

Plant Water Stress Affects Interactions Between an Invasive and a Naturalized Aphid Species on Cereal Crops

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Abstract

In cereal cropping systems of the Pacific Northwestern United States (PNW), climate change is projected to increase the frequency of drought during summer months, which could increase water stress for crop plants. Yet, it remains uncertain how interactions between herbivore species are affected by drought stress. Here, interactions between two cereal aphids present in PNW cereal systems, *Metopolophium festucae* (Theobald) subsp. *cerealium* (a newly invasive species) and *Rhopalosiphum padi* L. (a naturalized species), were tested relative to wheat water stress. When aphids were confined in leaf cages on wheat, asymmetrical facilitation occurred; per capita fecundity of *R. padi* was increased by 46% when *M. festucae cerealium* was also present, compared to when only *R. padi* was present. Imposed water stress did not influence this interaction. When aphids were confined on whole wheat plants, asymmetrical competition occurred; cocolonization inhibited *M. festucae cerealium* population growth but did not affect *R. padi* population growth. Under conditions of plant water stress, however, the inhibitory effect of *R. padi* on *M. festucae cerealium* was not observed. We conclude that beneficial effects of cocolonization on *R. padi* are due to a localized plant response to *M. festucae cerealium* feeding, and that cocolonization of plants is likely to suppress *M. festucae cerealium* populations under ample water conditions, but not when plants are water stressed. This suggests that plant responses to water stress alter the outcome of competition between herbivore species, with implications for the structure of pest communities on wheat during periods of drought.

Key words: agricultural entomology, community ecology, feeding behavior, wheat, insect–plant interaction

Climate modelers project increasing frequencies of extreme abiotic stress events in cereal-growing regions by mid-century (Chaves et al. 2003, Dai 2013), especially where crop production is already water limited as it is in the inland Pacific Northwest (Schillinger 2016). The effects of drought will occur simultaneously with pressure from pests and pathogens, which may in turn be indirectly affected by water stress on their host plants. Although the direct effects of drought stress on crop plants have been documented extensively (e.g., Hsiao 1973), the indirect effects on insect herbivores remain less well understood (Hale et al. 2003, Huberty and Denno 2004). Successful feeding and nutrient uptake by aphids, for example, requires adequate plant cell turgor pressure (Wearing and van Emden 1967, Holtzer et al. 1988, Archer et al. 1995), which is mediated by plant water content (Hsiao 1973, Drake and Gallagher 1984, Taiz and Zeiger 2002). Consequently, drought-stressed plants are usually inferior hosts for aphids (Kennedy et al. 1958, Huberty and Denno 2004, Davis et al. 2015a). However, the effects of plant drought stress on aphids often depend on the type of stress (e.g.,

chronic vs. acute; Pons and Tatchell 1995, Huberty and Denno 2004), the host plant species (Hale et al. 2003), and aphid species (Pons and Tatchell 1995). An assessment of drought–crop–aphid interactions is needed to inform pest management practices in regions where aphid species co-occur, as aphid species can respond uniquely to drought stress (Pons and Tatchell 1995, Hale et al. 2003) or to heterospecifics (Inbar et al. 1995, Gianoli 2000, Sandstrom et al. 2000, Gonzales et al. 2002).

A diverse community of economically important cereal aphids occurs sympatrically in wheat (*Triticum aestivum* L.) fields throughout the rainfed agricultural regions of the Pacific Northwest United States (PNW; Schotzko and Bosque-Pérez 2000, Bosque-Pérez et al. 2002, Qureshi and Michaud 2005). These include multiple naturalized species such as *Rhopalosiphum padi* L. (bird cherry-oat aphid), *Sitobion avenae* F. (English grain aphid), *Schizaphis graminum* (Rondani) (greenbug), *Diuraphis noxia* (Mordvilko) (Russian wheat aphid), and a recently detected exotic grass aphid, *Metopolophium festucae* (Theobald) subspecies *cerealium* (Halbert et al. 2013).

Metopolophium festucae cerealium was first reported in Oregon in 1994 (Halbert and Sandvol 1995), and large populations of the aphid have recently been detected in wheat in the PNW (Halbert et al. 2013, S.D.E., personal observations). Moreover, *M. festucae cerealium* colonization can cause above- and below-ground injury to both native prairie grasses and cereal crops (Davis et al. 2014). Presently, there is no information detailing whether the fitness of *M. festucae cerealium*, or damage caused by this species, is affected by cocolonization of host plants by naturalized cereal aphids. However, to understand pest population dynamics, it is important to determine if *M. festucae cerealium* is capable of cocolonizing crops with naturalized cereal aphid species, and the impacts of such interactions.

Studies evaluating interactions between sympatrically occurring aphids colonizing the same plant are few (Qureshi and Michaud 2005), and interactions between herbivores are seldom considered in the context of simultaneously occurring plant stress from abiotic factors such as drought. Here, we designed experiments to examine interactions between *M. festucae cerealium* and *R. padi*, a widespread cereal aphid species naturalized in the PNW. *Rhopalosiphum padi* is an agricultural pest worldwide (Blackman and Eastop 2007) and a competent vector of Luteoviruses (e.g., *Barley yellow dwarf virus*; BYDV) that cause plant disease (Plumb 1983, Rochow 1970, Finlay and Luck 2011), for which *M. festucae cerealium* is a nonvector (Sadeghi et al. 2016). We tested the hypothesis that plant water stress mediates interactions between these aphid species on wheat, evaluating aphid population growth when aphids colonized wheat in isolation or together using choice and no-choice assays. We also tested whether interactions depended on localized effects of feeding or systemic plant responses to herbivory. Broadly, our study allowed us to determine how interspecific interactions between herbivore species may vary based on water stress, and how such interactions can contribute to herbivore population dynamics.

Materials and Methods

Aphid Colonies

Colonies of both *M. festucae cerealium* and *R. padi* originated from females collected via sweep net in winter wheat fields near Moscow, ID (46.7317° N, 116.9972° W). Aphids were placed in 60 by 60 by 60 cm³ mesh enclosures (BugDorm 2120, MegaView Science Co. Ltd.; Taichung, Taiwan) containing 20-d-old potted (400-cm³ pots) winter barley (*Hordeum vulgare* L.) cultivar 'Eight-twelve', with each species maintained in a separate enclosure. Enclosures were kept in environmental growth chambers (Percival Scientific, Perry, IA; 25 ± 1°C SE, photoperiod of 16:8 [L:D] h, relative humidity: 30%). Once new nymphs were observed, they were immediately moved from the original colonies onto barley in new enclosures to ensure they were free of BYDV (Wu et al. 2014), and aphid colonies were provided new barley plants each week. Prior to use in experiments, both colonies tested negative for virus using ELISA.

Experiment 1—Interactions Between Wheat Water Stress and Aphid Species

Spring wheat plants cv. 'Kelse' (Kidwell et al. 2009) were sown individually in 400-cm³ pots containing ~110 g horticultural mix (Sunshine mix no. 1; SunGro Horticulture, Agawam, MA) in a greenhouse (27°C, photoperiod of 16:8 [L:D] h, 60% relative humidity). Watering treatments followed those described in Davis et al. (2015b): water was applied to pots on a gravimetric basis (grams H₂O/grams oven-dried soil) and consisted of two treatments, 0.1 and 0.8 g H₂O per g soil. In previous experiments these

treatments in the same greenhouse setting produced water-stressed and vigorous wheat plants, respectively (Davis et al. 2015a). Plants under the 0.1 g H₂O per g soil treatment exhibited increased leaf curling, reduced biomass, and eventually reduced seed set compared with the 0.8 g H₂O. Furthermore, the 0.1 g H₂O per g soil treatment elicits changes in phytohormone concentrations consistent with stress (Davis et al. 2015b). Watering treatments were initiated 7 d post-sowing and were delivered every 72 h throughout the course of the experiment. Water was administered by bottom-watering each pot and pots were contained individually in polystyrene bowls to ensure absorption of all experimentally applied water. To test the efficacy of watering treatments, predawn leaf water potentials (ψ_{leaf}) of aphid-free control plants were measured on secondary leaves excised from the stem within 1 cm of the ligule using a Scholander pressure chamber (PMS Instruments, Corvallis, OR), and water potential measurements were taken 10 d following initiation of watering treatments.

Fifteen-day-old wheat plants (i.e., subjected to watering regimes for 8 d at the time of aphid introduction) were fit with transparent cages constructed from dialysis tubing (3 cm length by 1 cm diameter, Spectrum Labs, Inc., Rancho Dominguez, CA) and stoppered with foam at each end to prevent aphid escape. Cages were placed on secondary leaves and positioned such that both adaxial and abaxial surfaces of the caged leaf material were exposed to aphids. Six mature, apterous females from aphid colonies were caged and allowed to feed and larviposit on plants for 24 h, after which all except four nymphs (foundresses) were removed. In total, 24 plants received *M. festucae cerealium*, 24 plants received *R. padi*, and 24 plants received both aphid species, such that the experimental design was consistent with a 2 × 2 factorial (two levels of watering treatments: 0.1 and 0.8 g H₂O per g soil; two levels of aphid species composition: single-species or mixed colony). Each plant received the same starting density of aphids to control for density-dependent effects. Thus, when both species were present in cages there were two foundresses of each species, and when each species was present in isolation there were four foundresses of a single species. Foundresses were checked daily and the numbers of offspring were recorded every 24 h for 12 d, and daily offspring production was standardized to the number of surviving foundresses on each plant to determine per capita fecundity. At the end of the experiment, aboveground biomass was harvested for each plant and oven dried for 24 h at 70°C to assess whether interactions of watering treatments and aphid identity affected wheat growth.

For this experiment, we analyzed the effect of watering treatments on predawn leaf water potentials and aboveground biomass using two-sample Student's *t*-tests. Aphid fecundity was analyzed using two-way ANOVA with water treatment (0.1 g or 0.8 g H₂O per g soil), aphid species treatment (individual and mixed colonies), and their interaction as fixed effects and mean daily per capita reproduction rate (offspring/female/day) of each aphid species as the response. We also included a blocking factor to account for greenhouse bench position (*b* = 3). We used Tukey's HSD test to make post hoc comparisons among treatment means. Statistical tests incorporated a type I error rate of $\alpha = 0.05$ for assessing significance, and all statistical tests were performed using JMP 11.0 software (SAS Institute, Cary, NC).

Experiment 2—Test of Previous Feeding by *M. festucae cerealium* on Population Growth of *R. padi*

A second experiment tested whether prior feeding by *M. festucae cerealium* impacted the reproduction of *R. padi*. Spring wheat plants

cv. Kelse were sown individually in pots as in Experiment 1, and water was administered to all pots at the 0.8 g H₂O per g soil rate beginning 7 d postsowing. Four mature, apterous *M. festucae cerealium* or *R. padi* females were placed on 15-d-old wheat plants, and females were allowed to feed and reproduce on caged leaf material for 7 d. After this period, these aphids and any offspring were removed and replaced with two mature *R. padi* apterae on the same caged leaf material, which were allowed to larviposit for 24 h. After 24 h, all except one *R. padi* nymph (foundress) was removed to yield a starting density of one aphid per plant. Foundresses were checked daily thereafter, and new nymphs were recorded and removed every 48 h until reproduction ceased. Thus, foundresses fed on wheat plants that had either (a) been previously exposed to 7 d feeding by *R. padi*, or (b) 7 d feeding by *M. festucae cerealium*.

Reproduction data were parameterized to construct life tables using the equations of Birch (1948) and Wyatt and White (1977). For each foundress, basic reproductive rate (R_o), generation time (T), age-specific fecundity (L_xM_x), and intrinsic rate of population growth (R_m) was determined. A blocking variable was included in the experimental design to account for the position of pots on the greenhouse bench ($b = 2$; north vs. south). The number of replicates was $n = 11$ for plants previously exposed to feeding by *M. festucae cerealium* and $n = 7$ for plants previously exposed to feeding by *R. padi*. The experiment was analyzed using one-way ANOVAs with feeding treatment as a fixed effect and *R. padi* basic reproductive rate (R_o), generation time (T), and intrinsic rate of growth (r_m) as response variables. The response of age-specific fecundity (L_xM_x) was analyzed using repeated-measure ANOVA with feeding treatment as a fixed effect and time (d) as a random effect. Statistical tests incorporated a type I error rate of $\alpha = 0.05$ for assessing significance, and all tests were performed using JMP 11.0.

Experiment 3—Whole-Plant Test of Aphid Species Interactions With Varying Water Stress

A third experiment was designed to investigate the effects of cocolonization by *R. padi* and *M. festucae cerealium* on population dynamics under two levels of water stress when aphids were allowed unrestricted movement on whole wheat plants. Wheat plants (cultivar Kelse) were sown individually in 1-liter pots containing 330 g horticultural mix. Plants were grown under the same greenhouse conditions as described for the previous two experiments. Water was administered to half the plants at a rate of 0.1 g H₂O per g soil and half the plants at a rate of 0.8 g H₂O per g soil as described in Experiment 1, with experimental watering initiated seven days postsowing.

Plants randomly received one of the four treatments: 1) only *R. padi* foundresses, 2) only *M. festucae cerealium* foundresses, 3) foundresses of both species, or 4) noninfested controls. Treatments were imposed 21 d following the initiation of watering regimes (28 d postsowing). To ensure efficacy of watering treatments, noninfested control plants were destructively sampled for measurements of predawn leaf water potential on the same day all other plants received aphid treatments. At the termination of the experiment, aboveground biomass was harvested for each plant and oven dried for 24 h at 70 °C. Six mature, apterous aphids per species were confined in clip cages and allowed to feed and reproduce on plants for 24 h, after which time all except five nymphs (foundresses) were removed and whole plants were enclosed individually using 1-by-1-mm mesh screen. In contrast to Experiment 1, plants receiving only a single aphid species had a starting density of five aphids, and plants receiving both species had a starting density of 10 aphids; this

design allowed for direct comparison of ending population sizes between aphid species across treatments. Foundresses were left to populate plants for an additional 21 d, at which point ending population sizes for each aphid species were recorded by census. Thus, the experiment incorporated eight possible treatment combinations (2 watering treatments \times 4 aphid species treatments), and each treatment combination was replicated 12 times for a total of $N = 96$ experimental units.

As in previous experiments, a blocking variable was incorporated to account for plant position on greenhouse benches ($b = 3$). One-way ANOVA was used to examine differences in plant leaf water potentials and aboveground biomass of noninfested control plants. Two-way ANOVA was used to examine the fixed effects of watering treatment, aphid species treatment, and their interaction on the response variable of final population size, which was log-transformed to conform to normality assumptions. As above, statistical tests incorporated a type I error rate of $\alpha = 0.05$ for assessing significance, and all tests were performed using JMP 11.0.

Results

Experiment 1—Interactions Between Wheat Water Stress and Aphid Species

Water-stressed wheat plants produced 62% less aboveground biomass than plants that received full water ($t = 21.03$; $df = 22$; $P < 0.001$). Moreover, at 10 d following initiation of watering treatments, predawn leaf water potentials for plants receiving 0.1 g H₂O/g soil water were significantly lower (0.41 MPa) than plants receiving 0.8 g H₂O/g soil water ($t = 2.94$, $df = 22$; $P = 0.007$, Table 1).

The effects of experimental treatments on aphid reproduction varied between the two aphid species. For *M. festucae cerealium*, the mean daily per capita fecundity was 0.59 nymphs ($SE = 0.034$). For this species, there was a marginally significant negative effect of heterospecific aphids on fecundity ($F_{1,39} = 3.39$, $P = 0.072$); however, fecundity was not significantly affected by watering treatment or the interaction between aphid presence and watering treatment (Table 2). Mean *M. festucae cerealium* reproduction was reduced by 19% on average when *R. padi* fed in the same cage. By contrast, the mean *R. padi* daily per capita fecundity was 1.36 nymphs ($SE = 0.125$), which was significantly higher than the reproductive rate of *M. festucae cerealium* ($t = 6.20$; $df = 44$; $P < 0.0001$). *Rhopalosiphum padi* reproduction was also significantly affected by aphid treatment, with 46% greater nymph production when *M. festucae cerealium* was present in the same cage compared to when they were absent (Table 3). *Rhopalosiphum padi* reproduction was not significantly affected by watering treatment or the watering treatment \times aphid species interaction (Table 2).

Experiment 2—Effect of Previous Feeding by *M. festucae cerealium* on *R. padi* Population Growth

Reproductive rate of *R. padi* feeding on wheat previously exposed to feeding by *M. festucae cerealium* was 36% greater than on wheat previously exposed to feeding by *R. padi* ($F = 95.5$; $df = 1, 15$; $P < 0.0001$). Specifically, *R. padi* foundresses feeding on wheat exposed to prior feeding by *M. festucae cerealium* exhibited 15% higher basic reproductive rates compared to foundresses feeding on wheat previously exposed to feeding by *R. padi* ($F = 8.48$; $df = 1, 15$; $P = 0.010$). Mean generation time was not affected by aphid feeding treatments ($F = 0.72$; $df = 1, 15$; $P = 0.41$; Table 4). These results were due to significant differences in age-specific fecundity among feeding treatment (Table 5), with *R. padi* foundresses feeding

Table 1. Wheat plant (cultivar Kelse) responses to experimental watering treatments, according to pot size

Pot size	Variable	Watering treatment	Mean \pm SE
400 cm ³	Predawn leaf water potential (MPa)	0.1 g H ₂ O/g soil	-0.62 \pm 0.14
		0.8 g H ₂ O/g soil	-0.21 \pm 0.01
	Dried aboveground biomass (g)	0.1 g H ₂ O/g soil	0.29 \pm 0.01
		0.8 g H ₂ O/g soil	0.79 \pm 0.02
1 L	Predawn leaf water potential (MPa)	0.1 g H ₂ O/g soil	-0.85 \pm 0.11
		0.8 g H ₂ O/g soil	-0.17 \pm 0.02
	Dried aboveground biomass (g)	0.1 g H ₂ O/g soil	1.55 \pm 0.14
		0.8 g H ₂ O/g soil	10.50 \pm 0.21

Table 2. ANOVA table summarizing results of experiment testing effects of competition between *Metopolophium festucae cerealium* and *Rhopalosiphum padi* feeding on cultivated wheat (*Triticum aestivum* cultivar Kelse) under two levels of water stress on the response of mean daily per capita fecundity of each aphid species

Variable	Source	SS	df	F	P
Offspring/female/day, <i>M. festucae cerealium</i>	Block	0.010	2	–	–
	Aphid treatment	0.185	1	3.394	0.072
	Water treatment	0.061	1	1.114	0.297
	Interaction	0.090	1	1.656	0.205
	Error	2.234	39		
Offspring/female/day, <i>R. padi</i>	Block	0.446	2	–	–
	Aphid treatment	7.652	1	13.419	<0.001
	Water treatment	0.340	1	0.598	0.444
	Interaction	0.061	1	0.107	0.745
	Error	22.239	39		

Table 3. Mean daily per capita fecundity (number of offspring per female) for *Metopolophium festucae cerealium* and *Rhopalosiphum padi* feeding on cultivated wheat (*Triticum aestivum* cultivar Kelse) under two levels of water stress

Aphid species	Water treatment	Aphid treatment	
		Heterospecific (both species present)	Conspecific (single species)
<i>M. festucae cerealium</i>	0.1 g H ₂ O/g soil	0.436 \pm 0.074	0.651 \pm 0.064
	0.8 g H ₂ O/g soil	0.597 \pm 0.067	0.635 \pm 0.067
<i>R. padi</i>	0.1 g H ₂ O/g soil	1.739 \pm 0.241a	0.837 \pm 0.217b
	0.8 g H ₂ O/g soil	1.839 \pm 0.217a	1.086 \pm 0.228ab

Values with letters denote Tukey's HSD test on the aphid treatment \times water treatment interaction (among the four values for each species).

on wheat previously exposed to *M. festucae cerealium* being more fecund between the age of 8 d and 16 d than foundresses feeding on wheat previously fed upon by conspecifics (Fig. 1).

Experiment 3—Aphid Species Interactions on Whole Plants With Varying Water Stress

Noninfested control plants receiving 0.1 g H₂O/g soil had significantly lower leaf water potential (mean difference = -0.68 MPa) than plants receiving 0.8 g H₂O/g soil ($F = 37.7$; $df = 1, 20$; $P < 0.0001$). Similarly, wheat plants receiving 0.1 g H₂O/g soil were significantly smaller than plants receiving 0.8 g H₂O/g soil ($F = 896.0$; $df = 1, 20$; $P < 0.0001$; Table 1).

The mean population size of *M. festucae cerealium* was significantly affected by watering treatment ($F_{1,42} = 4.81$; $P = 0.034$) and by aphid species composition ($F_{1,42} = 7.72$; $P = 0.008$), and there was a marginally significant interaction between these two variables ($F_{1,42} = 4.03$; $P = 0.052$). On average, *M. festucae cerealium* population sizes were 16% larger at the end of the experiment on plants watered at the 0.8 g H₂O/g soil level than on plants watered at the

Table 4. The effect of previous exposure to feeding (7-d exposure period) by either *Rhopalosiphum padi* or *Metopolophium festucae cerealium* on population growth parameters of *R. padi*

Variable	Feeding treatment	
	Previous feeding by <i>R. padi</i>	Previous feeding by <i>M. festucae cerealium</i>
Basic reproductive rate (R_0) ^a	26.3 \pm 1.17a	41.02 \pm 0.93b
Generation time (T) ^b	15.31 \pm 0.69	14.55 \pm 0.55
Intrinsic rate of growth (r_m) ^c	0.22 \pm 0.01a	0.26 \pm 0.01b

Values followed by letters indicate Tukey's HSD test.

^a Basic reproductive rate (R_0) refers to average number of offspring produced per foundress.

^b Generation time (T) represents average time (in days) between two consecutive generations.

^c Intrinsic growth rate (r_m) is the theoretical maximum population growth rate in the absence of density-dependent effects, where $(dN/dt)/(1/N) = r$.

0.1 g H₂O/g soil level (Table 6). We observed that *M. festucae cerealium* population growth was inhibited by the presence of *R. padi*, with mean population sizes reduced by 51% on average when both species colonized wheat plants simultaneously. The negative effect of the presence of *R. padi* on *M. festucae cerealium* was more pronounced on plants watered at the 0.1 g H₂O/g soil level than at the 0.8 g H₂O/g soil level, accounting for the interaction between aphid species composition and watering treatment. The mean population size of *R. padi* was significantly affected by watering treatment ($F = 58.00$; $df = 1, 37$; $P = 0.001$), but not by aphid species composition ($F = 1.90$; $df = 1, 37$; $P = 0.18$) or the aphid species composition \times watering treatment interaction ($F = 1.11$; $df = 1, 37$; $P = 0.30$). When feeding on plants watered at the 0.1 g H₂O/g soil level, mean *R. padi* population size was reduced by 70% compared to aphids feeding on plants watered at the 0.8 g H₂O/g soil level (Table 6).

Discussion

Previous studies have demonstrated neutral (Pons and Tatchell 1995, Bethke et al. 1998), negative (Kennedy et al. 1958, Sumner et al. 1983), or both (Hale et al. 2003) effects of host plant water

Table 5. ANOVA table summarizing repeat-measure statistical model comparing previous exposure to feeding (7-d exposure period) by either *Rhopalosiphum padi* or *Metopolophium festucae cerealium* on age-specific fecundity (L_xM_x) of *R. padi*

Source	SS	df	F	P
Block	0.323	1	–	–
Time (day)	1606.340	11	–	–
Feeding treatment	289.874	12	483.295	<0.0001
Error	6.121	125	–	–

stress on aphid performance. However, interactions between aphid species have seldom been considered in the context of abiotic stress imposed on host plants (Barton and Ives 2014). Here, an amensal interaction was observed between *M. festucae cerealium* and *R. padi* in whole-plant assays, but the relative magnitude of the negative effect on *M. festucae cerealium* increased on water-stressed plants, while it remained consistent across water-stress treatments for *R. padi*. The asymmetrical interactions between these two aphid species corroborate findings from studies involving other aphid species. For example, the cereal aphids *Sipha flava* and *Rhopalosiphum maidis* exhibit asymmetrical competitive interactions on *Sorghum halepense* (L.) Pers., and the outcome for each species depends on season (i.e., spring vs fall) in addition to the presence of natural enemies (Gonzales et al. 2002). Contrasting results by Gianoli (2000) found symmetrical competition between *R. padi* and *S. avenae* on seedling and tillering wheat plants, where reproductive rates of each species was negatively impacted by presence of the other. However, no abiotic stress was imposed on plants in these experiments.

Interactions between insect herbivores are commonly mediated by a shared host plant (Fritz et al. 1986, Mopper et al. 1990, Moran and Whitham 1990, Fritz 1992, Denno et al. 1995, Inbar et al. 1995, Gonzales et al. 2002). In many instances, insect herbivory can alter host plant quality to the benefit or detriment of the inducing insect and later-colonizing species (Hanhimaki 1989, Karban 1993, Karban and Baldwin 1997, Denno et al. 2000, Gonzales et al. 2002). Considering the generally poor nutritional quality of phloem sap, it has been suggested that some aphids manipulate phloem nutritional quality to their benefit, presumably through ultrastructural changes to plant cells induced by feeding on susceptible hosts (Al-Mousawi et al. 1983). Sandstrom et al. (2000) demonstrated that the aphids *S. graminum* and *D. noxia* ingested phloem sap with a substantially higher concentration of amino acids than *R. padi* when feeding on both wheat and barley. Furthermore, *S. graminum* and *D. noxia* induced macroscopic chlorotic lesions to infested leaf

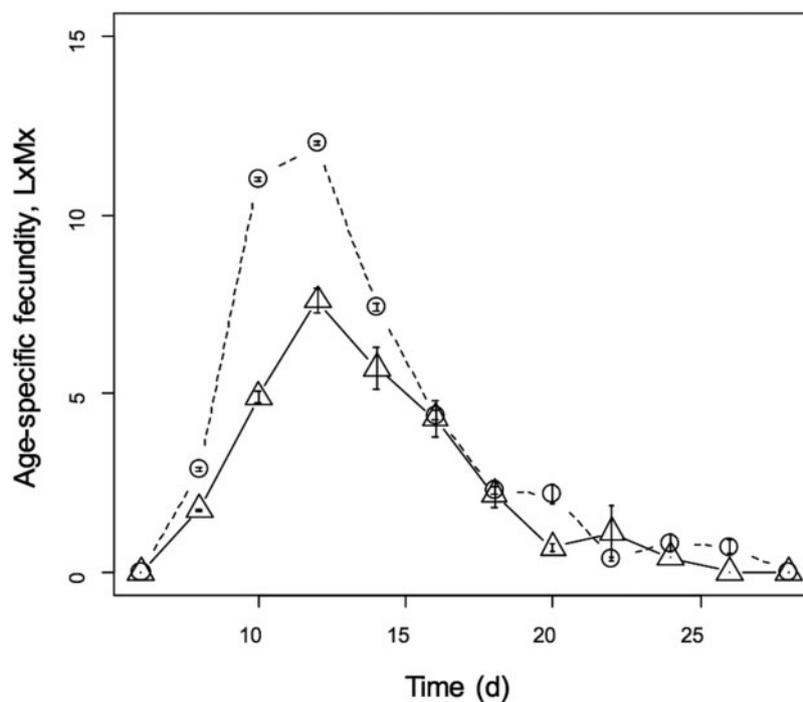


Fig. 1. Mean age-specific fecundity of *Rhopalosiphum padi* foundresses feeding on leaf tissue previously fed on by either *Metopolophium festucae cerealium* (circles, dashed line) or *R. padi* (triangles, solid line); bars show standard deviations.

Table 6. Mean population sizes (\pm SE) of *Rhopalosiphum padi* and *Metopolophium festucae cerealium* after 21 d of unrestricted feeding on whole wheat plants at two levels of water stress

Aphid species	Water treatment	Aphid species treatment		
		<i>R. padi</i> alone	<i>M. festucae cerealium</i> alone	Both species
<i>R. padi</i>	0.1 g H ₂ O/g soil	148 \pm 146	–	161 \pm 139
	0.8 g H ₂ O/g soil	493 \pm 125	–	579 \pm 125
<i>M. festucae cerealium</i>	0.1 g H ₂ O/g soil	–	171 \pm 24	49 \pm 22
	0.8 g H ₂ O/g soil	–	153 \pm 20	110 \pm 20

tissues, as does *M. festucae cerealium*, whereas *R. padi* did not. It should be noted that these lesions are symptoms of feeding activity and do not directly indicate nutritional manipulation by the herbivore; however, other reports exist linking aphid-induced chlorotic lesions with the enhanced performance of aphids. For example, Dorschner et al. (1987) found that an *S. graminum* clone incapable of inducing chlorotic lesions on a particular wheat cultivar experienced enhanced performance on plants previously infested by another *S. graminum* clone which had the ability to induce lesions. We likewise observed distinctive chlorotic lesions on leaf tissues exposed to *M. festucae cerealium* feeding, compared with *R. padi* feeding which produced no visual changes to plant tissues. This inability by *R. padi* to induce such lesions has been reported in other studies (e.g., Sandstrom et al. 2000, Ni and Quisenberry 2006). In addition, whereas *S. graminum* foundresses induce changes that enhance growth of their nearby offspring, *R. padi* do not (Qureshi and Michaud 2005). This indicates that *M. festucae cerealium* might be able to alter host plant nutritional quality, potentially to its benefit, as well as to the benefit of heterospecifics including *R. padi* when occupying the same leaf tissues. The interaction between water regime and presence of *R. padi* on *M. festucae cerealium* performance appears to stem from greater competition on water stressed plants, while no such interaction occurred for *R. padi* possibly because competitive effects are offset for *R. padi* by the documented increases in plant quality induced by cocolonizing *M. festucae cerealium*. While analyses of phloem sap are needed to directly support a hypothesis of feeding-induced nutritional enhancement (Sandstrom et al. 2000), the significant changes to *R. padi* life history traits on leaf tissue previously infested by *M. festucae cerealium* lead us to conclude that the mechanism(s) were plant mediated.

Basic biological information is limited for *M. festucae cerealium* in the PNW and in general (Davis et al. 2014). However, surveys for *M. festucae cerealium* show seasonal overlap with *R. padi* elsewhere; outbreaks of both have been reported during April in Europe (Massee 1935, Janson 1959) and on grasses in the spring (Hand 1989), and both aphids were detected in sweep net samples throughout the PNW during May and June of 2011 and 2012 (Halbert et al. 2013, Davis et al. 2014). Furthermore, Dent and Wratten (1986) observed evenly distributed *M. festucae cerealium* apterae within wheat plants in both laboratory and field settings. While spatial data were not recorded during our study, we observed generally even within-plant distributions for both aphid species when allowed to simultaneously colonize entire plants, showing no indications of avoidance or partitioning. Collectively, these findings suggest first, that *M. festucae cerealium* and *R. padi* both have the potential to infest wheat fields relatively early in the growing season and experience a temporal overlap; and second, that the distributions of both species cocolonizing the same wheat plant are not spatially separated, leading to potential colonization of the same (or closely neighboring) feeding sites. In surveys of more than 42 sites across

the inland PNW taken during the booting stage of the crop in 2011–2014, *M. festucae cerealium* and *R. padi* were often found coinfesting individual plants and fields (S.D.E., unpublished data).

The likelihood of spatiotemporal overlap and potential for competitive interactions between *M. festucae cerealium* and *R. padi* in the PNW must be considered together with our findings of differential impacts of host plant water stress on each aphid species. While a significant negative effect occurred for *R. padi*, the same -0.7 MPa water stress in potted wheat plants had no effect on *M. festucae cerealium* unless *R. padi* was present. The capacity of *M. festucae cerealium* to colonize water-stressed wheat compared to *R. padi* may be partially due to differing life history traits. According to Dent and Wratten (1986), the highest reproductive rate achieved by *M. festucae cerealium* on cereals was 28 nymphs after 10 d, whereas *R. padi* can produce as many as 40 nymphs after 6–8 d (Leather and Dixon 1981, Jiménez-Martínez et al. 2004). In all present experiments, *M. festucae cerealium* reproduction consistently occurred 3 d following that of *R. padi* (i.e., prereproductive periods of 10 and 7 d, respectively). In the whole-plant assay average per-plant abundance of *M. festucae cerealium* on plants only infested with this aphid was $\sim 80\%$ lower than *R. padi* when plants were adequately watered, and 70% lower than *R. padi* on water stressed plants (Table 6). This differential was exacerbated by greater reproduction of *R. padi* on plants coinfested with *M. festucae cerealium*, enhancing *R. padi*'s competitive advantage on water-stressed plants. Further testing is needed to determine the underlying mechanisms responsible for this outcome.

Findings from this study have potential implications for pest management in cereal cropping systems in the PNW and elsewhere. Interspecific interactions between two pest aphid species were complex, producing unique outcomes for each species that depended on the environmental context (i.e., water stress). Thus, variation in drought incidence or other environmental stressors in the field might influence the prevalence and pest status of both species and result in emergent effects on the overall insect herbivore community. Continued monitoring for *M. festucae cerealium* and *R. padi* in the PNW has potential to reveal future ecological trends for each species at the population level. If both species continue to have sympatric distributions and cocolonize fields, competitive pressure by *R. padi* could displace *M. festucae cerealium* populations in drought years. Alternately, *M. festucae cerealium* infesting wheat fields where *R. padi* and other potential competitors are generally absent may remain relatively unaffected by adverse environmental conditions. An additional possibility is that cocolonization will lead to increased reproduction by *R. padi*, thus promoting greater plant injury or potential virus spread across a shorter temporal window. Our study did not address implications of these effects on yield of wheat infested by one, the other or both aphid species. Future work should use field studies to assess this, and to include assessments of other biotic components (e.g., natural enemies) and other climatic stresses associated with drought (e.g., elevated temperature). Finally,

infection by BYDV also enhances *R. padi* performance on drought stressed plants (Jiménez-Martínez and Bosque-Pérez 2004, Davis et al. 2015a), which suggests the interaction of the combined stresses *M. festucae cerealium*, BYDV infection, and drought on *R. padi* should be assessed. Further investigations to these ends could help advance our understanding of the complex interactions between insect communities and the environment under projected conditions of increased drought frequency (Dai 2013).

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