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Source: Journal of Insect Science, 5(13) : 1-8

Published By: Entomological Society of America

URL: https://doi.org/10.1673/031.005.1301

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Qureshi JA, Michaud JP. 2005. Interactions among three species of cereal aphids simultaneously infesting wheat. 8pp. *Journal of Insect Science*, 5:13, Available online: insectscience.org/5.13

Journal of Insect Science

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# Interactions among three species of cereal aphids simultaneously infesting wheat

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Received 4 October 2004, Accepted 28 January 2005, Published 22 April 2005

## Abstract

Interactions among greenbug, *Schizaphis graminum* (Rondani), Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and bird cherry-oat aphid *Rhopalosiphum padi* (L.) were examined on wheat plants (*Triticum aestivum* L., cultivar TAM 107). Nymphs were released on the plants as conspecific and heterospecific pairs of either first or fourth instars and evaluated for survival, developmental time, fecundity, intra-plant movement, and affinity to plant tissues. Survival from first instar to onset of reproduction averaged 90-100% across all pair combinations. *Diuraphis noxia* developed faster as conspecifics than in any heterospecific combination, and faster as conspecifics feeding on the same plant tissue than on different tissues. Fecundity of *S. graminum* was higher for conspecifics that developed on the same plant tissue than for those feeding separately. There was evidence of amensalism (one species was harmed while the other was unaffected) in that *D. noxia* experienced delayed development feeding in tandem with *S. graminum*, and reduced fecundity with both *S. graminum* and *R. padi*. Furthermore, *S. graminum* nymphs had reduced survival when their mothers matured on a same plant with *R. padi*. Both *D. noxia* and *R. padi* changed position on the plant more often when developing with *S. graminum.* Survival of second generation *S. graminum* nymphs was reduced when this species developed and reproduced in tandem with *R. padi*. Preferred feeding locations were *S. graminum* - primary leaf, *D. noxia* - tertiary leaf and *R. padi* - stem and these were not altered in any heterospecific combinations. Heterospecific aphids had no impact on fecundity or progeny survival in any species combination when fourth instars matured and reproduced on plants not previously exposed to aphid feeding, supporting the inference that systemic, aphid-induced changes in plant physiology mediated the effects observed when first instars developed and reproduced on the same plants.

*Keywords:* amensalism, *Diuraphis noxia, Rhopalosiphum padi,* reproduction, development, *Schizaphis graminum*

## Introduction

To the extent that certain herbivores can alter the physiology of their host plant, and hence its nutritional value, there exists the potential for complex interspecific interactions among herbivores that are mediated by the host plant. As aphids feed from plant phloem elements, they inject saliva that often brings about changes in plant physiology (Prado & Tjallingii, 1994), usually for their own nutritional benefit (Petersen & Sandström, 2001). When more than one aphid species feed on the same plant the net changes in plant physiology will be some function of their combined effects. For aphid species that form closely spaced colonies, individuals may benefit from faster development when feeding in groups (Qureshi & Michaud, 2005). However, alterations in plant physiology induced by aphid feeding could potentially have positive, neutral, or negative effects on heterospecific aphids attempting to colonize the same plant. Amensalism (one species is harmed or inhibited and the other is unaffected), commensalism (one species derives some benefit while the other is unaffected), mutualism (an association in which both species benefit), and antagonism (both species are negatively affected via an indirect mechanism) are all plausible outcomes of interspecific interactions among aphid species that co-infest a host plant. Thus, host plant-mediated interactions among aphid species, rather than any direct form of competition, may be key factors influencing patterns of aphid species co-occurrence or niche partitioning in nature.

Three economically important aphids occur sympatrically in fields of wheat, *Triticum aestivum* L., throughout many regions of the USA where cereals are grown. These are the greenbug, *Schizaphis graminum*, the Russian wheat aphid, *Diuraphis noxia*, and the bird cherry-oat aphid, *Rhopalosiphum padi* (Homoptera: Aphididae) (Turney & Hoelscher, 1986; Schotzko & Bosque-Perez, 2000; Bosque-Pérez *et al.*, 2002). It has been shown that *S. graminum* and *D. noxia* are able to alter the amino acid profile of phloem contents in susceptible wheat (cultivar Arapahoe) for their own benefit (Telang *et al.*, 1999; Sandström *et al.*, 2000; Sandström & Moran, 2001), although they likely do so in very different ways. Notably, Telang *et al.* (1999) did not find any such effect for *D. noxia* on resistant wheat, cultivar Halt. Havlickova (1986) reported that feeding by *R. padi* on young wheat plants cultivars Mironovskaya 808 and Slavia resulted in increased concentrations of free amino acids, sucrose, glucose, and some phenolic

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compounds in above-ground plant parts, but caused a reduction in the concentration of free amino acids and other compounds in the roots. In contrast, Gianoli & Niemeyer (1997, 1998) have shown that *R. padi* infestation triggers the induction of defensive chemicals in the first leaf of wheat seedlings and that this response can vary with the tissue infested. Thus, some aspects of antibiosis-based plant resistance to aphids may involve mechanisms that interfere with the processes whereby aphids attempt to alter host plant physiology for their own benefit. Here we refer to changes in host plant chemistry brought about by aphid feeding as 'plant induction', whether the consequences are positive or negative for the aphids. If plant inductive processes are species-specific among aphids, we also might expect plant antibiosis mechanisms to be quite specific to aphid species. Notably, wheat varieties resistant to greenbug (e.g. cultivar TAM 110) are not resistant to Russian wheat aphid, nor vice versa (e.g. cultivars Halt, Stanton).

A variety of interactions have been reported for aphid species feeding on plants previously infested by conspecifics or different aphid species. For example, Messina *et al.* (2002) found that previous infestation of wheat by *R. padi* reduced the subsequent growth rate of a conspecific colony by 50%, but had no effect on a population of *D. noxia*. Similarly, biotype E of *S. graminum* had significantly improved fecundity on wheat cultivar Newton previously conditioned by *D. noxia*, but not on wheat conditioned by conspecifics (Formusoh *et al.*, 1992), a finding indicative of commensalism. Qureshi & Michaud (2005) observed that developmental time was decreased for nymphs of *S. graminum*, and increased for nymphs of *R. padi*, relative to that of their respective mothers that completed development on the same plants of wheat cultivar TAM 107, whereas there was no such effect for *D. noxia*. Gianoli (2000) found that the reproductive rate of English grain aphid, *Sitobion avenae*, on tillering wheat plants was negatively affected by a previous infestation of *R. padi*, a result suggesting amensalism.

Interactions among simultaneously occurring cereal aphids on the same plants have rarely been studied, but studies of other phloem-feeding Homoptera have revealed interactions ranging from synergism to antagonism. Alla *et al.* (2001) examined interactions between *R. padi* and the wheat leafhopper, *Psammotettix alienus*. They found that infestation by *R. padi* resulted in delayed development and increased mortality of *P. alienus* on the same wheat plants. Furthermore, in the presence of *R. padi, P. alienus* left their preferred feeding sites on the lower part of the plant and moved to upper plant parts. In contrast, Kidd *et al.* (1985) found a beneficial interspecific association between the grey pine aphid, *Schizolachnus pineti* and the spotted pine aphid, *Eulachnus agilis* on Scots pine, *Pinus sylvestris*. By feeding on the same shoots and needles as *S. pineti*, *E. agilis* was found to benefit from commensalism in terms of increased survival and faster growth, presumably by exploiting the plant induction brought about by *S. pineti*.

*Schizaphis graminum*, *D. noxia*, and *R. padi* have all been observed to simultaneously infest wheat plants (Bosque-Pérez *et al.* 2002, JAQ unpublished). In the course of rearing these species in the laboratory, we often find various combinations of these species developing together on the same plants, to the point where prevention of cross-contamination among colonies is a constant challenge. However, contamination of *D. noxia* colonies by *S. graminum* and *R. padi* seem to occur most frequently, as though colonies of *D. noxia* were preferentially invaded by the latter species. We have previously shown that these three species prefer different feeding sites on the plant and vary in their tendency to move among plant parts in the course of development (Qureshi & Michaud, 2005). In the present study, we examined interactions among *S. graminum*, *D. noxia*, and *R. padi* by comparing their acceptance of TAM 107 wheat, frequency of intra-plant movement, developmental time, and reproductive performance as they developed and reproduced on the same plants in heterospecific and conspecific pairs.

## Materials and Methods

### *Stock Colonies*

Stock colonies of *S. graminum* (Biotype 'I') were established from individuals collected at Agricultural Research Center-Hays in western Kansas during 2003 and maintained on sorghum cultivar 'P 8500'. Similarly, colonies of *D. noxia* (Biotype 'I') were initiated from individuals collected at the Hays center and maintained on wheat, *T. aestivum* cultivar 'Tomahawk', for several years. A colony of *R. padi* was established from individuals infesting wheat in a greenhouse at the Hays center during fall, 2003. We used wheat cultivar TAM 107 (PI 495594), released by Texas A&M University in 1984 (Porter *et al.*, 1987) as the host plant for rearing stock colonies and conducting all experiments as it represents an acceptable and suitable variety for all three aphid species (Qureshi & Michaud, 2005). Stock colonies of the three aphid species were maintained in isolation for more than ten generations at 20 ± 1º C under 'cool-white' fluorescent lighting set to a photoperiod of 16:8 (L:D) in Percival I-36VL growth chambers. Wheat seeds were planted in soil 8 cm deep in metal trays (26 x 36 cm) and germinated in a greenhouse. Ten to 12 day old plants were infested with aphids and then transferred to their respective environmental chambers. New trays of wheat seedlings were introduced for each colony every 12-13 days and manually infested with plant clippings from the old tray. Trays were watered as required.

### *Plants*

Nine to ten day old plants of TAM 107 wheat were used for these experiments. Plastic cones (2.5 cm diameter x 16 cm deep) were filled with soil and planted with three wheat seeds in each. After planting, cones were placed in plastic racks set in plastic trays filled with water for 48 h in the greenhouse. During this period, the cones drew up enough water from the tray to support plant growth throughout the experiment. Three to 4 days after germination, plants were thinned to leave a single seedling in each cone. Plants were grown for 9-10 days until they reached the 2-3 leaf stage, then cut to a height of 10 cm in order to facilitate repeated observations of aphids that are easily dislodged from tall plants.

### *Experiments*

Adult apterae of all three species were collected from their respective stock colonies and placed on wheat seedlings (2-3 per plant) to reproduce for a period of 24 h, yielding a synchronous cohort of 12 ± 12 h old first instar nymphs. Seedlings in individual cones (replicates) were each infested with two first instar nymphs on the stem and then covered with a ventilated clear plastic cylinder (2.3 cm diameter x 31 cm tall) and placed back in the rack. The six

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experimental treatments consisted of three heterospecific pair wise combinations of nymphs with three conspecific pair combinations serving as controls. There were twenty replications of each treatment.

The experiment was held in a growth chamber under the same environmental conditions as the stock colonies. Since the high light intensity that is optimal for maintaining plant quality also generates temperature gradients within the chamber, measurements of temperature (mean, minimum and maximum) and humidity were recorded daily using a digital temperature/humidity probe placed within a cylinder-covered cone on the same rack as the experimental replicates. The following data were recorded daily for each replicate: (1) presence or absence of the aphids on the plant (2) location of the aphids on the plant, (3) date of first reproduction by the aphids, (4) number of first instars nymphs of each species present, (5) total nymphs of each species present. Aphid locations on the plant were categorized as 'stem', 'primary leaf', 'secondary leaf', 'tertiary leaf', or 'flag leaf'. The number of first instar nymphs produced by each maturing aphid was tallied for eight days from the day of first reproduction. Since control treatments had two aphids of the same species reproducing together, total progeny were tallied for eight days from the first reproduction event and individual fecundity estimated by dividing by two.

A second experiment was performed similar to the first except that experimental plants were infested with fourth instar aphids. The rationale was to replicate the first experiment using older aphids that would interact on the plant for only a short period prior to reproduction, in contrast to the first instar aphids that would interact throughout their developmental and reproductive periods. Our hypothesis was that species interaction effects mediated by the host plant and evident in the first experiment would be absent in the second experiment where there was less time for plant induction processes to occur. There were 18 replicates per treatment and the data on the number of first instars nymphs and total nymphs of each species present were recorded daily for each replicate.

*Data Collection and Analysis*

Survival of first instar nymphs was measured as the proportion that achieved reproductive age, whereas the survival of their progeny was estimated as the number alive on day eight divided by the total number of first instars produced during the eight days of reproduction. Developmental time was calculated as the number of days from inoculation of first instars until the first reproduction event. Fecundity was tallied as the number of first instars produced by a foundress over eight days of reproduction. The proportion of time aphids spent on various plant parts, or off the plant, was estimated by dividing the total number of days the aphid was encountered at each location by its total developmental time. Position changes were tallied whenever an individual aphid was discovered on a plant part different from that it had been on the previous day. The frequency of position change on the plant was then calculated by dividing the number of times an aphid changed position on the plant by its total developmental time.

Survival of first instars to their first reproduction was analyzed and compared across treatments as binomial responses using GLIMMIX MACRO model and PROC MIXED (Littell *et al.* 1996) in SAS (SAS Institute 1999-2001) and data were transformed with logit link function. All the remaining variables were analyzed for differences across treatments with a one way ANOVA using PROC GLM in SAS followed by a least significant difference (LSD) procedure (Littell *et al.* 1996) for separation of means.

## Results

Mean daily temperature was 21.23 ± 0.8º C during the first experiment. Survival of first instars to first reproduction averaged 90-100% across treatments and was not significantly different for any species when conspecific pairs were compared to heterospecific pairs ($P > 0.05$). The GLIMMIX MACRO model used to test survival indicated a good fit for the analyzed data sets because deviance values were close to $\chi^2$ critical values and extra dispersion scale values were above 0.9 and close to 1.0.

In the first experiment, when seedling wheat plants were co-infested with first instar nymphs of all species combinations, *D. noxia* nymphs took longer to mature in the presence of *S. graminum* than in the presence of conspecifics ($F$ = 4.41; df = 2, 55; $P$ = 0.043), whereas their development rate in the presence of *R. padi* was intermediate and not significantly different from the other treatments (Fig. 1). The developmental times of *S. graminum* and *R. padi* nymphs did not differ from those of conspecific pairs when they developed in any heterospecific combination ($F$ = 2.84; df = 2, 56; $P$ = 0.067) ($F$ = 1.01; df = 2, 54; $P$ = 0.372). *Diuraphis noxia* maturing in conspecific pairs had higher fecundity than those maturing in pairs with either *S. graminum* or *R. padi* ($F$ = 5.78; df = 2, 55; $P$ = 0.005), whereas the fecundity of *S. graminum* and *R. padi* maturing in heterospecific pairs did not differ from those maturing in conspecific pairs ($F$ = 0.02; df = 2, 56; $P$ = 0.977) ($F$ = 1.31; df = 2, 54; $P$ = 0.278), (Fig 2).

We also used data from the first experiment to compare the developmental time and fecundity of conspecific aphid pairs that developed on the same plant tissue for at least five consecutive days with those that developed feeding on different plant tissues. Nymphs of *D. noxia* feeding consistently on the same plant tissue developed faster than those that developed on different tissues, whereas *S. graminum* pairs maturing on the same tissue had higher fecundity than those that fed and developed on different tissues (Table 1). All other comparisons of developmental time and fecundity were not significantly different between aphids that fed together versus separately.

The survival of progeny produced by *S. graminum* foundresses maturing in conspecific pairs was not different from that of foundresses that matured in the presence of *D. noxia*, but was lower for progeny whose mothers had matured with *R. padi* ($F$ = 5.03; df = 2, 56; $P$ = 0.009), (Fig. 3). Progeny survival for *D. noxia* and *R. padi* maturing in conspecific pairs was not different from that observed in any heterospecific combination ($F$ = 0.25; df = 2, 55; $P$ = 0.780 and $F$ = 0.25; df = 2, 54; $P$ = 0.782, respectively).

There was no difference among treatments in the frequency of position change on the plant for developing *S. graminum* nymphs ($F$ = 1.59; df = 2, 57; $P$ = 0.213), (Fig. 4). *Diuraphis noxia* changed position on the plant more often when developing in the presence of *S. graminum* than in conspecific pairs, but demonstrated an intermediate value in the presence of *R. padi* ($F$ = 3.27; df = 2, 56; $P$ = 0.045), (Fig. 4). Similarly, *R. padi* changed position more often

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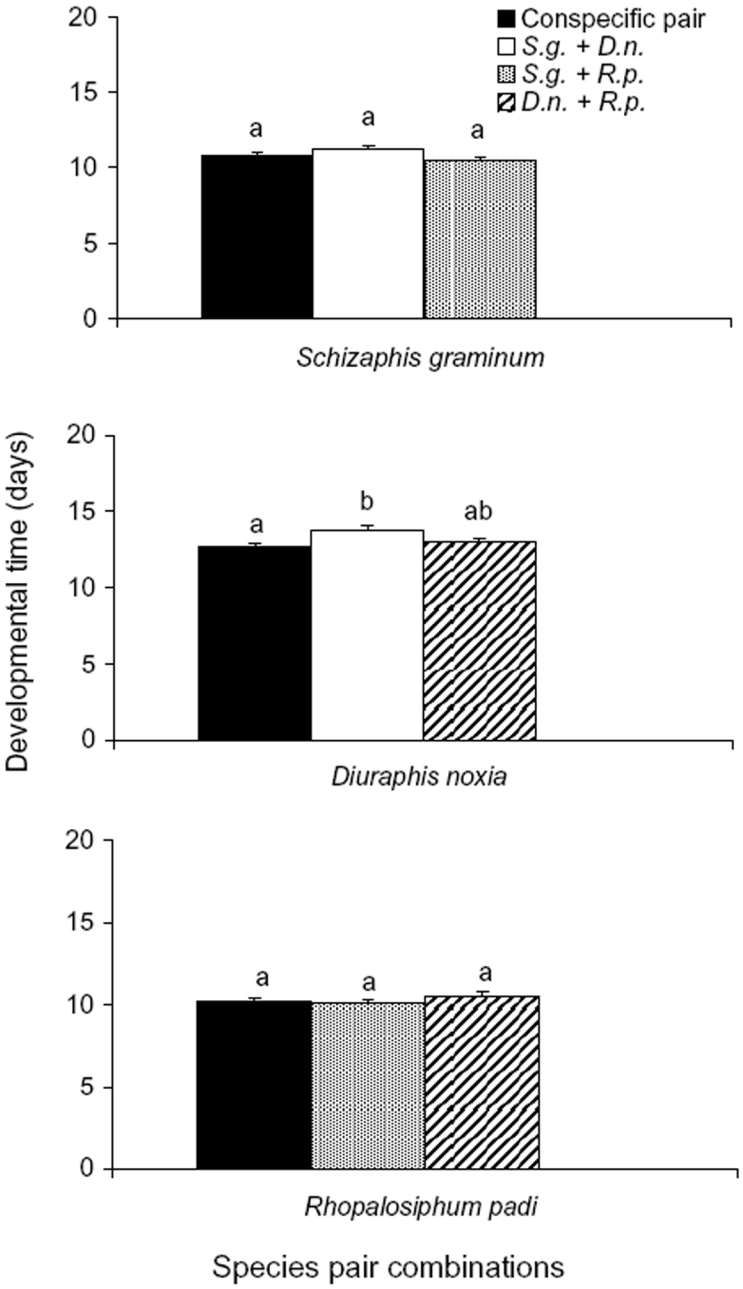


**Figure 1.** Mean developmental times (+ SEM) measured from birth to first reproduction of aphids that developed as conspecific or heterospecific pairs on TAM 107 wheat plants. Means bearing the same letter were not significantly different for particular species ($P > 0.05$, PROC GLM, LS MEANS).

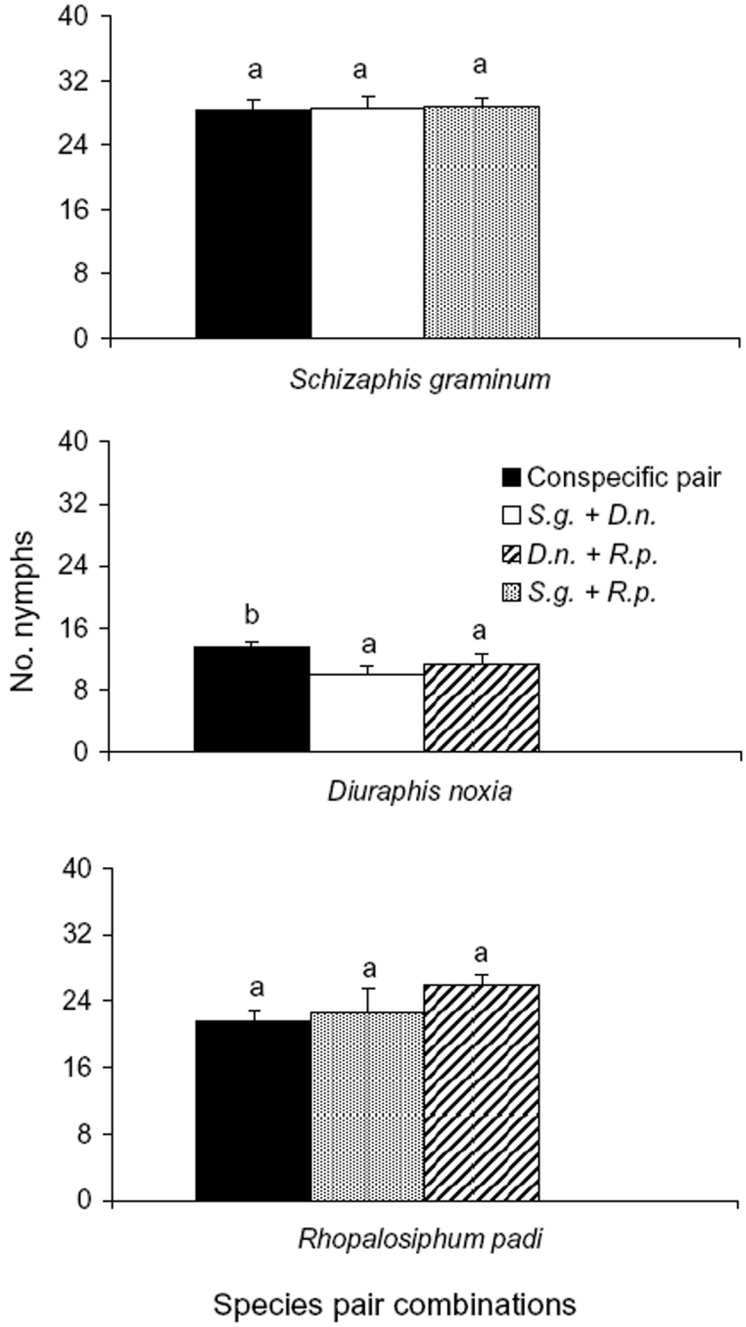


**Figure 2.** Mean fecundities (+ SEM) averaged over eight days of reproduction for aphids that developed and reproduced as conspecific or heterospecific pairs on TAM 107 wheat plants. Means bearing the same letter were not significantly different for particular species ($P > 0.05$, PROC GLM, LS MEANS).

in the presence of *S. graminum* than in the presence of *D. noxia* or a conspecific aphid ($F = 3.43$; df = 2, 58; $P = 0.039$), (Fig. 4).

Developing *S. graminum* nymphs spent 80-85% of their time on the primary leaf whether they were developing with a conspecific ($F = 52.68$; df = 5, 114; $P < 0.0001$) with *D. noxia* ($F = 72.95$; df = 5, 114; $P < 0.0001$) or with *R. padi* ($F = 39.20$; df = 5, 114; $P < 0.0001$). The order of plant tissue preference for *S. graminum* was primary leaf > stem > secondary leaf = tertiary leaf = flag leaf. Nymphs of *D. noxia* were present on the tertiary leaf for 57-70% of observations, significantly more than on any other plant tissue whether developing as conspecific pairs ($F = 15.92$; df = 5, 114; $P < 0.0001$) with *S. graminum* ($F = 19.00$; df = 5, 114; $P < 0.0001$) or with *R. padi* ($F = 26.42$; df = 5, 108; $P < 0.0001$). The order of tissue preference for *D. noxia* in conspecific pairs was tertiary leaf > primary leaf = secondary leaf > stem = flag leaf, whereas with *S. graminum* it was tertiary leaf > primary leaf >

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**Table 1.** Developmental time (Mean ± SEM, n) and fecundity (Mean ± SEM, n) of aphids that developed as conspecific or heterospecific pairs on either the same tissue for five consecutive days, or on different tissues, of TAM 107 wheat plants. Sg = *Schizaphis graminum*, Dn = *Diuraphis noxia*, Rp = *Rhopalosiphum padi*.

| | Sg and Sg | Rp and Rp | Dn and Dn | Sg and Dn | | Sg and Rp | |
|---|---|---|---|---|---|---|---|
| | | | | Sg | Dn | Sg | Rp |
| **Development time** | | | | | | | |
| Same tissue | 10.50 ± 0.34 (12) | 10.08 ± 0.33 (13) | 11.82 ± 0.33**a** (11) | 11.17 ± 0.40 (6) | 13.83 ± 0.60 (6) | 10.60 ± 0.27 (10) | 10.40 ± 0.34 (10) |
| Different tissues | 11.25 ± 0.41 (8) | 10.29 ± 0.42 (7) | 13.67 ± 0.37**b** (9) | 11.31 ± 0.31 (13) | 13.77 ± 0.32 (13) | 10.30 ± 0.34 (10) | 9.78 ± 0.43 (9) |
| *F* (df) | 1.98 (1, 18) | 0.15 (1, 18) | 14.07 (1, 18) | 0.07 (1, 17) | 0.01 (1, 17) | 0.49 (1, 18) | 1.30 (1, 17) |
| *P* | 0.176 | 0.706 | 0.015 | 0.793 | 0.919 | 0.493 | 0.270 |
| **Fecundity** | | | | | | | |
| Same tissue | 30.21 ± 1.46**b** (12) | 21.54 ± 1.38 (13) | 14.59 ± 1.03 (11) | 30.17 ± 2.88 (6) | 9.33 ± 1.45 (6) | 30.10 ± 1.33 (10) | 20.70 ± 3.89 (10) |
| Different tissues | 25.69 ± 1.39**a** (8) | 22.00 ± 2.65 (7) | 12.39 ± 1.08 (9) | 27.69 ± 1.77 (13) | 11.00 ± 0.72 (13) | 27.40 ± 1.47 (10) | 25.00 ± 4.14 (9) |
| *F* (df) | 4.54 (1, 18) | 0.03 (1, 18) | 2.17 (1, 18) | 0.58 (1, 17) | 1.35 (1, 17) | 1.86 (1, 18) | 0.57 (1, 17) |
| *P* | 0.047 | 0.866 | 0.158 | 0.457 | 0.261 | 0.190 | 0.459 |

Means within a column bearing different letters were significantly different ($P < 0.05$, PROC GLM, LS MEANS).

secondary leaf = stem = flag leaf and with *R. padi* it was tertiary leaf > primary leaf = secondary leaf with primary leaf > stem = flag leaf and secondary leaf = stem = flag leaf. *Rhopalosiphum padi* nymphs spent 66-88% of their time on the stem, significantly more than on any other plant tissue whether developing in conspecific pairs ($F = 276.80$; df = 5, 114; $P < 0.0001$) with *S. graminum* ($F = 24.68$; df = 5, 114; $P < 0.0001$) or with *D. noxia* ($F = 59.41$; df = 5, 108; $P < 0.0001$). The order of tissue preference for *R. padi* was stem > primary leaf > secondary leaf = tertiary leaf = flag leaf. The two tissues on which a species spent more time in all three species-pair combinations (primary leaf and stem for *S. graminum*, tertiary and primary leaf for *D. noxia*, and stem and primary leaf for *R. padi*) did not differ among species combinations in any case ($P > 0.05$).

The mean daily temperature was 22.32 ± 0.34º C during the course of the second experiment. Neither the fecundity of aphids transferred to experimental plants as fourth instars, nor the survival of their progeny, were significantly different among treatments for any aphid species, when aphids in conspecific and heterospecific pairs were compared (Table 2).

## Discussion

Changes in plant physiology due to feeding by these aphid species have already been described in wheat (Havlickova, 1986; Prado & Tjallingii, 1994; Telang *et al.*, 1999; Sandström *et al.*, 2000; Sandström & Moran, 2001). All three aphid species appeared to initiate distinct, species-specific, plant inductive processes that were systemic to varying degrees. Consequently, interactions among these aphid species appeared to be mediated by the host plant, although direct interactions among the aphids themselves cannot be ruled out. It is unlikely that the observed effects could have resulted from exploitation competition as the pairs of aphids employed in these experiments would not be able to extract more than a small fraction of available nutrients from the phloem, nor effect any appreciable resource depletion in the plant. Although certain aphid species exhibit direct aggression towards other insects, usually predators, this is known only in social aphids with sterile soldier castes (Rhoden & Foster, 2002) and has not been reported for these cereal aphids to our knowledge. In these experiments, using only two aphids per plant, we were able to document amensalism by both *S. graminum* and *R. padi* on *D. noxia*, and by *R. padi* on *S. graminum*, with all other interactions essentially neutral (Price 1997).

Of the three species, *S. graminum* can be considered the most aggressive in exploiting its host plant; it has the highest reproductive rate and causes rapid deterioration of plant quality via chlorosis (Gellner *et al.*, 1990; Qureshi & Michaud, 2005). The higher fecundity of *S. graminum* that developed in conspecific pairs on the same plant tissue for at least five consecutive days compared

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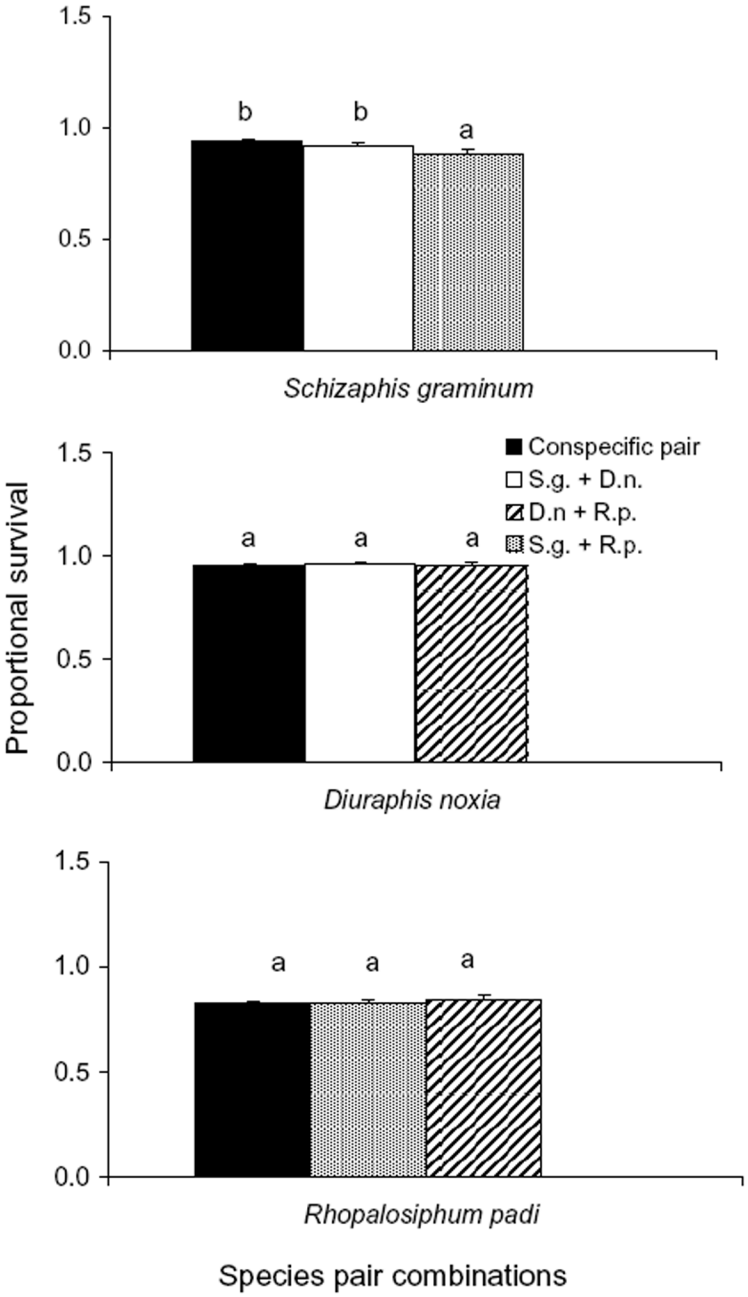


**Figure 3.** Proportional survival of progeny after eight days of reproduction by aphids that matured and reproduced in conspecific and heterospecific pairs on TAM 107 wheat plants. Means bearing the same letter were not significantly different for particular species ($P > 0.05$, PROC GLM, LS MEANS).

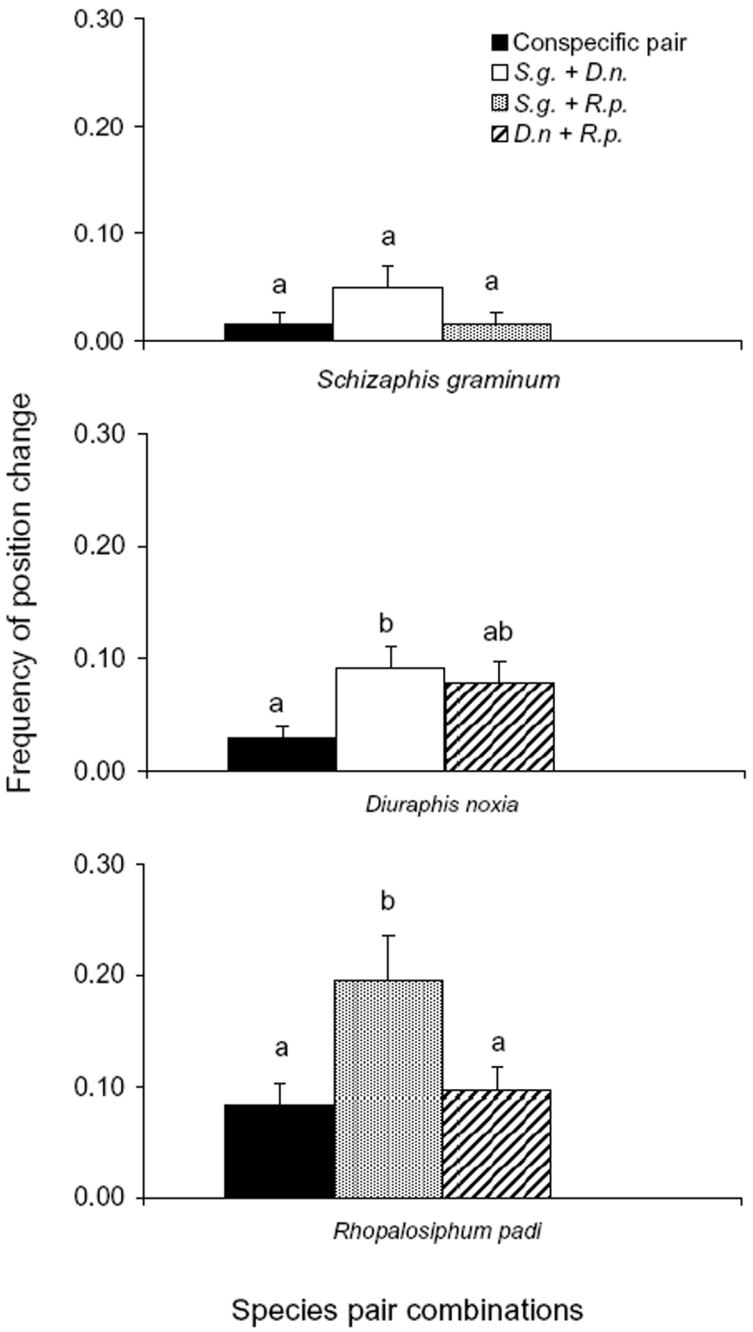


**Figure 4.** Frequency of position change (Mean + SEM) by immature aphids that developed as conspecific or heterospecfic pairs on TAM 107 wheat plants. Means bearing the same letter were not significantly different for particular species ($P > 0.05$, PROC GLM, LS MEANS).

to those that fed on different tissues (Table 1), suggests a benefit of conspecific group-feeding on reproductive rate that is localized within infested tissues. *Schizaphis graminum* is also known to significantly reduce translocation from the immediate vicinity of its feeding site without altering the integrity of phloem elements (Burd, 2002). Although both *D. noxia* and *S. graminum* feeding causes leaf chlorosis in wheat, the symptoms are slower to develop with *D. noxia* than with *S. graminum* and plants with uncontrolled colonies of *D. noxia* can survive considerably longer. In contrast, *R. padi* feeding symptoms appear much later than those of *D. noxia* or *S. graminum*, and uncontrolled colonies do not result in plant death, although plant productivity may be affected (Kieckhefer & Gellner, 1992). Thus *S. graminum* negatively impacted both development (Fig. 1) and reproduction (Fig. 2) of *D. noxia*, whereas *R. padi* negatively influenced only *D. noxia* reproduction and the nymphal survival of *S. graminum*. These results are consistent with plant induction by *R. padi* proceeding more slowly compared to *S. graminum* with more delayed effects on co-infesting aphid species.

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The fact that *D. noxia* developmental time was not significantly extended in the presence of *R. padi* confirms that a negative influence of *S. graminum*, rather than a lack of conspecific pair feeding benefits, was responsible for the delayed development. Furthermore, the higher rate of intra-plant movement by both *D. noxia* and *R. padi* in the presence of *S. graminum* (Fig. 4) is indicative of a response by the former species to plant induction by the latter.

*Diuraphis noxia* causes specific changes in host plant architecture (leaf rolling) that result in the creation of a 'cryptic niche' (Burd *et al.*, 1998), and the species has likely adopted sedentary feeding habits to capitalize on the benefits of feeding within this protected microhabitat (Telang *et al.*, 1999; Qureshi & Michaud, 2005). The faster development of conspecific pairs of *D. noxia* nymphs that remained feeding on the same leaf for at least five consecutive days compared to those that fed on different leaves (Table 1) is evidence of a benefit of group-feeding that also appears localized within the plant tissue, although *D. noxia* appears to have little effect on vein loading or phloem translocation at its feeding site (Burd, 2002). Consequently, it is conceivable that part of the cost paid by *D. noxia* developing in tandem with *S. graminum* was attributable to its increased frequency of intra-plant movement, either through a reduction in total feeding time, or because its own plant inductive processes were not localized on one part of the plant. This cost was apparently not paid by *R. padi*, possibly because this species is adapted to frequent position changes on the plant, even in the absence of heterospecific aphids (Qureshi & Michaud, 2005). Similarly, the higher fecundity of *S. graminum* that developed in conspecific pairs on the same tissue for at least five consecutive days compared to those that fed on different tissues (Table 1) indicates a benefit of group-feeding on reproduction in this species.

The presence of *R. padi* not only reduced *D. noxia* fecundity, it also reduced the survival of second generation *S. graminum* nymphs, both indications that feeding by the former species induces defensive host plant responses with amensal consequences for co-infesting aphid species. Amensal interactions have been previously demonstrated between *R. padi* and *S. avenae* (Gianoli, 2000) and *R. padi* and the wheat leafhopper, *P. alienus* (Alla *et al.*, 2001). These effects may result from *R. padi* feeding triggering the localized release of defensive compounds in the wheat plant (Gianoli & Niemeyer, 1997; 1998) that it seeks to avoid by frequent position change on the plant. Developing *S. graminum* nymphs, being relatively sedentary feeders, may have suffered from plant responses to *R. padi* feeding by not responding to their induction with position change on the plant. Interestingly, *R. padi* was the only aphid species to avoid any measurable negative impact in both heterospecific combinations and even displayed a trend toward higher fecundity after maturing in the presence of *D. noxia* (Fig. 2), although the effect was not significant because of high within-group variances in reproduction. Thus *R. padi*, perhaps the most generalist feeder of the three species and the only host-alternating aphid (Leather & Lehti, 1982), appeared to be the least negatively impacted in heterospecific interactions.

Although inter-specific interactions mediated by the host plant were clearly evident in this study, many of the host plant inductive processes seemed localized to some degree within plant parts. These aphid species differ significantly with respect to their preferred feeding locations on the plant (*S. graminum*: primary leaf, *D. noxia*: tertiary leaf, *R. padi*: stem) and these preferences were not altered by the presence of heterospecific aphids. Disparate feeding locations may reflect some degree of niche partitioning among these aphid species that share a range of host plants. The fact that there were no significant differences in fecundity or progeny survival among aphids transferred into conspecific or heterospecific pairs as fourth instars (Table 2) suggests that a period of more than several days of co-infestation by pre-reproductive aphids is required before any heterospecific impact can be realized. Thus interspecific

**Table 2.** Fecundity (Mean ± SEM) and proportional survival (Mean ± SEM) of progeny (averaged over eight days of reproduction) of fourth instar aphids that were transferred as conspecific or heterospecific pairs onto TAM 107 wheat plants.

| Species combinations | Fecundity (no.) | | | Proportional survival | | |
|---|---|---|---|---|---|---|
| | *S. graminum* | *D. noxia* | *R. padi* | *S. graminum* | *D. noxia* | *R. padi* |
| Conspecifics | 14.00 ± 0.67 | 11.72 ± 0.71 | 16.32 ± 1.00 | 0.88 ± 0.02 | 0.94 ± 0.01 | 0.80 ± 0.03 |
| *S. graminum* and *D. noxia* | 18.67 ± 1.98 | 9.44 ± 1.16 | _ _ | 0.91 ± 0.02 | 0.79 ± 0.06 | _ _ |
| *S. graminum* and *R. padi* | 16.44 ± 1.68 | _ _ | 15.00 ± 2.09 | 0.89 ± 0.03 | _ _ | 0.84 ± 0.03 |
| *D. noxia* and *R. padi* | _ _ | 11.59 ± 1.30 | 16.94 ± 2.01 | _ _ | 0.83 ± 0.06 | 0.80 ± 0.06 |
| *F* (df) | 2.28 (2, 51) | 1.42 (2, 50) | 0.31 (2, 48) | 0.55 (2, 51) | 2.42 (2, 50) | 0.25 (2, 48) |
| *P* | 0.113 | 0.250 | 0.733 | 0.580 | 0.099 | 0.776 |

Means within columns were not significantly different (P > 0.05, PROC GLM, LS MEANS

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interactions among these aphid species through altered plant physiology might not be an increasing, monotonic function of density as envisioned for classical interspecific competition (Faeth, 1992).

## Acknowledgments

We are thankful to USDA, APHIS, PPQ, and CPHST for financial assistance to Jawwad Qureshi, and John Reese, KSU Entomology Department for reviewing the manuscript. This article is Contribution No. 05-22-J from the Kansas Agricultural Experiment Station. Voucher specimens No. 158 are located in the Kansas State University Museum of Entomological and Prairie Arthropod Research.

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