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The role of aphid host preference in barley yellow dwarf virus epidemiology

Abstract

Viral infection can cause changes to a plant's morphology or chemical composition that may alter its desirability to the insect vector. In combination with viral persistence in the vector, prevalence of the disease, and the spatial distribution of infected plants, vector preference for virus-infected or uninfected individuals can strongly influence the rate of disease spread in plant communities (McElhany et al. 1995). Although it is known that the presence of a virus in the host plant can lead to a change in feeding behavior and an increase in fecundity (Ferreles et al. 1990, Fereres et al. 1989, Montllor and Gildow 1986), there is little evidence that vectors prefer infected hosts over uninfected hosts. In this study, I examined host preference of the grass-feeding aphids *Rhopalosiphum maidis*, *R. padi* and *Sitobion avenae* when offered a variety of grasses infected or uninfected with the PAV species of *barley yellow dwarf virus* (BYDV). The eight grass species used in the preference tests are commonly found in New York State and are known hosts of BYDV. Preference tests were carried out in cages, where adult aphids were allowed to choose among grass seedlings. To determine whether infection altered preference, aphids were offered either uninfected grass communities or communities that contained a mixture of infected and uninfected grass seedlings. Results from these trials indicated strong species-specific preferences by aphids for particular grasses. Although there was some indication that infection could alter preference, I found no evidence that infection caused a significant shift in preference ranking among grasses.

Introduction

For a vector-transmitted plant pathogen, the distribution of disease in a population is determined by the interaction of three factors: host plant, vector, and virus. The host preference of the vector determines which plant the vector chooses to feed on and this in turn determines which plants become infected. The host preference of a vector can be influenced by the nutritional quality of the host plant, as well as less obvious factors, such as the presence of natural enemies, the chemical composition of the plant caused by induced resistance, and the presence of disease. Often, plants that are infected by a pathogen are preferentially attacked by the insect vectors of the disease (Maris et al. 2004, Johnson et al. 2003, Eigenbrode et al. 2002). This vector host preference is not only important for determining the individual host plant that will become infected, but is also important from a community ecology perspective when in combination with two other factors related to disease: prevalence and persistence. Prevalence is the amount of disease present in the population and persistence is the amount of time that the disease remains in the population; these two factors in combination with vector host preference can strongly determine the distribution of disease in a population (McElhany et al. 1995).

Barley yellow dwarf virus (BYDV) is a phloem-limited luteovirus that is obligately transmitted by grass-feeding aphids (Power and Gray 1995). BYDV infects important grain crops such as corn, barley, and wheat and often causes significant economic losses in the cereal grain industry. Symptoms of BYDV include a yellowing discoloration of the leaves, reductions in growth, and decreased seed production of grasses; however, these symptoms are not always visible and enzyme linked immunoassorbent assay (ELISA) tests must be conducted to confirm the presence of BYDV.

Aphids are effective vectors of BYDV that move to host plants by crawling or flight, especially under environmental pressures such as crowding or depleted nutrition in which aphids become alate (develop wings). Aphid population size can be high, because they can reproduce rapidly through clonal parthenogenesis; aphids also occasionally reproduce sexually (Halbert and Voegtlin 1995). In New York State, there are three generalist grass feeding aphid species that are primarily responsible for transmitting BYDV, *Rhopalosiphum padi*, *R. maidis*, and *Sitobion avenae* (Power and Gray 1995).

In the late 1950s, four BYDV viral strains were identified in New York State: RPV, PAV, MAV, and RMV (Rochow 1958). Each viral strain can be transmitted by a restricted number of aphid species due to the specific virus transport mechanisms in the aphid that control the efficiency of virus transmission to the host plant (Gildow and Gray 1993). MAV is transmitted primarily by *S. avenae*, RPV is transmitted by *R. padi*, RMV is transmitted by *R. maidis*, and PAV is transmitted efficiently by both *R. padi* and *S. avenae* (Power and Gray 1995).

Currently, it is unclear which host plant species aphids prefer in upstate New York and if they prefer infected hosts over uninfected hosts. In general, insect vectors may preferentially attack infected plants because the presence of the pathogen results in a higher quality host (Belliere et al. 2004). The BYDV system appears to follow this trend (Ferreles et al. 1990, Fereres et al. 1989, Montllor and Gildow 1986). For BYDV-infected host plants, levels of sucrose and amino acids are increased, which appears to affect aphid feeding behavior and performance. For example, PAV susceptible host plants were probed less often by aphid vectors (which indicates a shorter exploration time and greater likelihood to feed) than PAV resistant host plants. Furthermore, aphids that fed on PAV infected host plants

showed higher fecundity than those that fed on uninfected plants (Ferreles et al. 1990, Fereres et al. 1989). The finding of fewer probes has also been correlated to the suitability of the host plants. *Schizaphis graminum* aphids appeared to have longer ingestion periods and fewer probes on infected oats than uninfected oats. Additionally, *S. graminum* aphids had a larger population and higher fecundity on infected oats, indicating that it is more suitable host as a host than uninfected oats (Montllor and Gildow 1986).

Although it appears that infection makes a plant a more suitable host, it is not clear whether aphid vectors show preference for host plants infected with BYDV. Some studies have found that aphids prefer host plants that are infected with virus (Ajayi and Dewar 1983). In a laboratory experiment, alate aphids were more attracted to infected oats and barley. This finding appears to be correlated with the yellowing of BYDV infected leaves (Ajayi and Dewar 1983). Additionally, field studies with BYDV infected wheat showed that the aphid species, *R. padi* was attracted to the yellowing of infected leaves (Power unpublished data). However, other studies have found that aphids preferred healthy hosts versus infected host plants (Power et al. 1994, Kieckhefer et al. 1976, Power unpublished data). Laboratory experiments with two different species of aphids, *S. avenae* and *R. padi*, found that aphids preferred healthy host plants to PAV infected host plants (Power et al. 1994a). Furthermore, other studies with alate *R. padi* and *S. avenae* provided with cut leaves (Kieckhefer et al. 1976) and field studies with *R. padi* aphids on oats (Power, unpublished data) found parallel results in which aphids preferred healthy host plants to infected host plants. Similarly, fecundity studies found higher fecundity on healthy plants when compared to BYDV infected plants, suggesting that infection lowers the quality of the plant host (Power et al. 1994b, Mowry 1990). These contradictory results concerning the benefits of infection status may

arise because the BYDV strain, aphid species, life-stage of aphids, and virulence of infection used in these studies often varied and were sometimes not specified.

In this study, I examined the host preference of aphid species, *R. padi*, *R. maidis*, and *S. avenae*, for several wild grass species that are common in New York State and either infected or uninfected with BYDV. There were two main goals of this study. First, I investigated the host preference of BYDV-vectoring aphids for eight common grass species when they were not infected with BYDV. Second, I tested whether aphid host preference for several grass species, including *Avena fatua*, *Bromus tectorum*, *Lolium multiflorum*, and *Setaria viridis*, changed in the presence of BYDV.

Materials and Methods

Experiment 1- Host plant preference in the absence of virus

The objective of Experiment 1 was to determine the host plant preference of three aphid species when presented with uninfected seedlings of eight grass species. The three different aphid species used in this experiment were *R. padi*, *R. maidis*, *S. avenae*, and a genetic variant called *S. avenae* (gray). For this study, eight annual wild grass species that are common in New York State and known to be susceptible to BYDV were tested; these included *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*. Previous BYDV preference studies have focused on crop grasses; the preference of aphids for these wild grasses has not been tested.

Host plant preference was determined by allowing aphids to choose among the eight grass species. The experimental design consisted of five pots for each aphid species with each pot containing an individual seedling from each of the eight grass species. The

seedlings were planted in a circle at equally spaced, randomized positions in an eight inch pot. To ensure that all seedlings were approximately two inches tall by the time of the experiment and to account for different species' growth rates, seeds of the eight grass species were planted at different times approximately two to three weeks before initiation of the experiment. Prior to the experiment, aphids were raised on barley in plant growth chambers at 20°C under a 16:8 light dark cycle (Power 1991). At the initiation of the experiment, twenty-four individual non-winged aphids were placed in the center of the pot and then caged with an eight-inch clear plexiglass cage with a mesh covered top that allowed sufficient air and light to infiltrate. At two, four, eight, and twenty-four hours after adding the aphids, the number of aphids on each seedling was counted to determine the grass species preference of each aphid species. At the twenty-four and forty-eight hours, the number of aphid nymphs on each seedling was counted to determine aphid fecundity on the different host species.

Statistics

Statistical analyses were measured using the statistical program, JMP4.1. Data on the number of aphids on each grass species over time was analyzed using a repeated measures analysis of variance. At twenty-four hours, the number of aphids on each grass species was analyzed using a two-way ANOVA (aphid species \times grass species). Because of a significant interaction between aphid species and grass species, one-way ANOVAs (with grass as the factor) were then run for each aphid species separately to determine if there was a significant difference in preference for grass species. For each aphid species there was a significant difference in grass species, so Tukey HSD analyses were performed to determine differences among grass species in ranking. The same analyses were performed on the number of nymphs to determine aphid fecundity on the different grass species.

Experiment 2, 3, 4- Host plant preference (virus)

I used similar methods for Experiments 2, 3, and 4, except that grasses infected with virus were added into the system to investigate whether aphid preference changed in the presence of virus. In this case only two aphid species, *R. padi* and *S. avenae* were tested because they both vector the BYDV strain of interest, *PAV*. Experiments 2, 3, and 4 are differentiated by the grass species used in each experiment. In Experiment 2, only two grass species, *A. fatua* and *B. tectorum*, were tested. In Experiment 3, *A. fatua*, *B. tectorum*, and *L. multiflorum* were tested. In Experiment 4, *A. fatua*, *B. tectorum*, and *S. viridis* were tested.

Again, seedlings differed in age to achieve similar heights; however, by the time of the experiment, seedlings had to be trimmed from about six inches to two inches to contain the seedlings in the cage. Seedlings designated as infected were inoculated with the *PAV* strain of BYDV using aphids. Aphids were fed on infected leaf tissue and then were individually transferred to experimental seedlings by paintbrush and allowed to feed on the host plant for up to one week to ensure successful transmission of the virus. After inoculation, cages were removed and seedlings were sprayed with horticultural oil to remove remaining aphids. Approximately one week after spraying, seedlings were tested for the presence of BYDV by ELISA to ensure the correct infection status for the experiments (Rochow 1986).

The experimental design consisted of uninfected and infected seedlings. Similar to Experiment 1, each pot contained only one aphid species, but the number of replicate pots varied among the three experiments. Experiments 2, 3, and 4 included nine pots per aphid species, three pots per species and five pots per species, respectively. In experiment 2, uninfected seedlings were not subject to aphid feeding and horticultural oil. This caveat in

experiment 2 was corrected in experiments 3 and 4, in which both infected and uninfected seedlings were subject to aphid feeding and horticultural oil. Uninfected and infected seedlings of each species were planted in eight-inch pots as described above. Aphids were raised on barley, and twenty-four non-winged aphids were released into the pots as in Experiment 1. At two, four, eight, and twenty-four hours, the number of aphids on each seedling was counted to determine host preference.

Statistics

For Experiments 2, 3, and 4, data on the percentage of aphids on each grass species over time was analyzed using a repeated measures analysis of variance. At the twenty-four hour interval, in Experiment 2 and the four hour interval in Experiments 3 and 4, the percentage of aphids on each grass species was analyzed using a three-way ANOVA (aphid species \times grass species \times infection) and all two-way interactions were included in the model. Since the interaction between aphid species and grass species was significant, a two-way ANOVA (grass species \times infection) was run for each aphid species separately. If there was a significant difference among grass species, I used the post-hoc Tukey HSD analysis to determine if significant pair-wise differences occurred.

Results

Experiment 1- Host plant preference in the absence of virus

When all plants were healthy, aphids showed strong preferences for particular grass species and these preferences differed among aphid species over time according to repeated measures ANOVA ($F=7.2408$, $p<0.0001$). At twenty-four hours, aphid species exhibited significant preferences for different grass species (Figure 1A, 2 way ANOVA, aphid species

×grass species interaction effect: $F=1.9113$, $p=0.0055$). The aphid species *S. avenae* preferred *A. fatua* to the other seven grasses (Figure 1B, 1 way ANOVA: $F=6.3442$, $p=0.0002$, Tukey's HSD: $p=0.05$). The same preference was exhibited by the gray variant of *S. avenae* (Figure 1C, 1 way ANOVA: $F=3.4153$, $p=0.0091$, Tukey's HSD: $p=0.05$). There was no significant difference in preference between *S. avenae* and the *S. avenae* gray variant (2 way ANOVA, aphid species × grass species interaction effect: $F=0.3844$, $p=0.8817$). In contrast, *R. maidis* preferred the grass species *P. capillare* to the remaining seven grass species (Figure 1D, 1 way ANOVA: $F=3.4153$, $p=0.0091$, Tukey's HSD: $p=0.05$). Finally, *R. padi* preferred *A. fatua* to the other grasses (Figure 5, 1 way ANOVA: $F=6.3988$, $p=0.0002$, Tukey's HSD: $p=0.05$).

The fecundity of different aphid species on the eight wild grass species differed significantly and mirrored aphid species preference at twenty-four hours (2 way ANOVA: aphid species × grass species interaction effect: $F=2.0563$, $p=0.0022$). *S. avenae* had highest fecundity on the grass species, *A. fatua* (Figure 2A, 1 way ANOVA: $F=5.4756$, $p=0.0005$, Tukey's HSD: $p=0.05$). The gray variant of *S. avenae* also had highest fecundity on the grass species, *A. fatua* (Figure 2B, 1 way ANOVA: $F=18.7721$, $p<0.0001$, Tukey's HSD: $p=0.05$). *R. padi* had highest fecundity on *A. fatua* and *L. multiflorum* compared to the other grass species (Figure 2C, 1 way ANOVA: $F=17.7494$, $p<0.0001$, Tukey's HSD: $p=0.05$). In contrast, the results for the aphid species, *R. maidis*, differed from the preference analysis because there were no significant differences in its fecundity on the host plants (1 way ANOVA: $F=1.9402$, $p=0.1004$).

Experiment 2- Host plant preference for *A. fatua* and *B. tectorum* (virus)

Aphid species showed strong preferences between host species. At twenty-four hours, *S. avenae* and *R. padi* differed in their preference for the grasses, *A. fatua* and *B. tectorum* (3-way ANOVA, aphid species \times grass species interaction effect: $F=14.4294$, $p=0.0003$). Similar to experiment 1, *S. avenae* most preferred *A. fatua* (Figure 3A, 1-way ANOVA: $F=6.7222$, $p=0.0142$, Tukey's HSD: $p=0.05$). Additionally, *R. padi* most preferred *A. fatua* (Figure 3B, 1-way ANOVA: $F=8.0808$, $p=0.0077$, Tukey's HSD: $p=0.05$). At the two hour interval, both aphid species significantly preferred uninfected seedlings to infected seedlings (2-way ANOVA, grass species \times infection interaction effect: $F=19.0826$, $p<0.0001$). By twenty-four hours, however, there was no significant difference in aphid species preference with respect to the infection status of the grass seedlings (2-way ANOVA, aphid species \times infection: $F=1.2162$, $p=0.2742$).

Experiment 3- Host plant preference of *A. fatua*, *B. tectorum*, and *L. multiflorum* (virus)

Experiment 3 revealed species-specific preferences by aphids for particular grasses, but little indication of any effect of infection status on preference. At four hours, *S. avenae* and *R. padi* differed in their preference for the wild grass species, *A. fatua*, *B. tectorum*, and *L. multiflorum* (3-way ANOVA, aphid species \times grass species interaction effect: $F=5.8800$, $p=0.0078$), but there was no significant difference in their preference for uninfected versus infected grass species (3-way ANOVA, aphid species \times infection interaction effect: $F=1.2141$, $p=0.2806$). Separate analyses of the two aphids indicated that *R. padi* showed a significant difference in its preference for grass species (Figure 4A, 1-way ANOVA: $F=4.3556$, $p=0.0378$) and preferred *L. multiflorum* (Tukey's HSD: $p=0.05$). In contrast, *S. avenae* did not show any significant difference in its preference for different grass species (Figure 4B, 1-way ANOVA: $F=1.5416$, $p=0.2609$).

Experiment 4- Host plant preference of *A. fatua*, *B. tectorum*, and *S. viridis* (virus)

Experiment 4 did not indicate species specific preference by aphids for particular grasses; furthermore, there was no evidence to suggest that BYDV infection may affect aphid host preference. The aphid species, *S. avenae* and *R. padi* showed no difference in preference for the wild grass species, *A. fatua*, *B. tectorum*, and *S. viridis*, whether infected or not.

Discussion

Aphid species vary in their host preference for different grass hosts. Within four hours, most aphids find and settle on their preferred host species. Among the aphid species tested here, the most commonly favored grass species was *A. fatua*. Aphid fecundity on host grasses followed the same trend as preference, with aphids showing the highest fecundity on *A. fatua* (Figure 5). This trend suggests that *A. fatua* is both the most preferred and the most suitable host, since aphids had greatest reproduction on it.

Although *R. padi* and *S. avenae* preferred *A. fatua*, one aphid species, *R. maidis*, did not follow this trend and instead favored the grass *P. capillare*. The differing preference of *R. maidis* in comparison to the other two aphid species is consistent with these aphids' status as pests of different crops. The common name of *R. maidis* is the corn leaf aphid, and it is considered a pest of corn. Therefore, its preference for *P. capillare* is logical because *P. capillare* is related to corn. Conversely, the common names of *S. avenae* and *R. padi* are the grain aphid and the bird cherry-oat aphid, respectively. Corn is not closely related to oats or other small grains, whereas *A. fatua* is in the same genus as cultivated oats, *A. sativa*.

Furthermore, *R. padi* and *S. avenae* are known as pests of oats and other small grains and strongly prefer *A. fatua*.

Although the taxonomic relatedness of the grass species was important in host preference, I did not detect any effect of genetic variation within an aphid vector species. In the uninfected host preference experiment (Experiment 1), the typical green aphid variant of *S. avenae* from Rochow's experimental system and a brown genetic variant of this species found by Stewart Gray were tested. Some studies have suggested that the brown variety has larger populations on barley than the green variety (Weber 1985), which leads one to question whether preference differs between the two variants. Since neither the preference nor the fecundity of the two variants was significantly different, it appears that this genetic variation in an aphid species may not be important in determining host grass preference or suitability.

Vector host preference is important when determining distribution, prevalence, and persistence of a plant virus (McElhany et al. 1995). The preferences of the different aphid species tested here for uninfected wild grass seedlings suggest that aphid species strongly differ in their host preference, but experiments with infected grass seedlings indicated that these preferences were not usually modified by infection status of the host. In the uninfected host preference test, aphid species *S. avenae* and *R. padi* most favored *A. fatua* and *L. multiflorum*, but showed lesser preference towards *B. tectorum* and *S. viridis*. In Experiments 2 and 3, grass seedlings were infected with BYDV, but aphids showed a similar host preference ranking of grass species when compared to the uninfected test. These similar preference rankings suggest that infection status may be irrelevant for vector host preference, since the uninfected host preference ranking is not altered in the presence of BYDV.

Therefore the composition of the grass species in a plant community appears to be more important than the infection status of the plants in determining the severity of a BYDV outbreak.

Although most of the evidence indicated that infection did not shift the preference ranking among grasses, there was some indication that infection could alter preference. In Experiment 2, aphid species showed a significantly smaller preference for seedlings infected with BYDV compared to uninfected seedlings at two hours. This finding suggests that the introduction of BYDV to the grass seedlings has some potential to affect the preference of aphid species; however, the trend in Experiment 1 showed that preference was established at the four hour interval. Hence, at two hours, aphids may still be exhibiting random exploration. Nevertheless, this inconsistency may be a result of the flawed experimental design in Experiment 2, in which aphid feeding and horticultural oil was not applied to both uninfected and infected seedlings. However, this early two-hour result does not seem considerable since infection status did not affect preference for all other time intervals, which is consistent with the latter experiments.

The inconsistency in the results of Experiment 2 could be a consequence of additional limitations in the experimental design. In the last three experiments in which seedlings were infected with BYDV, the number of replicates was limited due to the inability to successfully infect all of the grass samples with BYDV. Furthermore, the introduction of BYDV to grass seedlings affected the experiments because there was a lower survival rate (and number) of aphids due to exposure to residual pesticide. In a broader context, the use of a single BYDV strain, *PAV*, rather than the entire suite of BYDV species may be significant in determining aphid host preference because the remaining BYDV species may have influenced aphid

preference differently. Moreover, the other BYDV species would have allowed for the examination of other aphid vector species, such as *R. maidis*. Thus, greater sample size, the use of different BYDV strains, and different aphid species vectors may have altered results.

Despite such inconsistencies, it appears that infection did not cause a significant shift in the preference ranking among grasses. In the context of aphid host preference, knowledge of the makeup of a plant community may aid in determining BYDV spread and prevalence among grass species. The prevalence of a virus in a plant community can be increased by the presence of a reservoir host species that is highly susceptible to the virus through pathogen spillover, which may lead to infection in less susceptible host species in that community. For example, plant communities of *D. sanguinalis*, *E. crus-galli*, and *P. capillare* showed an increase in BYDV prevalence as the proportion of the reservoir species *A. fatua* increased in the community (Power and Mitchell 2004). My finding that *A. fatua* was the most preferred grass species among aphid species suggests that grass communities that have high proportions of *A. fatua* may have increased prevalence of BYDV. It is likely that the high preference of aphid species for *A. fatua* strongly affects the number of aphids that immigrates to a high density *A. fatua* community and can transmit BYDV.

Pathogen spillover is not only notable by increasing the presence of viral infection but can also lead to multi-species interactions through apparent competition among the grass species in a community. In an infected grassland community, apparent competition occurs when the presence of a viral disease in one population leads to the reduction or exclusion of other populations in that community. In plant communities of *D. sanguinalis*, *L. multiflorum*, and *S. lutescens*, the presence of *A. fatua* not only led to pathogen spillover but also apparent competition between *A. fatua* and *L. multiflorum* and *D. sanguinalis* (Power and Mitchell

2004). Apparent competition was evident through a relative decrease in biomass for *L. multiflorum* and *D. sanguinalis* in BYDV infected communities when compared to uninfected communities (Power and Mitchell 2004). In the context of aphid host plant preference, apparent competition is important because a grass species that is the most preferred host plant and strongest competitor in the presence of disease could out-compete and possibly exclude its weaker competitors from the community. For instance, *A. fatua* is considered effective in BYDV transmission due to its high virus titer such that aphids can acquire BYDV very efficiently (A. Power, personal communication). In combination with the high level of BYDV transmission, role as a strong competitor, and high host preference among aphid species, it is possible that the presence of *A. fatua*, BYDV infection, and apparent competition could lead to the exclusion of other grass species from the community.

Pathogen spillover and apparent competition may alter the composition of a native grassland community when an exotic reservoir species is introduced. In a California grassland community, the introduction of *A. fatua* greatly increased the proportion of native *Elymus glaucus* grasses that were infected with BYDV. The increased infection prevalence in *E. glaucus* corresponded with an increasing density of aphids as the proportion of *A. fatua* increased. It is likely that the introduction of *A. fatua* led to greater aphid density since aphid species were found to prefer it to native species in laboratory preference experiments (Malmstrom et al. 2005a). The grass species *E. glaucus* is one of many native California bunchgrasses that are inclined to BYDV infection in the presence of exotic grasses. This infection can lead to a reduction in growth and seedling establishment, which is an outcome of apparent competition by exotic introduced species (Malmstrom et al. 2006, Malmstrom et al. 2005a). Consequently, the increased prevalence of BYDV among native grass species

may lead to the replacement of these species by exotic grasses, thus altering the grassland community composition (Malmstrom et al. 2005b). Therefore, the modification of grassland community structure may be strongly mediated by the immigration of aphids to the community, which is largely due to the high host plant preference of aphids for preferred host plants, such as *A. fatua*.

Vector host preference of aphid species is one dynamic in the multi-species interactions that affect the composition of a grassland community. Aphid vector preference may be important in the distribution and prevalence of BYDV in a wild grass community. In the absence of infection, aphid species showed strong host preference for, and modified fecundity on, different wild grass species. There was some indication that infection could alter preference; however, I found no evidence that infection caused a significant shift in preference ranking among grass species.

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Appendix

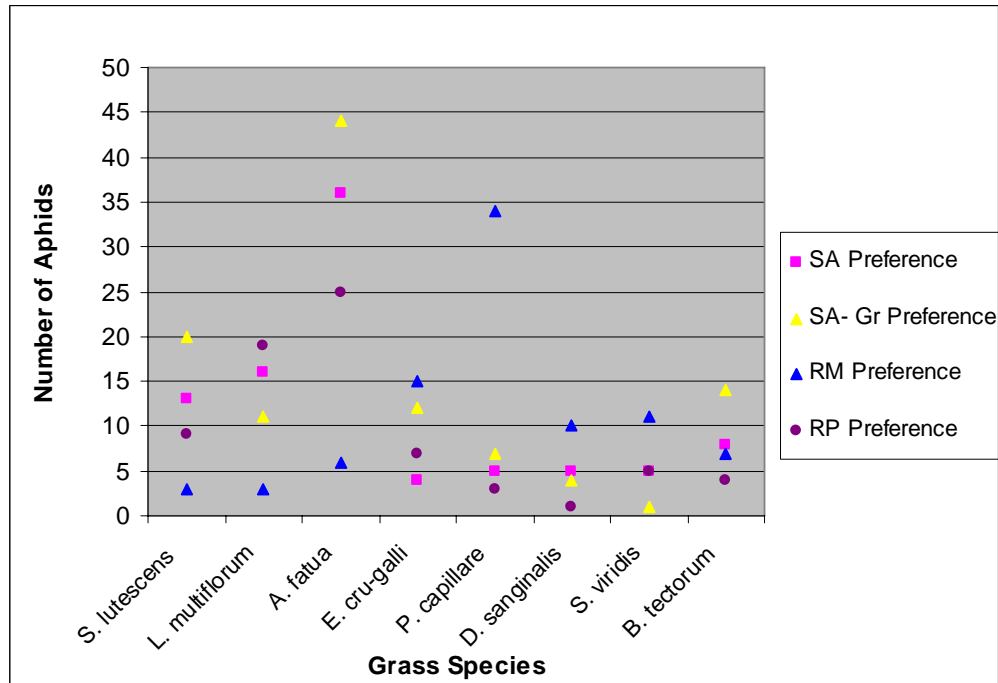


Figure 1A. Preference of aphid species *Sitobion avenae* (SA), *S. avenae* variant gray (SA-Gr), *Rhopalosiphum maidis* (RM), *R. padi* (RP) for uninfected wild grass species at the twenty-four hour interval. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*.

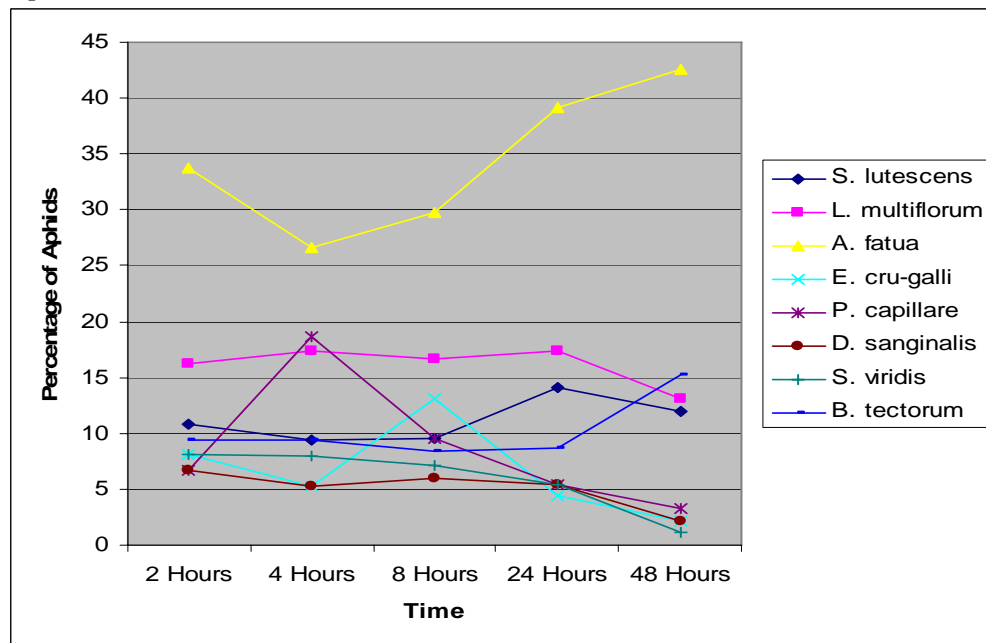


Figure 1B. Preference of aphid species *Sitobion avenae* for eight uninfected wild grass species over a two to forty-eight hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*.

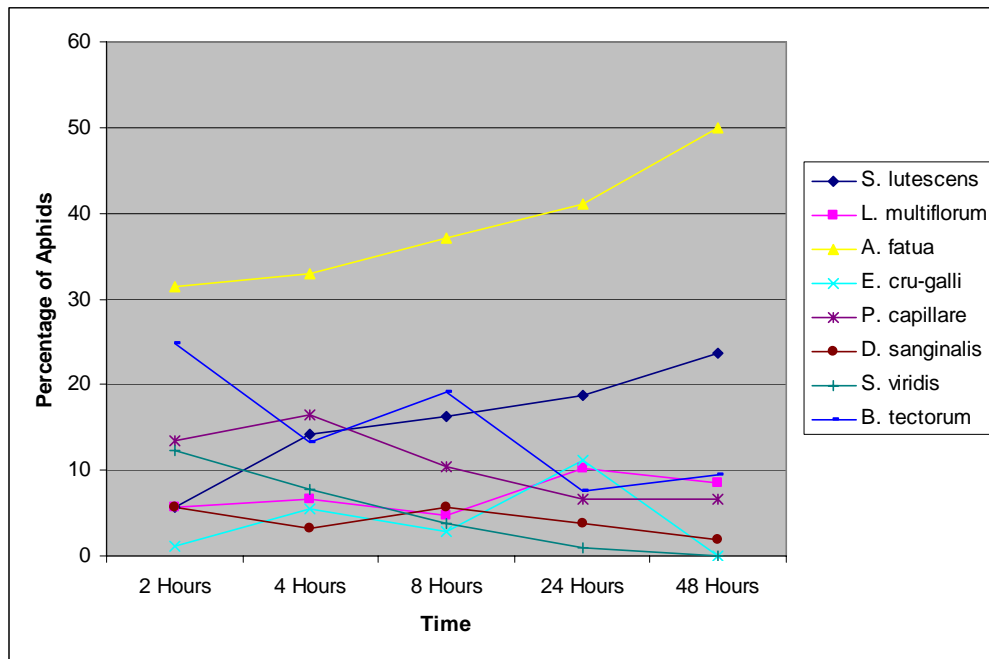


Figure 1C. Preference of aphid species *Sitobion avenae* variant gray for eight uninfected wild grass species over a two to forty-eight hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*.

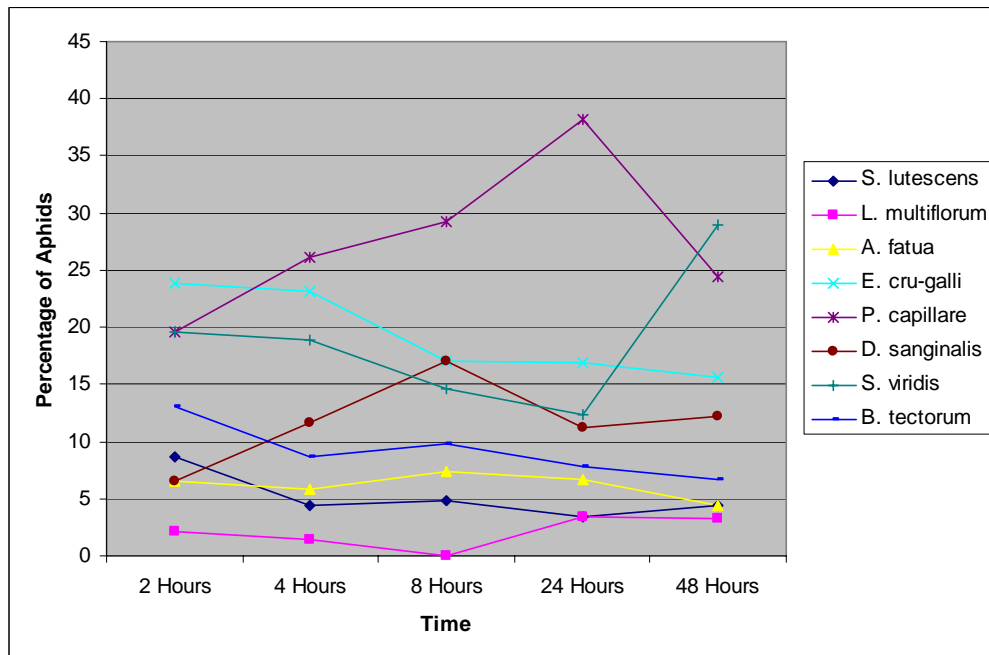


Figure 1D. Preference of aphid species *Rhopalosiphum maidis* for eight uninfected wild grass species over a two to forty-eight hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*.

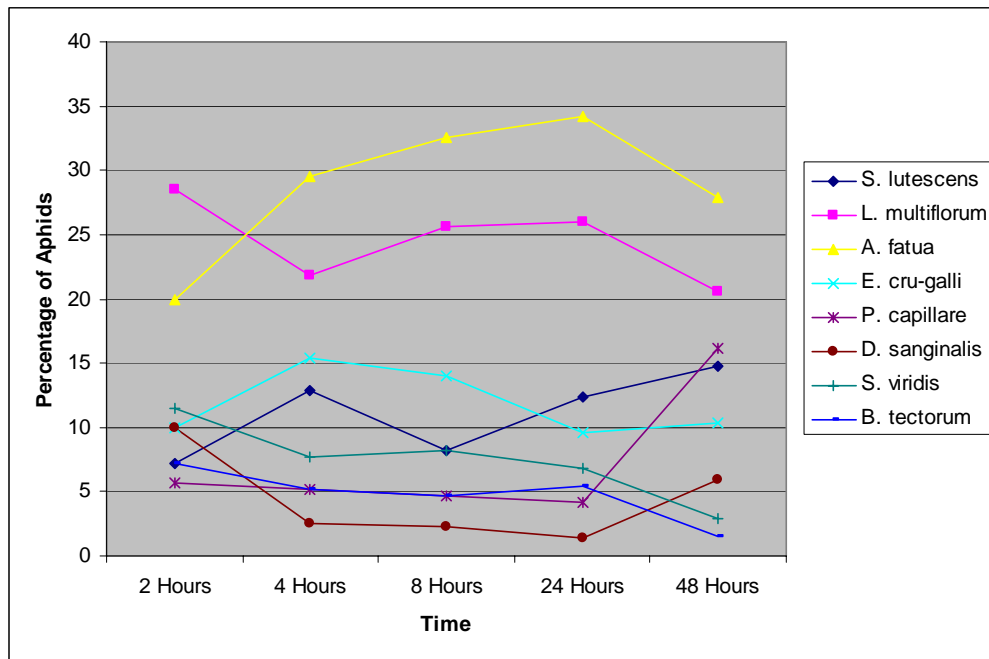


Figure 5. Preference of aphid species *Rhopalosiphum padi* for eight uninfected wild grass species over a two to forty-eight hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*.

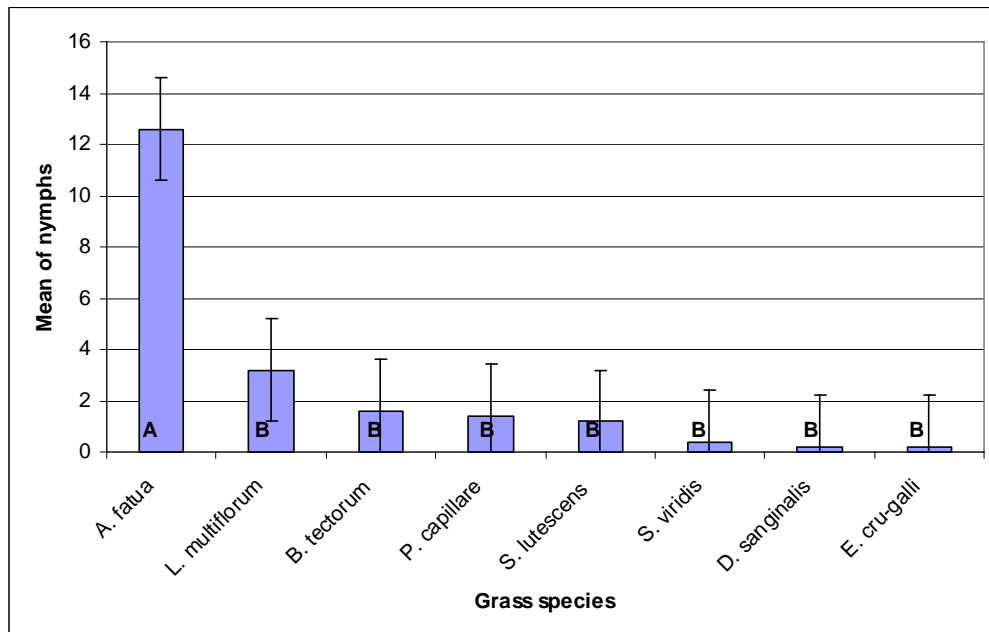


Figure 2A. Fecundity of aphid species *S. avenae* on eight uninfected wild grass species at a twenty-four hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*. Means followed by the same letters do not differ in significance.

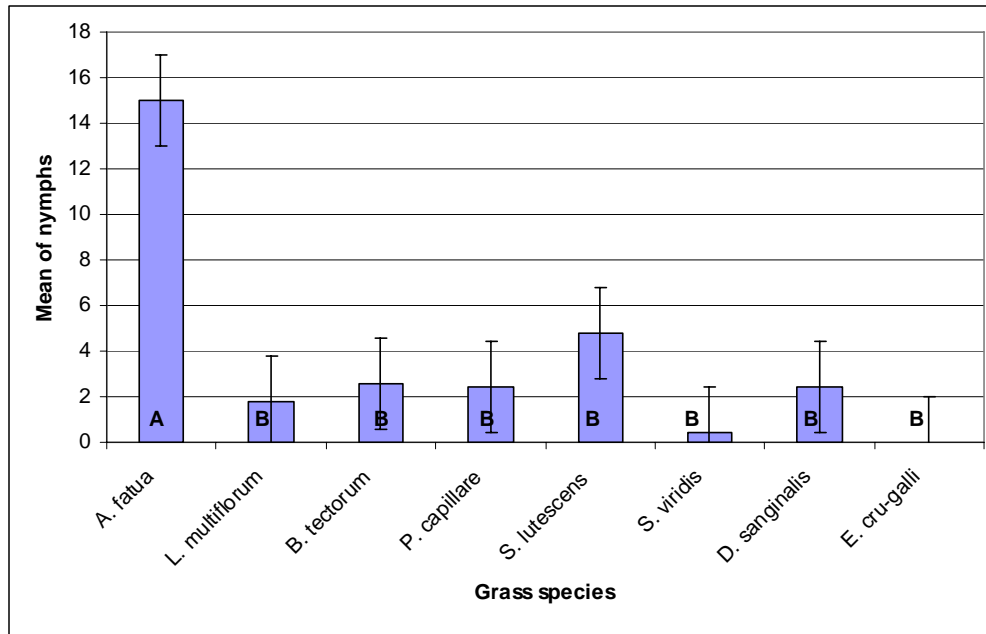


Figure 2B. Fecundity of aphid species *S. avenae* variant gray on eight uninfected wild grass species at a twenty-four hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*. Means followed by the same letters do not differ in significance.

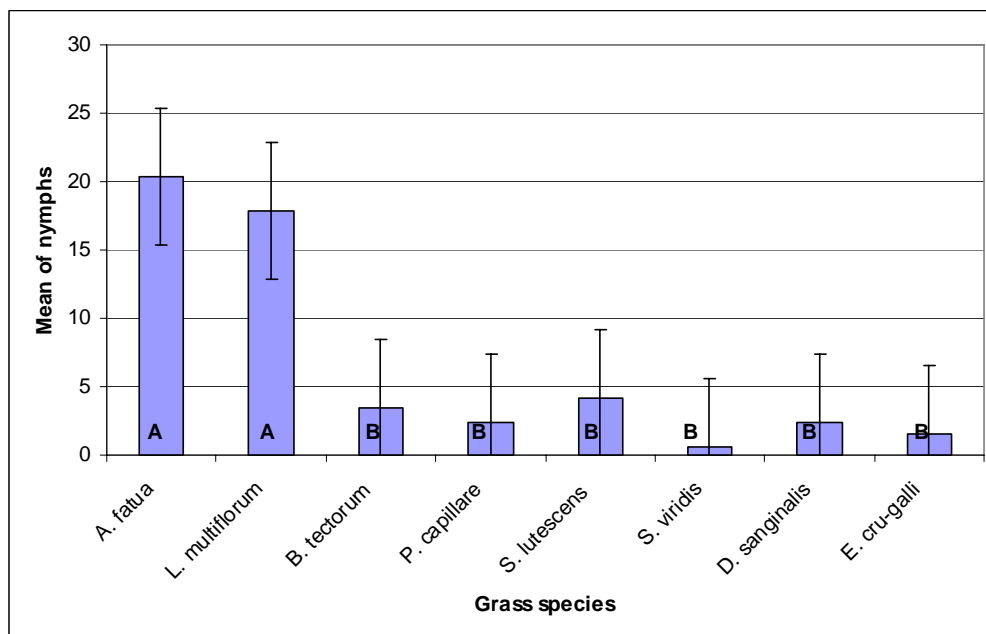


Figure 2C. Fecundity of aphid species *R. maidis* on eight uninfected wild grass species at a twenty-four hour period. The eight wild grass species include *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*. Means followed by the same letters do not differ in significance.

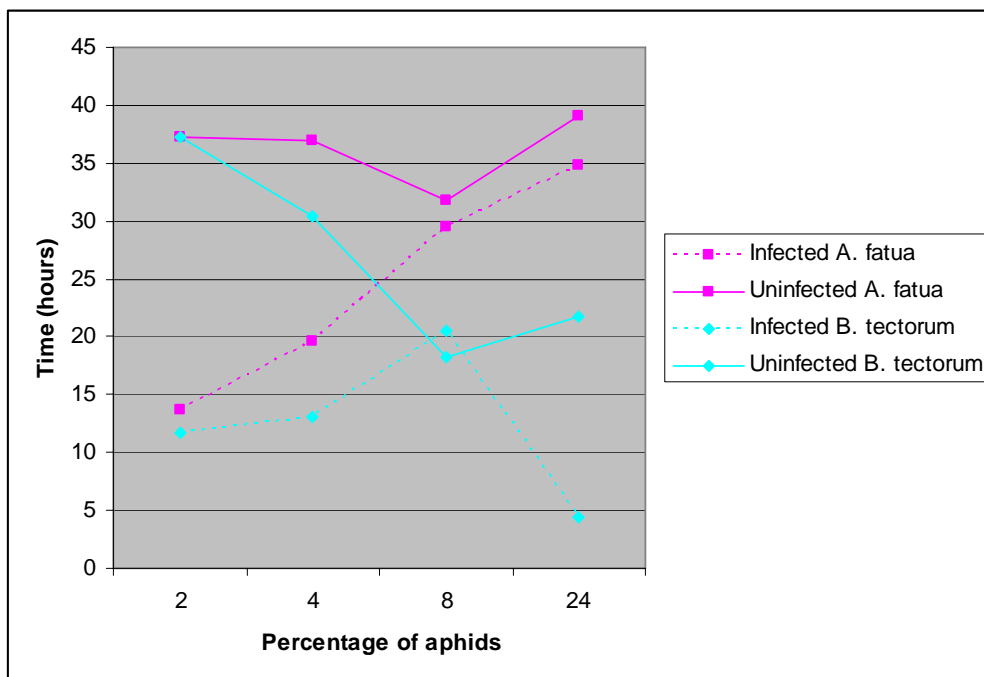


Figure 3A. Preference of aphid species *Sitobion avenae* for infected and uninfected seedlings of *Avena fatua* and *Bromus tectorum* over a two to twenty-four hour period.

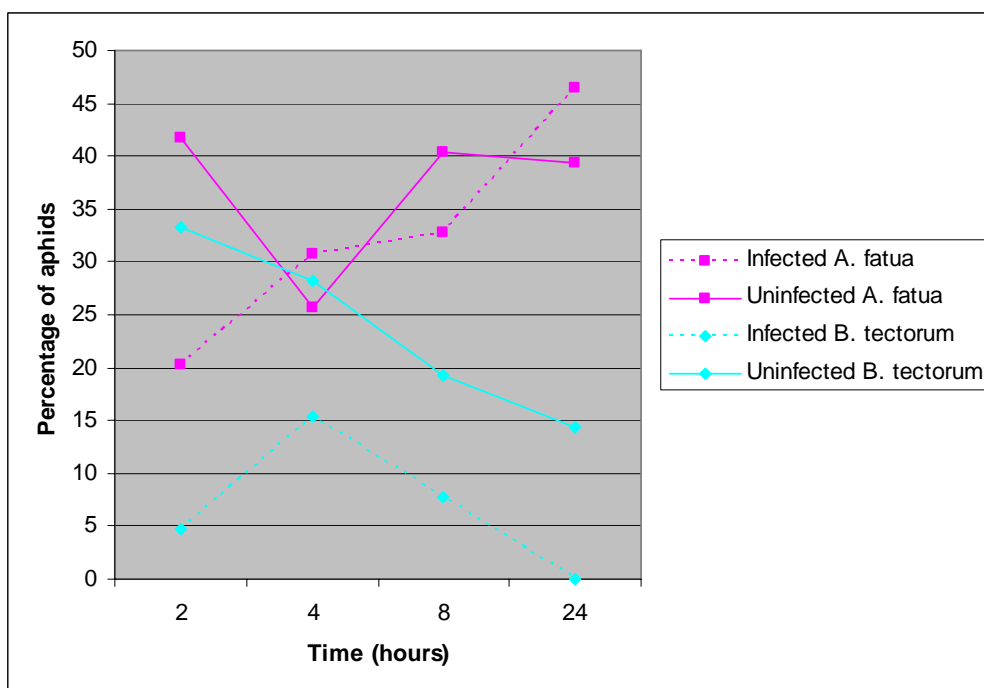


Figure 3B. Preference of aphid species *Rhopalosiphum padi* for infected and uninfected seedlings of *Avena fatua* and *Bromus tectorum* over a two to twenty-four hour period.

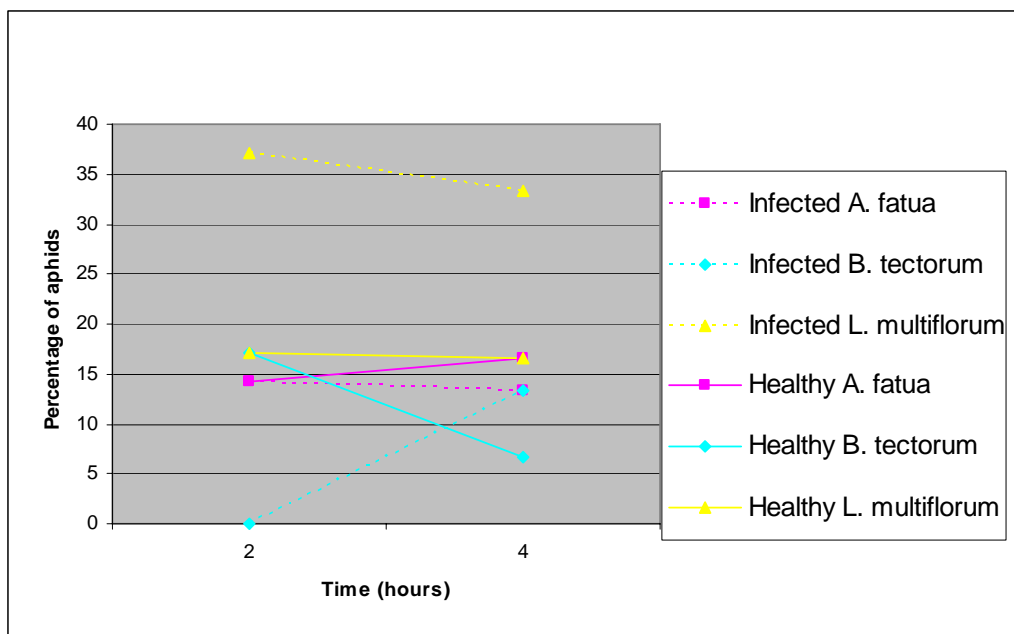


Figure 4A. Preference of aphid species *Rhopalosiphum padi* for infected and uninfected seedlings of *Avena fatua*, *Bromus tectorum*, and *Lolium multiflorum* over a two to four hour period.

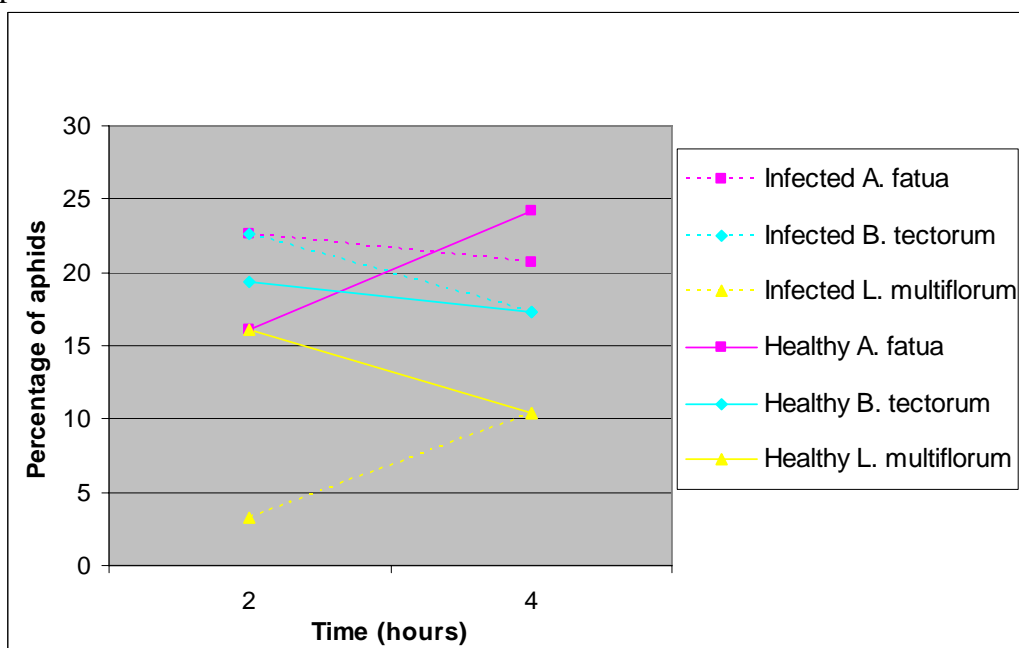


Figure 4B. Preference of aphid species *Sitobion avenae* for infected and uninfected seedlings of *Avena fatua*, *Bromus tectorum*, and *Lolium multiflorum* over a two to four hour period.

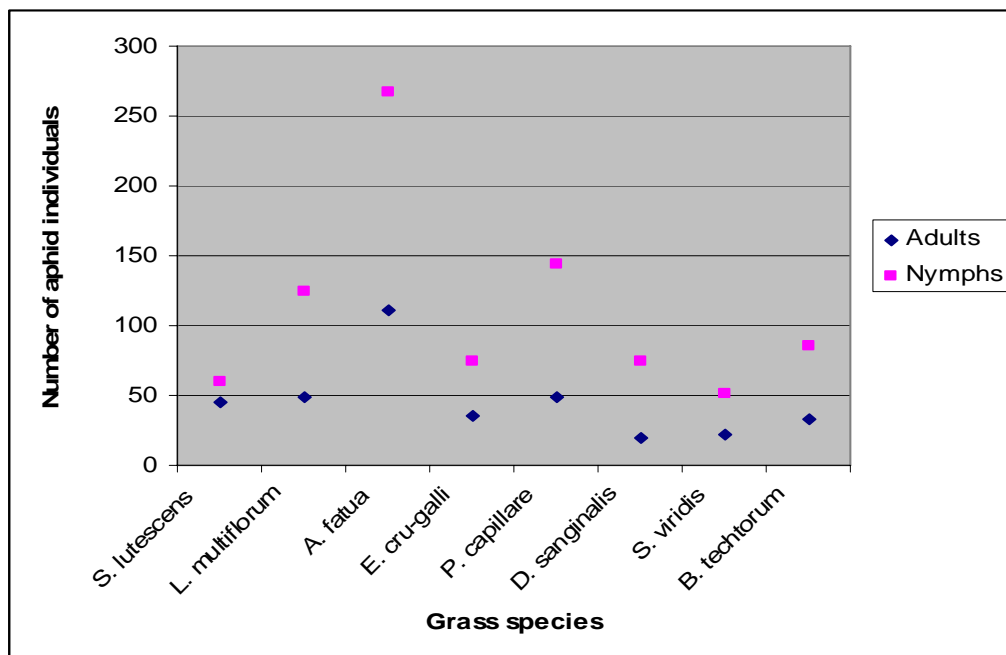


Figure 5. Total combined preference and fecundity of aphid species *Sitobion avenae* (SA), *S. avenae* variant gray (SA- Gr), *Rhopalosiphum maidis* (RM), *R. padi* (RP) for eight wild grass species at the twenty-four hour interval. The eight wild grass species are *Avena fatua*, *Bromus tectorum*, *Digitaria sanguinalis*, *Echinochloa cru-galli*, *Lolium multiflorum*, *Panicum capillare*, *Setaria lutescens*, and *S. viridis*.