Temporal and Spatial Dynamics of *Empoasca fabae* (Harris) (Homoptera: Cicadellidae) in Alfalfa

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ABSTRACT We describe the dynamics of potato leafhopper, *Empoasca fabae* (Harris) (Homoptera: Cicadellidae), populations in a 4-ha alfalfa field over 2 yr. Population growth and spatial structure were strongly influenced by days after cutting. Capture of *E. fabae* by suction traps above the boundary layer along with sex ratios of in-field populations suggested that immigrants contributed to population growth throughout the second and third alfalfa growth cycles. Initial sex ratios were strongly female biased (1995, 80%; 1996, 90%), with the degree of bias decreasing and approaching a 1:1 ratio through the third growth cycles. A higher proportion of the population was located in the edge relative to the interior plots in three of four alfalfa growth cycles. Spatial correlation between females and males was initially low, but increased as density increased; this correlation also decreased immediately after alfalfa harvest, and significantly increased over time after harvest. These data suggest that dynamic in-field spatial organization exists for *E. fabae*. Although the entire field was colonized, we hypothesize an edge-biased colonization process, initiated by females for at least the second growth cycle in the northeastern United States, followed by density-dependent movement away from crowded areas of declining host quality.

KEY WORDS *Empoasca fabae*, temporal and spatial dynamics, proportion maps, alfalfa, *Medicago sativa*

DAMAGE RELATED TO *Empoasca fabae* is often especially apparent along field margins, although few observations about field-scale spatial patterns of population density, or colonization, have been published. Kieckhefer and Medler (1966) suggested that adults aggregate at field margins and elevated areas, and these aggregations may be influenced by microclimate. Flinn et al. (1990) noted that *E. fabae* recolonized alfalfa in a population gradient from field edge to midfield, and Fleischer (1982) recorded higher densities along transects near recently harvested edges. Spatial patterns may result in frequency distributions of samples that deviate from a Poisson, and non-Poisson distribution patterns have been reported in alfalfa (Simonet and Pienkowski 1979, Simonet et al. 1979) and potatoes (Walgenbach and Wyman 1985).

Although *E. fabae* does not overwinter in the northern United States, it annually recolonizes the northern part of its summer range from southern source populations (Pienkowski and Medler 1964, Taylor and Relings 1986, Taylor 1993, Taylor and Shields 1995). Migrants are predominately female (Medler et al. 1966, Flinn et al. 1990, Taylor 1993). It is multivoltine (Delong 1938) and polyphagous, reproducing on 200 plant species in 26 families, and can feed on many additional plant taxa (Flanders and Radcliffe 1989, Lamp et al. 1989, Lamp and Zhao 1993). Habitats within a region influence the abundance of adults within a specific alfalfa field (Lamp and Zhao 1993), and the strip cropping or relatively small fields that characterize northeastern United States' agroecosystems may influence both temporal and spatial patterns.

Knowledge of *E. fabae's* field-scale spatial distribution could enhance pest management and sampling protocols. Targeting insecticides to spatial aggregations can slow resistance and conserve natural enemies (Midgarden et al. 1997), and the potential exists for varying the spatial deployment of resistant cultivars based on knowledge of colonization patterns (Blom and Fleischer 2001; Blom et al. 2002, 2004). However, alfalfa pest management strategies do not currently consider spatial patterns. Sequential sampling plans assume a Poisson distribution of sweep samples (Luna et al. 1983), and avoid field edges to avoid skewing a mean density estimate. A more accurate account could focus management at foci of existing populations, or areas of higher risk of immigration and establishment (Weisz et al. 1996, Blom et al. 2002).

The objectives of this study were to define the temporal and spatial dynamics of *E. fabae* in alfalfa on a field scale in landscapes common to the northeastern United States.

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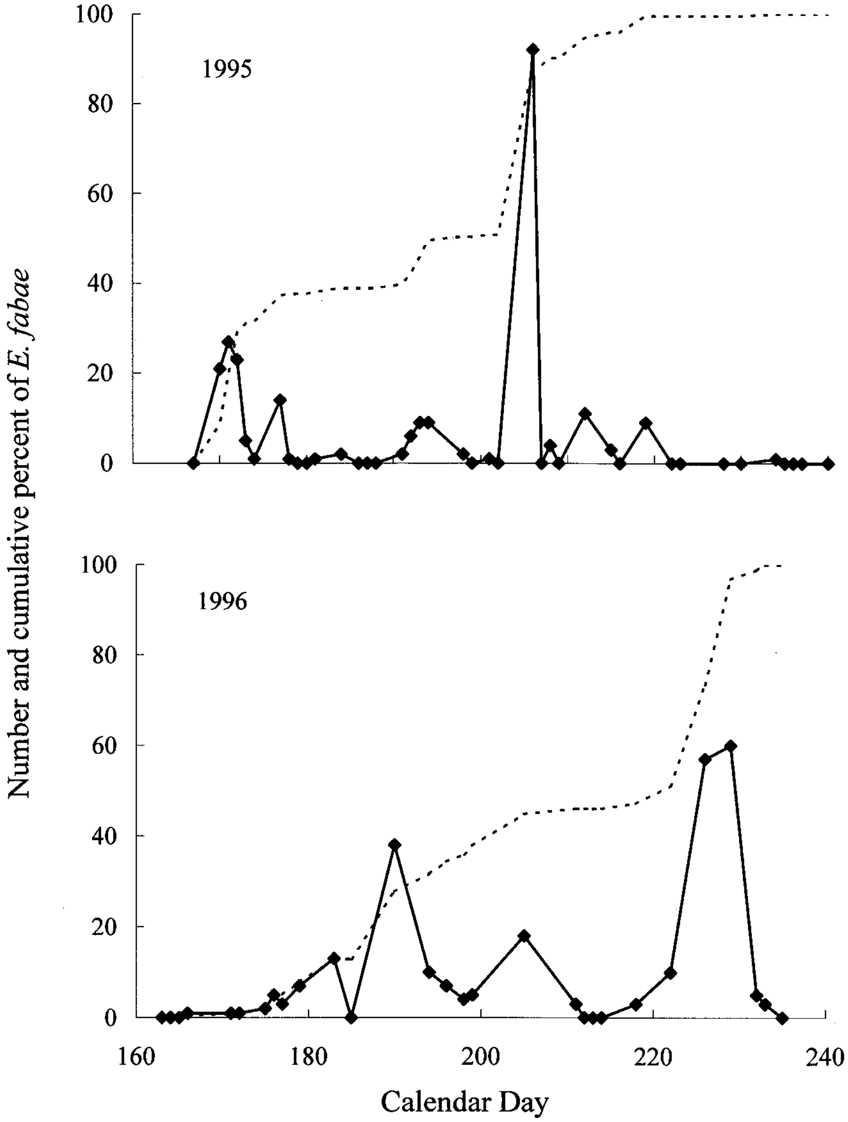

Fig. 1. Number (solid line) and cumulative percentage (dotted line) of *E. fabae* adults captured by the suction trap above the boundary layer.

Materials and Methods

E. fabae was sampled every 4–5 d during the second and third alfalfa growth cycles in 1995 and 1996 in a 4-ha (341 × 114 m) alfalfa field located in Centre County, Pennsylvania (Bayllets Farm). The field was harvested on a 40- to 42-d schedule, which resulted in four harvests per year. This field was seeded with *Medicago sativa* L. in the spring of 1994, and was not treated with insecticides or herbicides during this study. In both years, the 4-ha field was divided into 75 plots, each consisting of 529 m^2 (23 × 23 m) of alfalfa (36 plots had at least 1 border on a field edge, and 39 were interior plots). Plot corners were marked with yellow flags, and a pink flag with the plot number was placed in each plot center. In 1995, the lower and upper (341-m) sides of the field were bordered by 4-ha corn silage fields, followed by 3-ha alfalfa fields. In 1996, these lower and upper sides were bordered by 4-ha rye fields, followed by 3-ha alfalfa fields. In both years, the left (114-m) side was bordered by a narrow dirt road, followed by a grass pasture, and the right 114-m side was also bordered by a narrow dirt road, followed by a grass and weed field.

A suction trap, designed to detect long- and short-range *E. fabae* immigrants above the boundary layer, was maintained in the middle of a nearby field in both years. The fan (27-cm dual-inlet centrifugal blower), motor (one-third horsepower), and collecting jar sat in a 76 × 94-cm box that had a 25-cm (inside diameter) polyvinyl chloride pipe extending 64 cm above the

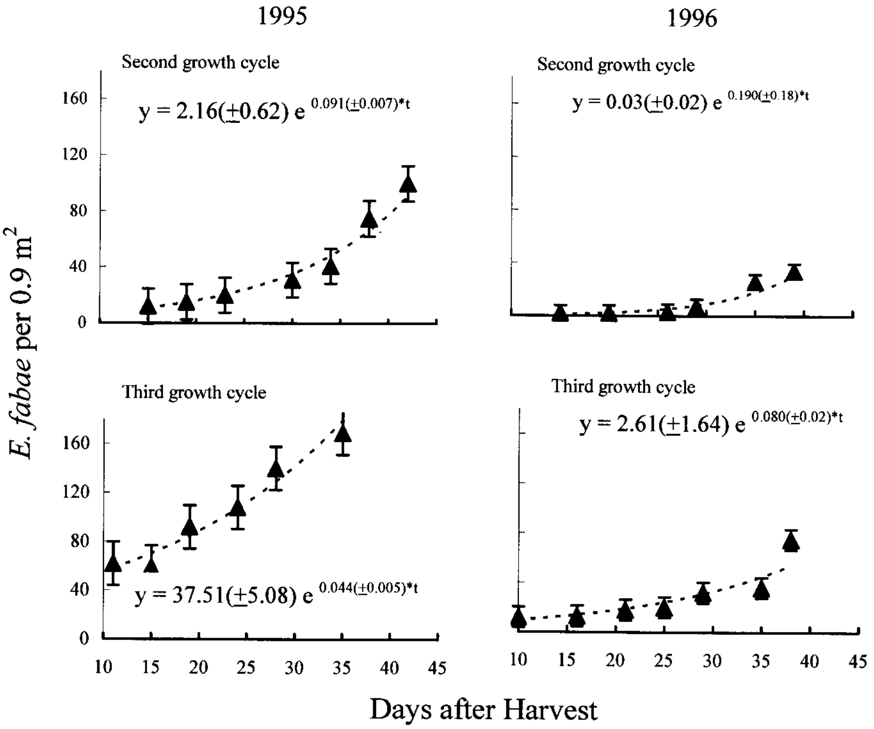

Fig. 2. Mean density of *E. fabae* adults (y) on alfalfa during the second and third alfalfa growth cycles in 1995 and 1996 fit to exponential models, $y = N_0(\pm SE)\ e^{r(\pm SE)t}$, where t = days after harvest. Asymptotic $R^2 > 0.96$ for 1995 and second cutting of 1996, and 0.88 for the third cutting of 1996. The parameter *r* combines net migration and reproduction.

box. Thus, the trap collected insects flying at least 158 cm above the ground. The fan operated at 1,725 rpm, which pulled in air at ≈58 m^3/min. Samples were collected at least once per week. Additionally, samples were collected after every rain event. Number and cumulative percentage of leafhoppers caught above

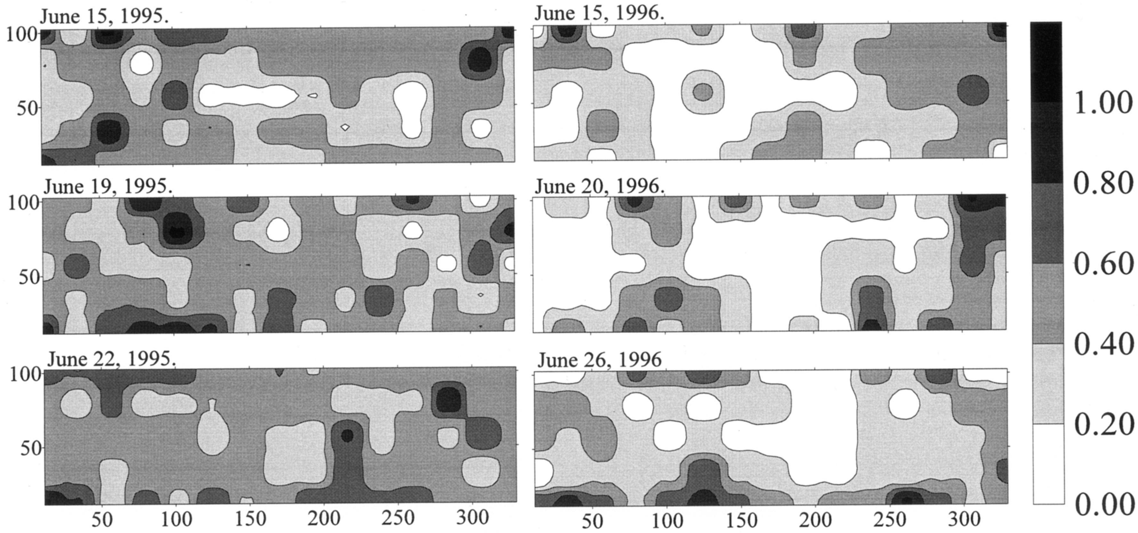

Fig. 3. Contour maps of the relative locations of *E. fabae* adults in a 4-ha alfalfa field during the second growth cycle in 1995 and 1996. Data from 75 529-m^2 plots; *x*- and *y*-axis in meters. Maps show the proportion of the total density for that date. Average densities of *E. fabae* for the entire field were: 12, 15, and 20 for 1995, and 2, 2, and 3 for 1996 per 0.90 m^2, respectively, on the dates represented.

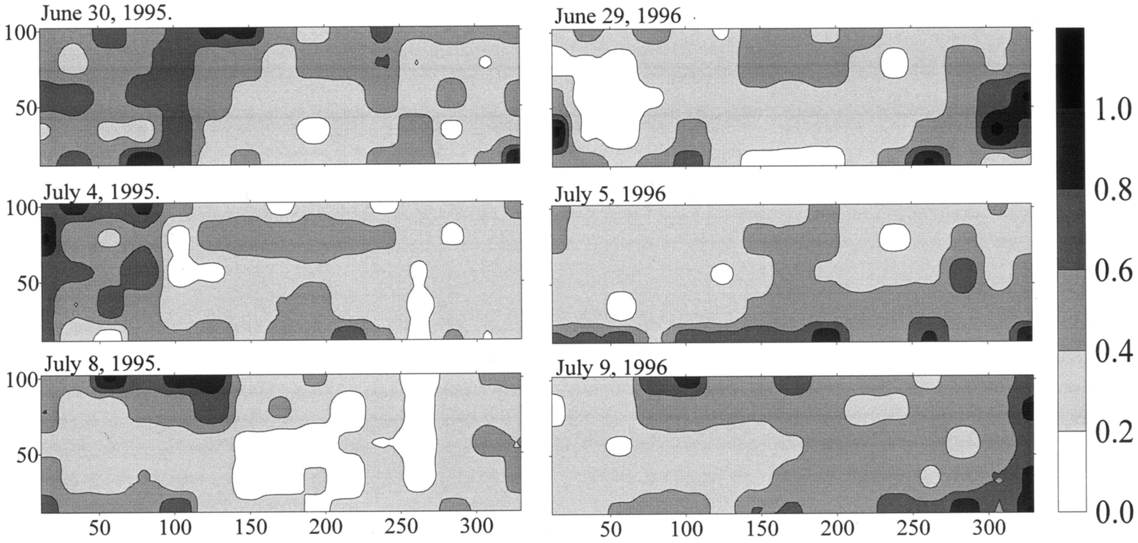

Fig. 4. Contour maps of the relative locations of *E. fabae* adults in a 4-ha alfalfa field during the second growth cycle in 1995 and 1996. Data from 75 529-m^2 plots; x- and y-axis in meters. Maps show the proportion of the total density for that date. Average densities of *E. fabae* for the entire field were: 31, 41, and 75 for 1995, and 7, 26, and 34 for 1996 per 0.90 m^2, respectively, on dates represented.

the boundary layer by the suction trap were plotted against each sampling date (calendar day [CD]) during the second and third growth cycles in 1995 and 1996.

Leafhopper samples within the field were taken with a D-Vac (Dietrick 1961), which provided absolute density estimates of adults (Fleischer 1982). Ten D-Vac suctions, each lasting ≈3 s, were taken in each plot while walking in a circular pattern in that plot. Suctions were taken ≈2 m apart in a circle equidistant from the center of each plot; thus, our in-field sampling unit was the area of the D-Vac collecting head (0.09 m^2) × 10 suctions, or 0.9 m^2. The 10-suction sample was placed inside a number 20 paper bag, stapled shut, placed in a cooler, and taken to a freezer. Leafhopper adults were counted and sexed. Mean density was regressed against days after harvest as an exponential increase for every alfalfa growth cycle in both years. Nonlinear regressions were identified using JMP (SAS Institute 1997). Sex ratio was plotted against time (CD).

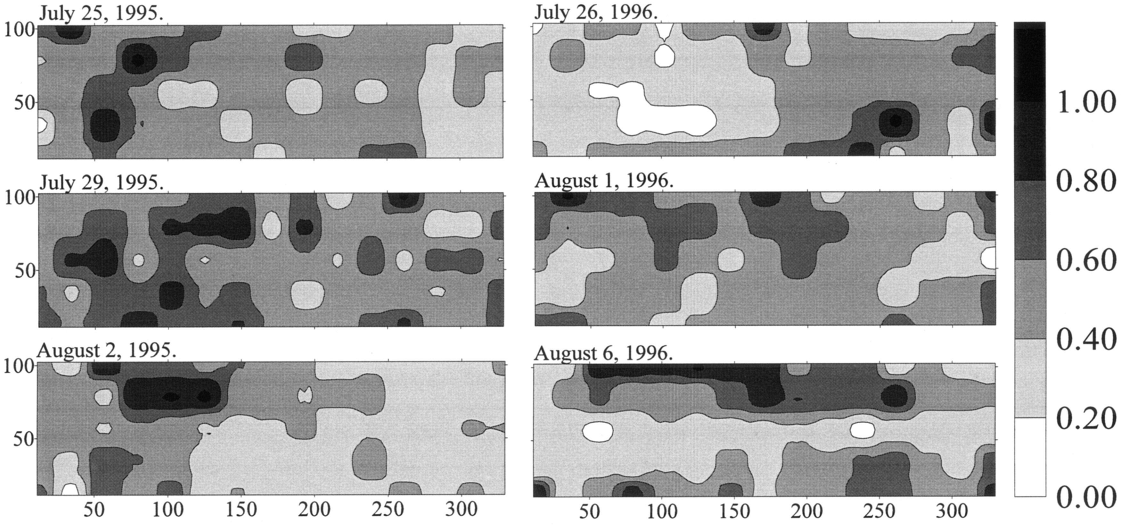

Fig. 5. Contour maps of the relative locations of *E. fabae* adults in a 4-ha alfalfa field during the third growth cycle in 1995 and 1996. Data from 75 529-m^2 plots; x- and y-axis in meters. Maps show the proportion of the total density for that date. Average densities of *E. fabae* for the entire field were: 62, 59, and 92 for 1995, and 12, 13, and 18 for 1996 per 0.90 m^2, respectively, on the date represented.

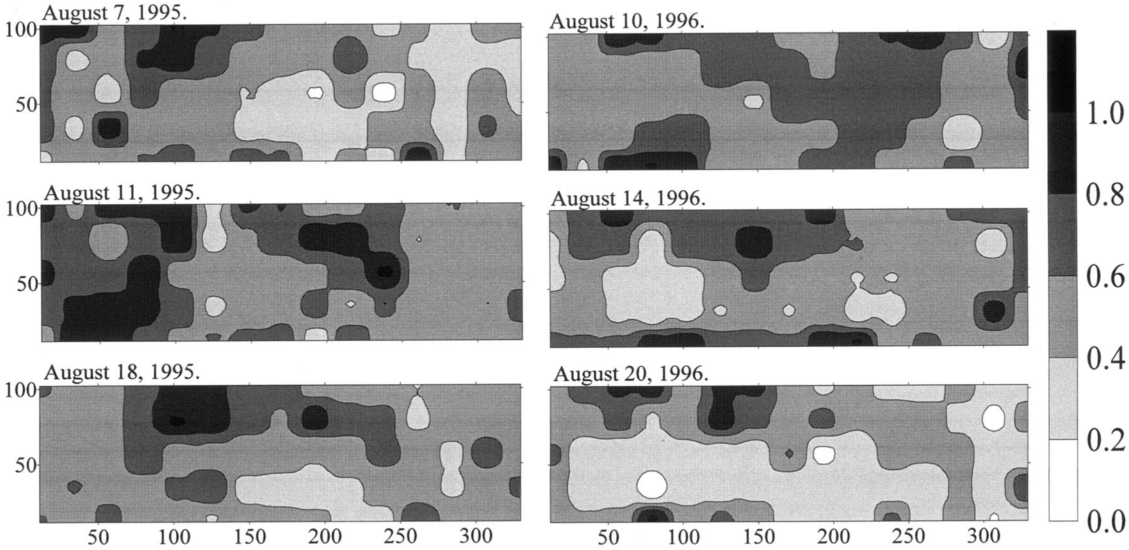

Fig. 6. Contour maps of the relative locations of *E. fabae* adults in a 4-ha alfalfa field during the third growth cycle in 1995 and 1996. Data from 75 529-m^2 plots; x- and y-axis in meters. Maps show the proportion of the total density for that date. Average densities of *E. fabae* for the entire field were: 108, 140, and 169 for 1995, and 20, 32, and 36 for 1996 per 0.90 m^2, respectively, on the dates represented.

Densities were spatially referenced to the centers of the 23 × 23-m plots. The spatial correlation between males and females was estimated using Pearson's correlation coefficient of the samples at each plot. We mapped the proportion of the maximum densities for each date, which helps to visualize consistency in spatial distribution over time by factoring out temporal trends. Proportions were computed by dividing the plot density by the maximum plot density in the field on that date, resulting in proportions that ranged from 0 to 1, and resulting maps display the proportion of the maximum density at each location. We constructed maps using inverse distance interpolation, with one over the distance to the fourth power ($1/d^4$) (Fleischer et al. 1999) using Surfer for Windows (Golden Software, Golden, CO, 1996). We graphed the average proportions from the 36 edge plots, and 39 interior plots, over time.

Results

E. fabae were collected above the boundary layer throughout the second and third growth cycles; this immigration process lasted ≈50–60 d in both years (Fig. 1). During 1995, the first immigration peak was at the beginning of the second growth cycle (CD 170, 19 d after harvest). The highest event, at the beginning of the third growth cycle (19–29 July; CD 200–210), was preceded by a small influx between 9 and 19 Jul (CD 190–200), and followed by a small influx between 29 July and 8 August (CD 210–220). In 1996, the first influx was observed at the end of the second growth cycle (29 June-9 July; CD 180–190). There was a second small influx at the beginning of the third growth cycle (24 July, 10 d after harvest), and the greatest influx was measured between 8 and 18 Aug (CD 220–231). During 1995, the cumulative percentage of *E. fabae* caught above the boundary layer started to increase on 15 Jun, 3 d earlier than in 1996. In 1995, ≈40% of the *E. fabae* detected above the boundary layer occurred during the first 7 d in the second alfalfa growth cycle, and another 40% came during the next 24 d. In 1996, the same percentage (40%) of *E. fabae* detected above the boundary layer arrived during the first 30 d, and the remaining 60% arrived during the next 13 d.

E. fabae was detected in the alfalfa with D-Vac suction sampling ≈10–15 d after the first harvest, when the alfalfa height was ≈7 cm. The mean density increased for all sampling intervals for both growth cycles in both years, despite differences in densities among alfalfa growth cycles and years. An exponential function of days after cutting captured most of the variation in mean density at the whole-field scale (Fig. 2, where the parameter r combines both net migration and reproduction). It is important to note that a linear function for the first 30 d after harvest, followed by an exponential increase (Emmen 1999), also successfully modeled this population increase. An important difference between both years, however, was that population densities were lower in 1996 than 1995, which was probably because of warmer and dryer weather in 1995. Mean densities per 0.90 m^2 (the D-Vac collection head area) of *E. fabae* averaged 12–100 for the second growth cycle of 1995, 62–169 for the third growth cycle of 1995, 2–34 for the second growth cycle of 1996, and 12–75 for the third growth cycle of 1996.

Even in the presence of this field-scale exponential growth in mean density, maps depicting the spatial locations of population proportions show aggregations

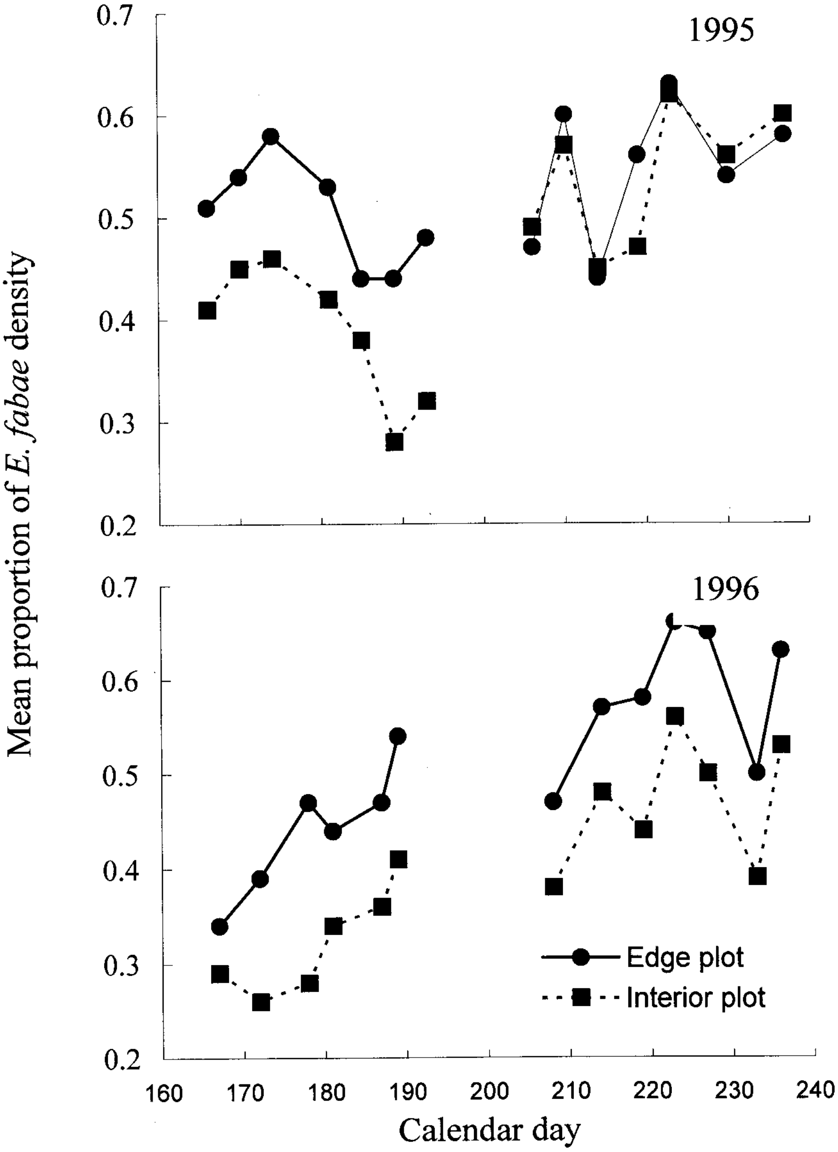

Fig. 7. Proportion of the maximum density of *E. fabae* adults on alfalfa in 1995 (top) and 1996 (bottom).

of leafhopper populations (Figs. 3, 4, 5, and 6) that were most pronounced when densities were low. In general, the population increased from the edge to center plots of the field in both years. A higher proportion of the population was located in the edge relative to the interior during the second growth cycle of 1995 (Fig. 7). The greatest difference occurred at the end of the second alfalfa growth cycle in 1995 (CD 189 and 193; 8 and 12 July, respectively). On these dates, exterior plots had ≈1.5 times as many *E. fabae* as the interior plots. However, this edge-biased pattern did not persist into the third growth cycle in 1995 (Fig. 7). In 1996, the edge-biased densities were present for both growth cycles (Fig. 7). The greatest difference occurred during the second and third sampling dates of the second alfalfa growth cycle (CD 171 and 177; 20 and 26 June, respectively), when exterior plots had ≈1.5 and 1.7 as many *E. fabae*, respectively, as the interior plots. During the third growth cycle in 1996, the greatest difference between exterior and interior plots (1.3) were observed at 21 and 29 d after harvest (CD 218 and 226; 6 and 14 August).

In both years, sex ratios of *E. fabae* adults below the boundary layer (from the D-Vac samples) were initially strongly female biased, and approached a 1:1 ratio over time (Fig. 8). The proportion of females averaged ≈80% during the second growth cycle of 1995, and ranged from 61 to 85%. In 1996, the proportion of females averaged 90% during this period, and ranged from 75 to 100%. During the third growth cycle,

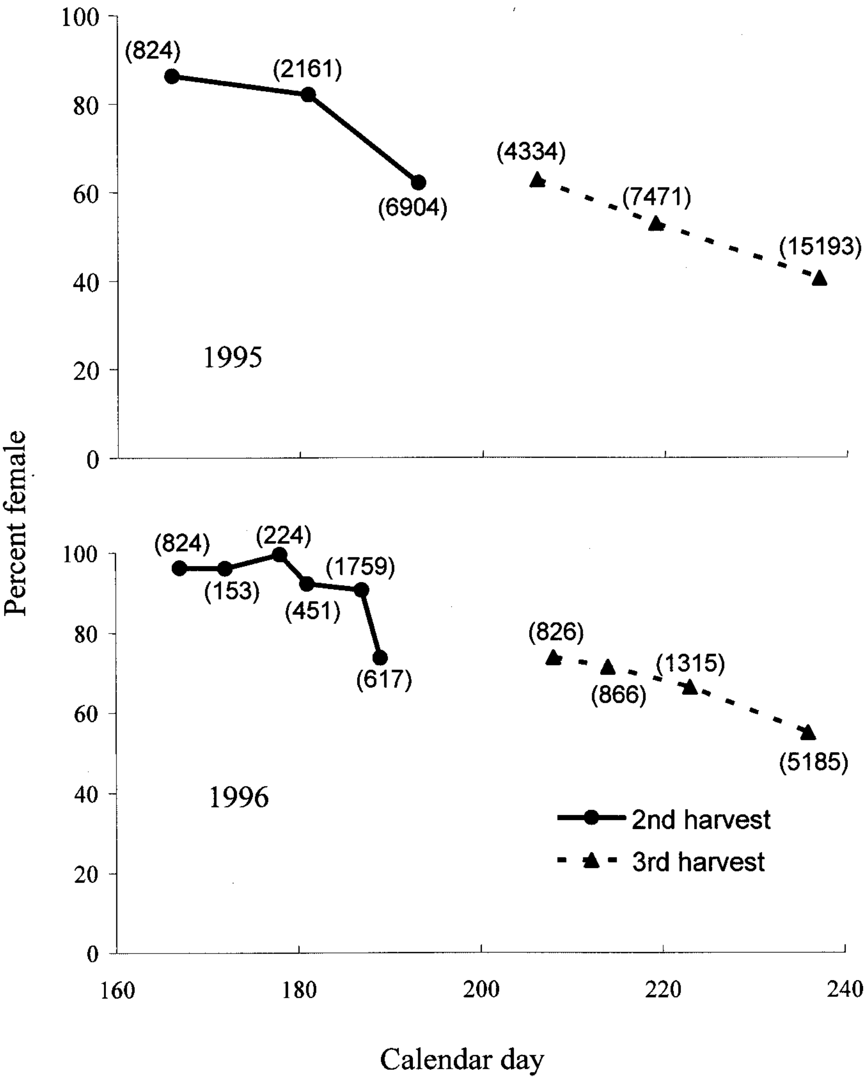

Fig. 8. Sex ratio of *E. fabae* adults during the second and third alfalfa growth cycles in 1995 (top) and 1996 (bottom). Sample size provided in parentheses.

these sex ratios were much closer to 50%. The percentage of females ranged from 40 to 60%, and 55 to 75%, in 1995 and 1996, respectively.

The temporal-dependent degree to which males and females occupied the same areas in the field was expressed as the correlation of their densities at each plot over time (Fig. 9). The densities of males and females were significantly correlated in space (*P* for all correlations in 1995, and all except the first date in 1996 was <0.01; *P* for this first date in 1996 was <0.03; $n = 75$ for all dates, except CD 224, where 1 outlier was deleted, resulting in $n = 74$). In 1995, correlations after harvest started fairly high ($r = 0.52$ and 0.61 at the beginning of the second and third harvest, respectively), and increased ($r \approx 0.8$ or greater by the end of both harvests). In 1996, correlations started lower ($r = 0.25$ at the beginning of the second harvest), but then increased to values similar to that seen in 1995 ($r = 0.78$ by the end of the third harvest). As population density and time after cutting increased, males and females steadily increased this tendency to occupy the same locations throughout the field in both years.

Discussion

Adults were captured above the boundary layer throughout the second and third growth cycles, reflecting continuous immigration. Adults sampled in the field (using D-Vac samples) could not be distinguished between long-distance migrants and adults generated from in-field reproduction in the sampled or nearby fields. However, *E. fabae* require ≈350 degree days (≈30 d) to develop from egg to adult (Flinn 1986). Therefore, as in Flinn et al. 1990, we hypothesize that the suction-trap captures and in-field adult population increase during the first ≈30 d of the sec-

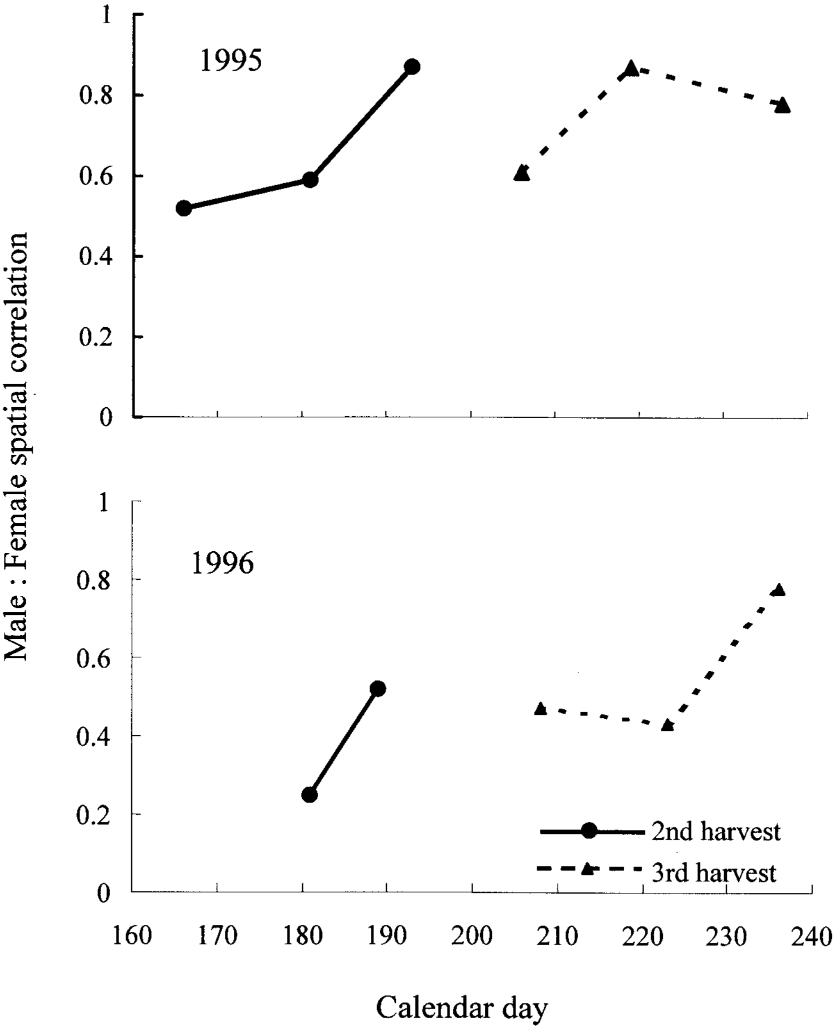

Fig. 9. Temporal-dependent spatial correlation between males and females of *E. fabae* during the second and third alfalfa growth cycle in 1995 (top) and 1996 (bottom).

ond growth cycle were primarily because of immigrants.

The sex ratio of leafhoppers during the second growth cycle in both years was female biased, which is consistent with Medler et al. (1966), who reported *E. fabae* sex ratios as high as 80% in the early spring, declining to 50% female later in the season. This supports a hypothesis of females comprising the majority of immigrants. The sex ratio of eggs is 1:1 (Decker et al. 1971). Therefore, as a result of unbiased sex ratios from within-field reproduction, sex ratios approached 1:1, and this occurred more quickly in 1995 than 1996. The continued female-biased sex ratio in 1996 may also reflect differential survivorship: female *E. fabae* can live 30–50% longer than males without food or water at 4.4–15.6°C (Decker and Cunningham 1967).

E. fabae were detected ≈10–15 d after the first cutting, as the alfalfa reached 7 cm, and densities increased consistently. For the first 30 d, this increase was linear, presumably because of higher rates of immigration than emigration, and during the last ≈10 d (≈30–42 d after cutting), population growth was exponential, presumably influenced by within-field reproduction. The population increase during the third growth cycle was also likely because of some fifth instars surviving harvest that were added to the reinvading adults from neighboring fields. Populations of *E. fabae* decline dramatically after harvest, and adults that move out of the field at harvest must reinvade the new crop. Thus, population growth in alfalfa reaches a peak just before harvest, and the peaks increase from the second to the third harvest. In both years, maximum densities occurred in late August.

Even though we detected appreciable rates of movement with suction-trap sampling, and we worked in rectangular fields, populations tended to occupy edge relative to interior plots, especially early in the population exponential increase. This agrees with limited studies in alfalfa after harvest (Fleischer 1982, Flinn et al. 1990), and in soybeans, in which densities were higher in edge than interior rows adjacent to recently harvested alfalfa (Poston and Pedigo 1975). Multiple hypotheses could explain this spatial pattern. Dispersal rates and patterns could change with adult age, or the higher densities along edges may reflect a tendency to return to the field after emigration. Host plant quality may vary within the field, with a higher probability of higher suitability along edges. We hypothesize that measurably more long- and/or short-distance immigrants arrive at the edge relative to the interior of the field, where they find suitable host, feed, congregate, and reproduce before dispersing away. This process may be density dependent, in which immigrants disperse at a rate that is influenced by declining space between individuals, or declining host quality caused by feeding, both of which are influenced by new immigrants and newly emerged individuals. These results suggest a two-step hypothesis of *E. fabae* within-field spatial patterns: edge-biased colonization (initiated by females) followed by density-dependent movement away from crowded areas of declining host quality. Further work is needed to determine the population processes that result in these dynamic within-field spatial patterns.

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