Implications of Pea Aphid Host-Plant Specialization for the Potential Colonization of Vegetables Following Post-Harvest Emigration from Forage Crops

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ABSTRACT The pea aphid, *Acyrthosiphon pisum* (Harris), attacks a wide range of legumes including many important forage and vegetable crops. Although economic injury levels for pea aphids are seldom exceeded in forage crops, aphid densities can reach extremely high levels during a single harvest cycle. After harvest of forage crops, large numbers of pea aphids may disperse into proximate vegetable fields. The objective of this study was to determine the potential impact of immigrating pea aphids on vegetable crops adjoining forage crops in the agricultural landscape. Pea aphids collected from alfalfa and clover were evaluated for their ability to survive on and their propensity to feed on vegetable crops. The survival of pea aphids collected from clover and alfalfa was significantly higher on these forage crops than on peas, green beans and lima beans in laboratory transplant experiments. In additional laboratory experiments, alfalfa-adapted aphids produced significantly fewer aphid offspring on lima beans than on alfalfa, and the adults and offspring had significantly higher mortality on lima bean leaves than on alfalfa leaves. Analysis of aphid feeding with an electronic monitor confirmed that alfalfa-adapted pea aphids feed on phloem sap from alfalfa but never feed on lima beans. These results led us to predict that pea aphids immigrating from alfalfa and other forage crops during harvest would not establish persistent, damage-causing populations in nearby vegetable crops. Our field data on pea aphid populations in lima beans were consistent with this hypothesis. High densities of pea aphids were found in lima beans immediately after harvests of nearby alfalfa fields, but high aphid densities did not persist >3 d. Our study suggests that although aphids can emigrate from forage crops to vegetable crops at densities above published action thresholds, the amount of damage actually caused by these forage-crop adapted aphids in higher-value vegetable crops will be minimal. It may be unnecessary to treat aphids in lima beans and other vegetables when aphids have immigrated from harvested forage crops. These findings suggest that pest management decision-making in vegetables can be improved by considering the source of immigrating pests such as pea aphids.

KEY WORDS *Acyrthosiphon pisum*, lima bean, dispersal, host range, economic injury level

FORAGE CROPS ARE a primary component of many agroecosystems and they can be an important source of insect pests that migrate into other crops (Stoltz and McNeal 1982, Schaber et al. 1990, Pedigo 1996). Most of the crops that are vulnerable to attack from pests emigrating from forage crops are fruits and vegetables, which tend to have a much higher value on a per area basis than forage crops like alfalfa, clover, other legumes and grasses. In New York, vulnerable vegetable crops cover <1% of the area planted to alfalfa, yet the average value of these vegetables on a per area basis is nearly three times higher (see Table 1). Thus, a full understanding of the biology and population dynamics of insect pests in forage crops is imperative for the effective management of many high-value vegetables and fruits.

One of the main forces driving the ecology of forage systems grown for hay is periodic harvesting, which takes place three to five times per growing season, depending on the crop and the environmental conditions. When forage crops are harvested almost all insects in the field either die or migrate. Mass migrations of both pests, including *Lygus* spp., western flower thrips, *Frankliniella occidentalis* (Pergande), the alfalfa weevil, *Hypera postica* (Gyllenhal), *Sitona scissifrons* Say, and the pea aphid, *Acrythosiphon pisum* (Harris), have all been recorded as postharvest immigrants from alfalfa into other crops (Stoltz and McNeal 1982, Harper et al. 1990, Schaber et al. 1990).

In our study we focused on the dispersal of pea aphids from alfalfa to lima beans after the harvest of alfalfa. Alfalfa is one the most widely used forage crops and high densities of pea aphids can develop in alfalfa between harvests (Losey 1996). Two characteristics of pea aphids that make them particularly important as potential migratory pests are a wide host range and parthenogenic reproduction. Pea aphids feed only on legumes, but within this plant family they can cause significant damage to peas, dry beans, alfalfa, clover, and fresh beans, both snap and lima (Stoltz and Mc-

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Table 1. Comparison of hectares in production, value per hectare and economic threshold for pea aphids on alfalfa versus lima and snap beans, and peas in New York

Crop	No. of hectares[a]	Value[a] ($/ha)	Economic threshold (aphids/stem)
Alfalfa	259,004	645	50 (<25.4 cm)[b] 100 (>25.4 cm)[b]
Lima and snap beans (fresh)	1,578	4,873	2.5[c]
Lima and snap beans (processing)	8,175	1,609	2.5[c]
Peas	5,828	1,453	2.5[d]

[a] New York Agricultural Statistics Service (1996).
[b] Cooperative Extension Service (1998b).
[c] Cooperative Extension Service (1998a).
[d] Maiteki and Lamb (1985).

Neal 1982, Yencho et al. 1986, Cooperative Extension Service 1998a). Once dispersing pea aphids find a suitable field they can reach damaging densities quickly because of their parthenogenic reproductive system and short generation time. However, not all aphids reaching a new crop after dispersing from harvested alfalfa have an equal chance of establishing. Several studies have shown that although pea aphids as a species have a fairly wide host range, individual strains or groups of clones produced parthenogenically by a single mother are often highly specialized on a single host plant (Via 1989, 1991; Sandstrom 1993). Thus, pea aphids that were thriving in alfalfa before harvest may not do well on a new crop colonized after harvest. Aphid host plant specialization may have important implications for pest management because even large immigrant aphid populations that are well above action thresholds may ultimately have little or no impact on a crop if their rate of feeding or survival is low.

The overall goal of our study was to determine the pest potential of pea aphids immigrating from harvested forage crops for vegetables located nearby. Specifically, our four objectives were as follows: (1) to compare the ability of aphids collected from alfalfa and clover to survive on these forage crops versus several vegetable crops, (2) to assess the survival and reproduction of alfalfa-adapted aphids on lima beans, (3) to quantify the feeding of alfalfa-adapted aphids on lima beans, and (4) to determine if pea aphid densities in lima beans were influenced by harvest of nearby alfalfa fields.

Materials and Methods

Survival of Aphids Collected from Alfalfa and Clover on Forage and Vegetable Crops. To determine the pest potential of pea aphids immigrating from harvested forage crops to vegetable crops, we compared the survival of pea aphids collected from alfalfa and clover on the these two forage crops, fava beans, peas, two varieties of lima beans, and two varieties of green beans. Apterous pea aphids were collected with sweep nets and aspirators from three alfalfa and two clover fields near Ithaca, NY. Collection sites in each field were separated by at least 10 m to ensure that each site contained distinct aphid clones. Because there are demonstrated differences in their biology (Kugler and Ratcliffe 1983, Losey et al. 1997), both red and green morph aphids were collected at each collection site so that their host range could be compared. To eliminate the possibility of mortality or behavioral effects caused by parasitism, all survival assays were run on the offspring (F_1) of field-collected aphids. To obtain F_1 offspring, field-collected aphids from a single collection site were placed in groups of five into 100 by 15-mm polystyrene petri dishes that were modified to contain a 35 by 10-mm petri dish that held moist cotton to maintain plant material. Sprigs of alfalfa or clover were placed in each arena. Within 24 h, each field-collected aphid produced an average of four to five offspring.

The survival rate of the first-instar aphid offspring was then assayed by placing them on potted plants caged in plastic buckets with mesh windows. Plant species tested included alfalfa ('Oneida'), clover ('Medium Red'), peas ('Progress'), fava beans ('Broad Windsor'), lima beans ('Maffei 15' and 'Henderson Bush'), and green beans ('Derby' and 'Provider'). All plants were potted in 10.16-cm pots and ranged from 5 to 7 wk old. All crop species and varieties are common in New York except fava beans. Fava beans were included in the study because they are known to be an excellent aphid host plant and can provide a benchmark as a high quality host plant.

Both red and green morph aphids were placed on each plant at densities of three to five aphids so that total aphid densities ranged from six to 10 aphids per plant. Each aphid on a given plant came from a different collection site in the field and thus was a distinct aphid clone. Aphids were maintained on plants for 6 d. This period was chosen because it would allow the first-instar aphids to become adults (at 20°C) and because it would minimize the probability that any nonfeeding aphids could survive (Losey and Denno 1998). After 6 d all plants were sampled destructively and surviving red and green aphids were counted. The proportions of both aphid morphs surviving on each plant type were analyzed with an analysis of variance (ANOVA) (PROC GLM, SAS Institute 1989) and means were compared with a Bonferroni procedure. Because of heteroscedasticity, proportions were arcsine square-root transformed before analysis. Standard errors in Fig. 1 are based on unpooled, untransformed data.

Survival and Reproduction of an Alfalfa-Adapted Aphid Strain on Alfalfa and Lima Beans. To determine the ability of alfalfa-adapted aphids to survive and proliferate on lima beans after colonization, we compared the survival, number of offspring, and number of exuvia produced by 2- to 3-d-old alfalfa-adapted, adult aphids on sprigs of either alfalfa or lima bean. Aphids used in this experiment were from a single clonal colony (L9), originally collected from alfalfa (near Ithaca, Tompkins County, NY), which is maintained on alfalfa plants and is known to be well

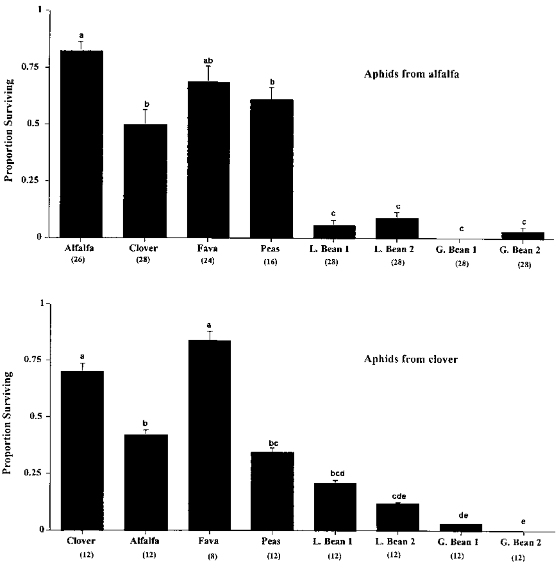

Fig. 1. Mean proportional survival (±SEM) of pea aphids collected from clover and alfalfa on eight plant species. Numbers in brackets represent the number of pea aphid clones tested on that plant species. Bars with the same letter represent mean proportional survival rates that are not significantly different at $P = 0.05$. Lima bean 1 = Maffei 15. Lima bean 2 = Henderson Bush. Green bean 1 = Derby. Green bean 2 = Provider.

adapted to alfalfa (Via and Caillaud 2000). Ten aphids were gently brushed onto the sprigs of alfalfa and lima bean in the experimental arenas, and survival and number of exuvia were evaluated after 3 d at 20°C, ≈50% RH and 16:8 photoperiod. Each plant treatment was replicated 10 times. Aphids not clearly dead were observed for at least 2 min and gently prodded to determine their status. Survival assays were conducted in the modified petri dishes described above.

The number of surviving aphids, offspring and exuvia produced during the experiment were compared for both plant species using a one-way ANOVA (SAS Institute 1990). The values were transformed to meet the assumptions of the analysis ($[\log_{10}(n + 1)]$; Sokal and Rohlf 1981).

Aphid Feeding on Alfalfa and Lima Beans. To determine the extent to which alfalfa-adapted aphids feed on lima beans, we compared the feeding behavior of L9 aphids on lima beans and alfalfa. We recorded stylet penetration of aphids on both plant species with the direct-current-electrical penetration graph (DC-EPG) developed by Tjallingii (1978, 1988). The feeding behavior of 17 aphids on alfalfa and 18 aphids on lima beans were monitored continuously for 5 h under fluorescent light at an ambient room temperature of 22°C following the protocol of Caillaud et al. (1995a, 1995b). We recorded feeding on eight channels, but technical problems often prevented successful recordings on one or more channels. Replications of successful recordings were blocked by date as follows: two alfalfa and three lima bean on 26 June, two alfalfa on 27 June, three alfalfa and four lima bean on 30 June, three alfalfa and four lima bean on 1 July, three alfalfa and four lima bean on 2 July, and three alfalfa and three lima bean on 3 July.

A full range of aphid activities can be determined from the analysis of EPG recordings including walking, penetration, saliva injection, ingestion of water, and ingestion of plant sap (Tjallingii 1988, 1990). EPG recordings were analyzed with the STYLET 2.1 software (Tjallingii 2000). We focused on a single waveform referred to as E2 that denotes a sustained ingestion of phloem sap. Because it is during this feeding phase that the aphid actually ingests nutrients from the plant, the amount of time spent in this phase is a good indicator of the suitability of a plant for the aphid. The mean time (in minutes) individual aphids on alfalfa and lima bean spent in E2 over the 5-h recording period was compared using a one-way ANOVA (SAS Institute 1990). These values were transformed to meet the assumptions of the analysis ($[\log_{10}(n + 1)]$; Sokal and Rohlf 1981).

Effect of Alfalfa Harvest on Aphid Densities. To determine if alfalfa harvesting was correlated with aphid densities in nearby lima bean fields, we sampled for aphids in a 100 by 50-m lima bean field that was ≈1 km from a large alfalfa field (≈10 ha). We took five suction subsamples of randomly selected lima bean plants on 10 dates during the 1996 growing season, using a D-Vac suction sampler with a 0.093-m^2 orifice. Each subsample consisted of 30-s placements of the suction orifice over three plants. Collection bags were sealed and returned to the laboratory where the number of aphids was recorded. Samples were taken on 16 and 29 June, 6, 11, 18, 22, 25, and 30 July, and 4, 7, 15, and 20 August. The alfalfa field was harvested on 2 July and 2 August. Both fields were at the Central Maryland Research and Education Center in Beltsville, Prince Georges County, MD. The number of aphids in each subsample was divided by three to express results as numbers of insects per plant. Values were log-transformed to meet the assumptions of the analysis ($[\log_{10}(n + 1)]$; Sokal and Rohlf 1981) and then regression analysis was used to determine the relationship between alfalfa harvesting dates and aphid densities in lima beans.

Results

Survival of Aphids Collected from Alfalfa and Clover on Forage and Vegetable Plants. Aphid clones collected from alfalfa and clover were found to be highly adapted to survival on these plants. For both alfalfa and clover, a significantly higher proportion of aphids survived when returned to the plant species from which they were collected (0.78 ± 0.04) compared with clones placed on vegetables (peas, green or lima beans; 0.14 ± 0.016; $P = 0.0001$) (Fig. 1). Aphids from clover had significantly higher survival on vegetable plants (0.19 ± 0.03) than aphids from alfalfa (0.12 ± 0.02; $P = 0.0066$). Aphid color morph did not have a significant effect on survival on vegetable plants ($P = 0.2630$), although a slightly higher proportion of

Table 2. Survival, reproduction and feeding of an alfalfa-adapted aphid clone (L9) on alfalfa and lima beans

	Alfalfa	Lima Beans	P value[a]
Adult survival[b]	98.0 ± 0.01	52.5 ± 0.07	0.0001
Offspring produced[c]	116.0 ± 7.96	80.3 ± 8.64	0.0063
Offspring survival[b]	95.0 ± 0.01	59.7 ± 0.11	0.0001
Exuvia recovered	35.3 ± 2.74	5.2 ± 2.69	0.0001
Feeding time[d]	17.7 ± 9.43	0.0 ± 0.00	0.0073

[a] Significance based on comparison of alfalfa versus lima with a one-way ANOVA.
[b] Mean ± SEM proportion surviving based on the number of living and dead aphids in each dish.
[c] Mean ± SEM number of immature aphids per dish.
[d] Mean ± SEM minutes spent in E2 as measured by the EPG.

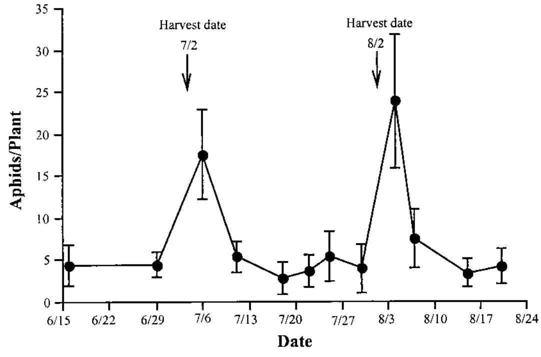

Fig. 2. Mean number of pea aphids per lima bean plant sampled in a lima bean field with a D-Vac sampler on 12 dates in the summer of 1996. Bars around each mean represent standard errors. Arrows represent the harvest dates of a nearby (1.5 km) alfalfa field.

red morph aphids survived on vegetable plants (0.16 ± 0.02) than green morph aphids (0.13 ± 0.02).

Because the origin of aphid clones (alfalfa versus clover) had a significant effect on survival on vegetables, the two sets of data were analyzed and are presented separately (Fig. 1). Regardless of origin, aphid survival was highest on the plant from which they were collected and on fava beans and the proportion of aphids surviving did not differ significantly between these two plants. This confirms the almost universal acceptance of fava bean as a pea aphid host. The exact phytochemical explanation for this phenomenon is not known. The next best hosts for both clover and alfalfa aphids were the other forage plant and peas. In general, all aphids collected did poorly on green and lima bean varieties. Survival was slightly but not significantly lower on green beans than lima beans.

Survival of Alfalfa-Adapted Pea Aphids on Alfalfa and Lima Beans. Adult aphid survival after 3 d was significantly higher on alfalfa than on lima bean. Survival of the immature offspring of these aphids was also significantly higher on alfalfa than on lima bean (Table 2).

The mean number of offspring produced per arena was higher on alfalfa than on lima beans (Table 2). We could not determine if this was caused by the lower adult survival or by lower numbers of offspring per adult because no recording was made of when in the 3-d period the offspring were born or the adults died. Based on the mean number of exuvia recovered, on alfalfa versus on lima bean, significantly fewer immature aphids molted to the second instar on lima bean (Table 2). It could not be determined if this was caused by lower offspring survival in the first instar or the inability of the immatures to reach some threshold weight on the lower quality plant.

Alfalfa-Adapted Pea Aphid Feeding Behavior on Alfalfa and Lima Beans. Aphids fed significantly longer on alfalfa sprigs than on lima bean sprigs (Table 2). In fact, none of the aphids tested on lima bean exhibited an E2 signal (which denotes sustained sap ingestion). We observed many more marked potential drops (signifying intracellular "tasting"), and E1, a precursor to E2 which signifies saliva injection (Tjallingii 1990), on alfalfa than on lima bean (J.E.L., unpublished data).

Effect of Alfalfa Harvest on Aphid Densities. The density of aphids in lima beans averaged five aphids per plant with very little variation except for the two samples taken directly after the harvest of the nearby alfalfa field (Fig. 2). On 6 July and 4 August, aphid densities reached 17.6 and 24.0 aphids, respectively. These high densities were each recorded on the first sampling date after a harvest of the alfalfa field (Fig. 2). In both cases, aphid densities were below eight aphids per plant by the next sampling date which was 5 and 3 d later, respectively.

The general pattern of aphid population density in lima beans in relation to alfalfa harvest is one of very high densities directly after harvest followed by rapid decline and then persistence at a fairly low level till the next harvest (Fig. 2). The relationship between aphid densities in lima beans and the number of days since alfalfa harvest was highly significant ($F = 14.80$, $P < 0.001$).

Discussion

Our results indicate that a small proportion of the pea aphid clones in alfalfa and clover have the potential to survive, reproduce, and feed in vegetable crops, even though pea aphids colonize these crops following forage crop harvest in densities above calculated economic injury levels (Fig. 2). During our field study, pea aphids appear to have colonized lima bean fields from alfalfa fields harvested in the immediate vicinity. It cannot be definitively specified that the "spikes" in aphid density in the lima bean field were caused by immigrants from the alfalfa field because the aphids were not marked. However, the two density spikes corresponded very closely with the alfalfa harvest dates (Fig. 2). The rapid decline in aphid density following the spikes is the precise result that would be predicted if most of these pea aphids were immigrants that were adapted to alfalfa. If the aphid density spikes were simply population fluctuations of resident aphids adapted to lima beans, then we would expect a rapid increase in natural enemies or a climatic event, such as hail or an extremely heavy rain, to have caused the decline. No such density-dependent or independent mortality source was recorded in this closely monitored lima bean field (Eubanks 1997, Eubanks and Denno 1999).

Although aphids from alfalfa can apparently colonize lima beans over a considerable distance, the presence of even a very high density of pea aphids will not necessarily cause damage to the crop. To cause feeding damage to a plant, large numbers of aphids must be present and feeding for an extended period. Actively feeding aphids can cause damage directly by removing photosynthate from the phloem and indirectly through lost production resulting from lost tissue (Barlow et al. 1977). Our data show that aphids arriving from alfalfa have a relatively short lifespan in lima beans. Alfalfa-adapted aphids did have some offspring on lima but this is not surprising because they will larviposit on wet filter paper as well (C. M. Caillaud, personal communication). The reproductive output of alfalfa-adapted aphids is much lower on lima beans than on alfalfa and the offspring have a high mortality rate (Table 2). Based on our data, there is very little chance of aphids immigrating from alfalfa sustaining a high-density population on lima beans.

Even the migrant aphids that do survive on lima beans would seem unlikely to directly damage the bean plants because we found no evidence that they feed on them (as indicated by the EPG recordings) (Table 2). Another possible source of damage from pea aphids moving from alfalfa to lima beans is the transmission of bean common mosaic virus (Zettler 1967). Our results indicate that this is highly unlikely. In addition to finding no E2 signal that denotes sustained sap ingestion on our EPG recording we also found no E1 signal that indicates the stage in which the aphid saliva, along with any persistent virus, is injected into the plant (Prado and Tjallingii 1996). Although our results indicate the risk is low, disease transmission between forage and vegetable crops cannot be totally discounted because a small proportion of aphid clones from clover and alfalfa did survive in vegetables and some viruses can be transmitted without the injection of saliva. A survey of the feeding potential of a large number of clones, although labor intensive, would allow a prediction of the potential for disease transmission.

Our results have important implications for the management of aphids in lima beans and other vegetable crops. The most general implication is that the immediate origin of pests should be considered in pest management decision-making. A high density of aphids that have immigrated into a vegetable field but that is not adapted to that crop does not pose the same threat as similar densities of resident, adapted aphids.

Suggesting quantifiable changes in how aphids are managed in lima beans is complicated by the variety of insect sampling units used in various pest management programs. Our data on aphids was taken in units of aphids per plant. Unfortunately, we could find no published source that expressed an economic injury level action threshold in these units. However, several sources give an action threshold for peas in terms of aphids per plant ranging from 0.3 (Yencho et al. 1986) to 10 (Cooperative Extension Service 1998a). We suggest that this range may be reasonable for lima beans as well because the threshold for both lima beans and peas when expressed as aphids per stem is ≈2.5 (see Table 1). We found density spikes of 17.6 and 24.0 aphids per plant (see Fig. 2) that is well above the 10 aphids per plant action threshold. If our lima bean field was scouted during the peak densities the generally accepted guidelines would indicate that the field warranted treatment. This would clearly be an inappropriate decision in this case and would lead to costly and unnecessary application of pesticides. Two steps that could be taken to avoid these unnecessary applications if aphid densities appeared to be above the action threshold would be to determine if any forage fields have been recently harvested in the immediate area, and if possible, wait several days and resample. An additional factor that could be used as evidence to support a decision to resample is the presence of a high proportion of alate individuals because this is the form most likely to successfully reach a vegetable field from a forage field. However, caution should be exercised in interpreting a high proportion of alatae because crowding and low plant quality (Sutherland 1967), which are signs of a potential pest outbreak, can also lead to the increased production of alatae. A high proportion of alatae and evidence of recent forage harvest in the immediate area are probably the best indication to wait and resample.

Host specialization has also been documented within two other polyphagous aphid species, *Sitobion avenae* (F.) (Weber 1985a), and *Myzus persicae* (Sulzer) (Weber 1985b), implying that similar sampling schemes could be applied to a wide range of systems. Further data on dispersal and host specificity we will facilitate major improvements in the management of aphids that migrate between crops.

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