *C. flagelliseta* found on the upper leaf surface was influenced by the total density of mites per leaf. For each year, the following regression was estimated separately for each canopy level:

$$\Pr op_t^l = \sum_{l=L}^{H} \beta_1 Pop_t^l + \sum_{l=L}^{H} \gamma_l Pop2_t^l + \beta_l \Pr op_{t-1}^l + e_t^l \quad [1]$$

where $\Pr op_t^l$ is the proportion of rust mites living on the upper surface of leaves from canopy level $l$ ($l$ indicates if the variable was observed in the high [H], mid- [M], or low [L] canopy), $t$ is the month the sampling was performed, $t-1$ is the previous sampling date to $t$, $Pop_t^l$ is the total density of mites per leaf observed in canopy level $l$ for the month $t$, and $e$ is the residual. Proportions of mites on the upper surface were calculated by averaging the proportions for all the leaves sampled in each canopy stratum. To complement the time series analyses, we ran a multiple regression for each sampling date (year 1, six sampling dates; year 2, 13 sampling dates) by using 1) total density of mites (as a continuous variable) and 2) canopy level (as a nominal variable) as independent variables (SAS Institute 2000). Each stratum contributed a single observation (year 1, $N = 3$ strata $\times$ 10 trees; year 2, $N = 3$ strata $\times$ 12 trees). We corrected the critical alpha level (0.05) for multiple tests by using the sequential Bonferroni technique (Rice 1989).

## Results

Rust mite density estimates obtained with the in-field subsampling technique were positively correlated with the densities measured in the laboratory ($F_{1,15} = 25.4$; $P = 0.0002$; $R^2 = 0.64$; Fig. 1).

Similar patterns of seasonal dynamics and within-plant distribution were observed in both years of the study. First, we found that rust mite densities varied seasonally (MANOVA, time effect, year 1: $F_{5,20} = 5.7$; $P = 0.002$; year 2: $F_{12,22} = 31.9$; $P = 0.0001$; Fig. 2). In both years, mite populations peaked in July (Fig. 2). In year 2, mite numbers also reached a second, smaller peak during the winter (Fig. 2B). In both years there was also a significant effect of vertical canopy stratum on mite density (MANOVA on cumulative rust mite-days, year 1: $F_{2,24} = 41.7$; $P = 0.0001$; year 2: $F_{2,33} = 68.3$; $P = 0.0001$). The young leaves located in the upper canopy harbored consistently lower densities of rust mites than leaves in the middle or lower canopy (Fig. 2). In year 1, mite densities in the mid- and the lower canopy were similar (Fig. 2A), whereas in year 2 the lower canopy harbored significantly higher mite densities than did the mid-canopy (Fig. 2B).

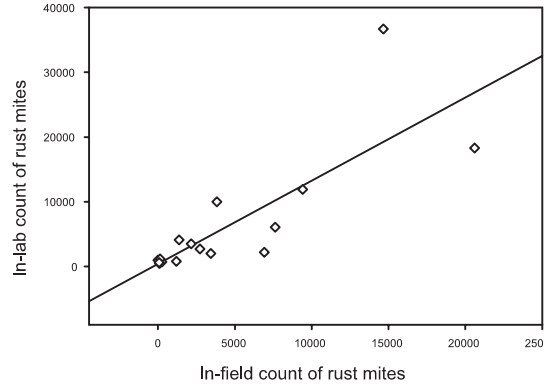


**Fig. 1.** Relationship between *C. flagelliseta* counts per leaf obtained using the subsampling technique in the field, and full counts performed in the laboratory ($N = 16$). y = 413.4 + 1.3x; $R^2 = 0.64$; $F_{1,15} = 25.4$; $P = 0.0002$.

The distribution of *C. flagelliseta* across the upper versus lower surfaces of leaves was highly variable across the 2 yr of study, seasonally, and across vertical plant strata (Figs. 3 and 4). There was, however, a general pattern for a larger proportion of the rust mites to be present on the upper surface of leaves when the overall mite population densities were very high (Fig. 5). For both years, time series analyses revealed that the proportion of mites found on the upper leaf surface was positively correlated with total mite densities in the lower section of the canopy only (Table 1). Moreover, the relationship seemed to be nonlinear (Table 1): as total rust mite densities increase, more individuals tend to inhabit the upper leaf surface until it reaches a plateau. When regressions were performed separately for each date, we found that the effect of mite density was expressed predominantly at times when overall mite densities were relatively high: for year 1, the density effects was significant in June ($P < 0.05$) and nonsignificant in July, August, September, and November 2000 and January 2001 ($P > 0.05$); for year 2, density effects were significant in June, July, August, September, and October 2001 ($P < 0.05$), and nonsignificant for April, May, November, and December 2001, and January, February, March, and April 2002 ($P > 0.05$). Also, when regressions were performed separately for each date, the effect of canopy strata was significant in most cases (year 1, July, August, and September 2000; year 2, April May, June, August, September, October, and December 2001, and January and March 2002; $P < 0.05$), and nonsignificant in few instances (year 1, June 2000; year 2, July and November 2001; $P > 0.05$).

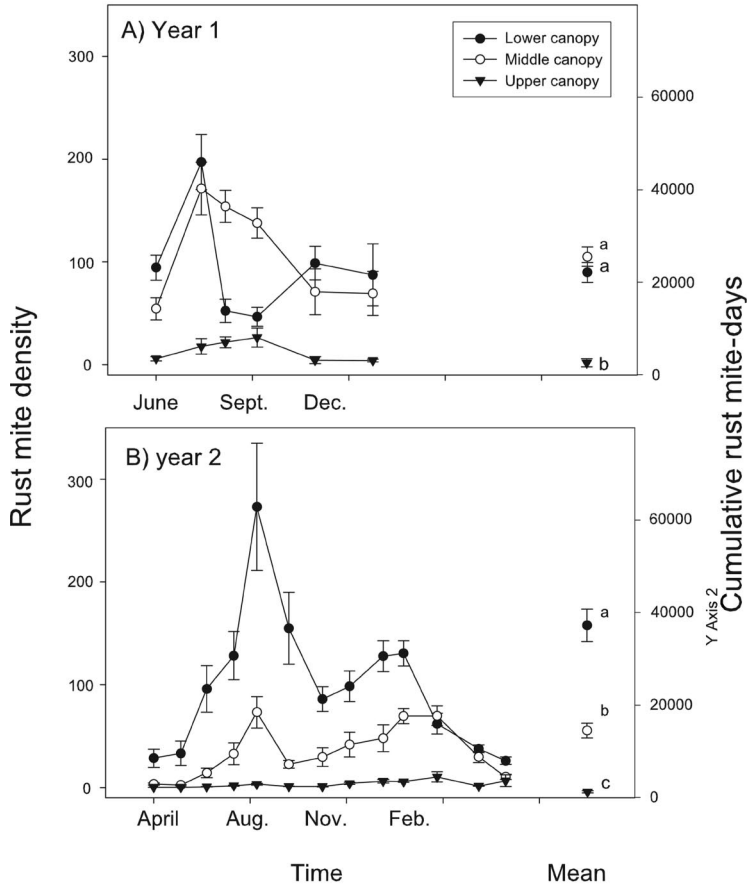


**Fig. 2.** Density of *C. flagelliseta* (total number of motile instars per subsampling unit, mean ± SE), and cumulative mite-days (mean ± SE) (yy axis) from (A) June 2000 to January 2001 (year 1) and (B) April 2001 to April 2002 (year 2), on papaya leaves located in three different plant strata. Within each year, cumulative mite-days with the same letter are not significantly different (Tukey–Kramer test, $P \geq 0.05$). In some cases, the error bars are too small to be shown.

## Discussion

In this study, we found that population densities of *C. flagelliseta* peaked during the summer. Mites were most abundant in the mid- and lower vertical strata of the plant canopy and least abundant on the youngest leaves found in the upper canopy (Fig. 2). Finally, when populations reach relatively high densities in the lower plant canopy, mites tended to move from the lower to the upper leaf surfaces in response to leaf overexploitation (Fig. 5; Table 1).

*C. flagelliseta* is present year-round, and its population densities vary seasonally, with the highest densities occurring in the summer, and the lowest densities in the late winter (Fig. 2B). The weather may contribute to this seasonal variation. Although seasonal temperature fluctuations within the tropics are less dramatic than in temperate regions, summer at our field site on Oahu, HI, is both warmer and dryer than winter (Armstrong and Bier 1983) and may therefore be more favorable for mite population growth. The sharp decline in rust mite densities that followed the summer peak in both years of the study (Fig. 2) may be attributed to the high numbers of leaves that died prematurely due to intense herbivory by *C. flagelliseta.* We show elsewhere that rust mites produce a substantial acceleration of leaf senescence (V.F. et al., unpublished data). The slower turnover of papaya leaves in the fall and winter may be responsible for the small increase in *C. flagelliseta* density that was observed in year 2 as a second peak in mite densities (Fig. 2B).

Leaf age classes found within different canopy strata are a dominant feature of the within-plant distribution of *C. flagelliseta.* We found that the mite is most abundant in the lower and the mid-parts of the plant canopy, which harbor older leaves (Fig. 2). This finding may indicate that rust mites preferentially colonize old leaves over young leaves, or exhibit higher survival or reproduction on mature foliage. Cells of young leaves may contain a higher concentration of proteinases and thus be less palatable to mites (El Moussaoui et al. 2001). Alternatively, and perhaps more likely, the higher densities of rust mites on older leaves may simply reflect the poor dispersal ability of

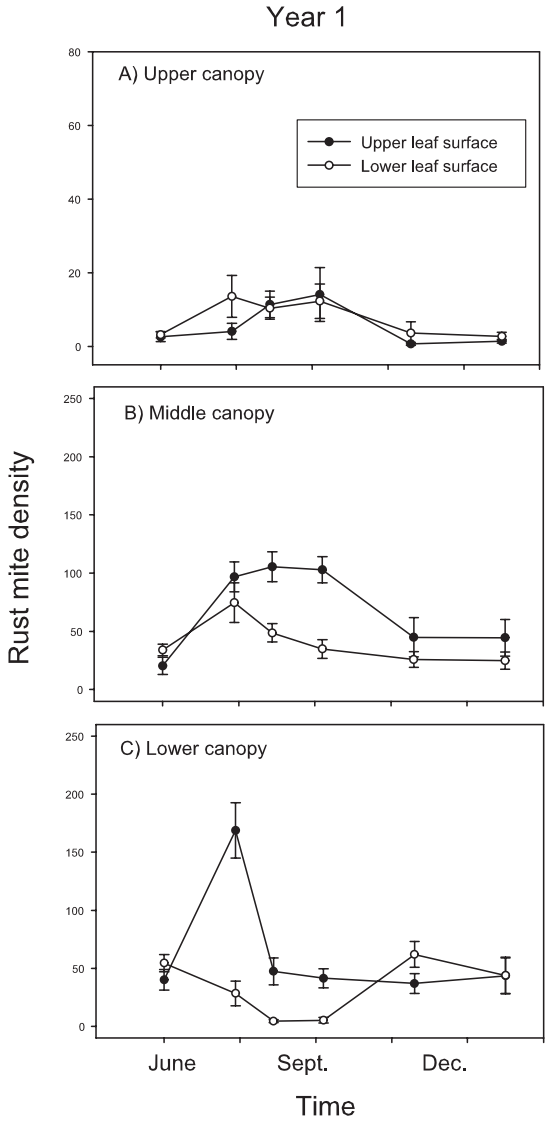


**Fig. 3.** Density of *C. flagelliseta* (no. of motile instars per subsampling unit; mean ± SE), from June 2000 to January 2001 (year 1) on the upper and the lower surfaces of papaya leaves located in (A) the upper canopy (note the different scale for the y-axis), (B) mid-canopy, and (C) lower canopy. In some cases, the error bars are too small to be shown.

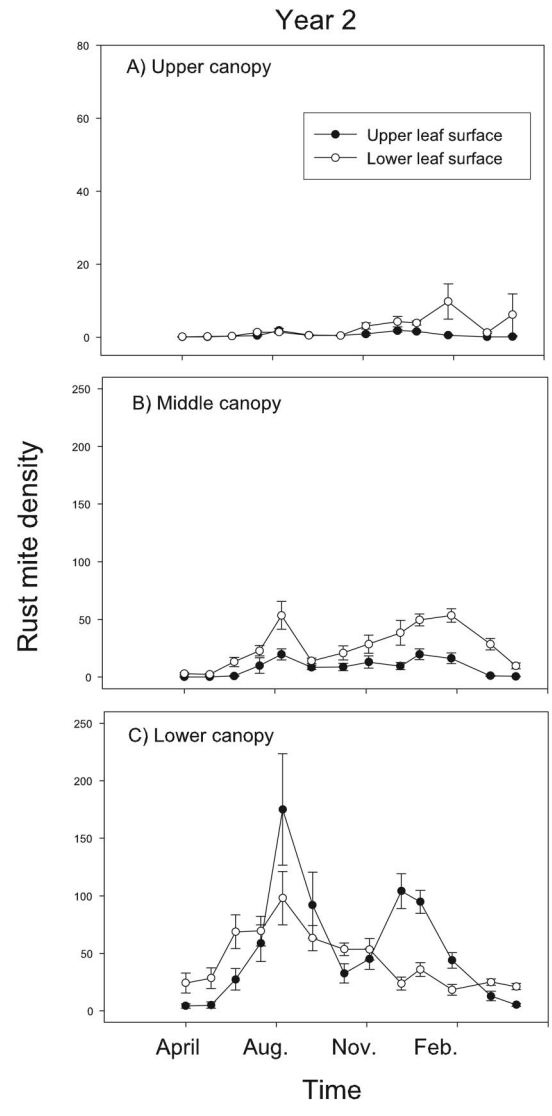


**Fig. 4.** Density of *C. flagelliseta* (number of motile instars per subsampling unit; mean ± SE), from April 2001 to April 2002 (year 2) on the upper and the lower surfaces of papaya leaves located in (A) the upper canopy (note the different scale for the y-axis), (B) mid-canopy, and (C) lower canopy. In some cases, the error bars are too small to be shown.

the rust mite: only a few colonizers may land on young leaves, and their populations may grow on the leaf with minimal mortality or dispersal as the leaf ages and occupies progressively lower positions within the plant canopy. Vuorisalo et al. (1989) investigated the within-plant distribution of the eriophyid *Eriophyes laevis* Nalepa, a gall maker on alder, and found, as we did, that mites were most abundant on the oldest plant parts. They attributed this result to the low dispersal ability of the mites.

We found that *C. flagelliseta* can be present on either the lower or the upper leaf surfaces (Figs. 3 and 4). However, regression analyses indicated that for leaves located in the lower canopy, the proportion of rust mites found on the upper leaf surface is positively correlated with the overall density of rust mites, especially at times of the year when rust mite populations peak (summer). This result suggests that mites move to the upper leaf surface in response to overexploitation of the lower leaf surface by conspecifics. Interestingly, the nonlinearity of the relationship suggests that once the total density gets sufficiently high, migration of mites to the upper leaf surface gradually slows down and stops occurring (Table 1). The lower canopy harbors the older leaves, usually already

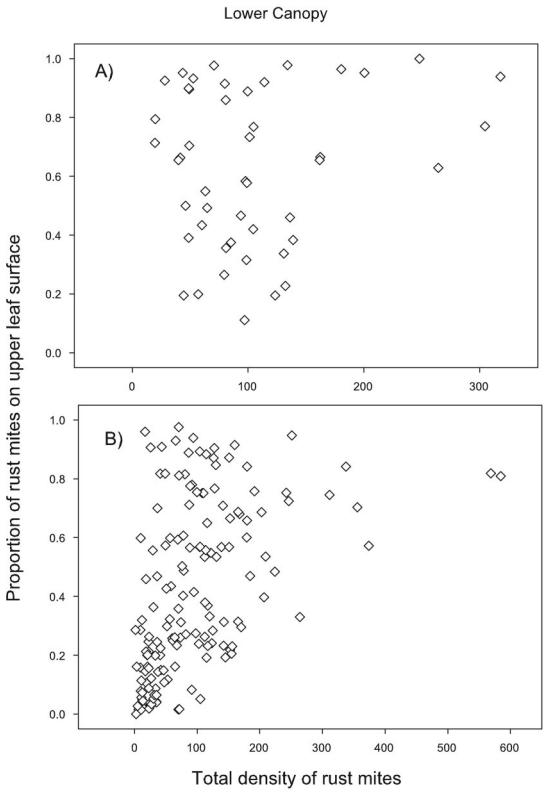


**Fig. 5.** Relationship between the proportion of *C. flagelliseta* on the upper leaf surface and the total density of mites (mean number of motile instars per subsampling unit) on leaves located on the lower stratum of the papaya tree canopy across year 1 (A) and year 2 (B).

heavily exploited by herbivores. Under this interpretation, we do not expect any correlation between mite density and use of the upper leaf surface when overall population densities are low or moderate. This is in accord with the results of regression analyses performed on individual dates: none of the regressions was significant for the samplings performed during the late fall, winter, and spring, when rust mite densities were relatively low. The nonsignificance of the time series analyses for the mid- and the upper canopy levels also may be attributed to the low or moderate densities of mites usually found on their foliage, and the younger age of these leaves, and therefore the smaller amount of cumulative leaf exploitation that could have occurred. We also believe that *C. flagelliseta* prefers to feed on the lower leaf surface over the upper leaf surface, because when we sampled we consistently observed extremely large numbers of *C. flagelliseta* exuviae on the lower surface of leaves that harbored high densities of mites on their upper surface, which indicates that populations were high on the lower leaf surface before the populations reached high densities on the upper surfaces. We discarded the possibility that rust mites move to the lower leaf surface to molt because we also find cast skins on the upper surfaces (V.F., personal observation). Lower leaf surfaces offer protection from sunlight, and many eriophyid mites tend to avoid direct exposure to the sun (Muraleedharan et al. 1988, Pena and Baranowski 1990, Hall et al. 1991).

In the light of these results, those obtained in a previous study (Fournier et al. 2003), and unpublished data, we suggest the following scenario for processes influencing the within-plant distribution of *C. flagelliseta.* Borne by air currents, the mites land on both leaf surfaces but either move to the lower surface, or stay on lower leaf surfaces when mite densities are low (Figs. 3A and 4). During the summer, when mite populations reach very high densities on the lower leaf surface, individuals tend to move to the upper leaf surface when the epidermal cells on the lower leaf surface, their preferred food resource, become heavily exploited. In the late summer, when the mites massively migrate to the upper leaf surface, we observe upward rolling of the leaf margin and the formation of leaf rolls (Fournier et al. 2003). Furthermore, due to greater exposure to wind currents, the upper leaf surfaces may offer a better location than the lower leaf surface to initiate the takeoff behavior for passive aerial dispersal when leaf quality decreases (Nault and

**Table 1. Results from time series analyses performed on each canopy level to determine the relationship between the proportion of *C. flagelliseta* living on the upper leaf surface and the total density of *C. flagelliseta* per leaf**

| | Canopy level | | |
|---|---|---|---|
| | Lower | Mid | Upper |
| Year 1 | | | |
| Total density | 0.05[a] (0.18)[b] | 0.18 (0.23) | 0.19 (−0.90) |
| Total density[2] | 0.08 (−0.0004) | 0.27 (−0.0007) | 0.22 (0.01) |
| Previous sampling date | 0.09 (0.23) | 0.16 (0.22) | 0.01 (0.43) |
| Observations (*N*) | 41 | 39 | 35 |
| $R^2$ | 0.94 | 0.94 | 0.83 |
| Year 2 | | | |
| Total density | 0.0001 (0.002) | 0.58 (0.0007) | 0.31 (−0.01) |
| Total density[2] | 0.0001 (−0.000002) | 0.88 (0.000001) | 0.41 (0.0001) |
| Previous sampling date | 0.003 (0.19) | 0.11 (0.14) | 0.0001 (0.35) |
| Observations (*N*) | 143 | 124 | 112 |
| $R^2$ | 0.88 | 0.72 | 0.53 |

[a] *P* value.
[b] Estimated coefficient.

Styer 1969, Bergh and Weiss 1993, Sabelis and Bruin 1996).

These results have direct implications for the management of *C. flagelliseta*, especially for the development of a scouting program. First, our study suggests that *C. flagelliseta* can be found at high densities for a large part of the year; therefore, it may be necessary to sample year-round, with a possible decrease in sampling intensity during the late winter/early spring. Second, the sampling should target leaves located in the mid- and lower canopies, because the largest mite populations are found within these strata. Finally, because *C. flagelliseta* can occupy either the upper or the lower leaf surfaces, sampling should include both leaf surfaces.

## Acknowledgments

We are grateful to Emily Bjerre, Jo Diez, Lee Laney, Janice Pereira, John Ueshiro, Susan Migata, Mark Hanzawa, and Jeffrey Daite for technical assistance. Special thanks go to James Amrine for identifying the mite species and to James Eaves for performing the time series analyses. The manuscript was improved by comments from Conrad Cloutier and Greg English-Loeb. This work was supported by a USDA–ARS grant for Minor Crops Research (Agreement no. 59-5320-9-226) to J.A.R and M.W.J. and scholarships from the Natural Sciences and Engineering Research of Canada and the Fonds de Recherche sur la Nature et les Technologies du Québec to V.F.

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*Received 18 November 2003; accepted 4 June 2004.*