Host plant resistance promotes a secondary pest population

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Abstract. Insecticides can cause secondary pest outbreaks that weaken the benefit of chemical pest control. These detrimental nontarget effects motivate the use of alternative pest management strategies such as host plant resistance and intercropping. However, when alternative pest management strategies effectively suppress primary pests, they also have the potential to promote secondary pest populations via competitive release. The potato leafhopper (Empoasca fabae) is a key pest of alfalfa, and leafhopper-resistant cultivars are being widely adopted by growers in the Midwest and Northeast United States. We conducted a field experiment comparing leafhopper-susceptible alfalfa, leafhopper-resistant alfalfa, and leafhopper-resistant alfalfa intercropped with orchardgrass. Leafhopper-resistant alfalfa reduced potato leafhopper abundance and protected the crop from protein loss, but there was no benefit of intercropping leafhopper-resistant alfalfa with orchardgrass. Importantly, the abundance of a secondary pest, the pea aphid (Acyrthosiphon pisum), was twice as high in the leafhopper-resistant plant treatments compared to the leafhopper-susceptible treatment. Field sampling and microcosm experiments confirmed that the increase in pea aphids was caused, at least in part, by release from competition with leafhoppers. These results suggest that, when host plant resistance against insects is employed, efforts to monitor and manage secondary pest populations are warranted.

Key words: competition; host plant resistance; pea aphid; pest management; potato leafhopper.

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INTRODUCTION

Significant advances in pest management and dramatic increases in pesticide use over the last 70 yr have helped to control agricultural pests (Tilman et al. 2002, Pimentel 2005, Thelin and Stone 2013), but animal pests still reduce agricultural yields by ~10% worldwide (Oerke 2006), with more severe losses occurring in food-insecure regions (Savary et al. 2019). Moreover, pest pressure on crops is expected to increase considerably due to global change: For example, cereal yield losses due to insects are predicted to increase by 10–25% per degree of global mean surface warming (Deutsch et al. 2018). Even when insecticides are used, yield losses can occur because insect pests evolve resistance to the insecticides used to control them (Denholm et al. 2002), and because insecticides have negative effects on beneficial species. For example, insecticides are often more harmful to (nontarget) natural enemies than to the pests themselves (Stark et al. 2004), leading to a resurgence of the focal pest after insecticide application. In addition,
many herbivores in agroecosystems are maintained at low, non-damaging levels by naturally occurring predators and competitors. When insecticides negatively impact these latter species, secondary pest outbreaks can result. Together, resistance evolution, pest resurgence, and secondary pest outbreaks reduce the efficacy of insecticides (Metcalf 1980, Hardin et al. 1995). Reduced efficacy, and negative effects on environmental and human health, limit the utility of chemical insecticides for pest management (Igbe-dioh 1991, Pimentel 2005).

There is an urgent need for environmentally sound, and effective, alternatives to insecticides. Host plant resistance, where crops are bred or genetically engineered to reduce pest damage, addresses this need and has become an essential pest management tool (Dent 1991). However, just as with insecticides, host plant resistance can impact the predators and competitors of target pests, and these nontarget effects may influence its efficacy. While the effects of host plant resistance on predators and parasitoids have received considerable attention (Boethel and Eikenbary 1986, Thomas and Waage 1996), the hypothesis that host plant resistance can promote secondary pest populations via competitive release has received less attention (Mattson et al. 1989, Zeilinger et al. 2016). Competitive interactions among herbivore species are widespread, and reviews of competition among phytophagous insects show that (1) it occurs in over 60% of the pairwise interactions that have been investigated, (2) it is just as common in managed (i.e., agricultural) systems as in unmanaged systems, and (3) its effects are often asymmetrical and moderated by host plant resistance (Denno et al. 1995, Kaplan and Denno 2007). For example, host plant resistance against a variety of pests has been achieved by engineering crops to express Bt toxins that target specific taxa (e.g., Lepidoptera). In southeastern United States, Bt cotton has strongly suppressed the primary lepidopteran pest (Helicoverpa zea), but secondary pest outbreaks involving stinkbugs have emerged. Careful experiments have confirmed that these outbreaks are caused, at least in part, by competitive release (Zeilinger et al. 2016). Evidence for host plant resistance-mediated competitive release also exists for Western bean cutworm (Striacosta albicosta) on Bt corn (Dorhout and Rice 2010) and for spruce budworms (Choristoneura fumiferana) on aphid-resistant balsam fir genotypes (Mattson et al. 1989). These secondary pest outbreaks limit the benefit of host plant resistance against primary pests and could result in the continued use of environmentally damaging insecticides.

Intercropping, where two or more crop species or genotypes are planted together, provides another environmentally friendly alternative to insecticides (Vandermeer 1992). Intercropping can control pest populations because herbivores have difficulty locating their host plants when they are surrounded by non-host plants (resource concentration hypothesis), and because non-host plants can increase natural enemy abundance by providing enemies with alternative resources and/or a favorable microclimate (enemies hypothesis; Root 1973). Numerous studies have investigated the effects of intercropping on pest suppression, and a meta-analysis of these indicates that intercropping generally reduces insect pest abundance and increases enemy abundance (Letourneau et al. 2011). However, herbivore species differ in their ability to locate host plants in diverse plant mixtures (Potting et al. 2005), and they differ in their vulnerability to predation (Denno et al. 2003). Therefore, interspecific differences in herbivores’ response to intercropping are expected, and when a non-host intercrop strongly suppresses one pest but has little or no direct effect on another, competitive release may occur.

In the Northeast and Midwest United States, the potato leafhopper (Empoasca fabae) is an important pest of alfalfa (Medicago sativa), soybean (Glycine max), snap bean (Phaseolus vulgaris), and potato (Solanum tuberosum; Chasen et al. 2014). Potato leafhoppers use their stylets to repeatedly lacerate plant vascular tissues, and this mechanical damage, combined with the release of saliva containing digestive enzymes, causes visible injury to the plant called “hopperburn.” The expression of hopperburn varies among host plants and can involve the chlorosis, necrosis, and curling of leaves, premature leaf drop, and stunted plant growth (Backus et al. 2005). Potato leafhopper feeding reduces the nutritive value of plants and can lead to plant-mediated competition with other herbivores. In potato, leafhoppers compete with the
Colorado potato beetle (*Leptinotarsa decemlineata*). They colonize the crop before the beetle, reduce plant quality, and reduce oviposition, larval performance, and survival of the later arriving beetles (Lynch et al. 2006, Kaplan et al. 2007). Whether plant-mediated competition between potato leafhoppers and co-occurring herbivores occurs in other crops, such as alfalfa, has not been investigated. In the Northeast and Midwest United States, the potato leafhopper is the most damaging pest of alfalfa and there are 13 additional herbivore species identified as potential pests of alfalfa (Undersander et al. 2019). Efforts to control the potato leafhopper in alfalfa have the potential to release these species from competition.

In alfalfa, potato leafhoppers are controlled by pesticides, host plant resistance, and grass intercrops (Chasen et al. 2014). These control methods are not highly specific to the potato leafhopper in the way the *Bt* toxin is specific to its target pests, but they may affect the leafhoppers more strongly than their competitors, setting the stage for competitive release of secondary pests. Potato leafhopper resistance in alfalfa is conferred by glandular trichomes. These trichomes provide both physical and chemical resistance to leafhoppers (Ranger and Hower 2001, 2002), although the primary cause of resistance is thought to be chemical (Ranger et al. 2004). Early leafhopper instars can be entrapped by the glandular exudates (Ranger and Hower 2001), the glandular trichomes significantly increase the rate at which nymphs jump or fall off the plant (Ranger and Hower 2002), and extracts from the glandular trichomes deter settling by leafhopper adults (Ranger et al. 2004). While the physical deterrence provided by glandular trichomes likely extends to similarly sized herbivores, the chemical deterrence may be more specific to potato leafhoppers because the commercially available cultivars have been selected and bred for resistance to this species. Moreover, the potato leafhopper has a broad host range that includes over 200 plant species, but it is unable to complete development on monocots (Lamp et al. 1994). While numerous studies have demonstrated that the presence of non-host grasses can strongly reduce potato leafhopper abundance in alfalfa (Lamp 1991, Roda et al. 1997, Degooyer et al. 1999, Straub et al. 2013), they appear to have no such effect on at least one co-occurring pest species, the pea aphid (*Acyrthosiphon pisum*; Straub et al. 2013).

The objectives of this study were to test the hypothesis that host plant resistance against potato leafhoppers promotes secondary pests via competitive release, and to test the hypothesis that intercropping leafhopper-resistant alfalfa with non-host grasses will further enhance potato leafhopper suppression and thus the competitive release of secondary pests.

**Methods**

**Field establishment**

The experiment was planted at Northern Star Farm in Trappe, Pennsylvania, USA (40°12'18.72" N, 75°27'57.15" W), in a field that was planted with soybean the previous year. The field was treated with lime and glyphosate prior to planting and was planted with a no-till drill on 28 April 2014. The three treatments were leafhopper-susceptible alfalfa (Pioneer 55V50), leafhopper-resistant alfalfa (Pioneer 55H94), and the latter cultivar intercropped with orchardgrass (Potomac). Orchardgrass is commonly intercropped with alfalfa because it is a high-quality forage grass that persists for several years despite frequent cutting (Hall 2008). The alfalfa monocultures were seeded at 23 kg/ha, and the intercropped alfalfa and orchardgrass plots were seeded at 9.5 and 10.6 kg/ha, respectively. On 1 June 2014, weeds in the alfalfa monocultures were controlled with an application of monocot selective herbicide sethoxydim (Poast, BASF, Research Triangle Park, North Carolina) and ammonium salt of imazethapyr (Pursuit, BASF, Research Triangle Park, North Carolina). Large broadleaf weeds were removed from the intercropped alfalfa by hand.

The three treatments, leafhopper-susceptible alfalfa (S), leafhopper-resistant alfalfa (R), and intercropped leafhopper-resistant alfalfa (IR), were replicated eight times. When plots occur in linear arrays, an ordered spatial arrangement protects against preexisting gradients in environmental conditions better than complete randomization (Hurlbert 1984). Thus, in one row of plots the sequence S, IR, R was repeated four times. In a second row of plots, the sequence R, S, IR was repeated four times. Plot sizes in the first and
Insect sampling

Foliage insects were sampled from the centerline of plots using 36 cm diameter sweep nets. The longer (85 m) plots received 30 sweeps, and the shorter (36 m) plots received 15 sweeps. Plots were maintained on a 4- to 5-week growth cycle, and samples were taken during three consecutive weeks following a cut during four growth cycles, called sample periods from here on. In 2014, samples were taken on 11 June, 16 June, 23 June (sample period 1), and 7 July, 16 July, 21 July (sample period 2). In 2015, samples were taken on 11 June, 15 June, 22 June (sample period 3), and 13 July, 20 July, 28 July (sample period 4). Plant treatment effects on the potato leafhopper (E. fabae), pea aphid (A. pisum), meadow spittlebug (Philaenus spumarius), tarnished plant bug (Lygus lineolaris), and grasshoppers (Acrididae) were investigated. The latter four taxa are occasional pests of alfalfa (Undersander et al. 2019).

Plant sampling

The abundance of alfalfa-feeding pests is likely to vary with alfalfa stem density, which was lower in the intercropped alfalfa treatment. To account for stem density effects, this variable was measured each week that insect sampling occurred. Two or three 0.25-m² quadrats were haphazardly selected within each plot, and alfalfa stem density was recorded. Mean stem density from the three weeks of sampling was calculated for each plot and used in statistical analyses. Alfalfa stem densities (mean ± SD) for the S, R, and IR treatments were 112 ± 17, 98 ± 12, and 59 ± 12 stems/0.25 m², respectively.

Forage protein content is an important component of forage quality that is negatively affected by potato leafhoppers (Flinn et al. 1990). Thus, forage biomass and protein content were measured at the end of sample periods 3 and 4. A 0.6-m³ mesh exclosure (BugDorm model no. 3120; MegaView Science, Taichung City, Taiwan) was placed in each plot immediately following the cut, and it was vacuumed to remove insects. These exclosures permitted comparison of plant treatments in the absence of herbivores. At the end of the sample periods, the plant material was harvested from the exclosures. In addition, three 1-m² forage samples were harvested from each plot to compare plant treatments in the presence of herbivores. The fresh mass of the samples was recorded in the field and converted to dry mass using a conversion factor calculated by drying a subsample. From each plot, one handful of plant material from the exclosures and three handfuls of plant material from the open field (one from each 1-m² sample) were analyzed for protein content by an agricultural services laboratory (Agri-Analysis).

Microcosm experiments

A microcosm experiment was conducted to investigate whether the leafhopper-susceptible alfalfa and leafhopper-resistant alfalfa differ in quality for pea aphids. Single plants were grown in an incubator at 22.5°C with 16:8 L:D in 6.5 cm square pots and provided with three beads of Osmocote (14:14:14) and −0.25 g of lime. Plants were 45 d old at the time of the experiment, and plant heights (mean ± SD) were 23.1 ± 6.9 and 23.3 ± 4.8 cm for the leafhopper-susceptible and leafhopper-resistant cultivars, respectively. Single plants were transplanted to 17 cm diameter pots and enclosed with a plastic tube (15 cm diameter, 30 cm height) and mesh top to create the microcosms. Pea aphids were collected from an alfalfa field as nymphs and reared for 48 hr on fava bean until they were adults. A single adult apterous aphid was placed on each leafhopper-susceptible (n = 15) and leafhopper-resistant (n = 17) plant. Microcosms were kept at 20°–24°C under 16:8 L:D. After 72 hr, all adults had survived and reproduced, and the number of offspring was recorded.

A second microcosm experiment was conducted to investigate the potential for competition between potato leafhoppers and pea aphids. Leafhopper-susceptible and leafhopper-resistant alfalfa plants were grown in 12 cm diameter clay pots with −3 g lime and fertilized with Miracle-Gro (24:8:16) every 3-4 weeks. The plants were cut at 4- to 5-week intervals. At the time of the experiment, the plants were 133 d old and plant heights (mean ± SD) for the leafhopper-susceptible and leafhopper-resistant cultivars were 18.8 ± 3.3 and 16 ± 3.6 cm, respectively. The pea aphids and potato leafhoppers came from...
colonies reared on fava bean. Microcosms were the same as described above.

The competition experiment was a 2 × 2 factorial design with plant (leafhopper-susceptible, leafhopper-resistant) and leafhopper (present, absent) as factors. Each treatment was replicated ten times. All microcosms received a single adult apterous aphid of similar age, and a single adult leafhopper was introduced to the leafhopper present microcosms. After seven days, the total number of aphids on each plant was recorded. Some of the aphids did not survive the transfer from fava to alfalfa and were excluded from the analysis. After exclusion, sample sizes were as follows: leafhopper-susceptible alfalfa, leafhopper absent (n = 7), leafhopper-susceptible alfalfa, leafhopper present (n = 7), leafhopper-resistant alfalfa, leafhopper absent (n = 9), and leafhopper-resistant alfalfa, leafhopper present (n = 7).

Statistical analyses

Insect abundances from sweep sampling (insects/sweep) were analyzed by repeated-measures MANOVA. Plant treatment × sampling period interactions were not significant, so mean values for the four sampling periods were used in the final analyses. Stem density for each plot was included in the statistical models. Plant treatment effects on forage yield and protein content were investigated separately for the herbivore-exclosure and open-field samples with ANOVA. Plant treatment × sampling period interactions were not significant, so mean values for the two sampling periods were used in the final analyses. In the case of forage protein content in the herbivore exclosures, the data were non-normal and were analyzed by a nonparametric Kruskal–Wallis test. Univariate regression was used to explore the relationship between forage protein content and potato leafhopper and pea aphid abundance in the open field. For these analyses, mean insect abundance for the six weeks of sampling in sample periods 3 and 4 (the same sample periods in which the forage protein content data were collected) was used.

To test for interspecific competition in the field, we looked for negative correlations between potato leafhopper and pea aphid abundance. Univariate regression was conducted separately for each plant treatment to control for the confounding effects of plant treatment on insect abundance. Data from each of the four sampling periods were included to take advantage of variation in insect densities that occurred between sampling periods. For each sample period and insect, the mean value from the three weeks of sampling was used. Each plot appeared in the analysis four times (once for each sample period), so plot effects were removed and the residual variation in leafhopper and aphid abundance was used in the analysis. For the plant quality microcosm experiment, a t-test was used to compare aphid reproduction on leafhopper-susceptible and leafhopper-resistant cultivars. For the microcosm competition experiment, ANOVA with factors for plant treatment, leafhopper, and their interaction was conducted. All analyses were conducted in (JMP Pro v.13, SAS Institute, Inc., Cary, North Carolina, USA).

Results

Insect abundance analyses

For potato leafhoppers, the plant treatment × week interaction was significant (Table 1). There was no difference among treatments in week 1, but by week 3, there were significantly more leafhoppers on leafhopper-susceptible alfalfa than on the other two plant treatments (week 3 ANOVA, \(F_{2,21} = 15.71, P < 0.001\); Fig. 1A). Tukey post hoc analyses indicated no difference between the R and IR treatments. Pea aphids showed the opposite pattern. The plant treatment × week interaction was significant (Table 1). Differences between plant treatments grew through time, and there were significantly fewer pea aphids on leafhopper-susceptible alfalfa than on the other two plant treatments (week 3 ANOVA, \(F_{2,21} = 11.87, P < 0.001\); Fig. 1B). Tukey post hoc analyses indicated no difference between the R and IR treatments. The time-averaged abundance of pea aphids (± SE) was twice as high in the leafhopper-resistant plant treatments (8.4 ± 2 aphids/sweep) compared to the leafhopper-susceptible plant treatment (4.2 ± 1.2 aphids/sweep). Plant treatment effects were not significant for the other alfalfa insect pests (Table 1).

Forage analyses

In the herbivore exclosures, there was no difference among plant treatments for forage protein...
Table 1. Repeated-measures MANOVA results for the effects of plant treatment (PT), stem density (SD), week, and their interactions on alfalfa insect pests.

| Source          | df       | Leafhopper† | Pea aphid‡ | Spittlebug§ | Plant bug¶ | Grasshopper# |
|-----------------|----------|-------------|------------|-------------|------------|--------------|
|                  |          | F          | P          | F           | P          | F            | P            | F           | P          |
| Between subjects |          |            |            |             |            |              |              |             |            |
| PT               | 2, 20    | 7.55       | 0.004      | 12.03       | <0.001     | 3.24         | 0.060        | 1.65        | 0.217      | 0.481       | 0.625        |
| SD               | 1, 20    | 0.64       | 0.431      | 0.017       | 0.896      | 5.31         | **0.032**    | 4.74        | **0.042**  | 0.077       | 0.784        |
| Within subjects  |          |            |            |             |            |              |              |             |            |
| Week             | 2, 19    | 5.30       | **0.015**  | 5.79        | **0.011**  | 0.22         | 0.803        | 5.92        | **0.010**  | 3.89        | **0.038**    |
| PT × week∥      | 4, 38    | 5.58       | **0.001**  | 5.45        | **0.001**  | 0.36         | 0.836        | 1.89        | 0.131      | 0.53        | 0.714        |
| SD × week∥      | 2, 19    | 4.42       | **0.027**  | 1.80        | 0.192      | 0.01         | 0.993        | 0.43        | 0.657      | 1.34        | 0.285        |

Note: Bolded values indicate statistical significance (P < 0.05).
† Potato leafhopper, *Empoasca fabae*.
‡ Pea aphid, *Acyrthosiphon pisum*.
§ Meadow spittlebug, *Philaenus spumarius*.
¶ Tarnished plant bug, *Lygus lineolaris*.
# Grasshopper, Acrididae.
∥ Wilks’ lambda test statistic.

Fig. 1. (A) Abundance of potato leafhoppers during three weeks of forage regrowth after cutting. (B) Abundance of pea aphids during three weeks of forage regrowth after cutting. Data are means ± 1 SE and were collected during four sample periods (see Methods for sample dates). Susceptible and resistant are different alfalfa cultivars and are in reference to potato leafhoppers, not pea aphids. Intercropped resistant alfalfa was planted with orchardgrass. Asterisks indicate significant differences among plant treatments by week. In weeks with significant differences, Tukey post hoc analyses indicated that the susceptible alfalfa differed from the resistant and intercropped resistant alfalfa, but there was no significant difference between the latter two treatments for potato leafhoppers or pea aphids.

content (χ² = 1.84, df = 2, P = 0.399) or dry matter yield (F₂,2₁ = 2.74, P = 0.088). In the open field, there was a significant difference among plant treatments in forage protein content (F₂,2₁ = 8.34, P = 0.002), such that leafhopper-susceptible alfalfa had lower protein content (21.4 ± 0.21%) than the leafhopper-resistant plant treatments (22.7 ± 0.23% and 22.6 ± 0.28%, for R and IR, respectively). Dry matter yield did not differ among plant treatments in the open field (F₂,2₁ = 1.39, P = 0.270).

To examine whether the reduced protein content of leafhopper-susceptible alfalfa may have been caused by the higher leafhopper pressure in
the open field, the relationship between leafhopper abundance and protein content was investigated. As expected, leafhopper abundance was negatively correlated with forage protein content ($\beta = -0.87$, $R^2 = 0.32$, $P = 0.004$; Fig. 2A). In contrast, pea aphid abundance was positively correlated with forage protein content ($\beta = 2.53$, $R^2 = 0.47$, $P < 0.001$; Fig. 2B).

**Interspecific competition and plant quality analyses**

If interspecific competition occurs in the field, then pea aphid and potato leafhopper abundance should be negatively correlated. Moreover, competition should be strongest in the leafhopper-susceptible alfalfa, where leafhopper numbers are highest. There was a strong negative correlation in leafhopper-susceptible alfalfa ($\beta = -4.18$, $R^2 = 0.51$, $P < 0.001$; Fig. 3A), a weak negative correlation in leafhopper-resistant alfalfa ($\beta = -3.27$, $R^2 = 0.14$, $P = 0.037$; Fig. 3B), and no correlation in intercropped leafhopper-resistant alfalfa ($\beta = -1.17$, $R^2 = 0.03$, $P = 0.325$; Fig. 3C).

In the microcosm experiment investigating plant quality effects on aphid reproduction, there was no significant difference in offspring production by adults on leafhopper-susceptible and leafhopper-resistant alfalfa ($t_{28.6} = -0.96$, $P = 0.342$; Fig 4A). In the microcosm experiment investigating interspecific competition, the presence of a leafhopper significantly reduced the final abundance of aphids ($F_{1,26} = 9.46$, $P = 0.005$). Final aphid abundance was not influenced by host plant resistance or by the interaction between leafhoppers and host plant resistance ($P > 0.4$; Fig. 4B).

**Discussion**

Host plant resistance against potato leafhoppers significantly reduced leafhopper abundance and protected the crop from protein loss, but also resulted in ~100% increase in the time-averaged abundance of pea aphids. Leafhopper and pea aphid abundance were negatively correlated, and this negative correlation was strongest in leafhopper-susceptible alfalfa, indicating that competitive release from leafhoppers promotes pea aphid population growth in leafhopper-resistant alfalfa. The microcosm experiment confirmed that leafhoppers can strongly suppress pea aphid population growth. Taken together, these results suggest that, like insecticides, host plant resistance can promote secondary pest populations that may weaken the benefit of controlling the primary pest.

![Fig. 2](image.png)  
**Fig. 2.** (A) Relationship between potato leafhopper abundance and forage protein content. (B) Relationship between forage protein content and pea aphid abundance. Figure axes are arranged to illustrate the likely causal pathways, with increasing leafhopper abundance causing a reduction in forage protein content (A), and the leafhopper-caused reduction in forage protein content causing a decrease in pea aphid abundance (B). Data are means from two sample periods (see Methods for sample dates).
Our finding that leafhoppers reduce the protein content of the forage is consistent with other studies (Flinn et al. 1990). We expected that host plant resistance would also increase dry matter yield, as has been previously shown (Flinn et al. 1990, Sulc et al. 2014). In the study by Sulc et al. (2014), the overall abundance of leafhoppers was significantly higher than in the current study which may help to explain why effects on yield were not observed here. Importantly, an orchardgrass intercrop provided no benefit in terms of leafhopper control when leafhopper-resistant alfalfa was used. Thus, while intercropping leafhopper-susceptible alfalfa with orchardgrass can protect alfalfa from leafhoppers (Roda et al. 1997), an orchardgrass intercrop appears to be redundant when leafhopper-resistant alfalfa is already being used for leafhopper control.

In the microcosm competition experiment, the presence of a single leafhopper reduced aphid reproduction by 46%. We did not observe reduced interspecific competition on leafhopper-resistant alfalfa in the microcosm experiment, as might be expected, but this can be explained by the fact that leafhoppers were confined to the microcosm and could not emigrate from resistant plants as they are likely to do in the open field (Roda et al. 1997).

The mechanism(s) by which potato leafhopper feeding negatively impacts aphid reproduction is unclear. Potato leafhopper feeding on alfalfa causes injury to the vascular tissue that reduces the photosynthetic rate of the plant and the crude protein content of the leaves (Flinn et al. 1990, Lamp et al. 2007). Protein content reflects nitrogen availability in the plant, and aphids are nitrogen-limited and respond positively to nitrogen concentration (Awmack and Leather 2002). Thus, potato leafhopper feeding may reduce pea aphid reproduction by reducing nitrogen availability. Our results are consistent with this mechanism—potato leafhopper abundance was
negatively correlated with forage protein content, while pea aphid abundance was positively correlated with forage protein content, suggesting leafhoppers reduce plant nitrogen content which limits pea aphid population growth. It is also possible that leafhoppers induce the production of plant defensive compounds that negatively impact the aphids. Herbivore-induced plant defense has been observed in alfalfa (Agrell et al. 2003), but to our knowledge, this has not been investigated in relation to potato leafhoppers and pea aphids. Moreover, whether plant-mediated competition among potato leafhoppers and pea aphids is reciprocal warrants further investigation. Potato leafhoppers are circular migrants that overwinter in the southern Gulf States and migrate north to the Midwest and eastern United States in the spring (Chasen et al. 2014). In contrast, pea aphids can overwinter in the egg stage in the northern United States (Via 1992). Thus, if pea aphids do negatively impact potato leafhoppers via plant-mediated competition, it would be most likely in established (i.e., second year and older) alfalfa in the early season because pea aphid eggs hatch in the field and aphid populations can begin to establish before leafhoppers arrive.

While higher pea aphid populations in leafhopper-resistant alfalfa appear to result from competitive release from leafhoppers, higher plant quality and/or release from predators in leafhopper-resistant alfalfa may also contribute. We did not find evidence for the former mechanism, but the latter mechanism seems plausible. The glandular trichomes that confer resistance to leafhoppers impede the foraging efficiency of a leafhopper parasitoid (Lovinger et al. 2000) and may have similar effects on small-bodied aphidophagous predators and parasitoids. In addition, some generalist predators consume both pea aphids and leafhoppers, and decreased leafhopper abundance in leafhopper-resistant alfalfa could reduce shared predator abundance and release pea aphids from apparent competition (Holt 1977). Understanding the effects of leafhopper-resistant alfalfa on the predation of pea aphids remains an interesting and open area of inquiry.

The consequences of larger pea aphid populations in leafhopper-resistant alfalfa require further investigation. One study reported the economic threshold for pea aphids in leafhopper-susceptible alfalfa to be 70 aphids/sweep (Cupe rus et al. 1982), while another reported an 80% lower economic threshold (Stucker 1986). Pea aphid numbers sometimes exceeded the latter threshold in this study, but only in leafhopper-resistant alfalfa. Importantly, even if pea aphid damage in leafhopper-resistant alfalfa does not warrant the cost of insecticides, there may still be

Fig. 4. (A) Effect of host plant resistance against potato leafhopper on pea aphid reproduction in a microcosm experiment. (B) Effect of potato leafhopper on pea aphid reproduction in a microcosm experiment. In (B), data from leafhopper-susceptible and leafhopper-resistant alfalfa are aggregated because the main effect of cultivar and the cultivar × leafhopper interaction were not significant. For (A and B), data are means ± 1 SE. **P < 0.01.
a nontrivial cost that could be avoided with alfalfa cultivars that offer high resistance to both pests.

Competition between potato leafhoppers and aphids may occur in other crops where these taxa co-occur, such as potato, soybean, and snap bean (Chasen et al. 2014). Aphids can damage crops both by feeding and by vectoring plant viruses. While aphid-vectored plant viruses are not a major concern in alfalfa, they are in potato (Syller 1996), soybean (Clark and Perry 2002), and snap bean (Mueller et al. 2012). In these crops, potato leafhoppers could lower virus transmission by limiting aphid populations, or increase virus transmission by reducing plant quality and promoting interplant movement by aphids. Crops that are vulnerable to potato leafhoppers, aphids, and aphid-vectored viruses provide an interesting opportunity to investigate how nonvectors and vectors interact to affect plant virus dynamics (e.g., Chisholm et al. 2019).

In some systems, herbivorous insects may serve as alternative prey that ultimately benefit pest control by promoting populations of generalist predators (Settle et al. 1996). In alfalfa, there is evidence for apparent competition between the pea aphid and potato leafhopper, with pea aphids having an indirect negative effect on potato leafhoppers by attracting shared predators (Ostman and Ives 2003). Thus, it may be the case that larger aphid populations protect leafhopper-resistant alfalfa by promoting predation of the more damaging potato leafhopper. Future studies investigating the effects of pea aphids on leafhopper-resistant alfalfa should consider the direct, indirect, and net effects of these secondary pests on alfalfa. Moreover, in other agroecosystems where host plant resistance is employed, efforts to monitor and manage secondary pest populations are warranted.

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