Plant resistance to the Russian wheat aphid: effects on a nontarget aphid and the role of induction

Frank J Messina,[1] Ashley J Bloxham

Department of Biology, Utah State University, Logan, Utah 84322–5305,
United States of America

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Abstract—Several resistant lines of wheat, *Triticum aestivum* (L.) (Poaceae), have been developed to control populations of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae). We examined the potential effects of *D. noxia* resistant lines on another aphid, the bird cherry-oat aphid (*Rhopalosiphum padi* (L.) (Hemiptera: Aphididae)), which commonly co-occurs with *D. noxia*. Because one type of resistance (mediated by the *Dn*1 gene) is purported to be induced rather than constitutive, we also determined the degree to which the suitability of resistant and susceptible plants is modified by previous infestation. Although resistant lines were derived from five different sources, we did not detect any differences in the population growth of *R. padi* on resistant and near-isogenic susceptible plants. The performance of *D. noxia* was reduced as expected on resistant plants but was unaffected by whether or not plants had been previously infested. In contrast, the performance of *R. padi* was reduced on plants that had been previously infested but was unaffected by whether plants were resistant or susceptible to *D. noxia*. Because neither species' performance was especially low on previously infested, resistant plants, there was no evidence that prior aphid feeding induces a higher level of resistance.

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Résumé—Plusieurs lignées résistantes du blé tendre, *Triticum aestivum* (L.) (Poaceae), ont été développées pour lutter contre les populations du puceron russe du blé, *Diuraphis noxia* (Mordvilko) (Hemiptera : Aphididae). Nous avons étudié les effets potentiels des lignées résistantes à *D. noxia* sur un autre puceron commun, le puceron bicolore des céréales, *Rhopalosiphum padi* (L.) (Hemiptera : Aphididae). Puisqu'on croit que la résistance médiée par le gène *Dn*1 est induite plutôt que constitutive, nous avons aussi déterminé dans quelle mesure une infestation antérieure rend les plants résistants et vulnérables plus ou moins appropriés à l'insecte. Bien que les lignées résistantes proviennent de cinq sources distinctes, il n'y a pas de différence dans la croissance des populations de *R. padi* sur les plants résistants et les plants vulnérables quasi-isogéniques. Le succès de *D. noxia* est réduit, comme prévu, sur les plants résistants, mais il n'est pas modifié par une infestation antérieure de la plante. En revanche, le succès de *R. padi* est restreint sur les plants qui ont subi une infestation antérieure, mais il ne varie pas selon que les plants soient ou non résistants à *D. noxia*. Puisque la performance des deux espèces n'est pas particulièrement réduite sur des plants résistants qui ont subi une infestation antérieure, il n'y a pas d'indication que l'alimentation préalable par les pucerons entraîne une résistance accrue.

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[1] Corresponding author: (e-mail: messina@biology.usu.edu)

Introduction

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), has been a sporadic pest of wheat, *Triticum aestivum* L. (Poaceae), since its detection in the United States of America in 1986 and in Canada in 1988 (Jones *et al.* 1989). The rapid spread of this aphid throughout western North America spurred a major effort to identify sources of plant resistance and to develop agronomically suitable, resistant cultivars (Souza 1998). Plant resistance has been considered an especially useful way to control *D. noxia*, because the aphid's habit of feeding within rolled wheat leaves may limit the effectiveness of contact insecticides and some natural enemies (Burd *et al.* 1993; Haile *et al.* 1999). Resistance genes have been isolated from several wheat accessions (Ma *et al.* 1998; Liu *et al.* 2001), and provide differing modalities of resistance.

The use of resistant crop cultivars influences more than the direct interaction between crop and pest. For example, plant traits that confer resistance to pests may simultaneously enhance or diminish the ability of natural enemies to reduce pest populations (Cortesero *et al.* 2000). Plants bred for resistance to a particular pest may also exhibit cross-resistance to other pest species (Agrawal and Karban 2000). In this study, we addressed two questions to gain a better understanding of the consequences of using resistant cultivars to control the Russian wheat aphid. Because *D. noxia* typically co-occurs with a suite of economically important cereal aphids (Schotzko and Bosque-Pérez 2000), we first asked whether plants bred for resistance to *D. noxia* reduce the population growth of another common pest, the bird cherry-oat aphid (*Rhopalosiphum padi* (L.) (Hemiptera: Aphididae)). Both aphids are phloem-feeders, but they might respond differently to compounds that confer antibiosis (Ni *et al.* 2001). In a set of greenhouse experiments, we included plants derived from five different sources of resistance to *D. noxia*, and compared the growth of *D. noxia* and *R. padi* populations on resistant lines and near-isogenic susceptible lines.

The second question addressed is the degree to which the level of resistance is modified by prior aphid feeding (Moran and Thompson 2001). Plant defense traits may be constitutive or may be induced by herbivore and pathogen attack (Karban and Baldwin 1997; Forslund *et al.* 2000). Some evidence suggests that one source of resistance to *D. noxia* (mediated by the *Dn*1 gene) depends on the production of pathogenesis-related proteins following aphid damage (van der Westhuizen *et al.* 2002). If the time required to induce resistance is short relative to its duration (Underwood 1998; van der Westhuizen *et al.* 1998*a*), we might expect poorer aphid performance on plants that have already been fed upon by aphids. We conducted two experiments that compared the growth of *D. noxia* and *R. padi* populations on *D. noxia* resistant and susceptible plants with different infestation histories. In an earlier study, prior feeding by *D. noxia* and *R. padi* had contrasting effects on the subsequent quality of a susceptible wheat cultivar; previous infestation by *D. noxia* had little effect on subsequent population growth, whereas the growth of *R. padi* was significantly reduced on previously infested plants (Messina *et al.* 2002).

Materials and methods

Plant material

Advanced line IDO524 was produced from backcrosses that incorporated the *Dn*1 resistance gene into a soft-white, spring wheat (*T. aestivum* 'Penawawa'; Souza 1998). This dominant gene was derived from plant introduction line PI 137739 (Du Toit 1989; Schroeder-Teeter *et al.* 1994) and confers antibiosis-resistance to *D. noxia* (Smith *et al.* 1992; Formusoh *et al.* 1994). In a greenhouse experiment, densities of *D. noxia* were nearly 50% lower on *Dn*1-bearing IDO524 plants than on near-isogenic 'Penawawa' plants (Messina and Sorenson 2001). Some evidence suggests that the expression of resistance depends on genetic background of the recipient plant (van der Westhuizen *et al.* 1998*b*). Resistance may also need to be induced by aphid feeding rather than expressed constitutively (Heng-Moss *et al.* 2003). It appears that possession of the *Dn*1 gene leads to relatively high chitinase, peroxidase, and β-1,3-glucanase activity following aphid damage (van der Westhuizen *et al.* 2002), and salicylic acid has been implicated as a potential mediator of this response (Mohase and van der Westhuizen 2002).

Advanced line IDO498 is a hard-red, winter wheat derived from backcrosses that incorporated the *Dn*4 resistance gene into the susceptible *T. aestivum* 'Manning' (Souza 1998). Expression of the *Dn*4 gene, which was originally identified in PI 372129 (Quick *et al.* 1991), may limit the amount of leaf rolling, a common symptom of infestation by *D. noxia* (Ma *et al.* 1998). Resistance in PI 372129 has been characterized as mainly tolerance (Nkongolo *et al.* 1991; Burd *et al.* 1993), but plants containing the dominant *Dn*4 gene also appear to possess a moderate amount of antibiosis resistance (Hein 1992; Hawley *et al.* 2003; Randolph *et al.* 2003). Induction of peroxidase activity may be involved in resistance conferred by the *Dn*4 gene (Ni *et al.* 2001). In a direct comparison of IDO498 and the near-isogenic 'Manning', aphid population growth was 20%–30% lower on the former line (Messina and Sorenson 2001).

Three hard-red, winter wheat germplasms (A90415W-E-0r-13, A90416W-21, and A92051W-D-2) were derived from backcrosses of three different resistant accessions to the susceptible 'Manning' (Souza *et al.* 2002). Germplasms A90415W-E-0r-13 and A90416W-21 incorporate resistance from PI 94460 and PI 48650, respectively. PI 94460 and PI 48650 showed moderate to substantial tolerance to *D. noxia* infestation (Zwer *et al.* 1994). Germplasm A92051W-D-2 incorporates resistance from PI 47545, which contains a single dominant gene that confers moderate levels of both antibiosis and tolerance with respect to *D. noxia* (Smith *et al.* 1991; Linscott *et al.* 2001).

Experiments

Three experiments compared the growth of *D. noxia* and *R. padi* populations on susceptible and *D. noxia* resistant plants. We used 'Penawawa' *versus* IDO524 in Experiment 1; 'Manning' *versus* IDO498 in Experiment 2; and 'Manning' *versus* A90415W-E-0r-13, A90416W-21, and A92051W-D-2 in Experiment 3. In each experiment, seeds were germinated in a peat–vermiculite mixture in 1.5-L pots. Seedlings were thinned to one per pot and fertilized with 50 mL of a 20–20–20 N–P–K solution 5 days after planting. Ten days after planting, each plant was covered with a cylindrical, cellulose–acetate cage (4.1 cm diameter × 32 cm tall), and we used a camel-hair brush to add three apterous adults of *D. noxia* or *R. padi* to each plant. Cages had organdy-cloth windows on the sides and top for ventilation. Plants at this time bore two unfolded leaves and one emerging leaf (Zadoks stage 12; Tottman 1987). Aphids were obtained from anholocyclic laboratory colonies maintained on winter wheat *T. aestivum* 'Garland' (Messina *et al.* 2002); voucher specimens are in the Utah State University Insect Collection, Logan. Aphids were added to 30 (Exp. 1), 25 (Exp. 2), or 20 (Exp. 3) replicate plants per treatment.

After an additional 10–11 days, plants and aphids were harvested into jars containing 70% ethanol, and we later recorded the number of aphids per plant. The duration of the experiment represented approximately one and a half aphid generations so that recovered aphids included the offspring and grandoffspring of the original three females per plant. Two-way ANOVA was used to examine the fixed effects of plant cultivar and aphid species on aphid density. Counts were square-root transformed to satisfy assumptions of the ANOVA. During each experiment, greenhouse temperatures fluctuated between 20 and 30 °C in a daily cycle, and relative humidity varied from 50% to 80%.

Two additional experiments simultaneously examined the effects of plant resistance and previous infestation on the growth of *D. noxia* (Exp. 4) or *R. padi* (Exp. 5) populations. Each experiment used 'Penawawa' and IDO524 as hosts, and followed the protocol of Messina *et al.* (2002). Seedlings were prepared as described above. Seven days after planting, we placed cages on all plants and added 25 adult aphids (*D. noxia* in Exp. 4; *R. padi* in Exp. 5) to half of the plants. Plants bore one unfolded leaf and one emerging leaf (Zadoks stages 11 or 12). Aphids fed and reproduced for 5–6 days. Plants were then brought to the laboratory and all aphids on infested plants were brushed into a tray containing 50% ethanol. We counted the number of aphids removed from 10 to 12 plants per cultivar to estimate aphid density at the end of the primary infestation. Because mechanical stimulation alone might induce changes in plant chemistry (*e.g.*, Cipollini 1997), uninfested (control) plants were handled in the same way (*i.e.*, brushed over a tray containing 50% ethanol).

Control and previously infested plants were maintained in a growth chamber at 24 °C for 30 h, after which they were returned to the greenhouse, caged, and inoculated with three adults of *D. noxia* (Exp. 4) or *R. padi* (Exp. 5) per plant (n = 25–27 replicate plants per treatment). Plants bore three unfolded leaves (Zadoks stage 13) at this time. Plants and aphids were harvested into jars containing ethanol after 10–11 days. Two-way ANOVA was used to estimate effects of plant cultivar and infestation history on the number of aphids per plant at the end of the secondary infestation. We used two-sample Student's t tests to compare aphid densities (square-root transformed) on resistant and susceptible plants at the end of the primary infestation.

Results and discussion

Growth of *D. noxia versus R. padi*

Despite using five different sources of *D. noxia* resistance, we found no evidence that resistant plants affected population growth of *R. padi*. In the first experiment, the population growth of *D. noxia* was 25% lower on the *Dn*1-bearing IDO524 plants than on the near-isogenic 'Penawawa' plants, but the growth of *R. padi* was virtually identical on the two hosts (Table 1). Aphid counts were higher for *R. padi* than for *D. noxia* because the former species has a higher intrinsic rate of increase on wheat seedlings (Messina *et al.* 2002). Two-way ANOVA indicated an effect of aphid species on aphid density ($F_{1,115} = 224.78$, $P < 0.001$), but there was no effect of plant cultivar ($F_{1,115} = 0.94$, $P = 0.33$) nor any interaction between the effects of aphid species and plant cultivar ($F_{1,115} = 1.69$, $P = 0.19$). No significant interaction was detected because the level of antibiosis toward *D. noxia* was unusually weak in this experiment (see Exp. 4 below and Messina and Sorenson 2001). Nevertheless, if plants that received *R. padi* were excluded from the analysis, densities of *D. noxia* were higher on 'Penawawa' than on IDO524 ($F_{1,57} = 18.74$, $P < 0.001$).

Experiment 2 compared IDO498 and the near-isogenic 'Manning'. Because the type of resistance provided by the *Dn*4 gene is mostly tolerance (Burd *et al.* 1993), we did not expect a large difference in the density of either aphid species between hosts. Populations of *D. noxia* were about 14% smaller on IDO498 than on the near-isogenic 'Manning', whereas the density of *R. padi* was only 4% lower on the resistant host (Table 1). Aphid density differed between aphid species ($F_{1,95} = 239.40$, $P < 0.001$), but there was no effect of plant cultivar ($F_{1,95} = 1.83$, $P = 0.18$) and no aphid species × plant cultivar interaction ($F_{1,95} = 0.19$, $P = 0.67$). As noted earlier, however, IDO498 appears to possess mild antibiosis resistance toward *D. noxia* (Messina and Sorenson

Table 1. Number (mean ± SE) of aphids (*Diuraphis noxia* or *Rhopalosiphum padi*) on susceptible and *D. noxia* resistant wheat plants.

Experiment	Plant cultivar	Number of aphids per plant *D. noxia*	*R. padi*
1	Penawawa	149.3±6.0	430.9±33.5
	IDO524	111.9±5.6	437.6±31.3
2	Manning	136.0±6.5	339.1±19.4
	IDO498	117.5±4.0	324.2±20.9
3	Manning	132.7±11.4	300.2±22.8
	A90415W-E-0r-13	126.7±8.7	306.4±23.4
	A90416W-21	118.8±6.7	310.2±27.8
	A92051W-D-2	122.6±7.8	315.7±33.5

Note: Counts were obtained 10–11 days after each plant received three adult aphids. Sample sizes were 30 (Exp. 1), 25 (Exp. 2), or 20 (Exp. 3) replicate plants per treatment.

2001). A separate analysis of plants that received *D. noxia* indicated higher aphid densities on 'Manning' than on IDO498 ($F_{1,47} = 5.85$, $P = 0.02$).

Experiment 3 included three wheat lines (A90415W-E-0r-13, A90416W-21, and A92051W-D-2) recently released to control *D. noxia* (Souza *et al.* 2002). These plants exhibited no antibiosis resistance toward either aphid species. Mean densities of *D. noxia* were only 7%–11% lower on resistant plants than they were on 'Manning', and densities of *R. padi* were actually lowest on 'Manning' (Table 1). Two-way ANOVA produced the expected effect of aphid species ($F_{1,151} = 249.94$, $P < 0.001$), but no effect of plant cultivar ($F_{3,151} = 0.04$, $P = 0.99$) and no aphid species × plant cultivar interaction ($F_{3,151} = 0.18$, $P = 0.91$). Even after *R. padi* was removed from the analysis, the density of *D. noxia* did not vary among plant cultivars ($F_{3,76} = 0.38$, $P = 0.77$).

Wheat plants showing antibiosis toward *D. noxia* appear unlikely to reduce the population growth of *R. padi*. A recent study using the *Dn*5 gene as a source of antibiosis resistance showed that the population growth of *D. noxia* was substantially reduced on resistant plants, but population densities of *R. padi* and other cereal aphids were unaffected (Schotzko and Bosque-Pérez 2000). High specificity of *D. noxia* resistance perhaps should be expected because *D. noxia* and *R. padi* feed in different locations on wheat plants, elicit different changes in plant nutrients and secondary chemistry, and respond differently to the same changes in plant chemistry (Bergeson and Messina 1998; Sandström *et al.* 2000; Ni *et al.* 2001, 2002; Messina *et al.* 2002). Screening of other cereal pests can determine whether cross-resistance might still be found among cereal- and grass-feeding aphids that are more closely related to *D. noxia*, either phylogenetically or ecologically. Since many crops are attacked by a suite of related pest species, more research should be aimed at detecting cross-resistance and establishing the specificity of resistance mechanisms.

Effect of previous infestation

Two experiments examined aphid population growth as a function of both plant resistance and infestation history. Because traits that mediate resistance may need to be induced by aphid feeding, we were specifically interested in whether final population sizes would be especially low on *Dn*1-bearing resistant plants (IDO524) that had been infested previously. In Experiment 4, each plant in the previous-infestation treatment received 25 adults of *D. noxia*. After 6 days, these primary infestations reached mean (±SE) densities of 317.3 ± 12.5 aphids per 'Penawawa' plant *versus* 243.1 ± 13.4 aphids

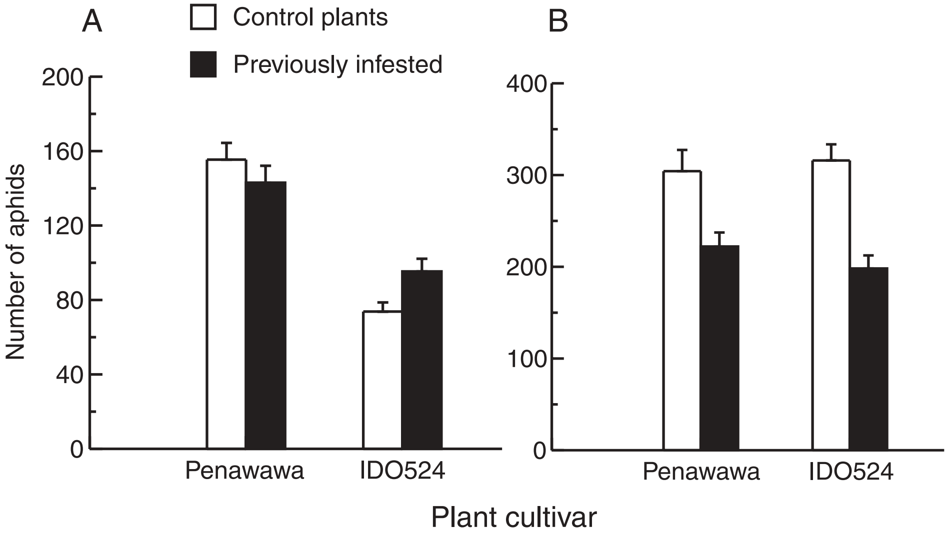

FIGURE. 1. Number (mean + SE) of aphids, *Diuraphis noxia* (A) and *Rhopalosiphum padi* (B), on susceptible (‘Penawawa’) and resistant (IDO524) wheat plants with different infestation histories. Counts were obtained 10–11 days after each plant received three adult aphids (*n* = 25–27 replicate plants per treatment).

per IDO524 plant ($t_{18} = 4.06$, $P = 0.001$). Although antibiosis resistance led to smaller populations on IDO524, the durations and sizes of the initial infestations on all plants should have been sufficient to induce changes in pathogenesis-related proteins and other potential defensive compounds (Forslund *et al.* 2000; Mohase and van der Westhuizen 2002).

After the primary infestation was removed, previously infested plants and control plants each received only three adults of *D. noxia*. Because each plant bore several leaves, any effect of infestation history would reflect variation in food quality rather than availability. Irrespective of infestation history, final aphid densities were lower on IDO524 plants than on the near-isogenic ‘Penawawa’ plants ($F_{1,100} = 79.70$, $P < 0.001$; Fig. 1A); however, no effect of infestation history was detected ($F_{1,100} = 0.94$, $P = 0.33$). In fact, the observed levels of resistance were opposite to the pattern that would be expected if resistance in IDO524 were elevated by previous infestation. Among control plants, final aphid densities were 52% lower on IDO524 than they were on ‘Penawawa’; among previously infested plants, the difference in aphid density between resistant and susceptible plants was only 33% (Fig. 1A). An interaction between the effects of plant cultivar and infestation history was detected ($F_{1,100} = 5.84$, $P = 0.02$).

Experiment 5 followed the same protocol but substituted *R. padi* for *D. noxia*. Mean (±SE) aphid densities of the primary infestation were similar on the two hosts (272.5 ± 11.3 on ‘Penawawa’ *versus* 251.7 ± 14.2 on IDO524; $t_{22} = 1.28$, $P = 0.23$), as would be expected if IDO524 possesses no antibiosis toward *R. padi* (see Table 1). Not surprisingly, plant cultivar also had no effect on final aphid counts ($F_{1,99} = 0.19$, $P = 0.66$; Fig. 1B). Population growth of *R. padi*, however, was influenced by infestation history, as densities were lower on previously infested plants than on control plants ($F_{1,99} = 31.25$, $P < 0.001$). Because the magnitude of this effect was similar on ‘Penawawa’ and IDO524 plants (Fig. 1B), there was no interaction between the effects of plant cultivar and infestation history ($F_{1,99} = 1.56$, $P = 0.22$). Thus, *D. noxia* was affected by plant cultivar but not infestation history, and the reverse was true for *R. padi*.

By using a factorial design, an earlier study showed that prior feeding by *D. noxia* on wheat seedlings had little effect on the subsequent performance of either itself or *R. padi*, whereas prior feeding by *R. padi* reduced its own subsequent performance but had little effect on the performance of *D. noxia* (Messina *et al.* 2002). The results of this study were similar, although we measured each species' performance only on plants previously infested by the same species. Resistance induced by prior *R. padi* infestation appears to be independent of the action of resistance genes for *D. noxia,* and its specificity (in which infestation by *R. padi* had little effect on the performance of *D. noxia*; Messina *et al.* 2002) precludes a simple mechanism such as reduced nutrient availability on *R. padi* infested plants.

For neither aphid species did we obtain evidence that aphid population growth was especially reduced on previously infested, resistant (IDO524) plants. The interaction between the effects of plant cultivar and infestation history in Experiment 4 suggested that, if anything, previous infestation by *D. noxia* lowered the level of antibiosis in IDO524 plants. This result may be artifactual, however, as it depended on the large difference in aphid density between control plants of 'Penawawa' and those of IDO524 in Experiment 4 (Fig. 1A), and would not have been obtained if this difference was more similar to that observed in Experiment 1 (Table 1). Our failure to detect increased antibiosis in previously infested IDO524 plants cannot be explained by insufficient time for induction to occur; Mohase and van der Westhuizen (2002) found that salicylic acid content and peroxidase activity increased in *Dn*1-bearing wheat plants within 12 h after infestation by *D. noxia* and continued to rise throughout the 120-h study period. To determine whether plant resistance is largely induced or constitutive, future studies should combine chemical assays of putative defense compounds with estimates of pest population growth, since increases in particular compounds following insect damage may not be causally related to variation in insect performance (Underwood *et al.* 2002).

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