Response of Resistant and Susceptible Barley to Infestations of Five *Diuraphis noxia* (Homoptera: Aphididae) Biotypes

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ABSTRACT Since 2003, four new biotypes of the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae), RWA2–RWA5, have been discovered that have the ability to damage most of the wheat germplasm resistant to the original Russian wheat aphid population (RWA1). Barley germplasm lines with resistance to RWA1 have not yet been evaluated against the newest biotypes. Our study compared how biotypes RWA1–RWA5 affected the growth and leaf damage of RWA1-resistant germplasm (STARS 9301B, STARS 9577B), moderately resistant germplasm (MR-015), and susceptible varieties (Schuyler, Harrington, and Morex) under greenhouse conditions. Russian wheat aphid population levels also were determined 14 d after plant infestation. STARS 9301B exhibited strong resistance by showing only small differences in leaf damage and growth parameters from the feeding by the biotypes. STARS 9577B showed greater differences in damage by the Russian wheat aphid biotypes than STARS 9301B, yet, the ratings were still within the resistant category (e.g., chlorosis rating 2.3–4.9). Leaf chlorosis ratings for MR-015 ranged from 5.0 to 6.9 and fell within the moderately resistant to susceptible categories for all the biotypes. The greatest difference in leaf chlorosis occurred in Morex where RWA2 showed less virulence than the other biotypes. Feeding by the Russian wheat aphid biotypes produced only small differences in leaf rolling and plant growth within plant entries. Population levels of the Russian wheat aphid biotypes did not differ within barley entries (n = 610–971) at the termination of the study (14 d). From our research, we conclude that the new Russian wheat aphid biotypes pose no serious threat to the key sources of resistance in barley (STARS 9301B and 9577B).

KEY WORDS plant resistance, genetic resistance, cereal pest, Russian wheat aphid, host race

In 2003, a new biotype of the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae), was detected in Colorado that was capable of damaging all resistant sources that were currently deployed in commercial wheat, *Triticum aestivum* L. cultivars in the United States (Haley et al. 2004). A recent investigation into the extent of Russian wheat aphid biotypic diversity in the states that bordered Colorado discovered three other Russian wheat aphid biotypes with unique biotype profiles when screened against the nine designated Russian wheat aphid resistance genes in wheat, *DN1* to *DN9* (Burd et al. 2006). A system for naming the Russian wheat aphid biotypes has been proposed (Burd et al. 2006) where designations of RWA1 is for the original Russian wheat aphid population collected from Bailey County, TX, in 1986 (Burd et al. 1993); RWA2 for the Colorado biotype that damages *Dn4* resistance in wheat (Haley et al. 2004); and RWA3, RWA4, and RWA5 for those biotypes collected in Texas and Wyoming that differentially damage *DN1–DN9* resistance in wheat (Burd et al. 2006).

The Russian wheat aphid is also a devastating pest of barley, *Hordeum vulgare* L., in states east of the Rocky Mountains (Mornhinweg et al. 2002) to the extent that some areas no longer grow barley (Bregitzer et al. 2003). Two Russian wheat aphid-resistant barley germplasm lines, STARS 9301B (Mornhinweg et al. 1995) and STARS 9577B (Mornhinweg et al. 1999), have been developed with resistance to RWA1, and they showed excellent potential for managing Russian wheat aphid with genetic resistance (Bregitzer et al. 2003). However, it is not known how RWA1 resistant germplasm reacts to the new Russian wheat aphid biotypes.

The objectives of our study were to determine how biotypes RWA2–RWA5 virulent to wheat affected the growth and leaf damage of RWA1-resistant and -susceptible barley germplasm in comparison with the original Russian wheat aphid population (RWA1) under controlled greenhouse conditions. Russian wheat aphid population levels also were monitored to determine how the resistant and susceptible barley germplasm affected the population growth of each biotype.

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Table 1. Mean ± SE chlorosis ratings for each plant genotype after 14 d of feeding by each Russian wheat aphid biotype under greenhouse conditions, April 2005

Russian wheat aphid biotype	Leaf chlorosis rating[a,b]					
	STARS 9301B	STARS 9577B	MR-015	Schuyler	Harrington	Morex
1	3.1 ± 0.3aD	4.9 ± 0.4aC	6.9 ± 0.3aB	8.4 ± 0.2aA	7.1 ± 0.9aAB	8.3 ± 0.3aA
2	2.7 ± 0.2aD	3.9 ± 0.3bC	6.1 ± 0.3aB	7.3 ± 0.5aAB	7.6 ± 0.5aA	5.0 ± 0.6bBC
3	3.1 ± 0.3aC	3.0 ± 0.3cC	5.0 ± 0.4bB	7.0 ± 0.5aA	7.7 ± 0.2aA	7.3 ± 0.4aA
4	2.7 ± 0.3aC	2.3 ± 0.2cC	5.6 ± 0.6abB	8.0 ± 0.3aA	7.0 ± 0.7aAB	7.5 ± 0.4aA
5	3.0 ± 0.0aB	2.9 ± 0.3cB	6.9 ± 0.6aA	8.0 ± 0.2aA	7.4 ± 0.6aA	7.1 ± 0.6aA

[a] Chlorosis rating is based on 1, healthy, no damage to 9, 95–100% chlorosis or necrosis (Burd et al. 1993).
[b] Means within a column followed by the same lowercase letter or within a row followed by the same uppercase letter, are not significantly different ($P > 0.05$; Kruskal–Wallis test).

Materials and Methods

Two Russian wheat aphid-resistant barley germplasm lines, STARS 9301B and STARS 9577B, were compared with a moderately resistant barley line (MR-015) and three Russian wheat aphid-susceptible commercial varieties (Schuyler, Harrington, and Morex). STARS 9301B was selected from PI 366450 (Mornhinweg et al. 1995), STARS 9577B was selected from CI 4165 (Mornhinweg et al. 1999), and MR-015 was a selection from CI 13683 (D.W.M., unpublished data). The Russian wheat aphid biotypes used in this study were offspring from the original North American Russian wheat aphid population (RWA1) collected Bailey County, TX, in 1986 (Burd et al. 1993) and is avirulent to wheat resistance genes *Dn*3 through *Dn*7; three biotypes collected in 2002–2003 and described by Burd et al. (2006) with the designation of RWA3 (Floyd County, TX) that was virulent to *Dn4* and *Dn7*, RWA4 (Lubbock County, TX) that was virulent to *Dn7*, and RWA5 (Park County, WY) that was virulent to *Dn1-3* and *Dn8-9*. These biotypes were obtained from USDA–ARS–PSWCRL at Stillwater, OK. RWA2 was obtained from Colorado State University, Ft. Collins, and was originally collected in Baca County, CO, in 2003, where it was found to be virulent to *Dn4* (Haley et al. 2004). The biotypes were maintained on Schuyler barley under greenhouse conditions for ≈1 yr at USDA–ARS, Stillwater.

The study was conducted in a greenhouse during early April with temperatures ranging from 10 to 18°C at night and from 20 to 32°C during the day. Light was supplemented by two 800-W halogen lights per 1.5 by 3.0 m^2 of table space that provided a total of 945 $\mu E\ m^{-2}\ s^{-1}$ with a photoperiod of 14:10 (L:D). Plants were started from seed in 7.0-cm-diameter plastic pots. The barley seedlings were infested during the one-leaf stage (100–130 mm in height) with 20 adult apterous Russian wheat aphids and covered by 32.0-mm-diameter plastic tube cages. The movement of aphids onto the plants was facilitated by placing 20 aphids into a 1.5-ml microcentifuge tube that was inserted into the soil at the base of a plant. A dead leaf piece 5.0 cm in length was gently placed in the vial and bridged to the plant to facilitate aphid movement and infestation process. The experimental design was a five biotype × six plant genotype factorial design arranged a randomized complete block design with seven replications. A set of untreated control plants were paired with infested plants to make growth comparisons.

The plant entry–biotype combinations were evaluated 14 d after infestation when the susceptible entries had become 90% chlorotic. All plants were then clipped at the crown and the aphids were brushed from the leaves and counted. Total plant length and damage assessments were made. The damage assessments on each plant included a leaf chlorosis rating, and leaf rolling rating, number of leaves per plant, and the direct measurement of plant height (millimeters). We used a chlorosis rating of 1–9: 1, healthy; 2, 1–5% and spotted; 3, 5–20%; 4, 21–35%; 5, 36–50%; 6, 51–65%; 7, 66–80%; 8, 81–95%; and 9, 95–100% or dead (Burd et al. 1993). Leaf rolling was rated using a 1–3 scale: 1, flat; 2, folded or less than fully rolled; and 3, fully rolled (Burd et al. 1993). Categorical data on leaf chlorosis and rolling for biotypes within each plant genotype and for plants within each biotype was subjected to a one-way nonparametric analysis using a Kruskal–Wallis analysis of variance (ANOVA) (NPAR1WAY), and, if significant, biotype and plant comparisons were made through pairwise comparisons using the Kruskal–Wallis test. Continuous data on the difference in Russian wheat aphid numbers and height of infested plants were analyzed by a two-way ANOVA, and the treatment means were compared ($P = 0.05$) by using the least squared means pairwise comparisons procedure.

Results and Discussion

Leaf chlorosis that resulted from the feeding of the Russian wheat aphid biotypes significantly differed in the RWA1-susceptible barley Morex ($\chi^2 = 14.06$, df = 4, $P = 0.007$) and RWA1-resistant STARS 9577B ($\chi^2 = 24.58$, df =, $P < 0.0001$) and MR-015 ($\chi^2 = 10.39$, df = 4, $P = 0.03$). RWA1 caused a higher level of chlorosis than the other Russian wheat aphid biotypes on STARS 9577B (Table 1). However, our results for RWA1 are consistent with Mornhinweg et al. (1999) who reported STARS 9577B to rate a 3.0, whereas Morex rated a 9.0 when using a 1–9 chlorosis damage scale. RWA2 through RWA5 showed less virulence in comparison with RWA1 on STARS 9577B, indicating that this resistance source as well as STARS 9301B were resistant. Therefore, these two key resistant

Table 2. Mean ± SE leaf rolling ratings for each plant genotype after 14 d of feeding by each Russian wheat aphid biotype under greenhouse conditions, April 2005

Russian wheat aphid biotype	Leaf roll rating[a,b]					
	STARS 9301B	STARS 9577B	MR-015	Schuyler	Harrington	Morex
1	1.6 ± 0.2aB	1.6 ± 0.3aB	3.0 ± 0.0aA	3.0 ± 0.0aA	3.0 ± 0.0aA	3.0 ± 0.0aA
2	1.1 ± 0.1aC	1.1 ± 0.1aC	2.6 ± 0.2aA	2.9 ± 0.1aA	3.0 ± 0.0aA	2.4 ± 0.3bBC
3	1.7 ± 0.3aB	1.3 ± 0.2aB	2.3 ± 0.2aA	3.0 ± 0.0aA	3.0 ± 0.0aA	3.0 ± 0.0aA
4	1.9 ± 0.3aB	1.1 ± 0.1aB	2.6 ± 0.2aA	3.0 ± 0.0aA	3.0 ± 0.0aA	3.0 ± 0.0aA
5	1.4 ± 0.3aB	1.0 ± 0.0aB	2.3 ± 0.4aA	3.0 ± 0.0aA	3.0 ± 0.0aA	3.0 ± 0.0aA

[a] Leaf roll rating: 1, flat; 2, folded or not fully rolled; and 3, fully rolled.
[b] Means within a column followed by the same lowercase letter, or within a row followed by the same uppercase letter, are not significantly different ($P > 0.05$; Kruskal-Wallis test).

sources in spring barley expressed broad resistance to the five Russian wheat aphid biotypes

Chlorosis ratings are useful in functionally classifying barley performance to Russian wheat aphid into four groups: resistant (1–3 rating), moderately resistant (4–5 rating), moderately susceptible (6 rating), and susceptible (7–9 rating) (Mornhinweg et al. 1994). MR-015 is among the group of moderately resistant germplasm that was created at USDA–ARS, Stillwater, and chlorosis typically rated a 4 to 5 in open flat tests against RWA1 (Mornhinweg et al. 1994). We did show significant differences in chlorosis ratings among the Russian wheat aphid biotypes. However, the original RWA1 biotype on STARS 9577B and MR-015 produced one of the higher levels of chlorosis of the biotypes tested. Reduced levels of virulence in Russian wheat aphid populations would not be of great concern to barley breeding programs; thus, would not warrant a biotype designation based on the performance of MR-015 or STARS 9577B.

Morex barley is commonly used as a susceptible plant entry when assessing resistance in barley germplasm (Mornhinweg et al. 1995, 1999, 2002). However, we found leaf chlorosis for Morex to contrast among the Russian wheat aphid biotypes. Morex incurred high levels of leaf chlorosis from all of the Russian wheat aphid biotype infestations, rating 7.1–8.3, except for RWA2 where the damage rating was significantly less (5.0). Chlorosis ratings among the barley entries within each biotype differed significantly ($\chi^2 = 28.6$–33.9, df = 5, $P < 0.0001$) and were mainly a result of the lower chlorosis ratings in the resistant entries. An exception was for the chlorosis ratings for RWA2 on Morex, which differed significantly from the other susceptible barley varieties and performed equally to RWA2-resistant STARS 9577B. The two other RWA-susceptible entries, Schuyler and Harrington, had uniform susceptible levels of damage across all biotypes. Puterka et al. (1992) reported that common aphid-susceptible barley, triticale (*Triticosecale rimpaui* Wittm.), and wheat cultivars showed resistance to certain Russian wheat aphid isolates from different regions of the world. Recently, Burd et al. (2006) noted that a common RWA1-susceptible wheat, 'Yuma', was actually resistant to RWA5. The differential susceptibility of standard cereal cultivars to the Russian wheat aphid biotypes underscores the importance of having several different susceptible entries as controls in Russian wheat aphid resistance screening trials.

Leaf rolling ratings across biotypes within each plant entry were not significantly different ($\chi^2 = 0.0$–6.8, df = 4, $P = 0.14$–1.0), except for Morex ($\chi^2 = 12.7$, df = 4, $P = 0.01$). Kruskal–Wallis pairwise comparisons determined that leaf rolling for RWA2 was lower than the other biotypes for Morex, but at the $P = 0.06$ level ($\chi^2 = 3.5$, df = 1). The relationships of leaf rolling among plant entries within each biotype were significant ($\chi^2 = 29.8$–35.6, df = 5, $P < 0.0001$) and were a result of RWA1-resistant STARS 9301B and STARS 9577B having lower roll ratings than the other plant entries (Table 2). Moderately resistant MR-015 sustained levels of leaf rolling that did not differ significantly from the susceptible barley entries. Burd et al.

Table 3. Mean ± SE difference in plant height when comparing the RWA treated plant to an uninfested control

Russian wheat aphid biotype	Plant ht difference (mm)[a,b]					
	STARS 9301B	STARS 9577B	MR-015	Schuyler	Harrington	Morex
1	−5.5 ± 1.6abA	−3.6 ± 1.2aA	−6.4 ± 1.1aA	−7.3 ± 1.4aA	−7.3 ± 1.8abA	−5.9 ± 1.5abA
2	−3.8 ± 0.3abA	−4.9 ± 1.2aA	−8.4 ± 2.9aA	−7.6 ± 1.8aA	−6.4 ± 1.3bA	−8.5 ± 1.4aA
3	−3.8 ± 1.7abCD	−2.5 ± 0.5aD	−7.1 ± 1.0aBC	−8.5 ± 1.0aAB	−11.2 ± 1.7aA	−7.0 ± 1.5abBC
4	−6.1 ± 0.9aB	−2.9 ± 1.0aB	−4.6 ± 1.1aB	−10.4 ± 2.0aA	−7.1 ± 1.7bAB	−3.9 ± 0.7bB
5	−2.6 ± 0.9bBC	+0.9 ± 0.5bC	−6.4 ± 1.8aAB	−7.4 ± 2.0aA	−9.4 ± 1.0abA	−9.6 ± 1.6aA

Measurements were taken 14 d after of feeding by each Russian wheat aphid biotype under greenhouse conditions, April 2005.
[a] Difference in plant height based on treated plants in comparison with an untreated control.
[b] Means within a column followed by the same lowercase letter, or within a row followed by the same uppercase letter, are not significantly different ($P > 0.05$: least significant difference [LSD]).

Table 4. Mean ± SE number of leaves per plant 14 d after infestation with the Russian wheat aphid biotypes

Russian wheat aphid biotype	Leaf no.[a]					
	STARS 9301B	STARS 9577B	MR-015	Schuyler	Harrington	Morex
1	3.1 ± 0.1bB	3.7 ± 0.1abA	2.1 ± 0.1cC	2.0 ± 0.0bC	2.7 ± 0.3aB	2.1 ± 0.1bC
2	3.9 ± 0.1aA	3.6 ± 0.2abAB	3.1 ± 0.3aBC	2.7 ± 0.3aCD	2.3 ± 0.2aD	2.9 ± 0.3aD
3	3.9 ± 0.1aA	3.4 ± 0.2abA	2.8 ± 0.1abB	2.6 ± 0.2aBC	2.3 ± 0.2aCD	2.0 ± 0.0bD
4	3.6 ± 0.2abA	4.0 ± 0.0aA	2.4 ± 0.2bcB	2.0 ± 0.0bB	2.3 ± 0.3aB	2.0 ± 0.0bB
5	4.0 ± 0.0aA	3.2 ± 0.3bB	2.8 ± 0.1abB	1.9 ± 0.1bC	2.3 ± 0.2aC	2.0 ± 0.0bC

[a] Means within a column followed by the same lowercase letter, or within a row followed by the same uppercase letter, are not significantly different ($P > 0.05$; LSD).

(1993) regarded leaf rolling as a form of gall that was critical to biology and RWA. In this regard, the moderately resistant MR-015 would not be a suitable resistance source to use against these biotypes.

Plant height was not significant for the main effect of biotype ($F = 0.52$; df = 4, 173; $P = 0.71$), but it was significant for barley entry ($F = 12.05$; df = 5, 173; $P < 0.0001$) and the biotype × entry interaction ($F = 1.67$; df = 20, 173; $P = 0.04$). In general, the biotypes reduced plant growth in both the resistant and susceptible barley entries (Table 3). One exception was STARS 9577B, which exhibited a slight stimulation in growth (<1.0 mm) when fed upon by RWA5 versus a 2.5–4.9-mm reduction in growth when fed upon by the other biotypes ($F = 5.17$; df = 4, 28; $P = 0.002$). The biotypes were dissimilar in how they reduced barley height within RWA1-resistant STARS 9301B and STARS 9577B and RWA-susceptible Harrington and Morex. Moreover, the barley entries within a biotype also differed in growth response for only biotypes RWA3, RWA4, and RWA5, and the differences were not consistent between RWA1-resistant and -susceptible entries. In contrast, Burd et al. (1993) determined that plant stunting best predicted the quantitative damage response to RWA1 infestations in oats, wheat, and triticale and that both resistant and susceptible germplasm were stunted. The stimulation of growth in barley by Russian wheat aphid feeding has not been previously reported and indicates that certain biotype-plant entry combinations may have this potential. Our results indicate that the appearance of new Russian wheat aphid biotypes with variable effects on barely growth will make it more difficult to access the performance of barley germplasm in the field and greenhouse trials.

The number of leaves produced by infested plants at the end of the study was significantly affected by biotype ($F = 5.19$; df = 4, 173; $P = 0.0006$), plant entry ($F = 71.15$; df = 5, 173; $P < 0.0001$), and their interaction ($F = 3.14$; df = 20, 173; $P < 0.0001$). Leaf number ranged from 3.1 to 4.0 for the resistant barley entries in contrast to leaf numbers ranging from 1.9 to 2.9 for the susceptible barley entries and moderately resistant MR-015 (Table 4). RWA1 had a greater impact than the other biotypes except RWA4 in reducing leaf number of resistant STARS 9301B and MR-015. RWA5 significantly reduced leaf number in STARS 9577B in comparison with RWA4 even though RWA5 stimulated plant height. RWA1 feeding typically reduces leaf number in susceptible cereals and is highly correlated with plant stunting (Burd et al. 1993). This correlation may no longer apply with the appearance of new Russian wheat aphid biotypes.

Population levels of Russian wheat aphid were significant for the main effect of biotype ($F = 2.25$; df = 4, 173; $P = 0.05$) but not for plant entry ($F = 1.92$; df = 5, 173; $P = 0.09$) or main effect interaction ($F = 1.49$; df = 20, 173; $P = 0.08$). Populations ranged from 610 to 971 (SE range 45–110) aphids per plant, representing a population increase over a 14-d period from an initial $n = 20$ adults per plant (Table 5). Plant condition greatly deteriorate within 14 d on susceptible plants; thus, we could only access general effects of the barley entries on each biotypes population development. We found significant differences in population levels among Russian wheat aphid biotypes only on resistant STARS 9577B and MR-015. Yet, it was apparent that the Russian wheat aphid biotypes could reach high population levels on the RWA1-resistant or -susceptible plant entries, which lead us to conclude

Table 5. Mean ± SE number of aphids per plant 14 d after infestation by each Russian wheat aphid biotype ($n = 20$) under greenhouse conditions, April 2005

Russian wheat aphid biotype	Aphid pop level[a]					
	STARS 9301B	STARS 9577B	MR-015	Schuyler	Harrington	Morex
1	971 ± 110aA	773 ± 104abcAB	986 ± 100abA	763 ± 59aAB	742 ± 165aAB	654.71aB
2	820 ± 80aA	886 ± 76aA	871 ± 86abA	945 ± 120aA	779 ± 105aA	928 ± 68aA
3	846 ± 80aABC	657 ± 52bcC	1092 ± 162aA	977 ± 45aAB	798 ± 86aBC	976 ± 93aAB
4	773 ± 83aA	833 ± 52abA	888 ± 134abA	712 ± 143aA	905 ± 89aA	777 ± 110aA
5	882 ± 57aA	564 ± 65cB	669 ± 135bAB	858 ± 60aA	764 ± 66aAB	798 ± 78aA

[a] Means within a column followed by the same lowercase letters, or within a row followed by the same uppercase letters are not significantly different ($P > 0.05$; LSD).

that resistant barleys had no great antibiotic effects. Webster and Starks (1987) also determined that resistant STARS 9301B had modest antibiotic effects and reduced intrinsic rate of increase of RWA1 by only 18.5%.

The linear correlation of leaf chlorosis to leaf rolling ratings ($r = 0.78$, $n = 209$, $P = 0.013$) and leaf number ($r = 0.80$, $n = 209$, $P < 0.0001$) were significant but only moderately associated. Leaf chlorosis had a low linear correlation with plant height ($r = 0.40$, $n = 209$, $P < 0.0001$) and had no correlation to aphid population level ($r = 0.1$, $n = 209$, $P = 0.087$). These correlations between the damage components and aphid populations generally agree with those by Puterka et al. (1992) and Webster et al. (1996). They both concluded that the lack of a relationship between feeding damage and RWA1 population levels were evidence that resistance in barley is through tolerance, and this concept can be extended to the Russian wheat aphid biotypes on barley entries we examined.

In summary, the Russian wheat aphid biotypes showed distinct differences in how they affected leaf damage and growth of some RWA1-resistant and -susceptible barley entries. STARS 9301B performed uniformly in leaf chlorosis and leaf rolling and exhibited strong resistance to all of the Russian wheat aphid biotypes. The original RWA1 isolate was most damaging to STARS 9577B, whereas the other biotypes caused significantly less chlorosis, yet these damage ratings were still within the range of resistant (1–3 rating) to moderately resistant (4–5 rating). The biotypes produced significant variation in leaf chlorosis to MR-015, but the chlorosis ratings still fell within a moderately resistant or moderately susceptible category (5–6.9 rating). The greatest difference in leaf chlorosis occurred for Morex where the new Russian wheat aphid biotypes showed less virulence. Russian wheat aphid biotypes have been designated because they have overcome previously resistant sources of Russian wheat aphid resistance in wheat (Haley et al. 2004, Burd et al. 2006) and are useful agents to screen for new sources of resistance. From our research, we conclude that the emergence of new Russian wheat aphid biotypes on wheat pose no serious threat to the key sources of resistance in barley (STARS 9301B and 9577B). STARS 9301B exhibited stronger resistance than STARS 9577B to the Russian wheat aphid biotypes we tested. There was also resistance to the new Russian wheat aphid biotypes in barley entries that were previously determined to be susceptible to RWA1. The ability of the new biotypes to differentially affect plant damage and growth of some barely entries suggests that it will become more difficult to access the performance of barley germplasm to Russian wheat aphid infestations in field and greenhouse trials.

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