

Competition in Cereal Aphids (Homoptera: Aphididae) on Wheat Plants

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ABSTRACT The cereal aphids *Rhopalosiphum padi* L. and *Sitobion avenae* (F.) coexist on the same host plant but occupy different ecological niches. *R. padi* arrives first in the season and reaches its population peak before *S. avenae*. In addition, *R. padi* prefers the stem and lower leaves, whereas *S. avenae* is found mostly on the ears and upper leaves of the plant. In greenhouse experiments, the likelihood of competition between *R. padi* and *S. avenae* on wheat seedlings and tillering plants was evaluated. The reproductive rate of *S. avenae* on tillering plants was negatively affected by previous infestation by *R. padi*, and this effect was larger when *R. padi* infestation started at an earlier plant growth stage. Likewise, previous infestation by *R. padi* decreased *S. avenae* reproduction on seedlings. In contrast, previous infestation by *S. avenae* on the flag leaf of flowering plants did not affect *R. padi* on that plant part. When both aphid species co-occurred from the beginning, the presence of either aphid species negatively affected the reproductive rate of the other. *R. padi* consistently had a higher rate of population increase than *S. avenae*. The presence of the other aphid species did not affect within-plant aphid distribution or alate aphid production. Results were similar on wheat seedlings and tillering plants. Finally, alate *S. avenae* preferred uninfested seedlings over *R. padi*-infested ones, whereas no preference was observed when the experiment was performed with tillering plants.

KEY WORDS *Rhopalosiphum padi*, *Sitobion avenae*, competition, wheat

THE RELEVANCE OF interspecific competition in the community structure of herbivorous insects has been intensively debated over the past decades, recently experiencing a sort of resurrection because of a more experimental approach, which has led to significant insights into the factors that can mediate competition (see Lawton and Strong 1981, Denno et al. 1995). Agroecosystems are a good arena to evaluate the likelihood of interspecific competition in insects because of the great knowledge on the ecology of pest species that is available.

A characteristic feature of the distribution and abundance of the two major species of cereal aphids on their host plants is their temporal and spatial separation. The bird cherry-oat aphid, *Rhopalosiphum padi* (L.), arrives first in the season (late spring-early summer) when cereals are in the seedling or early tillering stage. The population peak is reached when plants attain the stem-elongation stage, and populations decline during ear emergence (Wiktelius et al. 1990). The English grain aphid, *Sitobion avenae* (F.), usually arrives later in the season, when plants are in the late tillering or stem-elongation stage, and reaches maximum numbers at the earing stage (Dean 1974, Wiktelius and Ekblom 1985). Even when both aphid species co-occur on the same plant, they have different feeding niches. *R. padi* prefers the stem and basal

leaves (Leather and Dixon 1981), whereas *S. avenae* is found mostly on the ears and upper leaves (Watt 1979). Thus, there is little spatial or temporal overlap in these species. Nevertheless, there is some evidence from field data indicating that the maximum seasonal abundance of *S. avenae* is inversely correlated with that of *R. padi* (Rautapää 1976, Wiktelius and Ekblom 1985, but see Honek 1985).

The spatio-temporal pattern of resource use by *R. padi* and *S. avenae* could be considered, by classical ecological theory, as a means to achieve coexistence (or avoid competitive exclusion) (Schoener 1974). The reported inverse relationship in maximum seasonal abundance could be regarded as indirect evidence of interspecific competition between these aphid species. The latter issue has rarely been addressed in the vast literature on the ecology of cereal aphids (for reviews see Vickerman and Wratten 1979, Leather et al. 1989, Feng et al. 1992).

The current study aimed to determine whether competition between the cereal aphids *R. padi* and *S. avenae* occurs on seedlings or tillering plants of wheat, *Triticum aestivum* L. Experiments included both temporal co-occurrence and precedence of either aphid species. Whereas, the former addressed the classical competition scenario, the latter examined the effect of previous infestation on the other aphid species. Experiments were performed in greenhouses but in synchrony with the field season and with the reported time of arrival of each

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species to the cereal fields, thus emulating natural phenology.

Materials and Methods

Experimental plants of wheat 'Paleta' were grown from seeds provided by INIA (Instituto de Investigación Agropecuaria, Chile). Seeds were planted in plastic pots filled with potting soil. Experiments with seedlings used 250-ml pots, whereas experiments with tillering and older plants used 1.5-liter pots. Aphid stock colonies, originating from parthenogenetic females collected in cereal fields in Uppsala, Sweden, were kept on wheat seedlings in a greenhouse. Experimental aphids were young adults (1–3 d after the last molt). All experiments were performed in greenhouses during the spring and summer of 1998. Temperature ranged from a minimum of $15 \pm 2^\circ\text{C}$ to a maximum of $28 \pm 3^\circ\text{C}/\text{d}$. Treatments were always interspersed on greenhouse benches. Nomenclature of the growth stages of wheat plants follows the decimal code of growth stages of cereals by Zadoks et al. (1974).

Effect of Previous Aphid Infestation. I performed three experiments to evaluate the consequences of previous aphid infestation on the performance of the other aphid species. The first experiment attempted to estimate in the greenhouse the effect of the presence and the time of arrival of *R. padi* in wheat fields on the performance of *S. avenae*. According to field practices, all experimental plants were sown on 6 May. Early and late colonization by *R. padi* was simulated by infesting seedlings at growth stage 13 and tillering plants at growth stage 21, respectively. A third group of plants was not infested and served as a control. The infestation consisted of placing six adult *R. padi* on the base of the stem. Plants were enclosed with a porous plastic bag to prevent aphid dispersal. When all experimental plants attained growth stage 22, 10 d after the infestation of tillering plants, four adults of *S. avenae* of similar size were placed in a clip cage (2 cm diameter, 2 cm height) attached to the distal part of an upper leaf in all three groups of plants ($N = 14$ plants per treatment). Eight days later, the total number of aphids in the clip cage was counted and the fundamental net reproductive rate (R , Begon et al. 1990, p. 149) of *S. avenae* was calculated from the equation $N_t = N_0 \times R^t$, where N_0 is the initial number of aphids and N_t is the number of aphids after t days. The percentage of alate *S. avenae* in each treatment was also determined. In addition, the effect of *R. padi* infestation on final plant biomass (dry weight) and the presence of chlorosis symptoms on the infested leaves were evaluated. For parametric comparisons (R values, plant biomass) a one-way analysis of variance (ANOVA) was applied and the Tukey test was used for mean comparisons. Biomass data were log-transformed before analysis to normalize their distribution. For nonparametric comparisons (percentage of alate aphids) a median test (Zar 1996, p. 156) was applied.

The second experiment assessed the consequences of early infestation by *R. padi* on an hypothetical

arrival of *S. avenae* at the seedling stage of wheat. Seedlings at growth stage 12 were infested on the stem base with six adult *R. padi*; uninfested seedlings were used as controls ($N = 14$ plants per treatment). Three days later, four adult *S. avenae* of similar size were placed within a plastic cylinder (3 cm diameter, 15 cm height) that enclosed the upper part of a seedling (i.e., the second leaf and the newly expanded third leaf). The bottom of the cylinder was closed by a piece of foam with a radial aperture, which surrounded the base of the upper leaves without inflicting any damage. In this way, *S. avenae* was isolated from *R. padi*, which was on the lower parts of the seedling. The top of the cylinder was closed with a fine mesh. Empty cylinders were attached to control seedlings. Four days later, the enclosed leaves were gently pulled up to include the elongated tissue within the cylinder. Seven days after placing the *S. avenae* adults on plants, the experiment ended and the total number of aphids in the cylinder was counted and the fundamental net reproductive rate (R) of *S. avenae* was calculated. The percentage of alate *S. avenae* in each treatment and the biomass (dry weight) of the seedlings also were determined. Differences in R values and plant biomass were determined with a one-way ANOVA, whereas a median test was used to compare alate aphid percentages.

The third experiment was designed to evaluate the effect of the arrival of *S. avenae* to mature plants on established colonies of *R. Padi*. This is of interest because *R. padi* eventually colonizes the upper parts of old plants when the rest of the plant is drying. Twenty-four tillering plants at growth stage 21 were first infested by six adult *R. padi* placed on the base of the stem. When plants attained the flag-leaf stage (growth stage 41), six adult *S. avenae* were confined in a clip cage attached to the flag leaf of 12 randomly selected plants. The other 12 plants received empty clip cages and served as controls. After 24 h, once aphids settled, clip cages were removed and the *S. avenae* population was allowed to develop freely on the plant. All 24 plants were then enclosed with a porous plastic bag to prevent *S. avenae* dispersal between plants. At that time, no *R. padi* was observed feeding on the upper parts of the wheat plant. Two weeks later, when plants attained the flowering stage (growth stage 59), colonies of *S. avenae* were located mostly on the ear, and some individuals of *R. padi* were observed feeding on the upper part of the main stem and on the flag leaf. Thereafter, all the aphids were removed from the flag leaf to homogenize the experimental substrate, and four adults of *R. padi* of similar size were placed in a clip cage attached to the basal part of the flag leaf. Eight days later, the total number of aphids in the clip cage was counted and the fundamental net reproductive rate (R) of *R. padi* was calculated. The percentage of alate aphids and the biomass (dry weight) of the ear also were determined. Statistical tests were applied as described above.

Aphid Competition. Evaluations of competition between *R. padi* and *S. avenae* were performed both at the seedling and at the tillering stage. For the experiment on seedlings, eight adults of each aphid species

were deposited singly and in combination (eight aphids of each species) on wheat seedlings at growth stage 12 (primary leaf totally expanded, secondary leaf unfolded and tertiary leaf visible) ($N = 12$ plants per treatment). Individuals of *R. padi* and *S. avenae* were placed on the base of the stem and on the upper leaf, respectively. Seedlings were then enclosed with a porous plastic bag to prevent aphid dispersal. Twelve days later, when plants attained growth stage 15 (5 leaves unfolded) and aphid densities were high, plants were carefully cut into two parts: upper part (third, fourth, and fifth leaves) and lower part (stem, first and second leaves). For each plant part, the aphid species, the morph (alate or apterous), and the total number of aphids were recorded. The proportion of the aphid colony distributed on each part of the plant, the percentage of alate aphids, as well as the fundamental net reproductive rate (R), were determined for both aphid species. To evaluate the effect of the presence of one aphid species on the other, comparisons were made between single and mixed colonies. Because the counting of aphids took 2 d, a period during which aphid populations certainly increased, the comparisons were paired according to the correlative order of evaluation. A *t*-test for dependent samples was applied when data distribution allowed parametric comparisons, otherwise a Wilcoxon matched-pairs test was used. Data on proportions or percentages were arcsine-transformed before parametric analyses.

The experimental procedures and sample sizes (12 plants per treatment) for the experiment of competition on tillering plants were the same as those of the experiment on seedlings. Plants were infested at the early tillering stage (growth stage 21) and evaluated 3 wk later, when plants attained growth stage 23 (main shoot plus three tillers) and aphid densities were high. Plants (tillers) were cut into two parts as described above, and measures as well as statistical evaluations were performed accordingly.

Preference of Alate *S. avenae* for *R. padi*-Infested Plants. Choice-tests were designed to determine whether *S. avenae* discriminates between *R. padi*-infested and uninfested wheat plants. Experiments were performed both at the seedling and at the tillering stage. The first experiment assessed the consequences of *R. padi* early infestation on preferences of alate *S. avenae* at the seedling stage. Seedlings at growth stage 12 were infested on the stem base with six adult *R. padi*; uninfested seedlings were used as controls ($N = 14$ plants per treatment). Six days later, all pots with plants were placed along two rows separated by 30 cm. Treatments were alternated. In the space between rows, 14 petri dishes where six alate *S. avenae* had been confined were placed on top of a plastic pot (20 cm height) put upside down. In this way, alate aphids could take off from a height similar to that of the host plants. Aphids were in a host-searching mood since they had been caught from the walls of the cages of stock colonies 1 h before. The experiment started when Petri dishes were opened, and 24 h later the number of alate *S. avenae* on each seedling was recorded. Although the spatial array of pots and petri

Table 1. Effect of *R. padi* infestation on wheat seedlings and on population parameters of *S. avenae* later developing on them. Means $\pm$ SE shown ($N = 14$ plants per treatment)

	Aphid reproductive rate	% alate aphids	Seedling biomass, g
Control	1.487 $\pm$ 0.009	0.62 $\pm$ 0.25	0.20 $\pm$ 0.01
Infested	1.406 $\pm$ 0.013	0.77 $\pm$ 0.47	0.12 $\pm$ 0.01

dishes could suggest a paired comparison, the fact that seedlings were not isolated from each other made the median test more appropriate.

The experimental procedures, sample sizes, and statistical evaluations for the experiment on tillering plants were the same as those used in the experiment on seedlings. Plants were infested at growth stage 14 (four leaves unfolded) and evaluated for aphid preference 2 wk later, when plants attained growth stage 21.

Results

Effect of Previous Aphid Infestation. Previous infestation by *R. padi* reduced the reproductive rate of *S. avenae* on seedlings ($F = 11.25$; $df = 1, 26$; $P < 0.001$, one-way ANOVA), although no effect was detected on the percentage of alate aphids ($\chi^2 = 0.71$, $df = 1$, $P = 0.40$, median test) (Table 1). Plant biomass was significantly lower ($F = 10.02$; $df = 1, 26$; $P < 0.001$, one-way ANOVA) in infested seedlings than in uninfested ones (Table 1). Similar results were observed on tillering plants. Thus, the performance of *S. avenae* was negatively affected by *R. padi* infestation ($F = 11.77$; $df = 2, 39$; $P < 0.001$, one-way ANOVA), the effects being larger when *R. padi* arrived at an earlier plant growth stage (Fig. 1). Plant biomass was reduced ($F = 9.69$; $df = 2, 39$; $P < 0.001$, one-way ANOVA), and

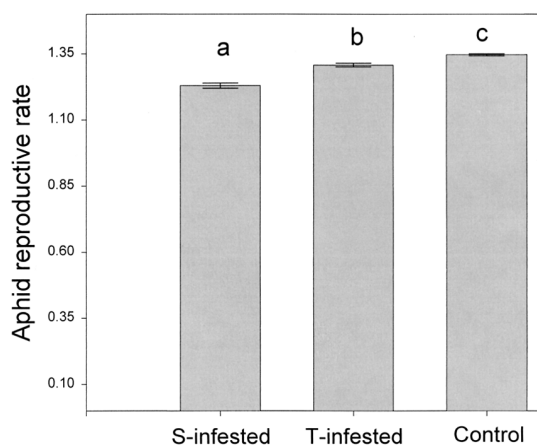


Fig. 1. Reproductive rate of *S. avenae* on wheat plants at the late tillering stage. Plants were previously infested by *R. padi* either at the seedling stage (S-infested) or at the early tillering stage (T-infested). Control refers to uninfested plants. Mean $\pm$ SE shown ($N = 14$ plants per treatment). Different letters indicate that means were significantly different ($P < 0.01$, Tukey test after a one-way ANOVA).

Table 2. Effect of infestation by *R. padi* at the seedling (S) and early tillering (T) stages on wheat plants at the late tillering stage and on the aphid *S. avenae* developing on them. Means $\pm$ SE shown ($N = 14$ plants per treatment)

	% alate aphids	Plant biomass, g
S-infested	3.77 $\pm$ 1.18	1.52 $\pm$ 0.15a
T-infested	2.22 $\pm$ 0.62	3.34 $\pm$ 0.14b
Control	1.85 $\pm$ 0.32	4.84 $\pm$ 0.13c

Means followed by different letters within a column are significantly different ($P < 0.01$, Tukey test).

the percentage of alate aphids was not significantly different ($\chi^2 = 17.2$, $df = 2$, $P = 0.42$, median test) (Table 2). Chlorosis symptoms distribution among treatments matched *R. padi* population load. The number of experimental leaves with chlorosis symptoms (of 14 replicates) were none for uninfested plants, one for late *R. padi* infestation, and 13 for early infestation. A significant effect of *S. avenae* infestation on the biomass of the ear of mature plants was observed, whereas no effect on the development of established colonies of *R. padi* was found (Table 3).

Aphid Competition. The reproductive rate of either aphid species was decreased in the presence of the other. This was true both on seedlings (*R. padi*: $t = 5.27$, $df = 11$, $P < 0.001$; *S. avenae*: $t = 2.22$, $df = 11$, $P = 0.024$, t -test for dependent samples) and on tillering plants (*R. padi*: $t = 2.66$, $df = 11$, $P = 0.011$; *S. avenae*: $t = 2.39$, $df = 11$, $P = 0.018$, t -test for dependent samples). This competitive effect was approximately symmetrical. Plant growth stage did not affect the reproductive rate of the aphids. Results also showed that the reproductive rate of *R. padi* was consistently higher than that of *S. avenae* (Fig. 2). No effect of aphid presence on within-plant distribution of the other aphid species was observed (Table 4). This held both on seedlings (*R. padi*: $t = 0.18$, $df = 11$, $P = 0.43$; *S. avenae*: $t = 0.22$, $df = 11$, $P = 0.52$, t -test for dependent samples) and on tillering plants (*R. padi*: $t = 0.04$, $df = 11$, $P = 0.70$; *S. avenae*: $t = 0.01$, $df = 11$, $P = 0.89$, t -test for dependent samples). Likewise, the production of alate aphids did not differ when the other aphid species was present (Table 4). Again, results were similar for seedlings (*R. padi*: $z = 0.66$, $P = 0.51$; *S. avenae*: $z = 1.39$, $P = 0.16$, Wilcoxon matched-pairs test) and tillering plants (*R. padi*: $z = 0.95$, $P = 0.34$, *S. avenae*: $z = 0.63$, $P = 0.53$, Wilcoxon matched-pairs test).

Preference of alate *S. avenae* for *R. padi*-infested plants. Fig. 3 shows that alate *S. avenae* significantly preferred uninfested seedlings over *R. padi*-infested

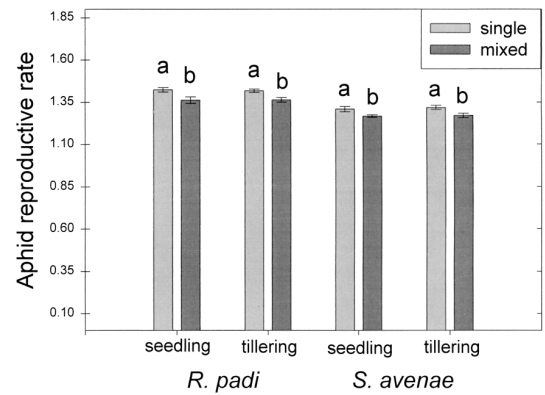


Fig. 2. Reproductive rate of the aphids *R. padi* and *S. avenae* developing in single (initial density: eight aphids) and mixed (initial density: eight aphids of each species) colonies on seedlings and tillering plants of wheat. Mean $\pm$ SE shown ($N = 12$ plants per treatment).

ones ($\chi^2 = 5.17$, $df = 1$, $P = 0.023$, median test), whereas no preference was observed when the experiment was performed with tillering plants ($\chi^2 = 0.8$, $df = 1$, $P = 0.369$, median test).

Discussion

Sitobion avenae performance is clearly affected by previous infestation of *R. padi*. Because of the high reproductive rate of *R. padi* on seedlings, even a short time of precedence (10 d) is enough to reduce *S. avenae* reproductive rate significantly. The experiment on tillering plants indicated that, regarding effects on *S. avenae* performance, it matters not only whether *R. padi* arrives but also at what time. In contrast, the settling of *S. avenae* on the ears of mature plants apparently does not affect the late development of the *R. padi* colony when it partially reaches the upper leaves of the plant. This result should be taken, however, with caution because data dispersion (standard error of aphid reproductive rate) in this experiment was considerably higher than those in the other experiments. A trend toward reduced reproductive rate of *R. padi* on *S. avenae*-infested plants was observed.

Plant biomass was dramatically reduced by aphid infestations, regardless of the growth stage. Infestation of wheat by *R. padi* has been shown to reduce aphid fecundity (Gianoli 1999) as well as to induce plant defensive chemicals (Gianoli and Niemeyer 1997). In

Table 3. Effect of *S. avenae* infestation on wheat plants and on population parameters of *R. padi* later developing on them. Means $\pm$ SE shown ($N = 12$ plants per treatment)

	Aphid reproductive rate ^a	% alate aphids ^b	Ear biomass, g ^a
Control	1.204 $\pm$ 0.017	1.62 $\pm$ 0.45	0.70 $\pm$ 0.03
Infested	1.171 $\pm$ 0.016	2.75 $\pm$ 0.67	0.56 $\pm$ 0.03
	$F = 2.06$; $df = 1, 22$; $P = 0.165$	$\chi^2 = 1.33$, $df = 1$, $P = 0.248$	$F = 12.28$; $df = 1, 22$; $P = 0.002$

^a One-way ANOVA.

^b Median test.

Table 4. Aphid population parameters in single and mixed colonies on wheat seedlings and tillering plants. Means $\pm$ SE shown ($N = 12$ plants per treatment)

	Proportion in upper leaves		% alate aphids	
	Seedling	Tillering	Seedling	Tillering
Rp	0.43 $\pm$ 0.06	0.78 $\pm$ 0.04	0.29 $\pm$ 0.13	6.28 $\pm$ 0.53
Rp (+ Sa)	0.53 $\pm$ 0.05	0.75 $\pm$ 0.05	0.36 $\pm$ 0.13	7.62 $\pm$ 0.61
Sa	0.84 $\pm$ 0.03	0.86 $\pm$ 0.03	2.38 $\pm$ 0.41	9.29 $\pm$ 0.78
Sa (+ Rp)	0.86 $\pm$ 0.02	0.89 $\pm$ 0.04	3.07 $\pm$ 0.44	10.17 $\pm$ 0.69

Rp, *Rhopalosiphum padi*; Sa = *Sitobion avenae*.

contrast, work done with another aphid species points to a benefit for aphid development of previous aphid infestation (Dorschner et al. 1987, Formoso et al. 1992), which may produce changes in plant nitrogen availability that are manifested by chlorosis symptoms (Dorschner 1990). The current data on chlorosis and on reproductive rate cast doubt on the prevalence of induced susceptibility (sensu Karban and Baldwin 1997) after aphid infestation, as manifested by localized chlorotic lesions. In general, it is still debatable whether there is a linear relationship between plant stress and insect performance (Koricheva et al. 1998).

Herbivory-induced changes in the host plant may mediate interspecific competition in insects (Faeth 1992, Masters and Brown 1992, Hougén-Eitzman and Karban 1995). In this work, for the sake of biological realism, inducer aphids were not removed from the plant. Thus, it is not clear whether competitive interactions resulted from such induced responses of the plant or from the sharing of a common resource—the phloem sap. Regardless of the mechanism involved, it is clear that, under the natural colonization regime, the presence of *R. padi* has a negative effect on *S. avenae*.

Competition between *R. padi* and *S. avenae* was symmetrical, unlike most of interspecific competitive interactions (Denno et al. 1995). Thus, negative effects of the presence of either aphid species on the reproductive rate of the other were significant and of

a similar magnitude. However, and in agreement with an early report (Markkula and Myllymäki 1963), the overall reproductive rate of *R. padi* was consistently higher than that of *S. avenae*. This suggests that, in the long run, *R. padi* could outcompete *S. avenae*, a phenomenon evident in aphid stock cultures in several countries (unpublished data). This competitive exclusion is not verified in the field, most probably because *S. avenae* is able to exploit the oldest stages of wheat plants (e.g., the ear), when *R. padi* populations are in decline.

It is noteworthy to acknowledge that the competition experiments lacked a control for the effect of intraspecific competition (e.g., Bergeson and Messina 1997). A higher number of conspecifics could produce the same reduction in aphid reproductive rate as that observed in mixed colonies (see Underwood 1997, p. 410). Thus, in my experiments, total number of herbivores is confounded by the presence of the other aphid species. Nevertheless, results do suggest interspecific competition because the presence of either aphid species, located on their natural feeding sites, negatively affected the performance of the other. What the experiments lacked is an assessment of the relative importance of interspecific competition versus intraspecific competition in the population growth of aphids.

Interestingly, results were qualitatively the same when the experiments were conducted on seedlings and on tillering plants. This is surprising if it is considered that tillering plants are not as suitable as seedlings for *R. padi* development on wheat (Leather and Dixon 1981). Moreover, it is documented that the later the arrival of *R. padi* to cereal fields in the season (i.e., arrival when plants are at the tillering stage instead of when they are seedlings), the lower the population peak (Wiktelius et al. 1990). Therefore, a greater advantage of *R. padi* over *S. avenae* in the experiment on seedlings would have been expected. However, the outcome of the interspecific interaction was very similar on both plant growth stages. A possible explanation for this could be that experiments on seedlings, by allowing aphid densities to reach a high level, ended with very late seedlings (five leaves) which could be already similar in quality to the following growth stage (i.e., tillering). The work that reported better performance of *R. padi* on wheat seedlings than on tillering plants was carried out on early seedlings (two leaves) (Leather and Dixon 1981).

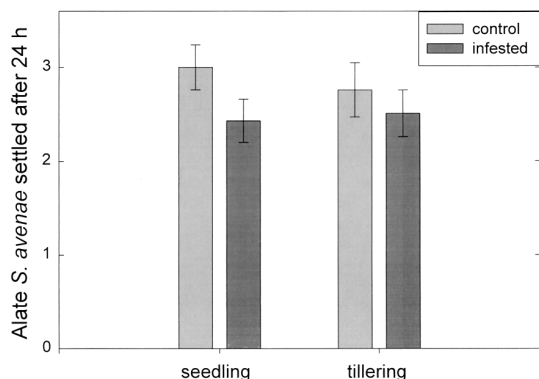


Fig. 3. Number of alate *S. avenae* settled (per plant) on either *R. padi*-infested plants or unfested plants after a choice test. Results shown for identical experiments on seedlings and on tillering plants (bars indicate mean $\pm$ SE, $N = 14$ plants per treatment). See text for methodological details.

Previous work addressing competition between *R. padi* and *S. avenae* on wheat had methodological flaws that impede drawing sound conclusions from them. These studies were either performed on plants at a phenological stage not relevant for the actual aphid-aphid interaction in the field (i.e., early seedlings) or used extremely low (and constant) aphid densities, hence artificially preventing resource limitation (Chongrattanameteekul et al. 1991a, 1991b; Thirakhuapt and Araya 1992a, 1992b).

In contrast to results on reproductive rates, neither the percentage of alate aphids nor within-plant distribution was affected by the presence of the other aphid species. Alate production, and hence imminent colony dispersal, is considered as a signal of deterioration of host quality (Dixon 1998). A report showed that more alate *R. padi* developed on plants previously infested with this aphid, interpreting it as an indication that aphid feeding reduced plant quality (De Barro 1992). Given that plant quality for the aphids developing in mixed cultures was indeed lower than in single cultures, as was evidenced by a reduction in reproductive rates, and that there was no increase in alate aphid production, my results do not support plant quality as a control factor over alate production in *R. padi* as well as in *S. avenae*. However, the limited temporal scale of my evaluations could have prevented the observation of increased alate production in the next aphid generations, as has been described earlier (chapter 6 in Dixon 1998). A trend toward a higher number of alate aphids on infested plants than on control plants was observed in all the experiments.

The patterns of preference of *S. avenae* for *R. padi*-infested-uninfested plants were not consistent. Whereas, *S. avenae* preferred uninfested seedlings, no choice was observed on tillering plants. Considering that *S. avenae* performance was negatively affected by previous infestation of *R. padi* both on seedlings and on tillering plants, the preference behavior of *S. avenae* on tillering plants does not seem to be adaptive, as is the case on seedlings. A recent report suggested the occurrence of interspecific recognition between these aphids on young seedlings of wheat (Johansson et al. 1997). However, because of the temporal features of their life cycle on cereal fields (see introduction), the tillering stage is a more relevant stage to study interactions between these aphids. Therefore, at present it is not currently possible to draw clear conclusions about the ecological significance of the observed preference patterns of *S. avenae*. Further experiments with a longer follow up on the location of *S. avenae* colonies would shed light on this topic, given that, among cereal aphids, this species shows the most active dispersal behavior between plants (Dean 1973).

Although this study was entirely conducted in the greenhouse, and hence extrapolations to the field must be done with caution, it nonetheless shows that *R. padi* and *S. avenae* do compete on wheat plants. Neither interference competition nor modification of feeding niches was observed when both aphid species co-occurred. This indicates that, as was shown earlier (cf., Denno et al. 1995), the spatial segregation of the host

plant by sap-feeders does not necessarily prevent competition. The mechanism underlying competition may be related either to the sharing of a common phloem resource or to modifications of the quality of this resource by insect feeding (i.e., induced responses of the plant). Although the competition is symmetrical, the higher reproductive rate of *R. padi*, together with its normal temporal precedence, would ensure a winning position for this aphid species.

The similarity of results on seedlings and tillering plants suggests that, regarding its interaction with *R. padi*, *S. avenae* would neither gain nor lose more by arriving to wheat plants earlier in the season. It is thereby hypothesized that the delayed arrival of *S. avenae* to cereal fields is not a consequence of competitive displacement by *R. padi*. Evaluation of the probable benefits to *S. avenae* of a further delayed arrival to the field is needed to substantiate or refute this hypothesis. In this regard, the possible role of environmental constraints in the temporal features of the life cycle of *S. avenae* should be investigated. Finally, the relative importance of aphid intraspecific competition should be determined to assess accurately to what extent the current findings relate to the real ecological scenario.

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