# Examining the Competitive Advantage of *Diuraphis noxia* (Hemiptera: *Aphididae*) Biotype 2 Over Biotype 1

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**ABSTRACT** The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) is a serious pest of small grains, such as wheat and barley. High population growth rates and a broad gramineae host range have allowed this aphid to successfully establish and become pestiferous across much of North America since its invasion in the mid-1980s. Resistant wheat cultivars were developed and provided control of *D. noxia* until 2003, when a new biotype (designated RWA2, as contrasted with the original biotype's designation, RWA1) emerged and rapidly spread through dryland winter wheat-growing regions. RWA2 displaced RWA1 more quickly than expected, based on RWA2's advantage in RWA1-resistant wheat cultivars. Previous research suggested that RWA2 may out-compete RWA1 in cooler temperatures. Thus, we sought to determine if RWA2 had a competitive advantage over RWA1 during the overwintering period. We placed a known distribution of RWA1 and RWA2 aphids in the field for the winter at three sites across a latitudinal gradient (from northern Colorado to Texas) to test for a competitive advantage between these biotypes. We found overwhelming support for an overwintering competitive advantage by RWA2 over RWA1, with evidence suggesting a >10-fold advantage even at our Texas site (i.e., the site with the mildest winter). This substantial overwintering advantage helps explain the quick dispersion and displacement of RWA1 by RWA2.

**KEY WORDS** Russian wheat aphid, overwintering, temperature, binomial distribution

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One of the primary pests of dryland winter wheat in North America is the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Morrison and Peairs 1998). *D. noxia*, an invasive pest, arrived into the United States in the mid-1980s (Morrison and Peairs 1998) and has the potential to cause substantial yield losses largely because it reproduces parthenogenically and has an exceptionally high intrinsic rate of increase (Merrill et al. 2009a). Until 2003, only one *D. noxia* biotype (designated as RWA1) was known to occur in North America (Shufran et al. 1997). In 2003, a biotype virulent to all available RWA1-resistant wheat cultivars was discovered in SE Colorado and was designated as RWA2 (Haley et al. 2004). RWA2 rapidly expanded throughout Colorado at a rate in excess of the rate expected based on its competitive advantage in RWA1-resistant wheat cultivars (Merrill et al. 2008a). *D. noxia* population growth rates change based on many factors, such as plant host (Webster et al. 1996, Merrill et al. 2008b), plant host condition or age (Girma et al. 1990, Hein 1992, Brewer and Noma 2002), physical environment (e.g., slope or soil type; Merrill et al. 2009b), and temperature (Michels and Behle 1988, 1989; Legg and Brewer 1995; Merrill et al. 2009a). In addition, differences in aphid population growth rates by biotype have been observed: Large competitive advantages have been found within host plant (Jyoti et al. 2006, Randolph et al. 2008) with the obvious extreme observed when plant host resistance is overcome by one biotype. Of the most relevance to this study, biotypes have demonstrated different growth rates within a temperature regime (Randolph et al. 2008). For example, in a temperature-controlled growth chamber, Randolph et al. (2008) found that RWA2 exhibited higher fitness than RWA1 under cool, early spring-like temperatures (13–18°C). Specifically, RWA2's intrinsic rate of increase and longevity were greater than that of RWA1 at 13–18°C. If extrapolated to colder temperatures, differences in the intrinsic rate of increase between these biotypes could account for the rapid expansion of RWA2 and the displacement of RWA1 by RWA2 (Merrill et al. 2008a). Mechanisms that would lead to a competitive advantage (e.g., growth rate differences, predator avoidance mechanisms, or differences in overwintering strategy) by aphid biotype are poorly understood but mechanisms such as feeding or resource acquisition differences that have been noted (Lazzari et al. 2009). We sought to test the hypothesis that RWA2 would hold a competitive advantage over RWA1 during the overwintering period by examining the relative population

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survival of these two biotypes in the field. Our null hypothesis was that if no competitive advantage existed between biotypes, then no change in overwintering survival rate would exist between RWA1 and RWA2 populations. If so, then the ratio of RWA1: RWA2 would remain stable throughout the winter and into the early spring, and thus, remain at approximately the fall infestation ratio. However, if RWA2 displaced or outperformed RWA1, the ratio of RWA1: RWA2 would decrease. Thus, we could test if one of the biotypes held a competitive advantage by examining changes from the ratio of biotypes infested before the winter to the ratio of biotypes observed in the spring.

## Methods

During the fall, fixed quantities of two *D. noxia* biotypes, RWA1 and RWA2, were infested onto dryland winter wheat. During the early spring, when symptoms became evident, we examined relative population density of RWA1 and RWA2 to determine if the relative densities of these two biotypes had changed. Tests were completed using a simple binomial probability test. Specifically, in the late fall, aphids were put out into the field at a 10:1 ratio of RWA1:RWA2. If no competitive advantage existed between biotypes, then the relative population density of RWA1 and RWA2 would remain reasonably stable from infestation to early spring sampling.

Two experiments were conducted to test for a competitive advantage of RWA2 over RWA1.

**Experiment 1.** 'Vona' wheat, which is susceptible to all *D. noxia* biotypes, was planted at the Agricultural Research, Development and Education Center (Fort Collins, CO: 41° N, 105° W. Annual temperature: 9.2°C. Mean January temperature: −1.9°C. Annual precipitation: 36.2 cm) on 12 September 2008 (climate averages from 1981 to 2010; PRISM 2004). Within this area, two plots measuring 1 m in length by 6 rows in width were infested with *D. noxia* in early December 2008. The aphids were mixed with cream of wheat as a carrier then applied with a Davis insect inoculator (Davis and Oswalt 1979). Each biotype mixture was applied separately so that *D. noxia* abundances per cubic centimeter and the *D. noxia* biotype ratios could be calculated. To determine the approximate number of *D. noxia* per application of the Davis inoculator, 1 $cm^3$ of the cream of wheat and *D. noxia* mixture was distributed into each of 10 petri dishes. The number of *D. noxia* in each dish was counted and dish totals were averaged to provide an average number of aphids per cubic centimeter mixture application. Each plot received 2 $cm^3$ of the RWA2 mixture (≈125.4 RWA2 per plot) and 8 $cm^3$ of the RWA1 mixture (≈1,338.4 RWA1 per plot) generating an approximate 10:1 RWA1: RWA2 ratio.

When damage symptoms manifested in the spring, infested tillers were clipped from the infested plots. Each tiller collected was placed in a separate Ziplock plastic bag and transported back to Colorado State University for processing. Pots were planted with one plant per pot of 'Yuma,' caged and allowed to grow to the four-leaf stage. To create isofemale lines, one aphid from one of the field collected infested tillers was introduced into a clip cage, which was attached to a leaf on one of the tillers in each pot. Each pot contained one aphid from one tiller so that each tiller collected had a representative isofemale colony. The pots remained caged throughout the experiment. When the isolated aphid reproduced and there were at least five aphids in the clip cage, the clip cage was removed so that the aphids were allowed to move about the plants in the pot and establish. When each isofemale colony reached an adequate size (i.e., >100 aphids), 10 aphids were transferred onto a pot containing one plant of each of the wheat cultivar differentials: Yuma (susceptible to RWA1 and RWA2) and 'Yumar' (resistant to RWA1 and susceptible to RWA2). The plant differentials were at approximately two- to three-leaf stage at transfer. When Yuma rated at an 8–9 on a 1–9 chlorosis scale (Webster et al. 1987, Burd et al. 1993), both plants in each pot were rated to determine aphid biotype. If only Yuma was damaged, then the biotype was designated RWA1, but if both plants rated at an 8–9, then the biotype was designated RWA2 (Weiland et al. 2008).

**Experiment 2.** Because results from the first experiment were strong, we decided to determine if there was a site effect or if results differed across a latitudinal gradient. We selected field sites at the Agricultural Research, Development and Education Center (Fort Collins, CO), near Lamar, CO (38° N, 103° W. Annual temperature: 12.0°C. Mean January temperature: −0.5°C. Annual precipitation: 36.4 cm) and at the Bushland ARS station, Bushland, TX (35° N, 102° W. Annual temperature: 14.3°C. Mean January temperature: 2.9°C. Annual precipitation: 50.8 cm; climate averages from 1981 to 2010; PRISM 2004). Small plots of 'TAM 107,' a hard red winter wheat known to be susceptible to all known RWA biotypes (Randolph et al. 2009), were planted at in the fall of 2010 and 2011. Plot size was at least 12 rows in width and 2 m in length and the wheat area infested was 6 rows in width by 1 m in length.

Plots were infested mid–late fall, when the plants were at least at the three-leaf stage, with 1,000 RWA1 and 100 RWA2 at a 10:1 RWA1 to RWA2 ratio. RWA1 and RWA2 were obtained from the colonies maintained at Colorado State University. The aphids were placed onto plants using two methods: 1) aphids were mixed with cream of wheat as a carrier then applied with a Davis insect inoculator (Davis and Oswalt 1979), or 2) aphids were infested by hand, by sprinkling them from plastic tubes onto plots. Plots were visually inspected before infestation to ensure that the area was not already infested with naturally occurring *D. noxia.*

At spring regrowth, and when *D. noxia* symptoms were evident, 50 infested tillers were clipped from plots at each site. Each tiller was placed in a separate Ziplock plastic bag. Tillers collected from Lamar, CO, and Bushland, TX, were placed in a cooler with an ice pack and sent overnight for processing at Colorado

Table 1. Overwintering weather conditions, sampling, and infestations dates, as well as the corresponding observed RWA1:RWA2 ratios for all sites (expected ratio is 10:1)

| Site | Years | Infestation date | Sampling date | Avg. temperature | Precipitation (cm) | RWA1:RWA2 ratio |
|---|---|---|---|---|---|---|
| Lamar, CO | 2010–2011 | 15 Nov. | 21 April | 2.62°C | 3.73 | 14:32 |
| Lamar, CO | 2011–2012 | 21 Nov. | 26 April | 3.57°C | 8.1 | 1:10 |
| Fort Collins, CO | 2008–2009 | 1 Dec. | 31 Mar.[a] | −0.23°C | 1.98 | 28:11 |
| Fort Collins, CO | 2010–2011 | 1 Dec. | 31 Mar.[b] | 0.79°C | 3.05 | No *D. noxia* |
| Fort Collins, CO | 2011–2012 | 21 Nov. | 17 April | 2.35°C | 0.76 | 10:23 |
| Bushland, TX | 2010–2011 | 17 Nov. | 11 April | 5.26°C | 2.31 | 22:24 |
| Bushland, TX | 2011–2012 | 15 Dec. | 9 April | 6.59°C | 7.16 | 10:20 |

[a] Multiple sample dates. Weather conditions reported are from 1 December 2008 to 31 March 2009.

[b] Localized extinction assumed. No infested tillers were found at this site in the spring of 2011.

State University. Isofemale colonies were developed and rated as RWA1 or RWA2 using the same methodology as in experiment 1.

**Statistical Design.** Binomial tests can be used to determine if an observed deviation from an expected distribution was probable (Ott 1993). Binomial probability distributions were calculated using a 10:1 RWA1:RWA2 ratio. The probability of observing the number of RWA2 biotype designations or greater was calculated using a binomial test calculated by the dbinom function in R statistical package (R Development Core Team 2008, Vienna, Austria). Because of sampling probabilities, observed data could vary from the initially placed ratio of RWA1:RWA2. For example, given an initial infestation of 10:1 RWA1:RWA2, if 20 aphids were biotyped, we would expect approximately two RWA2 and 18 RWA1. However, observations of 3 RWA2 and 17 RWA1 or 4 RWA2 and 16 RWA2 would not be unlikely. Because the inputs are known, probabilities of observing different outcomes can be calculated using a binomial probability distribution. That is, we can calculate the exact probability that 17:3 RWA1:RWA2 would be observed if we started with a population of 10:1 RWA1:RWA2, assuming that no competitive advantage was observed by either biotype.

## Results and Discussion

We hypothesized that if no competitive advantage existed between RWA1 and RWA2, the relative population densities would remain stable. That is, populations would respond in similar fashions to perturbations in overwintering conditions. Our data strongly suggest that this hypothesis should be rejected.

**Experiment 1.** Of the three seasons tested at the Fort Collins field site, the 2008–2009 winter was the coldest (average temperature of −0.23°C) and with 1.98 cm of precipitation (Table 1). In the spring, 39 infested tillers were successfully developed into isofemale colonies, and were tested and designated with a RWA1 or RWA2 biotype. Of the 39 colonies tested, 11 were found to be RWA2, 28 were found to be RWA1. Assuming equivalent overwintering abilities, the probability of observing a ratio of 28:11 RWA1:RWA2 or a more extreme ratio favoring RWA2 is 0.0003 (Fig. 1).

**Experiment 2.** Overwintering weather conditions for each site are listed on Table 1. At the Fort Collins site during the 2010–2011 overwintering season, temperatures were cold, although not exceptional, with an average daily temperature of 0.79°C from 1 December to 31 March (Table 1). Moisture accumulation was relatively high for this location during this period (3.05 cm). While overwintering weather conditions did not appear to be extreme, no infested tillers were found at the Fort Collins site in the spring of 2011 and localized extinction was assumed. However, successful overwintering of aphids occurred at the other two sites during the winter of 2010–2011. Isofemale colonies were developed from infested tillers at both Lamar (46 isofemale colonies established) and Bushland (46 isofemale colonies established). Of the isofemale lines from Lamar, 14 were designated RWA1 and 32 were designated RWA2 ($P < 0.0001$). Of the 46 isofemale colonies from Bushland, 22 were designated RWA1 and 24 were designated RWA2 ($P < 0.0001$). In 2011–2012, aphids survived at all three locations. Thirty isofemale colonies were developed from aphids in

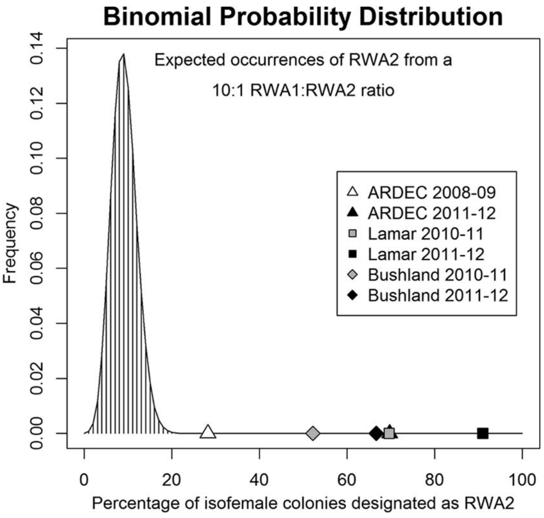

Fig. 1. Based on a 10:1 RWA1:RWA2 ratio of aphids in the field, Fig. 1 depicts the expected distribution (black lines) of the percentage of RWA2 designations under the assumption that no competitive advantage exists. Observations are denoted as indicated by the legend. All observations are well-distanced from expectations if the null hypothesis (no competitive advantage) were true.

Bushland, resulting in 10 RWA1 and 20 RWA2 biotype designations ($P < 0.0001$). Thirty-three isofemale colonies were developed from aphids at the Fort Collins field site, resulting in 10 RWA1 and 23 RWA2 designations ($P < 0.0001$). Eleven isofemale colonies were developed from the Lamar field site, resulting in 1 RWA1 and 10 RWA2 designations ($P < 0.00001$).

If no overwintering advantage existed between RWA1 and RWA2, the probability of observing these data were effectively zero ($P < 0.00001$). For example, the probability of collecting 23 RWA2 and 10 RWA1 from the Fort Collins site in 2011–2012 site is zero ($P = 8.748825e\text{-}16$). During the entirely of experiment 2, the highest probability of occurrence was $P = 1.078238e\text{-}13$, at the Bushland site in 2010–2011. That is, mathematically, there is zero chance that these data could have occurred randomly.

These results dramatically indicate that RWA2 has a competitive advantage over RWA1, which may help to explain the rapid displacement of the RWA1 biotype by the RWA2 biotype (Merrill et al. 2008a). The probability that no overwintering advantage is occurring is negligible. However, these results should not be extrapolated to the mechanism level. That is, we cannot tell from these experiments what kind of advantage exists. However, it is interesting that experiment 2 indicates that there may be a more distinct competitive advantage of RWA2 over RWA1 in the Colorado sites (i.e., sites with harsher winter conditions). For example, RWA2 showed a greater competitive advantage over RWA1 in Lamar than in Bushland. However, because of a lack of independence, weather data do not lend themselves to statistical interpretation. That is, we would need additional years with a gradient of overwintering severity to quantify the effects and effect sizes of weather variables on the relative growth rates of RWA1 and RWA2.

We cannot completely discount the possibility of experimental error such as sampling bias, immigration, or differential establishment at infestation. However, all of these errors would be linear in effect and would not compound over time (i.e., while the population sizes change nonlinearly, if no competitive advantage existed then populations would increase or decrease at equivalent rates, resulting in noncompounding errors from infestation or establishment). The exceptional effect size of the signal suggests that these errors must accrue to over an order of magnitude difference. For example, to accept that these data arose from sampling bias, one would have to assume that, from the symptomatic tillers, RWA2 infested tillers were sampled ≈14 times more frequently than RWA1 infested tillers. However, we have not seen any data in the literature or in our studies that supports the possibility of differential symptom expression by biotype on susceptible wheat. Thus, parsimony suggests that changes in the distribution of biotypes were nonlinear and compounding, such as differences in intrinsic rates of increase.

Regarding the possibility of immigration into our plots, attempts were made to confirm that no aphids were in the plots previous to infestation or in close proximity to the plots. Moreover, to observe these data, a substantial aphid flight must occur during the winter or early spring, which has not been supported by *D. noxia* flight monitoring data. Specifically, first state-wide detection of the spring *D. noxia* flight in Colorado based on suction trap data (five Colorado sites: Akron, Yellow Jacket, Lamar, Fort Collins, and Fruita 1988–1996) occurs toward the end of April (Hammon et al. 1999). If observations were ascribed to different rates of establishment on wheat following the artificial aphid infestation, data would suggest RWA2 to be more than an order of magnitude more successful (e.g., to observe these data, if 100% RWA2 established, only 7% of RWA1 could establish). We suggest that the probability of these sources of error causing the observed data are negligible, especially given previous evidence suggesting that RWA2 has an advantage over RWA1 under controlled, cool temperature conditions (Randolph et al. 2008). That is, a slight difference in population growth rates during the winter (i.e., an intrinsic rate of increase difference of 0.03 was found by Randolph et al. 2008 in cool conditions) would result in the observed data.

Overall, these data were surprising because of the overall strength of the signal with which RWA2 was outcompeting RWA1. For example, the complete reversal of the RWA1:RWA2 ratio at the Lamar site (2011–2012) shows a 100-fold advantage of RWA2 over RWA1. While this was the most extreme of the quantified advantages, it was not an outlier (Table 1). Each and every site that we tested showed RWA2 strongly outcompeting RWA1. The observed rapid displacement of RWA1 by RWA2 (Merrill et al. 2009c) can be explained (although not mechanistically) by this advantage. To better understand the mechanisms behind RWA2's advantage over RWA1, future research should examine relative cold tolerances, overwintering fitness, and other mechanisms that may provide a competitive advantage in dryland winter wheat regions.

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