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**LOCAL DISPERSAL OF THE POTATO LEAFHOPPER
(HOMOPTERA: CICADELLIDAE)
IN RESPONSE TO ALFALFA CUTTING**

By

John Charles Wise

A THESIS

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ABSTRACT

LOCAL DISPERSAL OF THE POTATO LEAFHOPPER (HOMOPTERA: CICADELLIDAE) IN RESPONSE TO ALFALFA CUTTING

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Local dispersal of the potato leafhopper (Homoptera: Cicadellidae) in response to alfalfa cutting was studied in 1989, in a 1.9 ha alfalfa field and bordering habitats, located in South-West Michigan. Yellow sticky traps, net sweeps, and area traps were used to determine the vertical distribution, habitat preference, and timing of adult dispersal out of alfalfa after cutting, and the spatial distribution of potato leafhoppers re-colonizing the field.

Dispersal patterns from the first alfalfa cutting suggest that long distance migrant populations may not have the ability to disperse out of the alfalfa in response to cutting. Dispersal patterns from the second cutting indicate that the locally produced populations disperse primarily at low heights (1.2 to 2.7 m), leaving the field almost immediately after cutting, and preferring black locust over cherry, oak and grass vegetation.

The spatial distribution of the potato leafhoppers in alfalfa indicates that following harvest, the tree vegetation surrounding the field acts as a temporary host until

conditions in the alfalfa become favorable for re-colonization.

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INTRODUCTION

The potato leafhopper, Empoasca fabae (Harris), is a major pest of alfalfa, potatoes, and beans, and a minor pest of other crops such as apple, celery, rhubarb, and clover. With the addition of non-crop plants, the potato leafhopper (PLH) is known to have over 200 hosts, most of which are suitable for reproduction of the insect (Poos and Wheeler 1943, 1949). The PLH occurs predominantly in the Mid-western states east of the 100th meridian to the Atlantic coast, and south throughout the Gulf states and northern Florida (DeLong 1965). To date there has been no clear evidence for the ability of the PLH to overwinter in Michigan or any other North-central or Eastern states receiving fewer than 250 frost-free days per year (Decker and Cunningham 1968). Populations of PLH have been found to over winter every year along the Gulf Coast, especially in the most southern parts of the Mississippi Delta region (Medler 1957).

Long-distance migration is the primary means by which the PLH disperses over the hundreds of kilometers of its geographic range each year. Major populations of PLH move over 800 kilometers on synoptic-scale weather systems in as few as 24 hours, to then be deposited in an area where there were previously no individuals (Pienkowski and Medler 1964).

The weather conditions associated with this transport are generally a low-pressure area over the Great Plains, a high-pressure area over the Atlantic Coast, a north-south cold front moving east, and a east-west front over the Northern states (Pienkowski and Medler 1964). These conditions often allow for a south-north flow of maritime tropical air from the Gulf states, which, if of sufficient speed and temperature, are capable of picking up and transporting the insects to the more northern states, and then depositing them along the cold front by rainfall or associated down drafts (Huff 1963). Low-level nocturnal jets of over 20 m/s at the 850 millibar level have been documented as being particularly effective in transporting PLH over long distances in short periods of time (personal communication, Carlson, 04-17-90).

After the long-distance migration and throughout the rest of the growing season, large numbers of individuals can move within more localized geographic areas (from one field to another), called local dispersal (Pienkowski and Medler 1966, Poos and Westover 1934, Poston and Pedigo 1975, DeLong 1965, Flanders 1989). Unlike long distance migration, local dispersal is primarily a voluntary flight without the support of synoptic wind patterns, and is thought to be initiated by overcrowding, decline of food quality and quality, food preference, adverse weather conditions, or loss of suitable habitat (Johnson 1960, Delong 1971).

There has been less attention given to localized dispersal than long-distance migration, and yet it is the main

mechanism by which large populations of PLH can suddenly appear in agricultural fields which are otherwise devoid of this pest, often causing severe economic damage to crops. Pienkowski and Medler (1966), and Poston and Pedigo (1975) studied the dispersal response of PLH to alfalfa cutting, finding mass movements primarily to the borders of adjacent plots, but their sampling designs did not account for the possibility of a much higher vertical flight by the PLH to more distant habitats. Lamp et al. (1989) studied the dispersal response of PLH to alfalfa harvest, and found increases in PLH populations in habitats adjacent to the cut field as well as habitats as far away as 200 meters. These researchers did not quantify whether those distant catches were from low-level movement or high vertical flights. Pienkowski and Medler (1966) also noted that the PLH dispersal pattern from the first cutting (long-distance migrant population) was different than that of the second cutting (locally generated population). Unlike the dispersal pattern from the second cutting, they showed that the migrant adults caught on sticky traps were not proportional to the higher PLH abundances estimated in the alfalfa before the cutting.

Local dispersal is also responsible for the recolonization of alfalfa by the PLH after cutting (Pienkowski and Medler 1962). After alfalfa is harvested, the field that previously provided adequate food and shelter for the PLH is stubble, becoming a much hotter and dryer environment. Most PLH adults disperse during cutting or shortly afterward as the

hay dries. Up to 95% of the nymphal population dies within the first week after cutting, leaving the field nearly barren (Simonet and Pienkowski 1979). As alfalfa regrowth begins, a renewed source of food and shelter is again available for the PLH. Flinn et al. (1990) studied PLH immigration, and found that after the first alfalfa harvest the PLH begins to recolonize the alfalfa when it reaches a height of 5 cm, maintaining a constant immigration rate until halfway into the crop growth cycle. They saw a similar trend after the second harvest, except that immigration of the PLH begins a little sooner. Kieckhefer and Medler (1966) saw distinct aggregations of adult PLH at margins and elevated portions of alfalfa fields, usually coinciding with periods of high seasonal population density. Following alfalfa harvest, they noted a one or two-week period where this aggregation pattern is lost. They expected that the accumulation of adult PLH along the field margins was a result of immigration from outside sources (Kieckhefer and Medler 1966).

The first objective of this study was to characterize the dispersal of PLH adults out of alfalfa, in response to the catastrophic loss of habitat from alfalfa cutting. In addition, the difference between the dispersal of the long-distance migrant population and that of the locally produced population was investigated.

The second objective of this study was to characterize the dispersal of PLH adults into alfalfa, following alfalfa cutting. In addition, the difference between the dispersal of

the long-distance migrant population and that of the locally produced population was examined.

The third objective of this study was to describe the overall temporal dynamics of the PLH in alfalfa and the surrounding habitats. The use of yellow sticky trap and net sweep sampling techniques as population density estimators in relation to the area trap sampling technique as an absolute population estimator was evaluated.

MATERIALS AND METHODS

Site description: A 1.9 ha alfalfa field, Medicago sativae L., and the surrounding vegetative habitats were chosen as the study site. The site is located at the Kellogg Biological Station in Hickory Corners, Kalamazoo Co., Michigan. The two-year-old alfalfa field was moderately contoured, the north-west corner having the lowest elevation, followed by the north-east corner, the south-west corner, and, finally, the south-east corner. There was an approximate 5 m change in elevation between the lowest and highest point in the field. Approximately 1600 m² of the north-west corner was partially infested with the perennial weed, curled dock (Rumex crispus L.). The alfalfa dominated the surface area until the middle of August, at which time the dock infested up to 40% of that corner. The higher elevations of the field were infested by the weed, daisy fleabane (Erigeron annuus L.), which became readily apparent when it flowered in late July. Bordering the south side of the field was a lightly wooded fence row, composed of young black cherry (Prunus serotina Ehrhart) and red oak (Quercus rubra Linnaeus) (about 9 m high), with a ground cover of grasses, asters and goldenrod. Bordering the east side of the field was primarily a heavily wooded fence row, composed of mature black cherry and red oak (about 13 m high), sprouting cherry and oak shrubs, with a ground cover of grasses, asters and goldenrod. Bordering the west side of the field was primarily an open field, composed of grasses and

some goldenrod. Bordering the north side of the field was a woodlot, composed of mature black locust (Robinia pseudoacacia Linnaeus) (about 14 m high) and sprouting black locust shrubs, with a ground cover of grasses, asters, goldenrod and brambles. Five habitat types were classified as 1) young cherry/oak, 2) mature cherry/oak, 3) grass field, 4) black locust, and 5) alfalfa (Figure 1).

DISPERSAL OF THE POTATO LEAFHOPPER OUT OF ALFALFA:

The dispersal of PLH adults out of alfalfa in response to alfalfa cutting was characterized by measuring the vertical distribution, habitat preference, and timing of departure into the surrounding habitats. The differences in local dispersal between the long-distance migrant population and the locally produced population, was determined by comparing the dispersal patterns resulting from the first alfalfa cutting to the dispersal patterns resulting from the second alfalfa cutting.

Trap construction and field design: Estimates of PLH abundance were made using yellow sticky traps and net sweeps. Yellow sticky trap samples were made at three permanent sampling sites, spaced 20 meters apart, along the inside edge of each of the four habitats surrounding the alfalfa field (Figure 2). At each permanent sample site, eight yellow sticky traps were hung on a vertical trapping structure, holding two traps at 1.2, 2.7, 4.3, and 5.8 m above the soil surface. The vertical trapping structure was constructed with

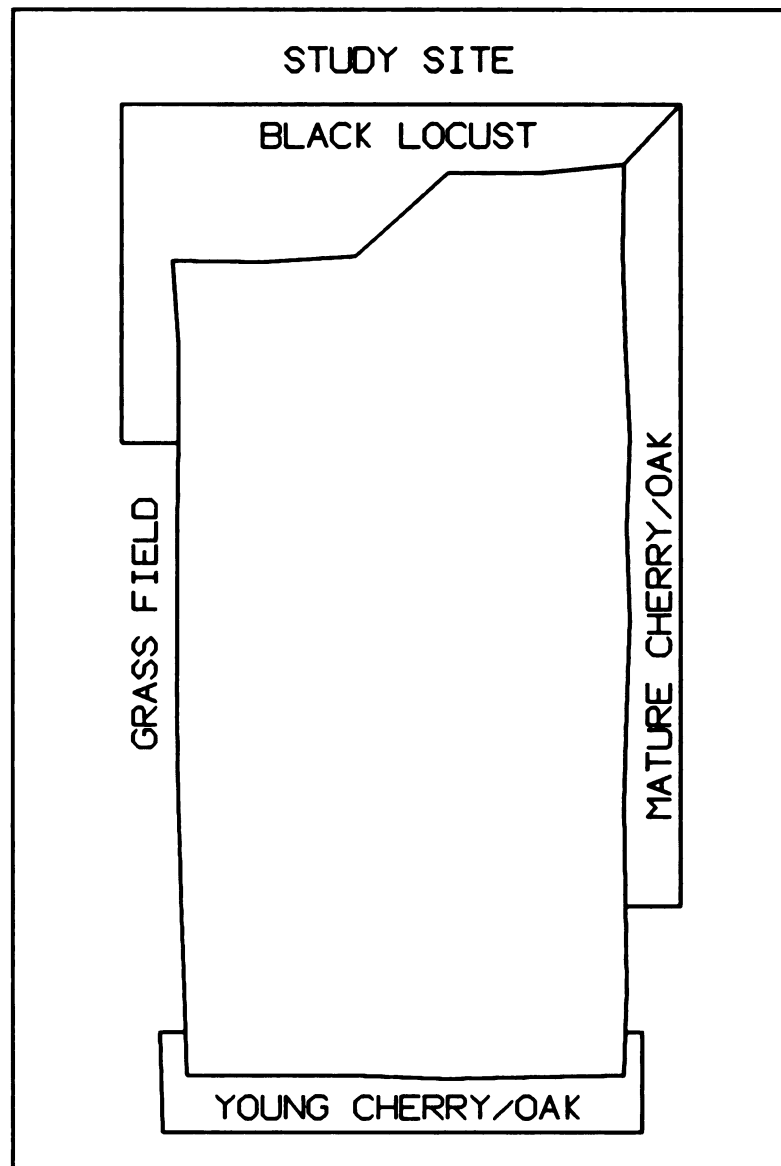


Figure 1. The 1.9 ha alfalfa field, and four bordering habitats.

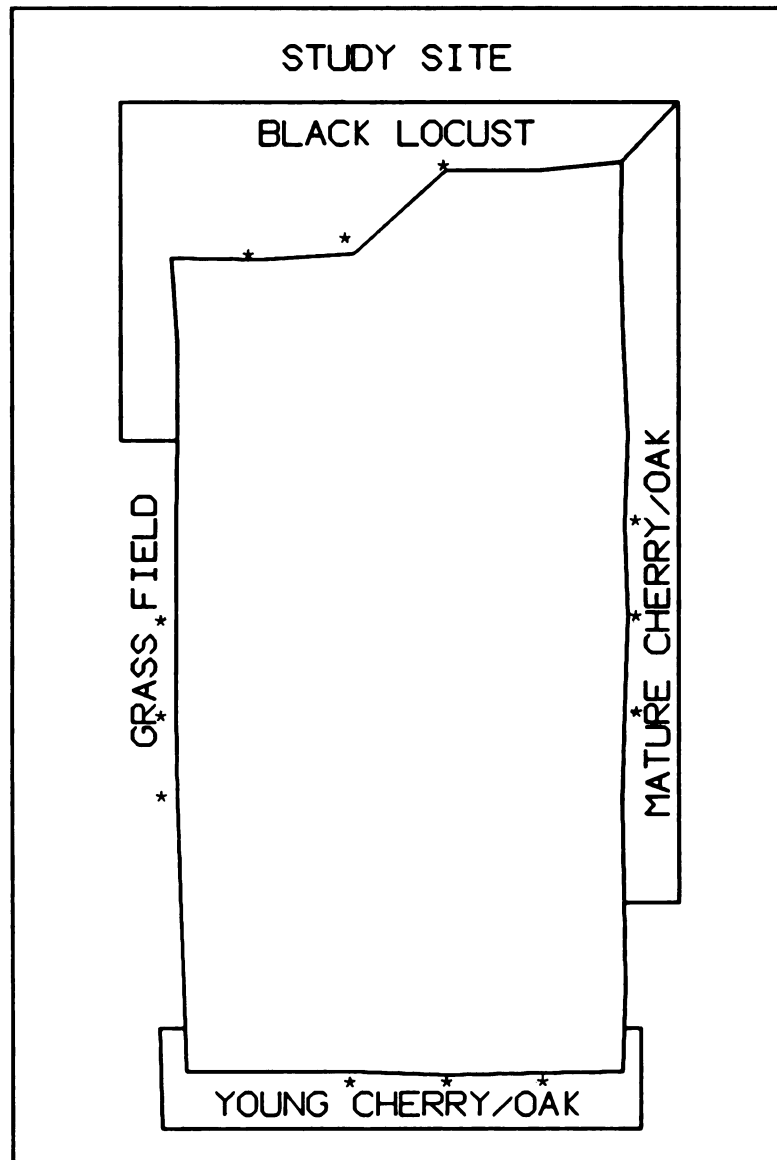


Figure 2. Twelve permanent sampling sites for vertical trapping structures and 'tree sweeps'.
* - permanent sampling sites.

a 1.9 cm diameter, 6.1 m long aluminum conduit pipe, inserted 30 cm in the soil, leaving a 5.8 m section above the soil level. Two unbaited Pherocon AM yellow sticky traps (Trece Inc., Salinas, Cal.) were tied to a groove on each end of a .64 cm, 1.2 m long wood dowel, taped horizontally to each preceding height on the vertical conduit with duct tape. A 1 m diameter helium balloon (Balloons Galore Inc., East Lansing, Mi.) was used to extend the height of one vertical trapping structure per bordering habitat, tethering yellow sticky traps at 15.3 and 30.5 meters above the center of each habitat with kite string, totaling two traps for each balloon. All yellow sticky traps were positioned to face the alfalfa/habitat edge that they were placed in. All yellow sticky trap and net sweep sample designs for the alfalfa habitat are described in the PLH re-colonization chapter, and population means are based on one yellow sticky trap per trap standard.

Three sets of net sweep samples were made, consisting of 10 sweeps per sample with a standard 38 cm sweep net in the tree foliage of each bordering habitat. These 'tree sweeps' were taken near each permanent sampling site at approximately 1.2 m and 4.3 m above the ground. This was done for each habitat's dominant tree species, totaling 12 samples for the young cherry/oak habitat (dominant species: black cherry and red oak), 12 samples for the mature cherry/oak habitat (dominant species: black cherry and red oak), six samples for the black locust habitat (dominant species: black locust), and

no sweeps on the west side because there were no trees in the sampling site areas (Figure 2). The sweep net was taped with duct tape to a 3 meter long aluminum conduit pole to extend the reach for the 4.3 m high net sweep samples.

Sampling procedure and site conditions: The first alfalfa harvest period lasted one day. The alfalfa was cut on 07 June and the un-baled hay removed as greenchop on 08 June. Prior to cutting, the alfalfa was 53 cm high, the black locust was just reaching first leaf, and black cherry and red oak were slightly less than first leaf. The weather conditions for the sampling periods before and after alfalfa cutting were similar, temperatures ranging from 6 C to 29 C each day and winds coming primarily from the south-west at moderate velocities. The accumulated degree-days > 10 C (from 01 January, 1989) for 07 June were 298.

Yellow sticky traps (1.2 m) were sampled for a one-week pre-harvest period before the first cutting, ending 05 June, for comparison with the sampling after the first cutting. Balloon traps were also sampled before the first cutting, for a 24 hour period ending 07 June. After the first alfalfa cutting, yellow sticky trap samples were made 24 hours after the cutting, and then on 15 June for an accumulative one week post-harvest PLH catch total. The balloon traps were sampled 24 h following the alfalfa cutting, ending on 08 June. Net sweep samples were made after the cutting on 15 June.

The second alfalfa harvest period lasted four days from the cutting of the alfalfa on 31 July to the baling and removal of hay on 04 August. Prior to cutting, the alfalfa was 62 cm high and the black locust, black cherry and red oak all had a mature cover of foliage. The temperature conditions for the sampling periods before and after the cutting were similar, ranging from 14 C to 31 C per day. Wind conditions were different, coming primarily from the east direction at a moderate velocity before the cutting and coming primarily from the west at a low velocity after the cutting. The accumulated degree-days 10 C for 31 July were 908.

Yellow sticky trap and net sweep samples were made to estimate PLH abundance for the four-day pre-harvest sampling period before the second cutting, ending 31 July (net sweeps made on 18 July), for comparison with the post-harvest sampling period. Balloon traps were sampled for PLH before the cutting for a 24 hour period, ending on 29 July. During the second alfalfa harvest period, yellow sticky traps from one vertical trapping structure from each of the four bordering habitats were sampled at 6, 18, 42, 48, and 96 hours after alfalfa cutting. This was done to determine the point in time when the PLH adults dispersed out of the alfalfa. These data were then summed for a four-day post-harvest catch total. Yellow sticky traps from the other two vertical trapping structures were sampled once at the end of the harvest period, on 04 August. Balloon traps were sampled on the same time sequence as the intensively sampled vertical

trapping structures, but ended on 02 August. Net sweep samples were made in the four bordering habitats at 6 and 48 hours after the cutting. PLH counts were then averaged for a harvest period estimate.

The sampling always began with the young cherry/oak habitat on the south side, and moved clock-wise around the alfalfa field. When sampling the yellow sticky traps, adult PLH were counted and removed from both sides of the trap, and, when saved for identification, were placed on a site-and-date-marked paper note card to be stored in a freezer. Sampling all twelve vertical trapping structures required about three hours, depending on the abundance of PLH. Yellow sticky traps were replaced every two weeks, or sooner if the condition of the trap deemed necessary. The net sweeps in tree foliage were made in the early evening when wind velocity was lowest. Samples were placed in zip-lock plastic bags or paper bags, which were marked for sample site and date, and then refrigerated for later PLH count and identification (DeLong 1931).

The data were analyzed using a two-way analysis of variance (ANOVA) to distinguish catch differences between the four habitats, and then the vertical height differences within each habitat.

DISPERSAL OF THE POTATO LEAFHOPPER INTO ALFALFA:

The dispersal of PLH into alfalfa after cutting was characterized by descriptively comparing their spatial

distribution in the field to PLH densities in the surrounding habitats, field topography, alfalfa height, and time since last cutting. The differences in local dispersal between the long distance migrant population and the locally produced population, was determined by comparing the spatial patterns resulting from the first alfalfa cutting to the spatial patterns resulting from the second alfalfa cutting.

Trap construction and field design: Samples of PLH were made using yellow sticky traps, net sweeps, and area traps. All three sampling techniques were used at permanent sample sites in a 20 by 20 meter grid design over the whole alfalfa field and the inside edge of all four bordering habitats, totaling 63 sample sites (Figure 3). The alfalfa field had a total of 34 permanent sample sites, the young cherry/oak habitat had six, the mature cherry/oak habitat had eight, the grass field habitat had eight, and the black locust habitat had seven permanent sample sites.

At each sample site, two unbaited Pherocon AM yellow sticky traps were hung 1.2 meters above the ground on a 'T' trap standard. The 'T' trap standard was constructed with a 1.27 cm, 1.5 meter long aluminum conduit pipe, inserted 30 cm vertically in the soil into a 1.9 cm diameter, 30 cm long aluminum conduit pipe, leaving a 1.2 m section above the soil surface. Two yellow sticky traps were tied to a groove cut on

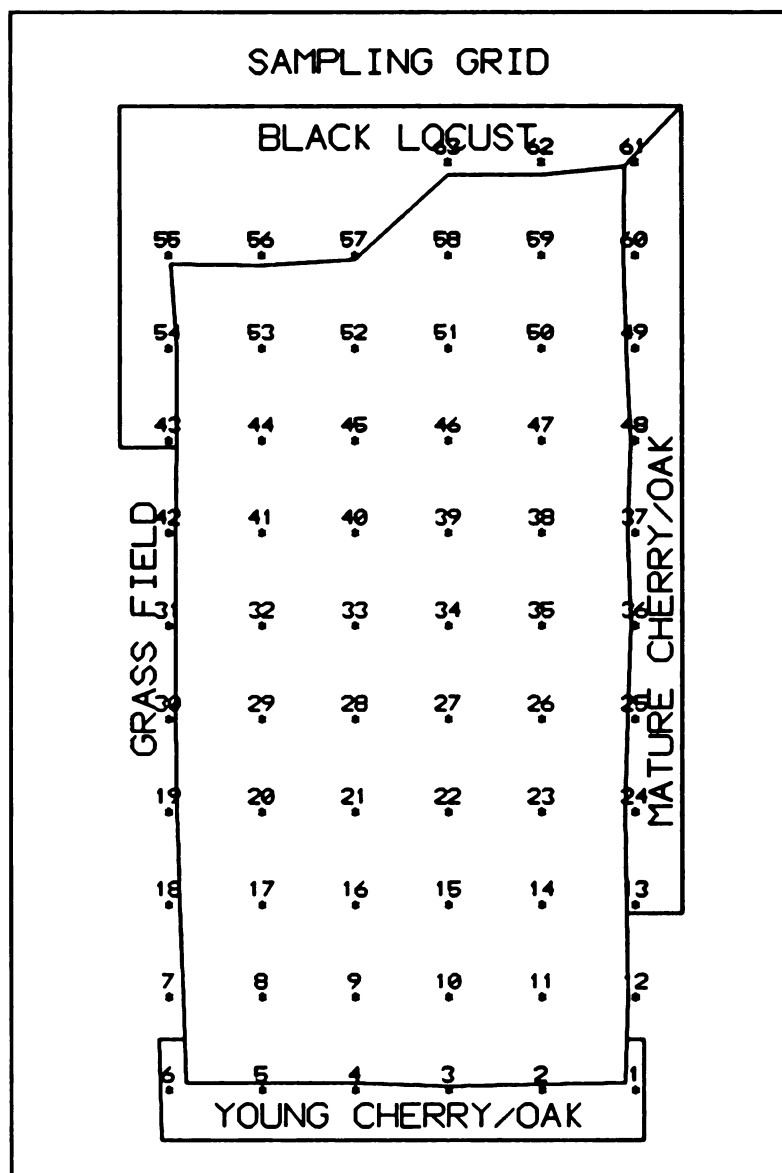


Figure 3. The 20 m by 20 m grid design of the 63 permanent sampling sites.

each end of a .64 cm diameter, 1.2 m long wood dowel, which was placed horizontally to the vertical conduit through a .64 cm drilled hole on a 1.27 cm (inside diameter), 6 cm long plastic PVC tube, which was fitted to the top of the conduit. All yellow sticky traps in the alfalfa were positioned to face north/south. Samples from the two traps per standard were recorded and analyzed separately; only one being used for the spatial distribution analysis.

Sweep samples were made at each permanent sample site for all five habitats. A sweep sample consisted of ten sweeps taken with a standard 38 cm sweep net in the ground cover, staying within a five meter radius distance of the permanent sample site. Net contents were placed in a zip-lock plastic bag or paper bag, which was marked with sample site and date, then refrigerated for later PLH count and identification.

Absolute densities of PLH were estimated near each permanent sample site for all five habitats, by using an area trap. This was done to determine PLH numbers per unit area (Cherry et al. 1977, Roltsch et al. 1990). The area trap was constructed using a 20 gal (75.7 l) plastic container, with a surface area of .3 square meters. A hole was cut out of the bottom of the container, and a 1/2 pt (.236 l) Kerr canning jar attached to the outside and filmed with motor oil. The area trap worked by placing the container over vegetation, and waiting for adult PLH fly to the light coming through the jar. After the PLH are in the jar, they are caught on the oil film in the jar. With a 1 m piece of twine, a 1.5 m aluminum

conduit pipe was tied to the top of the container, so that it could be placed over the vegetation from above without disturbing the PLH residing in the sampling area. The area trap was placed over the vegetation within a five meter radius of each permanent sample site and then left for ten minutes. The container was lightly tapped on its side before being checked, to agitate any remaining insects into flying into the glass jar. When the trap was checked, the PLH adults caught in the oil were counted and immediately removed so that the jar could be re-oiled (if needed) and used again.

Sampling procedure and site conditions: PLH counts with yellow sticky traps, located at each permanent sampling site, were made one week before the first alfalfa harvest period. After the alfalfa cutting on 07 June, post-harvest PLH counts were made on 08 June, 15 June, 22 June, and 01 July using the net sweep and area trap methods (yellow sticky traps were removed from the field to accommodate the harvest operation). Degree-days and alfalfa height were recorded for each sampling date.

For the second alfalfa harvest period, yellow sticky trap, net sweep and area trap samples were used to estimate PLH numbers for a one-week pre-harvest period before the cutting, ending 28 July. After the alfalfa cutting, post-harvest PLH estimates were made on 11 August, 18 August, and on 24 August. Degree-days and alfalfa height were recorded for each sampling date.

The sampling sequence for all three PLH sampling techniques began at the south-east corner (permanent sampling site #1) of the field, and ended at the north end of the field (permanent sampling site #63) (Figure 3). When sampling the yellow sticky traps, adult PLH were counted and removed from both sides of the trap, and when saved for identification were placed on a labeled note card to be stored in a freezer. Yellow sticky traps were normally sampled in the morning, requiring approximately four hours to complete all 1.2 m traps, depending on PLH abundances. Yellow sticky traps were replaced with new traps every two weeks, or sooner if the condition of the trap deemed necessary. The net sweeps and area trap sampling were only conducted when temperature, moisture and light conditions were appropriate. The net sweep and area trap sampling were usually conducted at the same time. The area traps were placed first at the permanent sample sites for a whole east-west row (i.e. sites #1-#6, #7-#12, etc.). Ten minutes later the net sweep samples made for that row, and the area traps were checked and moved to the next row as each sweep sample was finished.

The spatial distribution of the potato leafhopper was developed with the Surfer software program and displayed graphically for descriptive analysis (Golden Software 1990). Surfer is a menu driven contouring program that creates contour maps of gridded data input from ASCII or binary formatted data files. The inverse distance squared interpolation method and a search radius of the 10 nearest

points was used to compute a grid based on PLH estimates to develop contour maps of PLH distribution. The PLH contour interval levels were set for each sampling technique and for each of the two alfalfa harvest periods. The contour intervals were scaled according to the PLH numbers of the sampling date with the highest PLH counts. This was done separately for each alfalfa harvest period and each sampling technique. All other sampling dates in that harvest period and for that sampling technique were contoured using the same PLH contour intervals so that direct comparison of spatial distribution could be made.

TEMPORAL DYNAMICS OF THE POTATO LEAFHOPPER:

The overall temporal dynamics of the PLH in alfalfa and the surrounding habitats was described, beginning with its first arrival by long-distance migration, then reproduction and seasonal population growth, and ending with its late-season population decline and mortality. The value of yellow sticky trap and net sweep sampling techniques as population density estimators were tested by multiple regression analysis, using area trap sampling as the method to obtain the PLH population estimate.

Trap construction and field design: Estimates of PLH abundance and activity were made using yellow sticky traps, net sweeps, and area traps. All three sampling techniques were used at permanent sample sites in a 20 by 20 meter grid

design over the entire alfalfa field and the inside edge of all four bordering habitats, totaling 63 sample sites (Figure 3). Within the alfalfa field there were 34 permanent sample sites. The young cherry/oak habitat had six sites, the mature cherry/oak habitat had eight, the grass field habitat had eight, and the black locust habitat had seven permanent sample sites. Samples were taken from 04 June to 27 May. Trap construction and sampling sequence is previously described.

Early season samples, 26 April to 27 May, were taken from a slightly different field design than the 20 by 20 grid. Three yellow sticky trap transect lines ran from the north end of the alfalfa field into the black locust woods. The yellow sticky traps were constructed the same way as the grid traps, but were spaced 10 m apart rather than 20 m. There were a total of 24 yellow sticky traps in the alfalfa habitat, and 6 yellow sticky traps along the inside edge of the black locust habitat. PLH counts on yellow sticky traps and net sweeps (in alfalfa only) were made on a weekly basis at each sampling site. All PLH specimens caught were saved and the males identified to species to assure the accuracy of the first arrival estimates (DeLong, 1931).

For the sampling technique comparison, an un-weighted least squares regression model was used, with area trap values selected as the dependent (response) variable, and the yellow sticky trap and net sweep values selected as the independent (predictor) variables (NH Analytical Software, 1988). Only those sampling dates when all three sampling techniques, and

whose daily temperatures were above the PLH minimal flight thresholds, were used. The months of June, July, and August fit these requirements. Samples from the alfalfa habitat were used for the analysis.

RESULTS AND DISCUSSION

DISPERSAL OF THE POTATO LEAFHOPPER OUT OF ALFALFA:

First alfalfa harvest period: The mean number of PLH adults caught on yellow sticky traps in the four habitats surrounding the alfalfa field during the post-harvest period were much lower than the numbers caught during the one week pre-harvest period (Table 1). The maximum and minimum daily temperatures affecting flight threshold, and the wind speed and direction affecting PLH activity were similar for these two sampling periods (Table 2). The total precipitation during the pre-harvest period was much greater than that of the post-harvest period (Table 2). The heavy rains of the pre-harvest sampling period likely inflated the yellow sticky trap catch, by increasing PLH activity from mechanical agitation of foliage (Dysart, 1962). The same weather system was also responsible for first major influx of PLH from long-distance migration within the pre-harvest sampling period (personal communication, J D Carlson, 04-17-90). This may account partially for the greater pre-harvest catch, since the yellow sticky traps would have reflected the higher PLH activity level resulting from the search for host plants for feeding and ovipositing after arrival from long distance migration. Sweep samples were not made during the pre-harvest period, and therefore cannot be compared with the counts made during the harvest period.

Table 1. Mean number of potato leafhoppers caught on yellow sticky traps and in net sweeps, for the four bordering habitats (1.2 m to 5.8 m ht mean) and the alfalfa habitat.

habitat	yellow sticky traps				net sweeps		
	<u>first cutting</u>		<u>second cutting</u>		<u>first cutting</u>		<u>second cutting</u>
	05/28- 06/04	06/07- 06/15	07/27- 07/31	07/31- 08/04	06/04	06/15	07/18 08/03
grass field	*28.1bc	7.5b	18.5b	24.2c	-	-	-
Young che/oak	44.4ab	7.7b	92.6a	90.6ab	-	0.1b	6.2ab 24.5ab
mature che/oak	19.1c	4.6b	42.0b	105.3ab	-	0.8b	2.7b 11.8b
black locust	51.3a	25.0a	36.2b	138.8a	-	11.5a	11.7a 37.9a
habitat mean	35.7	11.6	47.3	89.7	-	4.1	6.9 24.7
alfalfa	24.9	-	302.3	-	-	0.0	39.1 8.4

Means followed by the same letter are not significantly different ($P < 0.05$; two way ANOVA).

* Values for 06/04 yellow sticky traps represent means for the 1.2 m trap height only.

Table 2. Weather data for pre- and post-harvest sampling dates of the first and second cutting periods.

	first cutting		second cutting	
	<u>pre-harvest</u>	<u>post-harvest</u>	<u>pre-harvest</u>	<u>post-harvest</u>
	(05/28 - 06/04)	(06/07 - 06/15)	(07/27 - 07/31)	(07/31 - 08/04)
ave maximum temp C	24.0	23.4	25.2	29.2
ave minimum temp C	14.0	12.7	14.5	17.2
wind speed (mph)	10 - 20	5 - 15	5 - 15	5 - 15
wind direction *	south-west	west, south-west	east, north-east west, south-west	
total precip (in)	6.1	0.8	0.8	0.5

* Wind direction refers to the direction from which the wind is coming. The data was taken from the Kellogg Biological Station, located approximately one km from the study site.

The mean number of PLH from yellow sticky traps in alfalfa for the pre-harvest sampling period was 24.9 (N=34, SE=2) and no PLH were caught when sweep samples were taken after the alfalfa was cut, on 08 June. The PLH population established in alfalfa therefore, diminished at the time the alfalfa was cut (Table 1). However, the post-harvest yellow sticky trap catch in the four bordering habitats did not reflect the expected catch resulting from dispersal, relative to the estimated PLH population in alfalfa (Table 1). This indicates that the insects may not have dispersed out of the alfalfa at cutting.

The PLH caught in yellow sticky traps and net sweeps during the post-harvest sampling period were significantly higher in the black locust habitat than any other of the habitats surrounding the alfalfa field (Table 1). The potato leafhoppers appear to have preferred this legume tree species over the other habitats, both before and after cutting. The vertical distribution of the PLH in all four habitats was nearly uniform, not including the balloon traps, which caught no PLH (Table 3).

Second alfalfa harvest period: The mean numbers of PLH from yellow sticky traps and net sweeps in the four habitats surrounding alfalfa during the post-harvest sampling period were much higher than the mean numbers from the pre-harvest period (Table 1). The mean sweep net catch of PLH in the alfalfa habitat before the cutting was 39.1 (N=34, SE=3.0) and

Table 3. Mean number of potato leafhoppers caught on yellow sticky traps at six heights in the four habitats surrounding an alfalfa field.

trap height (m)	first cutting: pre-harvest (5/28-6/04)				post-harvest (6/07-6/15)			
	grass field	young cher/oak	mature cher/oak	black locust	grass field	young cher/oak	mature cher/oak	black locust
1.2	28.14	48.50	18.38	24.91	7.67a	6.33a	5.00ab	18.17b
2.7	-	-	-	-	7.83a	7.67a	6.17a	22.67ab
4.3	-	-	-	-	6.67a	6.67a	4.00ab	29.50a
5.8	-	-	-	-	8.00a	10.00a	3.33b	29.67a
15.3	0.00 *	0.00	0.00	M	0.00	0.00	M	M
30.5	0.00 *	0.00	0.00	M	0.00	0.00	M	M
trap height (m)	second cutting: pre-harvest (7/27-7/31)				post-harvest (7/31-8/04)			
	grass field	young cher/oak	mature cher/oak	black locust	grass field	young cher/oak	mature cher/oak	black locust
1.2	41.33a	62.17c	51.67a	32.33a	45.00a	126.20a	202.20a	208.30a
2.7	19.67b	104.80ab	37.50a	41.33a	25.67b	91.33b	94.83b	146.70b
4.3	8.50c	125.80a	40.67a	37.17a	14.17c	82.83bc	71.83bc	116.50c
5.8	4.50c	77.67bc	38.17a	33.83a	12.00c	62.00c	52.17c	83.67d
15.3	0.00	0.00	0.00	2.00	3.00	2.00	5.0	26.00
30.5	0.00	0.00	0.00	0.00	1.00	1.00	1.0	0.00

Means followed by the same letter are not significantly different ($P < 0.05$; two way ANOVA).

* PLH catch at 15.3 m and 30.5 m 'balloon traps' represent only one replication, therefore were not tested for statistical significance. The PLH catch in balloon traps are based on a 24 hour sampling period.

after the cutting was 8.4 ($N=34$, $SE=0.7$). This indicates that the established population decreased as a result of cutting. The maximum and minimum daily temperatures affecting PLH flight threshold, and the wind speeds affecting PLH activity were similar for both sampling periods. Therefore, the increased catch in the bordering habitats and decreased catch in alfalfa was clearly a result of PLH dispersal in response to the cutting.

The PLH caught on yellow sticky traps during the post-harvest sampling period were significantly greater in the black locust than any of the other habitats surrounding alfalfa, and the young and mature cherry/oak habitats had significantly greater PLH catches than those in the grass field habitat (Table 1.). During the pre-harvest sampling period, the PLH numbers in the young cherry/oak were highest, and the PLH numbers in the other three habitats were statistically the same. The PLH caught in yellow sticky traps in the young cherry/oak habitat were higher possibly due to the east, north-east winds during this time, lending to PLH dispersal in the southern direction (Table 2). Sweep net counts in the tree foliage after alfalfa cutting were highest in the black locust habitat, next highest in the young cherry/oak, and lowest in mature cherry/oak (Table 1). Similar proportions were found before the alfalfa cutting for net sweeps in the bordering habitats. This indicates that PLH has a preference for black locust when dispersing in response

to alfalfa cutting, and prefers cherry and oak habitats secondarily over an open grass field.

The vertical distribution of PLH caught in yellow sticky traps (1.2 m to 30.5 m heights) during the pre-harvest sampling period was uniform for the mature cherry/oak and black locust habitats, with the young cherry/oak and grass habitats being non-uniform (Table 3). The vertical distribution of PLH during the post-harvest sampling period was non-uniform for all habitats, counts being significantly highest at 1.2 m and generally decreasing proportionally with height for all habitats (Figure 4). Very few PLH were caught in the balloon traps above the bordering habitats, except for 26 individuals caught at 15.3 m in the black locust habitat during the post-harvest sampling period. This indicates that in response to alfalfa cutting, PLH disperses into the surrounding habitats primarily at low heights (1.2 to 2.7 meters), but can fly as high as 30.5 m especially when preferred habitats are present.

The intensive sampling of vertical trapping structures during the post-harvest sampling period showed that for all four bordering habitats, 60% of the PLH (means averaged and compared for a six-hour time period) were caught in the sample taken six hours after the cutting, and 17% were caught in the sample taken 18 hours after the cutting (Table 4). Eighty eight percent of the 26 PLH caught at 15.3 m in the balloon traps over the black locust habitat were caught in the first six hours after the cutting. Of the PLH caught in net sweeps

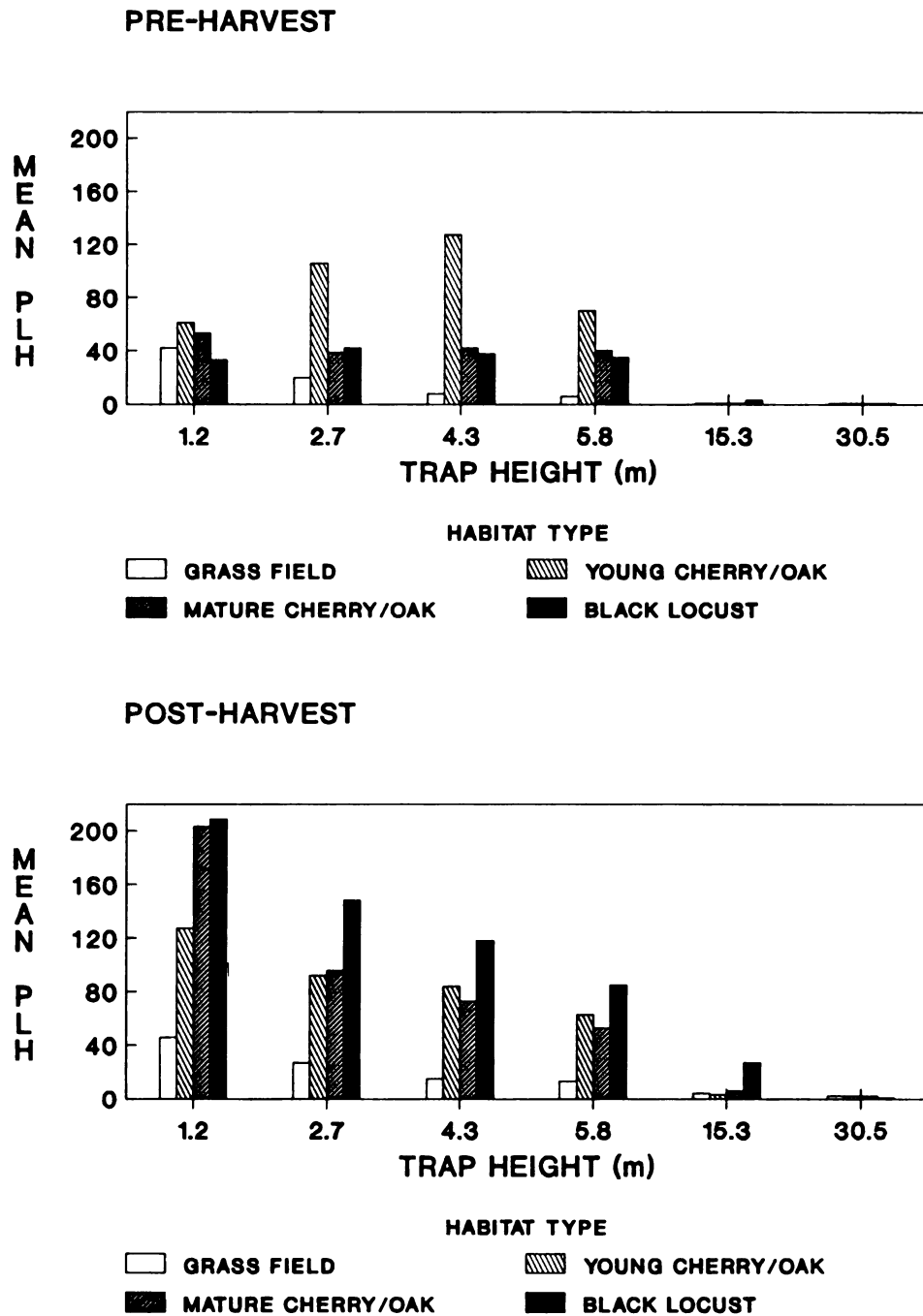


Figure 4. Vertical distribution of the potato leafhopper over six heights, collected from four habitats surrounding an alfalfa field, for the second alfalfa cutting.

Table 4. Percent of total potato leafhoppers caught on yellow sticky traps (1.2 m to 5.8 m ht) during the four day period of intensive sampling after the second cutting.

habitat	number of hours after second alfalfa cutting				
	6	18	42	48	96
grass field	63%	20%	12%	1%	4%
young che/oak	65%	14%	8%	5%	8%
mature che/oak	51%	19%	17%	7%	6%
black locust	64%	12%	9%	11%	3%

The percentages are based on the mean PLH catch for a six hour sampling time within each intensive sampling period, made in the four vegetative habitats.

made in tree foliage during the four-day post-harvest period, 80% were caught six hours after the alfalfa cutting. This indicates that in response to alfalfa harvest, most PLH leave the alfalfa field immediately after the cutting, dispersal reducing greatly after the first 24 hours.

Comparison of the two alfalfa harvest periods: Comparing the nearly uniform vertical distribution of PLH in the bordering habitats after the first cutting to the change from a nearly uniform vertical distribution before the second cutting to a strongly non-uniform vertical distribution after the second cutting, suggests that the long-distance migrant population did not disperse out of the alfalfa in response to the first cutting (Figure 4 and 5). This is similar to what Pienkowski and Medler (1966) observed during the first alfalfa harvest. They concluded that the migrant population either dispersed such that they were not caught in the traps surrounding the field, or they did not disperse out of the field at all after cutting. Since all of their sticky traps were less than 1 m high, they could not conclusively say whether the low catch was a result of PLH not actually dispersing out of the alfalfa, or the PLH possibly dispersing above the low sticky traps. The results from the multiple-height traps (VTS) in our study provides stronger evidence for Pienkowski and Medler's later conclusion of the migrant PLH not dispersing out of alfalfa at all.

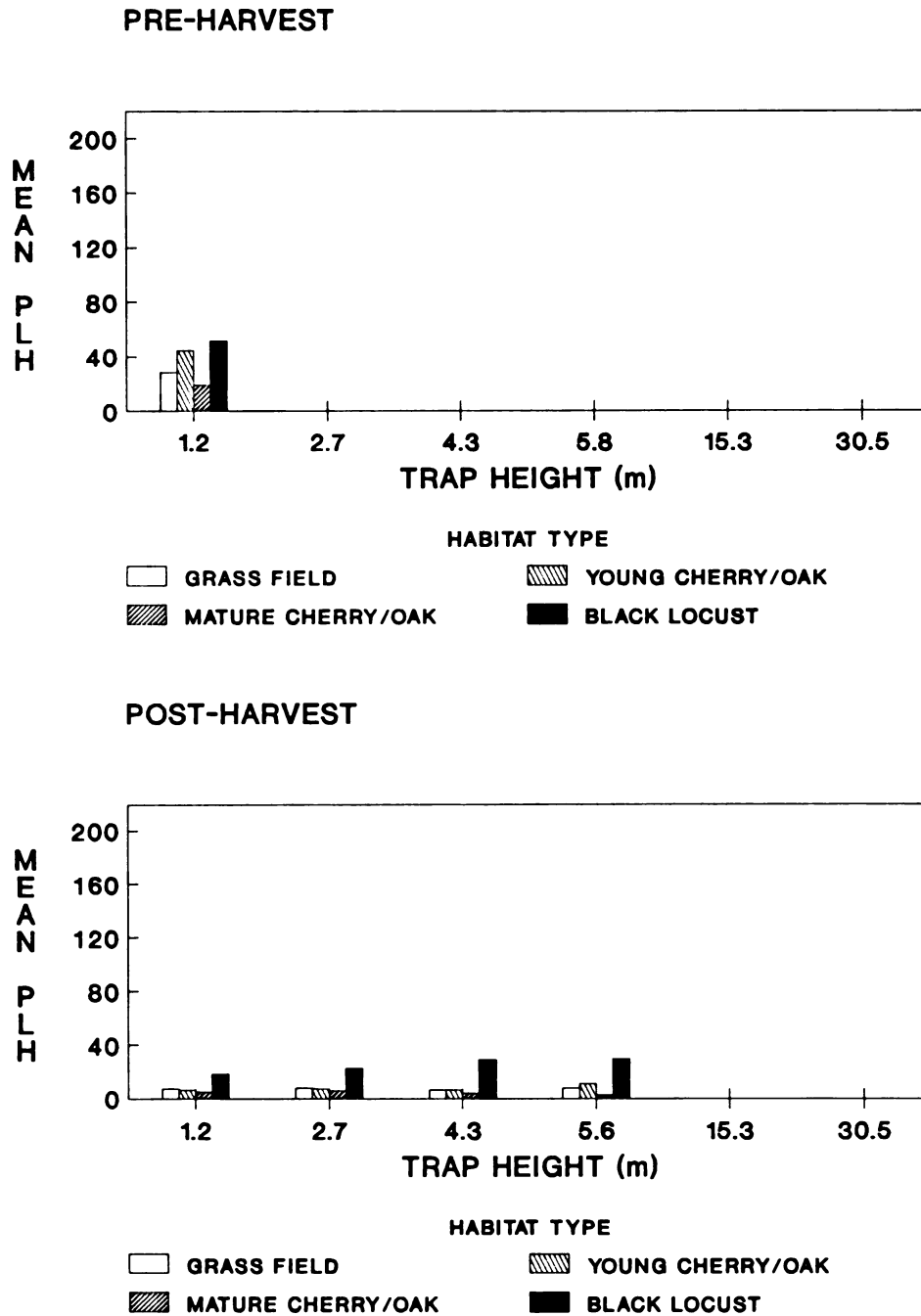


Figure 5. Vertical distribution of the potato leafhopper over six heights, collected from four habitats surrounding an alfalfa field, for the first alfalfa cutting. There were no samples taken at the 2.7, 4.3, and 5.8 m heights for the pre-harvest sampling period.

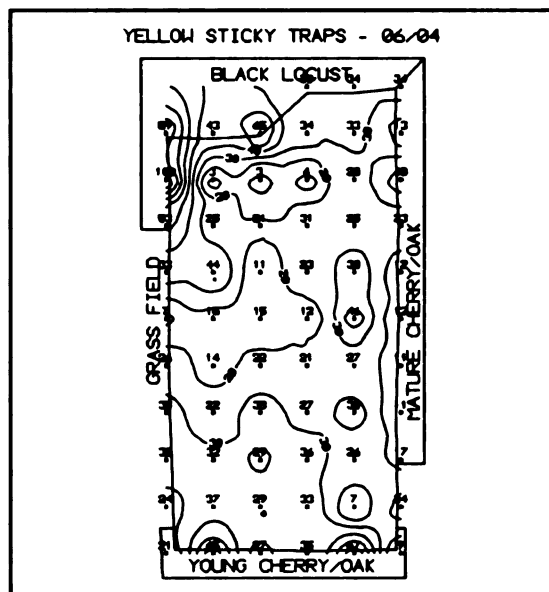
Since sweep samples 24 hours after the first cutting showed no adult PLH population in the alfalfa stubble, there may have been high mortality to the PLH from the mechanical harvest operation. Mortality may also have occurred from insect desiccation by exposure, since the day following the cutting was hot and dry (Table 2). This could be true if the flight capabilities of the potato leafhopper migrant population were lost shortly after long-distance migration, as Waloff (1973) described for mature females in a number of leafhopper species. This would result in a lower number of individuals being able to disperse into the surrounding habitats in response to the disturbance of cutting.

There are a number of explanations for how migrant PLH could lose their ability to disperse in response to cutting. One is that from the time female PLH leave their overwintering sites in the south, to the time they arrive in the north, the fertilized eggs that they carry are maturing and enlarging. Shields (1990) observed a significantly higher body length to wing length ratio in migrant females collected in New York, than in pre-migrant females collected in Louisiana. The effect of this "wing loading" on migrant females could be a diminishing ability to fly. Teraguchi (1986) saw that during migratory bouts, Empoasca females were carrying primarily small (assumably immature) eggs (personal communication, 03-16-90). The high vertical flights ended around the time that the eggs were expected to be large and mature (personal communication, Teriguchi, 03-16-90). Another possibility is

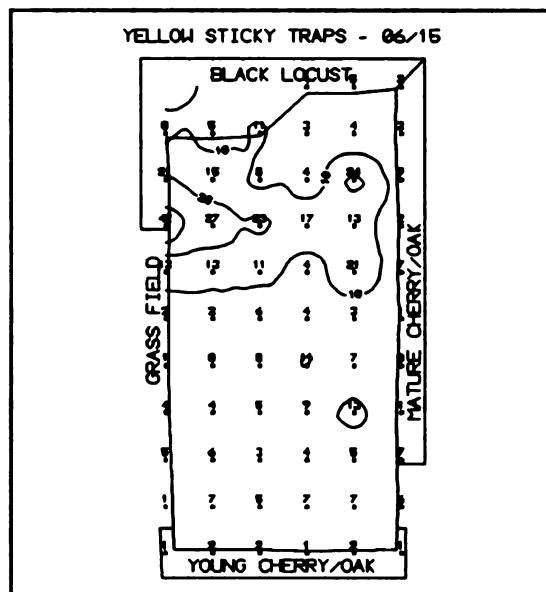
that PLH could lose some or all ability to fly as a result of muscle fatigue from the long-distance migration. Especially if an immediate explosive flight was required to avoid an on-coming alfalfa mower, the failure to do so because of less than optimal strength is plausible. Even if the ability to fly is not physiologically lost following long-distance migration, it is possible that PLH could acquire a sedentary behavior in response to finding a host plant for ovipositing. This would allow for local flight in search of host plants immediately after long distance migration, but a lack of dispersal for those females ovipositing in alfalfa at the time of cutting.

DISPERSAL OF THE POTATO LEAFHOPPER INTO ALFALFA:

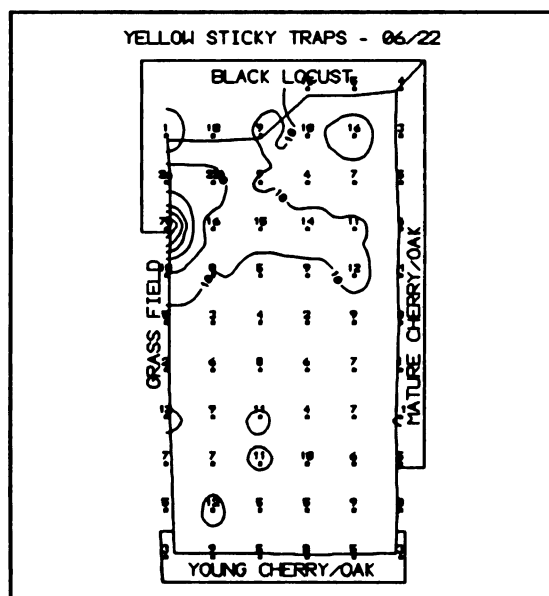
First alfalfa harvest period: The spatial distribution of PLH based on yellow sticky trap counts during the pre-harvest sampling period showed highest PLH numbers in the black locust habitat, followed by young cherry/oak, grass field, alfalfa, and mature cherry/oak (Figure 6a). The distribution of PLH in alfalfa was fairly uniform, except for the very low counts at the north end of the field near the black locust. The alfalfa was about 53 cm high before the first cutting. The first yellow sticky trap post-harvest sampling period had lower PLH counts in all habitats, except for a few sites at the north end of the alfalfa field where trap catch reached 27 PLH (Figure 6b). The spatial pattern in alfalfa was very similar



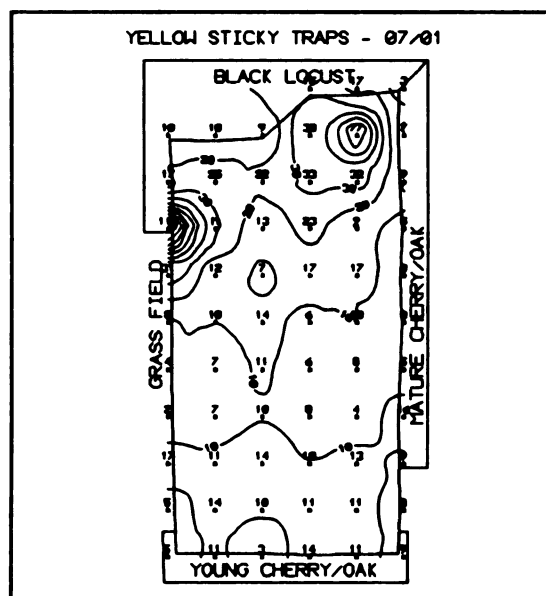
a



b



c



d

Figure 6. Spatial distribution of the potato leafhopper during the first alfalfa cutting, based on yellow sticky trap counts: a - pre-harvest sampling period; post-harvest sampling periods - b, c, d.

during the second post-harvest sampling period, except trap catches in the bordering habitats were higher in a few places (Figure 6c). These higher catches in the bordering habitats may be due to local PLH dispersal from other areas, since the counts in alfalfa remained fairly consistent. The third post-harvest sampling period had an increase in PLH trap catch throughout the whole alfalfa field, with higher densities at the north end of the field, and the bordering habitats remaining basically the same (Figure 6d).

The spatial distribution based on net sweep counts have a similar concentration in the north end of the alfalfa field after the cutting, except for the first two samples taken in the first week after alfalfa cutting (Figure 7). During this period, densities in alfalfa were zero or nearly so (Figure 7a, 7b). PLH established throughout the whole field by the second week after cutting, counts being slightly higher at the north end (Figure 7c). By 01 July, alfalfa field margins had greater counts than the interior of the field, the north end being the highest (Figure 7d). The alfalfa height was 7 cm on 15 June, 23 cm on 22 June, and 40 cm on 01 July.

The spatial distribution of PLH based on area trap counts was quite variable, showing no apparent immigration patterns over time (Figure 8). Since the PLH must fly to be caught in this trap, the potential flight inhibition of the long-distance migrants may have affected the estimates from these traps. Similar to the net sweeps, the counts were very low

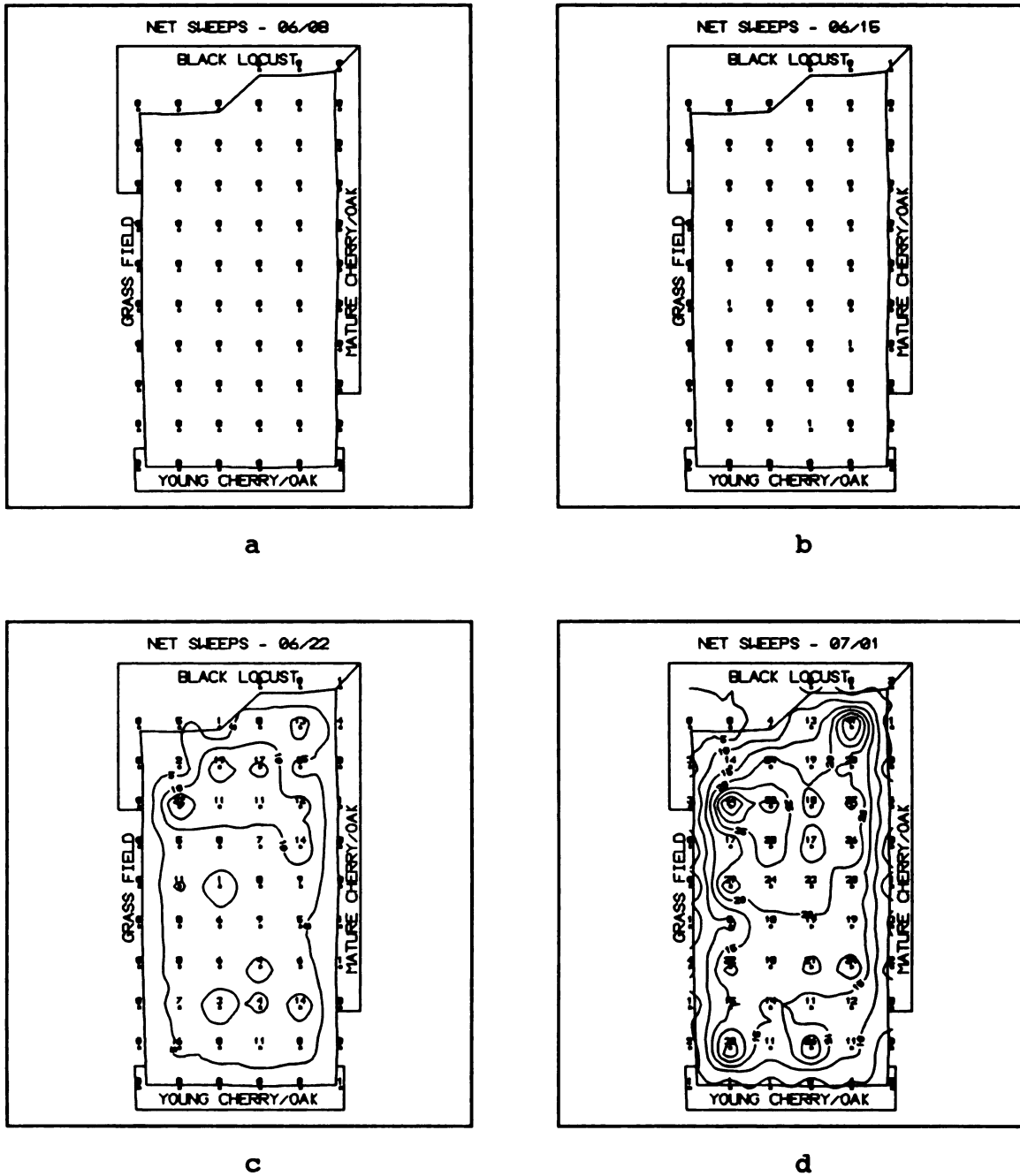


Figure 7. Spatial distribution of the potato leafhopper during the first alfalfa cutting, based on net sweep counts: post-harvest sampling periods - a, b, c, d.

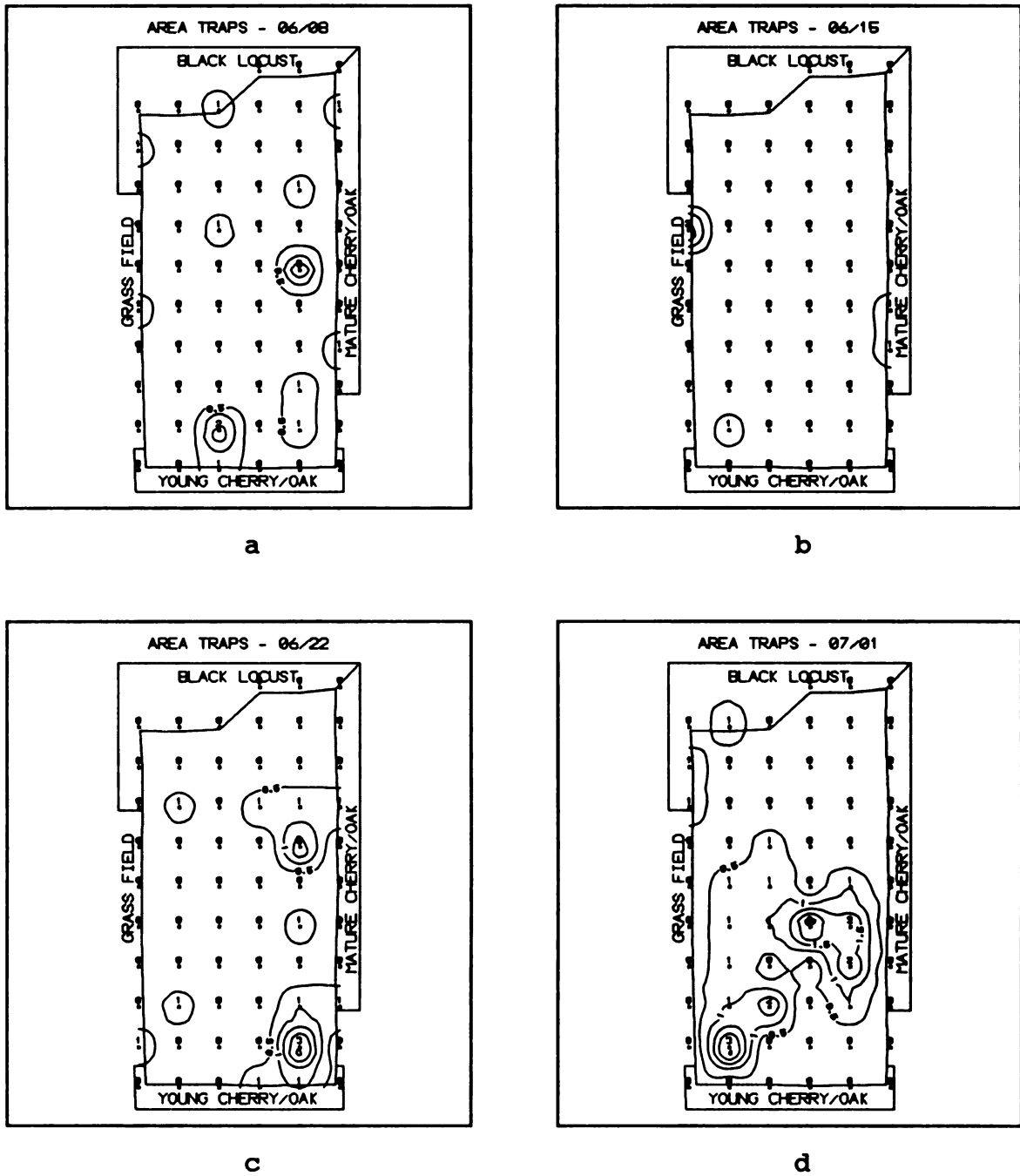


Figure 8. Spatial distribution of the potato leafhopper during the first alfalfa cutting, based on area trap counts: post-harvest sampling periods - a, b, c, d.

for the first two post-harvest sampling periods (Figure 8a, 8b).

Overall, re-colonization by PLH was distributed more near the black locust habitat, which was the greatest source of potato leafhoppers based on pre-harvest and post-harvest bordering habitat estimates (Table 1). The higher PLH densities near field margins, shown by the net sweeps was similar to what Kieckhefer and Medler (1966) saw in their distribution studies as population densities increased. The comparison of yellow sticky trap counts to those of the net sweeps and area traps indicates that the long-distance migrant adults fly into the alfalfa field soon after the cutting, but do not begin to establish themselves until there is alfalfa regrowth. We could not positively determine the source of all the PLH immigrants, since there were several brief long-distance transport episodes between 08 June and 01 July, that could have deposited PLH into the field and surrounding vegetation. The rate of re-colonization was fairly uniform over the whole field, the north end consistently having higher counts throughout the sampling periods.

Second alfalfa harvest period: The spatial distribution of PLH based on yellow sticky trap counts during the pre-harvest sampling period had highest potato leafhopper numbers in the alfalfa habitat, followed PLH counts in the mature cherry/oak, young cherry/oak, grass field, and black locust habitats (Figure 9a). The distribution of PLH in alfalfa was

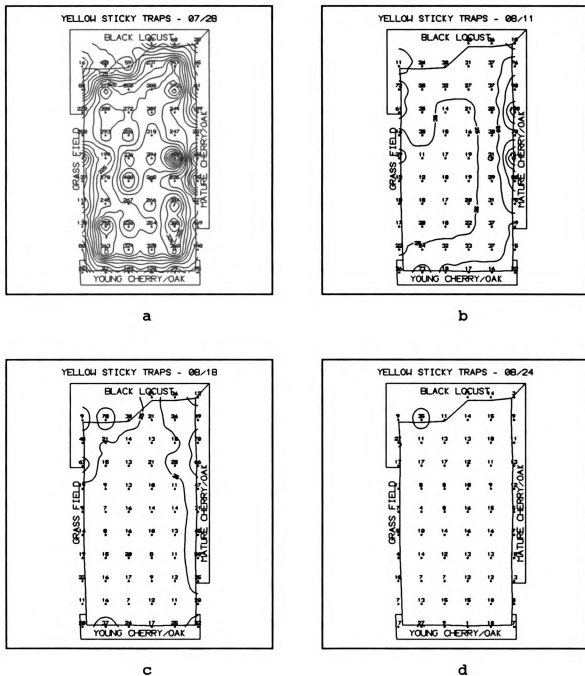


Figure 9. Spatial distribution of the potato leafhopper during the second alfalfa cutting, based on yellow sticky trap counts: a - pre-harvest sampling period; post-harvest sampling periods - b, c, d.

distinctly greater in the field margins than the interior. This was especially true near the south-east corner of the alfalfa field, which had the highest elevation. The alfalfa height before harvest was 64 cm. During the first post-harvest sampling period, the PLH were distributed predominantly along the field margins adjacent to the habitats with tree vegetation. The margins adjacent to the grass field and interior alfalfa plots had lower catches (Figure 9b). Patterns were similar for the second post-harvest sampling period, except the catches in the young and mature cherry/oak habitats were lower (Figure 9c). By the third post-harvest sampling period, the distribution of PLH was much more uniform throughout the alfalfa field, and the counts in bordering habitats were nearly equal to the PLH counts in alfalfa (Figure 9d).

The spatial distribution of PLH based on net sweep counts before the cutting was greatest along the east margin of the alfalfa field, especially at the higher elevations near the south-east corner (Figure 10a). During the first post-harvest sampling period, the distribution of PLH was nearly uniform, with the highest counts mainly in the north end (Figure 10b). A similar pattern can be seen in the second post-harvest sampling period, except for slightly higher catches on the east side and lower PLH counts in some of the bordering habitats (Figure 10c). By the third sampling period, the recolonization pattern was more uniform, with the highest counts randomly distributed throughout the field (Figure 10d). The

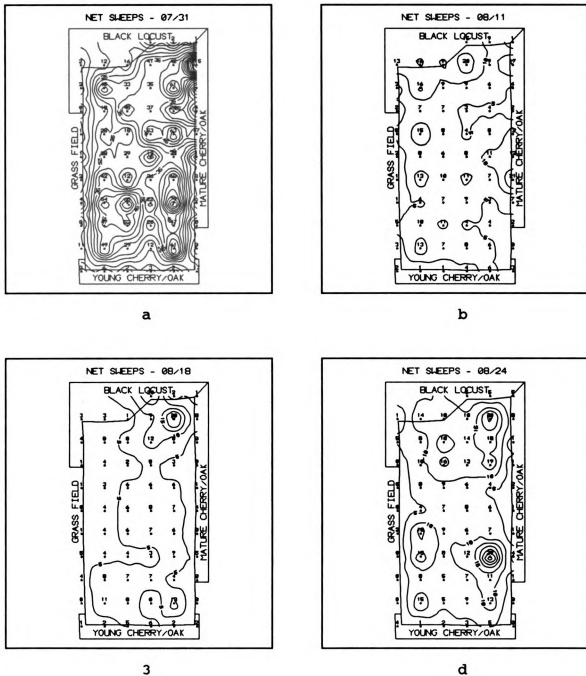


Figure 10. Spatial distribution of the potato leafhopper during the second alfalfa cutting, based on net sweep counts: a - pre-harvest sampling period; post-harvest sampling periods - b, c, d.

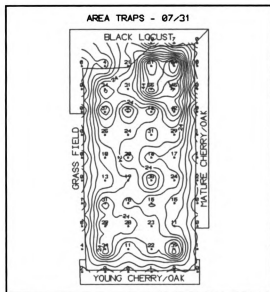
alfalfa height was 15 cm on 11 August, 30 cm on 18 August, and 42 cm on 24 August.

The spatial distribution of PLH based on area trap catch before the cutting showed highest population densities along the north and south margins of the alfalfa field (Figure 11a). The spatial distribution during the first post-harvest period was fairly random in the alfalfa habitat, the highest counts being in the black locust habitat (Figure 11b). During the second and third post-harvest sampling periods, the population was distributed more in the interior of the alfalfa field, and slightly higher at the north end (Figure 11c, 11d).

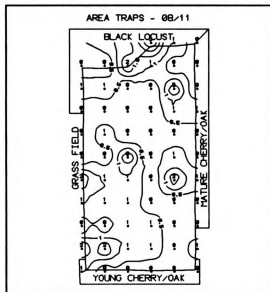
Overall, the pre-harvest distribution of PLH was highest along field margins, similar to that observed by Kieckhefer and Medler (1966) in periods of high population densities. After the cutting, the re-colonization of alfalfa by PLH was distributed more along margins adjacent to habitats with tree vegetation, which were the greatest sources of leafhoppers (Table 1). The locally produced population established in alfalfa much more quickly after cutting than the long-distant migrant population of the first cutting. This is similar to what Flinn et al. (1990) observed. By the last post-harvest sampling period, distribution of PLH was fairly uniform for all sampling techniques.

TEMPORAL DYNAMICS OF THE POTATO LEAFHOPPER:

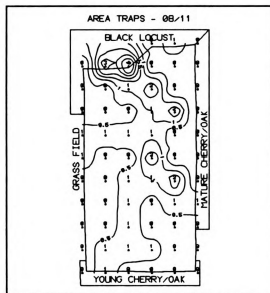
The first potato leafhoppers were caught on yellow sticky traps during the one week sampling period, ending 26 April (74



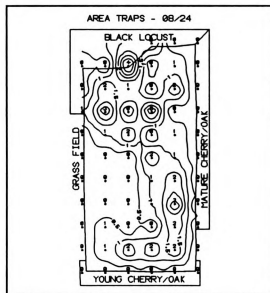
a



b



c



d

Figure 11. Spatial distribution of the potato leafhopper during the second alfalfa cutting, based on area trap counts: a - pre-harvest sampling period; post-harvest sampling periods - b, c, d.

Degree-Days > 10 C) (Figure 12). The one male specimen caught during this period was in the alfalfa habitat and was confirmed as Empoasca fabae . Subsequent single male specimens were caught on yellow sticky traps on 05 May (black locust) and 27 May (alfalfa). The PLH that established in this time are expected to have come from long-distance migration rather than a local over-wintering population, since there were a number of weak synoptic wind transport events during this time that could have deposited potato leafhoppers into the area. Also, the female-to-male ratio was quite high, indicating a long-distance migrant population (Flinn, 1990).

The first large catch of PLH was during the sampling period ending 04 June (268 degree-days) (Figure 12). These large numbers are postulated to have been a result of the first major influx of PLH from long-distance migration, and individuals were caught in all five habitats of the study site. Other PLH scouting networks in Michigan confirmed the large increase in PLH counts during that week (Whalon et al. 1989). Synoptic weather conditions were also ideal, with nocturnal 850 millibar winds in excess of 20 meters-per-second from the Gulf Coast source region to Michigan (personal communication, J. D. Carlson). The black locust habitat had the highest catch, followed by young cherry/oak, grass field, alfalfa, and then mature cherry/oak.

After the first alfalfa cutting (311 degree-days), the PLH population based on counts from yellow sticky traps was highest in the black locust habitat, followed by alfalfa,

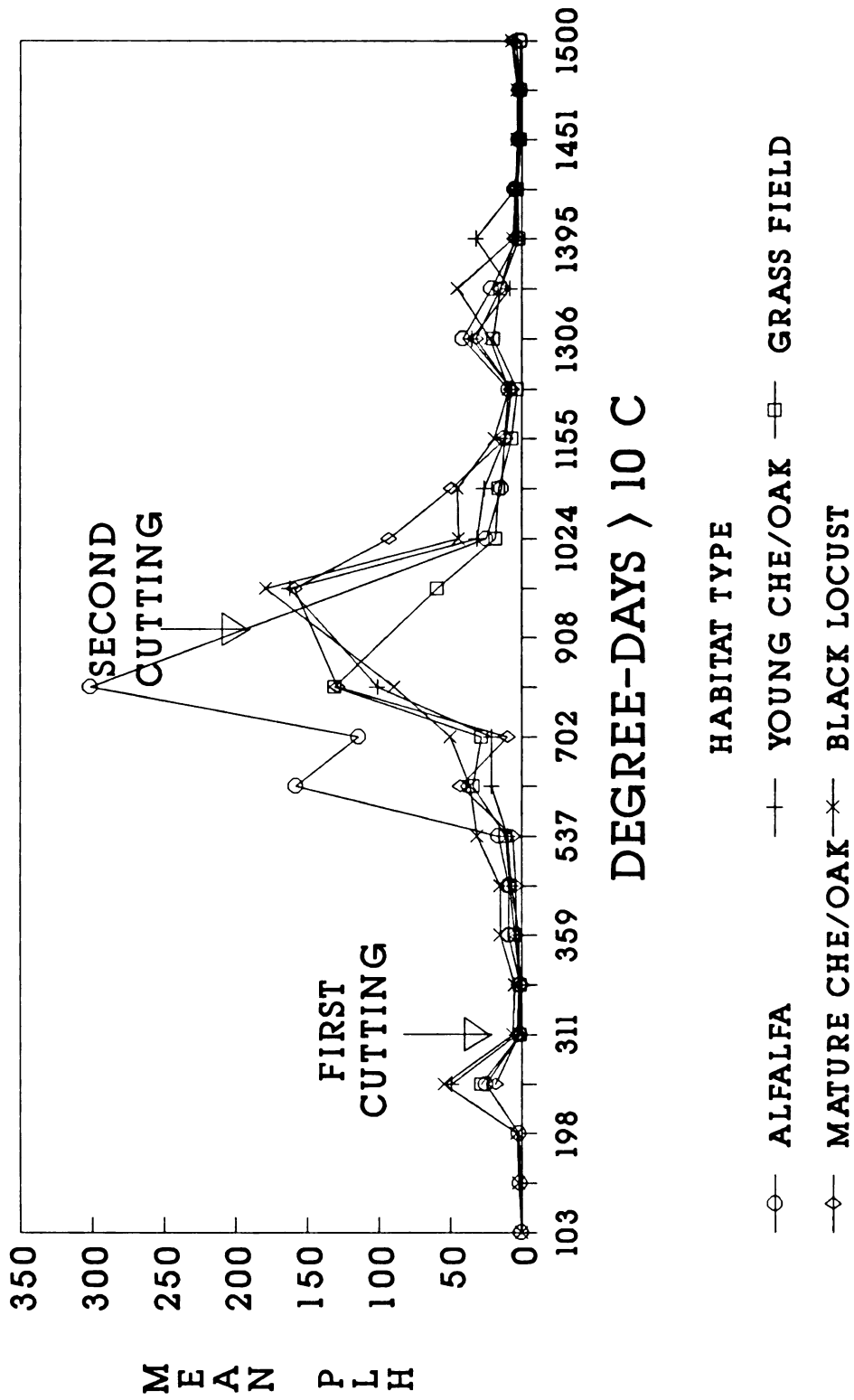


Figure 12. Temporal distribution of the potato leafhopper in the five vegetative habitats, represented by yellow sticky trap samples.

grass field, young cherry/oak, and then mature cherry/oak. This distribution remained basically the same, the total PLH population gradually increasing until sampling period 07 July (622 degree-days), when the first locally produced PLH adults were expected to be found (Hogg, 1985). There were a total of 354 degree-days $> 10^{\circ}\text{C}$ between the time of the first major influx of long-distance migrants to the sampling period ending 07 July. The increase in population density in the month of June was likely a result of a number of potential long distance transport episodes that occurred between 08 June and 01 July.

During the month of July, the PLH population increased in all five habitats; dramatically so in alfalfa, where counts of PLH were much higher than any of the other habitats. This was easily seen in all three sampling techniques (Figure 13). After the second alfalfa cutting (908 degree-days), the PLH population briefly diminished in alfalfa, and increased dramatically in all of the bordering habitats, except the grass field (Figure 12). This was clearly a result of PLH dispersal out of the alfalfa field into the bordering habitats. The alfalfa habitat was quickly re-colonized, and the population densities in the bordering habitats slowly declined. The alfalfa habitat did not again attain the highest densities until sampling period 07 September (1306 degree-days), based on counts from yellow sticky traps.

In the month of October, there was a general decline of PLH counts in all habitats (Figure 12). The three bordering

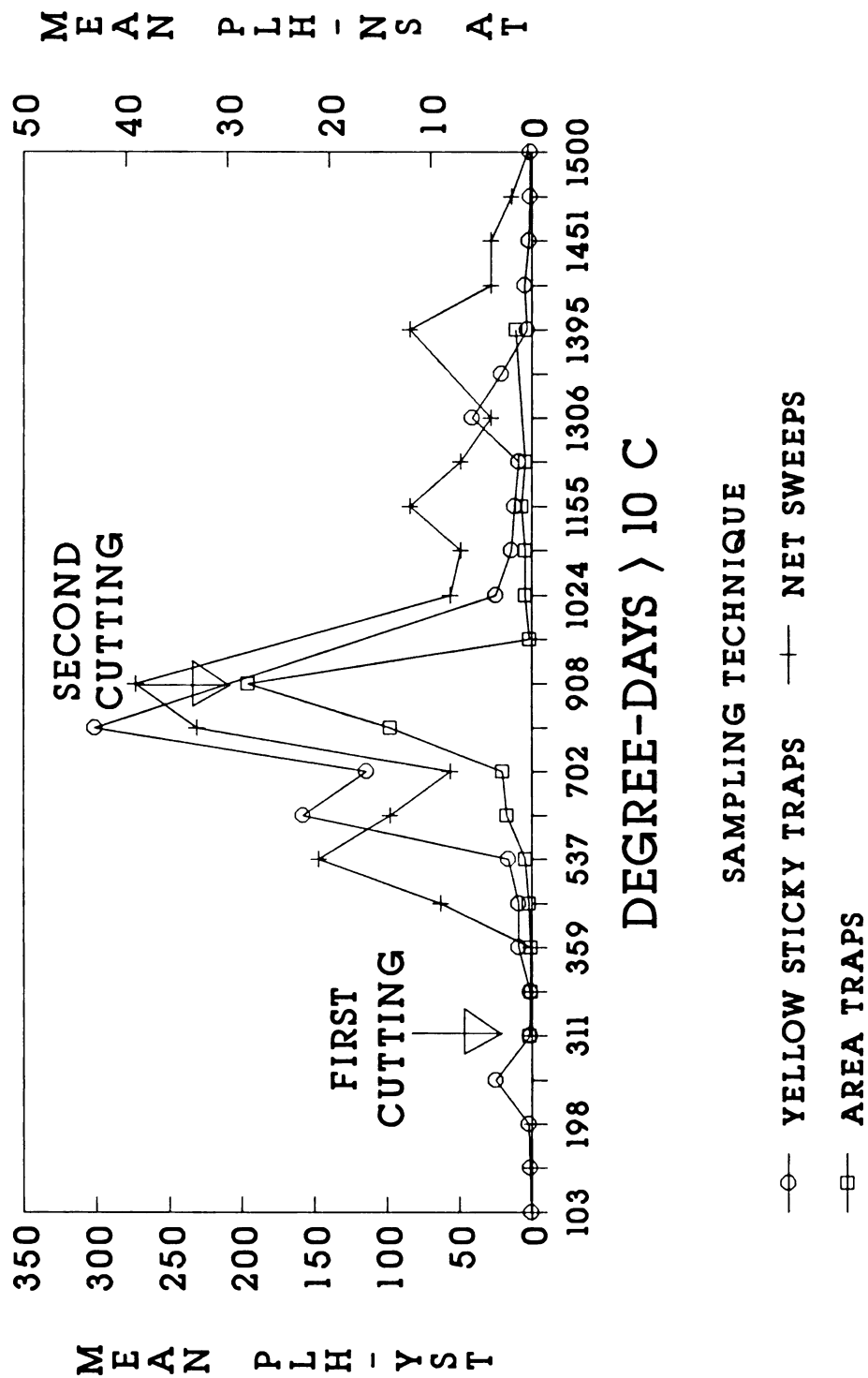


Figure 13. Temporal distribution of the potato leafhopper in alfalfa, represented by yellow sticky traps (YST), net sweeps (NS), and area traps (AT).

habitats attained higher densities than the alfalfa and grass field habitats. This is similar to what Lamp et al. (1989) observed in habitats containing tree vegetation near alfalfa fields, and is probably a result of the PLH seeking protection from cold weather in those habitats. Regressing net sweep values on the area trap values resulted in a significant overall regression ($F=16.51$, $P=.001$, $R^2=.64$). This indicates that the linear trends from the net sweep technique were similar enough to the linear trends of the area trap technique, so as to be important in explaining absolute density trends. Regressing yellow sticky trap values on the area trap values also resulted in a significant overall regression ($F=60.7$, $P=.00$, $R^2=.86$). This indicates that the linear trends from the yellow sticky trap technique were similar enough to the linear trends of the area trap technique, to be important in explaining absolute density trends. These regressions suggest that even though net sweep and yellow sticky trap techniques do not measure absolute density, the seasonal trends resulting from these sampling techniques are highly correlated with the seasonal trends resulting from absolute density sampling techniques (Figure 13).

CONCLUSIONS

DISPERSAL OF THE POTATO LEAFHOPPER OUT OF ALFALFA:

Dispersal patterns from the first alfalfa cutting suggest that long distance migrant populations of the potato leafhopper may not have the ability to disperse out of alfalfa in response to cutting, and may suffer high mortality shortly after cutting. Dispersal patterns from the second cutting indicate that the locally produced populations of the potato leafhopper disperse into the surrounding vegetation primarily at low heights (1.2 to 2.7 m), but can also fly as high as 30.5 m, especially when into a preferred habitat like black locust. When dispersing in response to cutting, most of the PLH leave the field immediately or within the first 24 hrs after the cutting. Dispersal patterns from the second cutting also indicate that PLH have a preference for black locust over cherry/oak, and cherry/oak over grass when dispersing, as well as during more sedentary activity.

DISPERSAL OF THE POTATO LEAFHOPPER INTO ALFALFA:

The dispersal patterns from the first and second alfalfa cuttings indicated that tree vegetation surrounding an alfalfa field acts as a temporary host for the potato leafhopper, until conditions become favorable in the alfalfa field for re-colonization. Yellow sticky trap samples showed that potato leafhoppers fly into the alfalfa field very soon after cutting, but do not establish themselves until the alfalfa

reaches around 15 cm in height. The locally produced populations establish in the new cover sooner than the long-distance migrant populations.

TEMPORAL DYNAMICS OF THE POTATO LEAFHOPPER:

The use of all three sampling techniques was important for an accurate description of the spatial and temporal dynamics of the potato leafhopper.

The use of area traps was important as an estimator of PLH population density because the technique is not influenced by environmental variables such as wind, alfalfa height, and movement from surrounding areas. The accuracy of the estimate was limited by the fact that PLH flight behavior is required for the technique to work, and because it only provided an estimate of the PLH population at one discrete time of the day. The population density estimate could be distinctly different if taken at another time of the day, since the insect population is moving throughout the day in response to the changes in climatic conditions.

The use of net sweeps to estimate PLH population density was important in that the technique requires no flight behavior on the part of the insect to attain the sample. The accuracy of the estimate is limited, though, by the fact that it is a function of alfalfa height, and that it only represents the one discrete time of the day that the sample was made. It, like the area trap, does not account for the constant change of the PLH population, as the day goes on.

The use of yellow sticky traps to estimate PLH population density was important in that it is the only technique which accumulates PLH over time. Rather than the estimate being based on one instantaneous sample, the trap gathers information about a population 24 hours a day. It also had the advantage of being able to be placed easily in a wide range of sampling locations, such as on a 30 m high helium balloon. There are a number of variables not related to insect density, though, that can significantly limit the accuracy of the yellow sticky trap estimate. In addition to insect density, the yellow sticky trap sample is influenced by color attraction, flight behavior, wind speed, and temperature. Therefore to accurately describe the spatial and temporal dynamics of the PLH population, more than one sampling technique is required.

MANAGEMENT STRATEGIES:

Timing alfalfa cuttings to harvest alfalfa just after PLH ovipositing is a standard recommendation for control. With the indication that long-distance migrants have limited flight ability after establishing in alfalfa, the adult can be made an additional target for the cutting practice.

In situations where a PLH susceptible crop (apples, grapes, soybeans, potatoes, etc.) is adjacent to an alfalfa field that is to be harvested, a 'trap crop' can be designed to intercept the PLH dispersing out of the cut alfalfa. The 'trap crop' should involve plants that highly attractive to

PLH (like black locust), and should be placed between the alfalfa field and the crop to be protected. Because of the PLH's vertical distribution during dispersal, the 'trap crop' should be as full and high as possible.

FUTURE RESEARCH:

There are a number of logical additions to this type of PLH dispersal research. First, the vertical trapping array along the inside edge of the bordering habitats should be expanded out from the alfalfa field, continuing the dimensions already set for the trap grid in the alfalfa. This would allow for the characterization of PLH vertical distribution, not only at the edge of the alfalfa field, but also at incremental distances away from the alfalfa and into the surrounding habitats. Designing the vertical trapping in a grid format will also produce a three dimension spatial description of PLH dispersal, since there is both vertical and horizontal sampling in the grid.

The other aspect that would help characterize PLH dispersal is a 'mark and recapture' study. This type of work would quantify the movements of small numbers of PLH in greater detail, to then help interpret the dispersal patterns of the broader spatial study.

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