Impact of *Diuraphis noxia* and *Rhopalosiphum padi* (Hemiptera: Aphididae) on Primary Physiology of Four Near-Isogenic Wheat Lines

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ABSTRACT The impact of feeding injury by the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), and bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) on susceptible and resistant wheat, *Triticum aestivum* L., near-isogenic lines 'Tugela' (susceptible), Tugela-*Dn1* (antibiotic), Tugela-*Dn2* (tolerant), and Tugela-*Dn5* (antixenotic) was evaluated by assessing photosynthetic parameters. Photosynthesis and closely related parameters, pigment composition, and nonstructural carbohydrates were measured at 1, 3, and 9 d after aphids were introduced on plants maintained under greenhouse conditions. Overall, *R. padi* had a higher reproductive capacity within a period of 9 d compared with *D. noxia* on all lines except Tugela-*Dn2*. Although the visible injury symptoms associated with aphid injury can be highly species specific, the data indicate that photosynthetic reduction is a common physiological pattern of wheat response to aphid feeding, irrespective of chlorosis elicitation. Although both aphids negatively affected net photosynthesis, *D. noxia* had a greater impact than *R. padi*, even when aphid numbers were considerably fewer for *D. noxia* (100–150 aphids per plant) compared with *R. padi* (>200 aphids per plant). The photosynthetic pigment and carbohydrate data suggest that the initial net photosynthesis reduction elicited by aphid feeding may not be directly related to the light reaction portion of the photosynthetic pathway via pigment losses. It is also unlikely that source–sink manipulation is the primary cause for the observed short-term inhibition of photosynthesis.

KEY WORDS plant–insect interactions, plant resistance, photosynthesis, photosynthetic pigments, herbivory

Wheat, *Triticum aestivum* L., hosts several aphid species (Hemiptera: Aphididae), such as Russian wheat aphid, *Diuraphis noxia* (Mordvilko); greenbug, *Schizaphis graminum* (Rondani); corn leaf aphid, *Rhopalosiphum maidis* (Fitch); bird cherry-oat aphid, *Rhopalosiphum padi* (L.); English grain aphid, *Sitobion avenae* (F.); and *Diuraphis tritici* (Gillette). Although piercing-sucking feeding behavior is similar across all aphid species, the development of injury symptoms associated with aphid feeding seems to be highly specific. For example, *R. padi* feeding on wheat does not elicit any visible injury symptoms, whereas *D. noxia* elicits highly visible leaf chlorosis.

The physiological and biochemical changes in wheat plants elicited by *D. noxia* feeding have been evaluated (Miller et al. 1994; van der Westhuizen and Pretorius 1996; Rafi et al. 1996; Haile et al. 1999; Ni et al. 2001, 2002; Ni and Quisenberry 2003; Macedo et al. 2003b). *D. noxia* usually feeds at the base of the youngest leaves of the plant, which is a strong sink for phloem-mobile mineral nutrients, amino compounds, and carbohydrates. By feeding at these sites, *D. noxia* can manipulate plant growth and development, altering carbohydrate-partitioning patterns of source–sink relationships within the plant (Burd et al. 1996). Additionally, Haile et al. (1999) demonstrated that *D. noxia*-resistant and -susceptible wheat cultivars respond differently to injury.

At a cellular level, *D. noxia* feeding is responsible for a sequence of events that can result in reductions in total chlorophyll (Fouche et al. 1984, Kruger and Hewitt 1984, Riedell 1989, Gellner et al. 1991, Burd and Todd 1992, Miller et al. 1994) and may possibly interfere with photosynthetic efficiency. Photosynthetic reductions associated with aphid-elicited loss of chlorophyll on potato, *Solanum tuberosum* L., also have been reported (Gibson et al. 1976, Ni et al. 2001).

Reductions in photosynthetic capacity elicited by aphids also might be a result of changes in transpiration rates, stomatal conductance, and root growth as demonstrated for susceptible wheat cultivars infested with greenbug (Gerloff and Ortman 1971, Ryan et al. 1987, Veen 1985, Wood et al. 1985, Wood and Tedders 1986, Riedell and Kieckhefer 1995). Reductions of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) regeneration with concurrent reductions

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on photosynthetic capacity also have been reported as a result of aphid feeding. Rafi et al. (1996) demonstrated that aphid feeding was responsible for reductions of the small and large units of Rubisco.

An important aspect of *D. noxia* management is host plant resistance, and improving our understanding of how *D. noxia* affects host physiology is important in identifying new targets for aphid resistance in wheat. Aphid resistance in wheat and barley, *Hordeum vulgare* L., has been extensively investigated (Du Toit 1989, Webster et al. 1991, Smith et al. 1992, Miller et al. 1994, Quisenberry and Schotzko 1994, Unger and Quisenberry 1997). The first *D. noxia*-resistant commercial cultivar of hard red winter wheat, 'Halt', was released in 1996 (Quick et al. 1996). Several studies have evaluated the impact of *D. noxia* feeding on different aphid-resistant wheat varieties, but they have produced inconsistent results (Burd and Elliott 1996; Rafi et al. 1996; van der Westhuizen and Pretorius 1995; Haile et al. 1999; Heng-Moss et al. 2003; Ni et al. 2001; Wang et al. 2004a, 2004b).

These variable results might be related to temporal aspects of the injury. The duration of infestation might be intimately linked with the biochemical and physiological response of wheat plants (Kriel et al. 1986, Aalbersberg et al. 1989, Hein et al. 1989, Hein 1992, Macedo et al. 2003b). In addition, previous studies demonstrated that although the mechanical injury pattern of different aphid species, such as *D. noxia* and *R. padi*, seems to be very similar, the salivary components in these species vary in composition, particularly oxido-reductases (catalase and peroxidase), which perhaps has a key role on injury-symptom development (i.e., leaf chlorosis) (Ni and Quisenberry 2003).

Macedo et al. (2003a, 2003b) demonstrated that reductions in photosynthesis from aphid injury are not initially associated with reductions in chlorophyll or with impairment of the light reactions of photosynthesis. Both studies indicated that the development of chlorosis and other photosynthetic impairments is consistent with injury associated with the formation of reactive oxygen species resulting from possible problems with quenching restoring excited photosynthetic pigments. Although a direct effect of aphid feeding on proteins associated with photosynthetic quenching is possible, problems in quenching are typically associated with end-product inhibition of photosynthesis.

Although Haile et al. (1999) demonstrated that *D. noxia*-resistant and -susceptible wheat cultivars respond differently to injury by *D. noxia*, no previous studies have compared physiological responses triggered by two aphid species. Therefore, the objective of our study was to assess the comparative impact of infestations by two aphid species—chlorosis-eliciting *D. noxia* and nonchlorosis-eliciting *R. padi*—in *D. noxia*-susceptible wheat line 'Tugela' and compare these to the impacts on the *D. noxia*-resistant near isogenic lines Tugela-*Dn1* (antibiosis), Tugela-*Dn2* (tolerance), and Tugela-*Dn5* (antixenosis).

Materials and Methods

Plants and Insect Materials. Both aphid species used in this study were obtained from colonies established from field collections. The *D. noxia* colony was established from collections in 1994 near Scottsbluff, NE. The *R. padi* colony was established from collections in 1996 near Lincoln, NE (Ni et al. 2001). A susceptible wheat variety, 'Stephens', was used to maintain both aphid colonies, as per previous studies (Macedo et al. 2003b, Heng-Moss et al. 2003). Colonies were maintained in Percival growth chambers (Percival Scientific, Perry, IA) at 21 ± 1°C, a photoperiod of 16:8 (L:D) h, and 40–50% RH at the Montana State University Plant Growth Center, Bozeman, MT.

The wheat lines evaluated were Tugela, a susceptible line to *D. noxia* injury, and the resistant near-isogenic lines Tugela-*Dn1* (antibiosis), Tugela-*Dn2* (tolerance), and Tugela-*Dn5* (antixenosis). Tugela was first released in 1993 (Du Toit 1988). Since then, several resistant cultivars have been released. Most of the resistant cultivars released contain the same single dominant gene (*Dn1*, *Dn2*, and *Dn5*) due to research efforts initiated in South Africa (Marasas et al. 1997).

Plants were grown individually in SC-10 Conetainers (3.81 cm in diameter by 21 cm depth) (Stuewe & Sons, Inc., Corvallis, OR) filled with equal parts of MSU PGC soil mix (equal parts of sterilized Bozeman Silt Loam soil: washed concrete sand and Canadian sphagnum peat moss) and Sunshine Mix one (Canadian sphagnum peat moss, perlite, vermiculite, and Dolmitic lime; Sun Gro Horticulture, Inc., Bellevue, WA) in a 32-m^2 greenhouse bay. The conetainers were placed in fitted racks, leaving sufficient space between paired individual conetainers to ensure adequate light interception by wheat seedlings. Plants were watered regularly and fertilized weekly with a 100 ppm mix (Peters 20–20-20 General). Greenhouse temperatures and RH were maintained at ≈22°C and 50% RH. Supplemental light was provided with GE Multi Vapor lamps (MVR1000/C/U, GE Lighting, General Electric Co., Cleveland, OH) with a photoperiod of 14:10 (L:D) h. The light intensity in the greenhouse at the canopy level, under a clear sky at midday was 970 μmol photons/m^2/s, recorded during photosynthetic measurements using a quantum sensor (model LI-190, LI-COR, Inc., Lincoln, NE).

Age-specific aphids were used in this study. Both aphid species were preconditioned following procedures by Budak et al. (1999). To infest wheat plants, either 0 or 15 aphids were introduced onto the second fully expanded leaf blade by using a camel's-hair brush. Aphids were confined on the seedlings using tubular, Plexiglas cages (30 cm in length by 4 cm in diameter). To ensure uniformity of environmental conditions, uninfested plants also were caged. Experiments were conducted in the same greenhouse bay used to grow experimental plant materials with the same environmental settings described above. The number of aphids was determined for each plant at 1, 3, and 9 d postinfestation.

The experimental design consisted of a split-split plot with four replications per treatment. Three evaluation dates (1, 3, and 9 d postinfestation) were considered the main plots within each trial. Aphid treatments (*D. noxia*, *R. padi*, and uninfested) were the subplots within each main plot, and lines (Tugela, Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5*) were considered the sub-subplots within each subplot. The experiment was repeated twice.

Aphid Reproductive Capacity. Aphid reproductive capacity was determined by following procedures described by Budak et al. (1999) for each insect species in different wheat lines at 1, 3, and 9 d postinfestation:

$$\text{Aphid reproductive capacity} = \text{final no. of aphids} - \text{initial no. of aphids}/\text{initial no. of aphids}$$

Net Photosynthesis and Closely Related Parameters. Determinations of leaf photosynthesis, transpiration, stomatal conductance, and intercellular CO_2 rates were recorded from the area injured by aphid feeding on each plant at 1, 3, and 9 d postinfestation. Photosynthesis measurements were taken using a portable photosynthesis system (model LI-6400, Li-Cor Inc.). Measurements were taken under 1,200 μmol photons/m^2/s light intensity, with 400 μmol/mol CO_2 reference concentrations at a constant flow of 500 μmol/s. Data were logged when the system was considered stable (i.e., photosynthesis changes were <0.1 μmol/m^2/s, and conductance changes were <0.05 μmol/m^2/s). In addition, the number of aphids was recorded on each evaluation date for all plants. Leaf material was then harvested and stored in a -80°C incubator for biochemical determination of chlorophyll content and composition of injured leaves as well as nonstructural carbohydrate assessments.

Pigment Characterization. Concentrations of total chlorophyll, chlorophyll *a*, chlorophyll *b*, chlorophyll *a*/*b* ratios, and carotenoids also were measured at 1, 3, and 9 d postinfestation. Measurements were taken from the area of feeding injury where the photosynthetic measurements were taken. For uninfested plants, the same area on corresponding leaves was used to measure the chlorophyll concentration to facilitate statistical comparison between infested and uninfested plants. Chlorophyll extraction followed methods by Wang et al. (2004a) and calculations of total chlorophyll, chlorophyll *a*, chlorophyll *b*, chlorophyll *a*/*b*, and carotenoid concentrations were based on the equation described by Bertrand and Schoefs (1997).

Nonstructural Carbohydrate Concentrations. After storage at -80°C, plant samples were dried at 70°C in a controlled airflow oven for 48 h, and then mechanically ground. Twenty-five milliliters of 0.02 M benzoic acid was added to a Folin-Wu tube containing 100 mg of plant sample. The mixture was autoclaved for 20 min on the steam cycle and slowly cooled. The autoclave procedure was repeated to ensure that nonstarch oligosaccharides and polysaccharides were hydrolyzed. Approximately 500-μl aliquots were then diluted to 750 μl with 50 mM potassium acetate, pH 5.0, and 0.02 M benzoic acid. Amylase/amyloglucosidase (250 μl) was added to the solution, which was then incubated at 42°C for 15 h. The glucose concentration was then determined according to the Nelson-Somogyi copper reducing method (Spiro 1966).

Statistical Analysis. Analysis of variance (ANOVA) procedures were performed to determine whether variances between experimental replicates were similar by inclusion in a model tested using the PROC MIXED procedure (SAS Institute 2001). The data were pooled when interactions between experiment replication and treatment were not significant. Pooled data were subsequently analyzed using mixed-model analysis (PROC MIXED, SAS Institute 2001). The effect of the aphid treatments on the wheat leaf photosynthetic capacity, total chlorophyll, chlorophylls *a* and *b*, carotenoids, and extractable glucose concentrations of the lines was evaluated for each measurement (Littell et al. 1996) with block and block-by-treatment assigned as random effects in the model. When appropriate, means were separated using Fisher least significant difference (LSD) procedure ($\alpha = 0.05$).

Results

Aphid Reproductive Capacity. We observed a significant difference in aphid numbers and their interaction with the explanatory variables aphid species, wheat lines, and postinfestation time ($F = 4.97$; df = 12, 72; $P < 0.0001$). An increase in aphid numbers was observed for all four lines within the 9-d study. We observed greater numbers of *R. padi* on both the *D. noxia*-susceptible Tugela and *D. noxia*-antibiotic Tugela-*Dn1* at the end of 9 d in comparison with the other lines, *D. noxia*-tolerant Tugela-*Dn2* and the *D. noxia*-antixenotic Tugela-*Dn5*. We also observed greater numbers of *R. padi* compared with *D. noxia* on all lines 9 d after infestation (Fig. 1).

Net Photosynthesis and Closely Related Parameters. Photosynthetic rate had a significant three-way interaction among aphid species, lines, and time postinfestation ($F = 5.34$; df = 12, 243; $P < 0.0001$). To facilitate comprehension of this three-way interaction, we will present our results in sections by aphid species.

Diuraphis noxia. We did not observe any significant differences in photosynthetic rates 1 d after infestation on the infested lines. Only Tugela-*Dn2* had a significant reduction in photosynthesis ($T = -2.66$, df = 243, $P = 0.01$). We observed significant photosynthetic rate reductions of 15.4, 27.9, and 20.4% for Tugela ($T = 2.44$, df = 243, $P = 0.0153$), Tugela-*Dn2* ($T = 5.06$, df = 243, $P < 0.0001$), and Tugela-*Dn5* ($T = 3.59$, df = 243, $P = 0.0004$), respectively. Injury by *D. noxia* did not affect photosynthesis of Tugela-*Dn1* 3 d after infestation. No significant differences in photosynthesis rates were observed 9 d postinfestation for infested Tugela-*Dn1*. However, significant reductions were observed on Tugela ($T = -2.55$, df = 243, $P =$

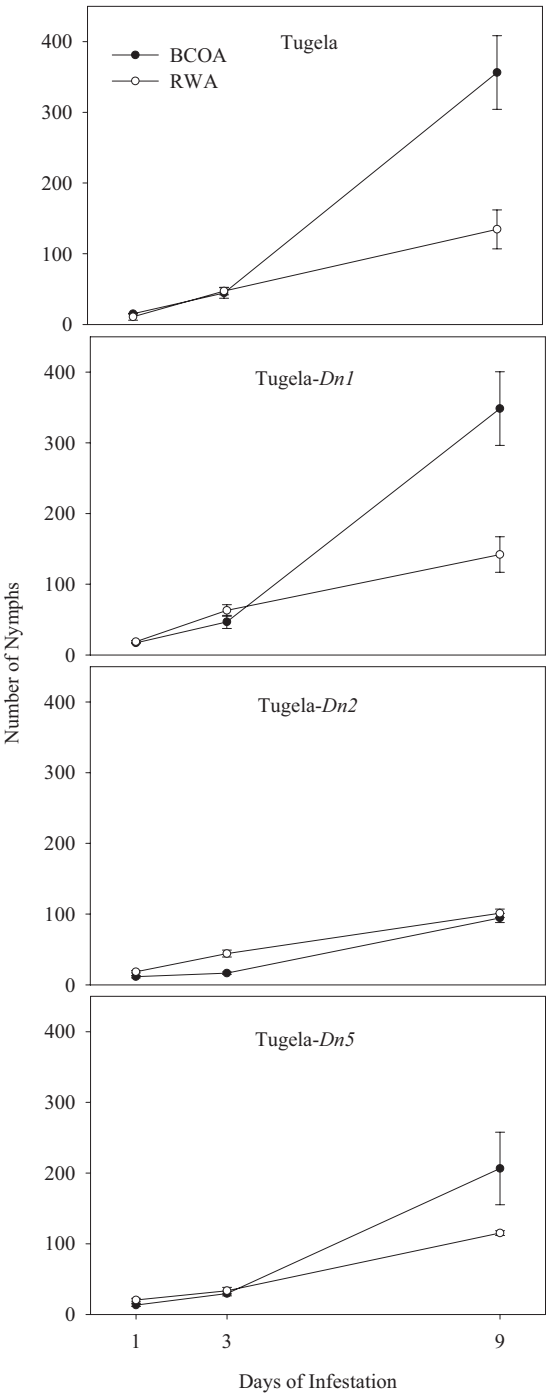

Fig. 1. Mean number of total aphids nymphs produced on each wheat near-isogenic line. The data are presented as days of infestation (x-axis) versus number of aphid nymphs (y-axis). BCOA, bird cherry-oat aphid; RWA, Russian wheat aphid.

0.0115), Tugela-*Dn2* ($T = -2.61$, df = 243, $P = 0.0095$), and Tugela-*Dn5* ($T = -5.58$, df = 243, $P < 0.0001$) at 9 d postinfestation (Table 1).

Changes in photosynthetic rates were accompanied by significant changes in closely related photosynthetic parameters, such as stomatal conductance, transpiration, and intercellular CO_2 concentrations. Aphid feeding had a significant impact on stomatal responses 1 d postinfestation ($F = 4.14$; df = 12, 243; $P < 0.0001$). We observed significantly lower stomatal conductance for infested Tugela-*Dn2* ($T = 3.85$, df = 243, $P = 0.0002$) and Tugela-*Dn5* ($T = 3.80$, df = 243, $P = 0.0004$) compared with the uninfested counterparts. At 3 d postinfestation, we observed significantly smaller stomatal conductance values in infested Tugela-*Dn2* ($T = 6.11$, df = 243, $P < 0.0001$) and Tugela-*Dn5* ($T = 3.70$, df = 243, $P = 0.0003$) compared with infested Tugela. Lesser stomatal conductance values were also observed in infested Tugela-*Dn1* ($T = 3.81$, df = 243, $P = 0.0002$), Tugela-*Dn2* ($T = 4.02$, df = 243, $P < 0.0001$), and Tugela-*Dn5* ($T = 3.14$, df = 243, $P = 0.002$) compared with the uninfested counterparts. After 9 d of feeding, no significant differences in stomatal conductance were observed between any infested and uninfested line.

We observed a significant impact of aphid feeding on transpiration rates of lines Tugela-*Dn2* and Tugela-*Dn5* 1 d after infestation. Significantly smaller transpiration rates were observed in infested Tugela-*Dn2* ($T = 6.38$, df = 243, $P < 0.0001$) and Tugela-*Dn5* ($T = 6.38$, df = 243, $P < 0.0001$) compared with the infested Tugela. When infested, both Tugela-*Dn2* ($T = 2.67$, df = 243, $P = 0.0081$) and Tugela-*Dn5* ($T = 2.24$, df = 243, $P = 0.026$) showed significantly lower transpiration rates compared with their uninfested counterparts. At 3 d postinfestation, we observed significantly lower transpiration rates in the infested Tugela-*Dn2* ($T = 3.11$, df = 243, $P = 0.002$) and Tugela-*Dn5* ($T = 5.10$, df = 243, $P < 0.0001$) compared with their Tugela counterparts. Conversely, infested lines showed significantly lower transpiration rates compared with their uninfested counterparts. When the aphids fed for 9 d, infested Tugela showed significantly lower transpiration rates compared with uninfested Tugela ($T = 2.96$, df = 243, $P = 0.003$). A similar response was observed for Tugela-*Dn5* ($T = 3.17$, df = 243, $P = 0.002$).

Intercellular CO_2 concentrations were significantly different between Tugela and Tugela-*Dn2* ($T = 5.20$, df = 243, $P < 0.0001$) or Tugela-*Dn5* ($T = 2.23$, df = 243, $P = 0.027$) 1 d after infestation. Infested Tugela had a greater intercellular CO_2 concentration than infested Tugela-*Dn2* or Tugela-*Dn5*. We only observed lower intercellular CO_2 concentrations between infested and uninfested plants for Tugela-*Dn2* ($T = 5.11$, df = 243, $P < 0.0001$). We did not observe any impact of aphid feeding on the intercellular CO_2 concentrations of any lines at three or 9 d after infestation.

Rhopalosiphum padi. Our results showed that the impact for *R. padi* and *D. noxia* on photosynthetic rates of the lines were similar. Only infested Tugela-*Dn2* had a 12.2% reduction of its photosynthetic rates 1 d after infestation ($T = -2.43$, df = 243, $P = 0.02$) compared with its uninfested counterpart. Signifi-

Table 1. Means ± SE of temporal changes in photosynthesis of different wheat near-isogenic lines (Tugela, Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5*) in response to aphid treatments (uninfested, *R. padi*, or *D. noxia*)

Days after infestation	Aphid	Tugela (susceptible)	Tugela-*Dn1* (antibiotic)	Tugela-*Dn2* (tolerant)	Tugela-*Dn5* (antixenotic)
1	Check	21.6 ± 1.1aX	24.5 ± 0.7bX	26.5 ± 1cX	22.7 ± 1.4abX
	R. padi	21.7 ± 0.9aX	22.5 ± 0.5aX	23.3 ± 0.6aY	22.2 ± 0.8aX
	D. noxia	21.1 ± 0.4aX	23.1 ± 1.4bX	23 ± 1.4bY	20.3 ± 0.9aX
3	Check	21.1 ± 0.4aX	23.6 ± 0.5bX	24.1 ± 0.5bX	23.4 ± 0.8bX
	R. padi	18.1 ± 1.3aY	22.5 ± 0.6bX	18.0 ± 1.2aY	20.4 ± 1.2aY
	D. noxia	17.8 ± 1.4aY	23.1 ± 0.2bX	17.4 ± 0.4aY	18.6 ± 0.4aZ
9	Check	19.3 ± 1.9aX	16.8 ± 0.8aX	16.7 ± 0.7aX	13.5 ± 1.6bX
	R. padi	14.4 ± 1.3aY	18.2 ± 0.8bY	19.7 ± 0.9bY	18.8 ± 0.9bY
	D. noxia	15.9 ± 1aY	14.8 ± 1.1aZ	20.1 ± 1.6bY	20.9 ± 0.9bZ

Means followed by different letters are significantly different ($\alpha = 0.05$); X, Y, and Z indicate differences within columns for each sampling date postinfestation (1, 3, and 9 d); a and b indicate differences within rows.

cantly lower photosynthetic rates were observed 3 d postinfestation only for Tugela ($T = -2.25$, df = 243, $P = 0.03$), Tugela-*Dn2* ($T = -4.55$, df = 243, $P < 0.0001$), and Tugela-*Dn5* ($T = -2.21$, df = 243, $P = 0.03$), with reductions of 14.2, 25, and 12.5%, respectively. At 9 d postinfestation, significant reductions were observed on infested Tugela ($T = -3.70$, df = 243, $P = 0.0003$), Tugela-*Dn2* ($T = -2.20$, df = 243, $P = 0.0289$), and Tugela-*Dn5* ($T = -3.97$, df = 243, $P < 0.0001$).

Similar to our observations for *D. noxia*, stomatal conductance, transpiration rates, and intercellular CO_2 were significantly affected by *R. padi* feeding. We observed significantly lower stomatal conductance 1 d postinfestation in Tugela-*Dn2* ($T = 5.29$, df = 243, $P < 0.0001$) and Tugela-*Dn5* ($T = -4.38$, df = 243, $P < 0.0001$) compared with their uninfested counterparts. We also observed lower conductance in infested Tugela-*Dn2* ($T = 4.60$, df = 243, $P < 0.0001$) and Tugela-*Dn5* ($T = 4.60$, df = 243, $P < 0.0001$) compared with the infested Tugela line. Three days postinfestation only the infested Tugela-*Dn1* ($T = 2.43$, df = 243, $P = 0.016$) and Tugela-*Dn2* ($T = 3.94$, df = 243, $P = 0.0006$) had significant lower stomatal conductance compared with their Tugela-infested counterparts. When compared with their uninfested counterparts, significant reductions were observed in Tugela ($T = 5.32$, df = 243, $P < 0.0001$), Tugela-*Dn1* ($T = 3.55$, df = 243, $P = 0.0005$), Tugela-*Dn2* ($T = 3.02$, df = 243, $P = 0.003$), and Tugela-*Dn5* ($T = 2.79$, df = 243, $P = 0.006$). Nine days postinfestation, we observed significant reductions in stomatal conductance in infested Tugela-*Dn2* ($T = 2.57$, df = 243, $P = 0.011$) and Tugela-*Dn5* ($T = 3.35$, df = 243, $P = 0.0009$) lines compared with the infested Tugela-*Dn1* line. No significant differences in stomatal conductance were observed between any infested and uninfested line, except Tugela-*Dn5* line ($T = 2.34$, df = 243, $P = 0.019$).

Significantly lower transpiration rates were observed in infested Tugela-*Dn2* ($T = 6.38$, df = 243, $P < 0.0001$) and Tugela-*Dn5* ($T = 6.38$, df = 243, $P < 0.0001$) compared with the infested Tugela. When infested, lower transpiration rates were observed on Tugela-*Dn2* ($T = 2.67$, df = 243, $P = 0.008$) and Tugela-*Dn5* ($T = 2.24$, df = 243, $P = 0.026$) compared with their uninfested counterparts. Three days postinfestation, we observed significantly greater transpiration rates in the infested Tugela-*Dn1* ($T = 2.78$, df = 243, $P = 0.006$) and Tugela-*Dn2* ($T = 3.41$, df = 243, $P = 0.0008$) compared with their Tugela counterparts. Conversely, all infested lines tested showed significantly lower transpiration rates when compared with their uninfested counterparts. After 9 d of feeding, the infested Tugela had lower transpiration rates than Tugela-*Dn2* ($T = 2.98$, df = 243, $P = 0.003$) or Tugela-*Dn5* ($T = 3.96$, df = 243, $P < 0.0001$). Additionally, we did not observed any significant difference between transpiration rates of infested lines compared with their uninfested counterparts.

Significant intercellular CO_2 differences between Tugela and Tugela-*Dn2* or Tugela-*Dn5* concentrations were observed 1 d after infestation. Lower intercellular CO_2 concentrations were observed in infested Tugela compared with infested Tugela-*Dn2* ($T = 4.67$, df = 243, $P < 0.0001$) or Tugela-*Dn5* ($T = 7.24$, df = 243, $P < 0.0001$). We also observed lower intercellular CO_2 concentrations in uninfested Tugela-*Dn2* ($T = 4.67$, df = 243, $P < 0.0001$) and Tugela-*Dn5* ($T = 6.76$, df = 243, $P < 0.0001$) compared with their infested counterparts. We did not observe any impact of *R. padi* on the intercellular CO_2 concentrations of any lines at three or 9 d after infestation.

Pigment Characterization. Total chlorophyll concentration, as determined by biochemical extractions, had a three-way interaction with the treatment factors time postinfestation, wheat line, and aphid species ($F = 2.46$; df = 12, 165; $P = 0.006$). Chlorophyll *a* concentrations also were significantly influenced by the interactions among treatment factors ($F = 2.75$; df = 12, 165; $P = 0.002$). There were no significant interactions between time postinfestation, aphid species, and lines for chlorophyll *b* concentrations. There was no effect of aphid species or the interactions with other parameters on this pigment. However, there was a significant effect of time postinfestation, lines, and the interactions ($F = 22.82$; df = 6, 165; $P < 0.0001$) (Table 3). In addition, carotenoids and chlorophyll *a*/*b* ratios were not significantly affected by any treatments imposed in this study (Table 2 and 3).

Diuraphis noxia. Feeding by *D. noxia* elicited significant responses in total chlorophyll content of the lines 1 d after infestation. Lower total chlorophyll

Table 2. Means ± SE of temporal changes of total chlorophyll concentrations (micrograms per gram of leaf) of different wheat near-isogenic lines (Tugela, Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5*) in response to aphid treatments (uninfested, *R. padi*, or *D. noxia*)

Days after Infestation	Aphid	Tugela (susceptible)	Tugela-*Dn1* (antibiotic)	Tugela-*Dn2* (tolerant)	Tugela-*Dn5* (antixenotic)
1	Check	237.9 ± 23.2aX	263.2 ± 17.2aX	714.9 ± 41.9bX	340.3 ± 48.6cX
	R padi	248.8 ± 13.9aX	202.1 ± 21.9aX	547.2 ± 52.3bY	635.5 ± 70.1bY
	D. noxia	235.9 ± 9.7aX	86.8 ± 7.9bY	532.5 ± 62.2cY	502.1 ± 56.7cY
3	Check	243.6 ± 14.7aX	307.1 ± 33.4bX	1452.9 ± 150.8cX	2307.1 ± 494.5dX
	R padi	709.6 ± 47.9aY	305.0 ± 10.1bX	1275.7 ± 204.6cX	2277.9 ± 124.1dX
	D. noxia	273.0 ± 17.9aX	258.6 ± 22.5aY	1431.2 ± 219.1bX	1456.9 ± 275.9bX
9	Check	133.3 ± 24.1aX	299.6 ± 41.3bX	383.6 ± 4.2cX	478.8 ± 47.9dX
	R padi	235.9 ± 12.1aY	284.0 ± 15.9bX	554.7 ± 28.1cY	552.6 ± 17.9cY
	D. noxia	213.9 ± 29.8aY	145.3 ± 8.6bY	247.4 ± 68.5aZ	479.1 ± 64.1cXY

Means followed by different letters are significantly different ($\alpha = 0.05$); X, Y, and Z indicate differences within columns for each day postinfestation (1, 3, and 9 d); a, b, c, and d indicate differences within rows.

contents were observed on infested Tugela and Tugela-*Dn1* compared with the remaining lines. In addition, *D. noxia* had a significant negative impact on total chlorophyll content of Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5* lines compared with the other aphid treatments (Table 2).

At 3 d after infestation, significantly higher total chlorophyll concentrations were observed on Tugela-*Dn2* and Tugela-*Dn5* compared with the other *D. noxia*-infested lines. When *R. padi*- and *D. noxia*-infested leaf-blades were compared, significantly greater total chlorophyll concentrations were observed in *R. padi*-infested Tugela and Tugela-*Dn1*. Nine days after infestation, Tugela-*Dn1* showed lower total chlorophyll concentrations compared with the other *D. noxia*-infested lines. In addition, *D. noxia* infested Tugela-*Dn5* had significantly greater total chlorophyll content than all lines tested. When aphid infested leaf-blades were compared, we observed significantly lower chlorophyll concentrations on *D. noxia*-infested Tugela-*Dn1* and -*Dn2* compared with either *R. padi*-infested or uninfested leaf blades (Table 2).

Chlorophyll *a* concentrations were significantly affected by aphid injury. Infested Tugela-*Dn2* and Tugela-*Dn5* had greater chlorophyll *a* concentration than Tugela and Tugela-*Dn1* lines at 24 h. Significantly lower chlorophyll *a* concentrations were observed on infested Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5* compared with their paired uninfested plants. In general, *D. noxia* injured leaf blades had lower chlorophyll *a* concentrations than those infested with *R. padi*. Three days after infestation, injured Tugela-*Dn2* and Tugela-*Dn5* had greater chlorophyll *a* concentrations than Tugela and Tugela-*Dn1*. In addition, greater chlorophyll *a* concentrations were observed in injured Tugela, Tugela-*Dn1*, and Tugela-*Dn5* plants infested with *R. padi* than *D. noxia* infested lines. At 9 d after infestation, we observed significant differences in chlorophyll *a* concentrations only between *D. noxia*-infested Tugela-*Dn1* and Tugela-*Dn5*. In addition, *D. noxia*-injured leaf blades of Tugela-*Dn1* and Tugela-*Dn2* had lower chlorophyll *a* concentrations than their paired *R. padi*-infested plants.

Rhopalosiphum padi. Significant differences were observed among infested lines after 1 d. Infested Tugela and Tugela-*Dn1* lines had significantly lower total chlorophyll concentrations than Tugela-*Dn2* or Tugela-*Dn5* infested lines. In addition, *R. padi*-infested leaf blades of Tugela-*Dn2* and Tugela-*Dn5* had lower total chlorophyll concentrations than of their paired uninfested plants. Three days after infestation, all lines infested with *R. padi* were significantly different from each other (Table 2). However, only the total chlorophyll from *R. padi*-infested Tugela was significantly different from either *D. noxia* or the uninfested paired plants. Aphid feeding had significant impact on total chlorophyll 9 d after infestation. In

Table 3. Means ± SE of temporal changes of chlorophyll *a* concentrations (micrograms per gram leaf) of different wheat near-isogenic lines (Tugela, Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5*) in response to aphid treatments (uninfested, *R. padi*, or *D. noxia*) over three postinfestation periods (1, 3, and 9 d)

Days after Infestation	Aphid	Tugela	Tugela-*Dn1*	Tugela-*Dn2*	Tugela-*Dn5*
1	Check	205.5 ± 21.2aX	207.7 ± 4.6aX	633.7 ± 38.4bX	263.5 ± 56aX
	R padi	201.1 ± 9.5aX	174.6 ± 17.2aY	476.2 ± 42.3bY	515.9 ± 32.3bY
	D. noxia	200.3 ± 7.3aX	75.8 ± 6.1bZ	458.9 ± 45.9cY	424.9 ± 45.5cZ
3	Check	208.3 ± 13.6aX	262.2 ± 28.8bX	1221.6 ± 130cX	1943 ± 415.5dX
	R padi	598.4 ± 39.6aY	258.1 ± 11.4bX	1055.9 ± 157.5cX	1905.7 ± 111.8dX
	D. noxia	230.2 ± 19aX	206.9 ± 17.9aY	1168.9 ± 173.5cX	1184.4 ± 217.7cX
9	Check	110 ± 19.2aX	238.6 ± 37.6bX	322 ± 3.8cX	404.5 ± 39.7dX
	R padi	196.8 ± 9.2aY	232.5 ± 13.1bX	467.5 ± 22.5cY	464.3 ± 16.3cX
	D. noxia	176.5 ± 25.3aY	116.9 ± 7.5bY	207.4 ± 57.5aZ	407.5 ± 56.1cX

Means followed by different letters are significantly different ($\alpha = 0.05$); X, Y, and Z indicate differences within columns for each day postinfestation (1, 3, and 9 d); a, b, c, and d indicate differences within rows.

Table 4. Means ± SE of temporal changes of chlorophyll *b* concentration (micrograms per gram leaf) of different wheat isogenic lines (Tugela, Tugela-*Dn1*, Tugela-*Dn2*, and Tugela-*Dn5*)

Wheat isoline	Chlorophyll *b* (μg/g) Days of Infestation		
	1	3	9
Tugela	38.6 ± 4.5aX	63.1 ± 9aX	33.3 ± 2.9aX
Tugela-*Dn1*	31.3 ± 8.3aX	47.8 ± 3.5aX	46.9 ± 4.4aX
Tugela-*Dn2*	75.3 ± 7.3aY	237.8 ± 24.9bY	62.9 ± 6.1aX
Tugela-*Dn5*	91.2 ± 16.1aY	336.3 ± 34.4bX	78.1 ± 4.2cY

Means followed by different letters are significantly different ($\alpha = 0.05$); X and Y indicate differences within columns; a and b indicate differences within rows.

general, all lines had total chlorophyll concentrations that were significantly different when infested with *R. padi*. The *R. padi*-infested plants from the lines Tugela, Tugela-*Dn2*, and Tugela-*Dn5* had greater total chlorophyll concentrations than the paired uninfested plants.

When infested, Tugela-*Dn2* and Tugela-*Dn5* had greater chlorophyll *a* concentration than Tugela or Tugela-*Dn1* at 24 h after infestation. Infested lines Tugela-*Dn1* and Tugela-*Dn5* had greater chlorophyll *a* concentrations than their paired uninfested plants. Three days after infestation, significant differences were observed among all lines (Tables 3 and 4). Similar results were observed on the lines 9 d after infestation (Table 3).

Nonstructural Carbohydrate Concentrations. The aphid species did not elicit significant changes in nonstructural carbohydrate concentrations, which were assessed via determination of extractable glucose present in the plant material when the lines were exposed to feeding for 1 d. However, significant differences occurred 3 and 9 d after infestation (Fig. 2).

Diuraphis noxia. Aphid feeding by *D. noxia* elicited significant changes only in Tugela. Infested Tugela had significantly lower glucose concentrations compared with its uninfested counterpart. No other significant differences were observed for any infested lines. After 9 d, injury by both aphids altered glucose concentrations of Tugela-*Dn1*, which had significantly higher glucose concentrations than infested Tugela-*Dn2* or Tugela-*Dn5*. In addition, Tugela infested with this species had glucose concentrations lower than infested Tugela-*Dn1*, Tugela-*Dn2*, or Tugela-*Dn5*.

Rhopalosiphum padi. This aphid species had a significant effect on infested Tugela, which had significantly lower glucose concentrations compared with infested Tugela-*Dn1*, Tugela Tugela-*Dn2*, or Tugela-*Dn5*. After 9 d, Tugela-*Dn1* showed significantly lower concentrations than Tugela-*Dn2* or Tugela-*Dn5*. Infested Tugela also had significantly lower concentrations than infested Tugela-*Dn2* or Tugela-*Dn5*.

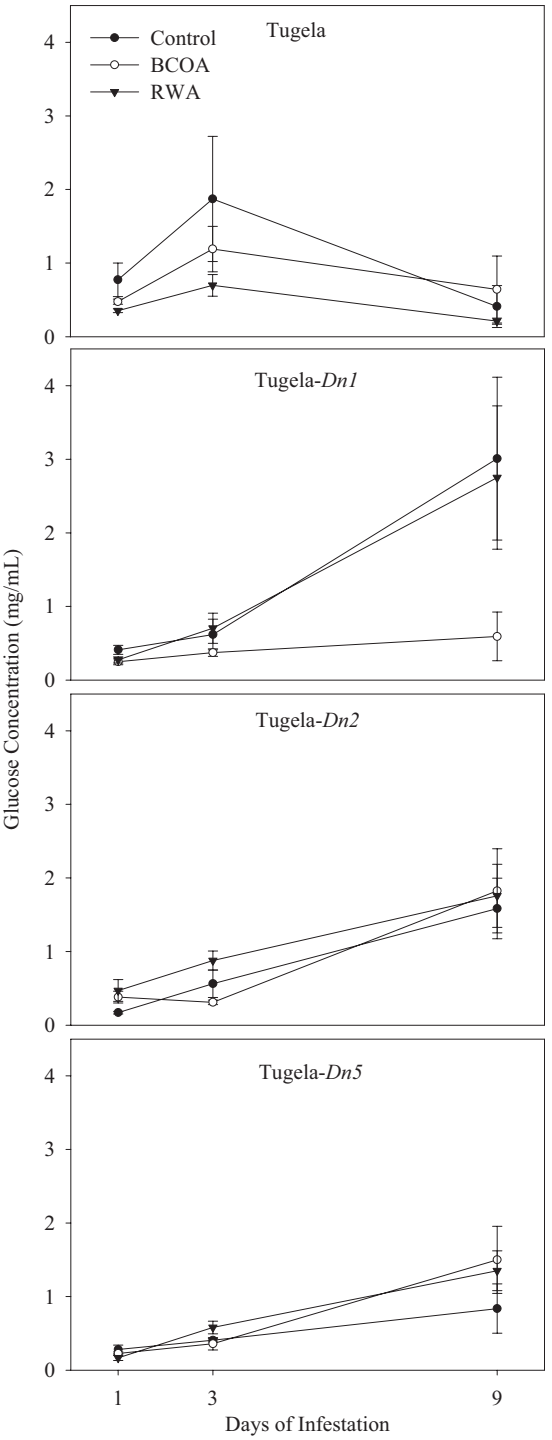

Fig. 2. Aphid impact on glucose concentration from aphid-infested and uninfested wheat near-isogenic line. The data are presented as days of infestation (x-axis) versus glucose concentration (y-axis). Control, uninfested; BCOA, bird cherry-oat aphid; RWA, Russian wheat aphid.

Discussion

Resistance mechanisms associated with the wheat near-isogenic lines in this study might have different impacts on the reproductive capacity of *D. noxia* and

R. padi. Overall, *R. padi* seemed to have a greater reproductive capacity within a period of 9 d compared with *D. noxia* on all lines except for the tolerant line Tugela-*Dn2.* Although Tugela-*Dn2* had similar impacts on both species, holding populations at 100 individuals, remarkable differences were observed in the lines expressing susceptible or antibiosis traits. These traits had no significant impact on reproductive capacity of *R. padi*, at least for the duration of the study. Heng-Moss et al. (2003) reported lower numbers of *D. noxia* on tolerant and antibiotic lines after a 7-d period of infestation compared with the susceptible line. The differences between our results and the results of their study could be due to differences in the initial number of aphids used to infest the plant materials. Heng-Moss et al. (2003) used 0 or 20 aphids per leaf blade, whereas this study began with 0 or 15 aphids per leaf blade. However, our results were similar to those reported by Wang et al. (2004b). Although their study was conducted in a growth chamber, they reported that *R. padi* was differentially affected by the resistance mechanisms expressed by these Tugela lines.

Although the visible injury symptoms associated with aphid injury might be highly species specific, our data indicate that there seems to be a common physiological pattern of wheat response to aphid feeding. The tolerant Tugela-*Dn2* showed a significant reduction in net photosynthetic rates 1 d after infestation. This indicates that, independent of the tolerance trait, aphids might have a short-term negative impact on wheat primary physiology. This potentially affects the capacity to cope with other biotic and abiotic stresses, such as pathogen infection, other types of herbivory, and adverse environmental conditions. The susceptible Tugela and antixenotic Tugela-*Dn5* lines also had net photosynthetic reductions by both aphid species at 3 and 9 d postinfestation. Although both aphids negatively affected net photosynthesis, *D. noxia* had a greater effect, even when aphid numbers were considerably less (100–150 aphids per plant) compared with >200 observed in the antixenotic line infested with *R. padi.* Our findings, therefore, support the findings of Ni and Quisenberry (2006) on the influence of injury-symptom formation by *R. padi* and *D. noxia.*

Based on our pigment and carbohydrate data, which were affected differently among the injured lines, the initial net photosynthesis reduction on plants due to aphid feeding might not be directly related to the light reaction portion of the photosynthetic pathway via pigment losses. This was previously reported for potato (Gibson et al. 1976, Ni et al. 2001). It is also unlikely that source-sink manipulation is the primary cause for the observed short-term inhibition of photosynthesis. Our data suggest that the main mechanism involved is related to stomatal limitation or CO_2 uptake, which potentially has a significant effect on Rubisco regeneration (Rafi et al. 1996).

Macedo et al. (2003b) observed similar results when characterizing the impact of *D. noxia* on the susceptible wheat variety 'Arapahoe'. Their results suggested that early stages of the development of *D. noxia* feeding injury symptoms (i.e., leaf rolling and chlorotic streaks) on susceptible seedlings is a light-activated process, even though the elicitor of the symptoms is aphid feeding. In addition, Macedo et al. (2003a) also observed that soybean aphids, *Aphis glycines* Matsumura, even in low densities were responsible for photosynthetic rate reductions of as much as 50% on infested soybean, *Glycine max* (L.) Merr., leaflets, including leaflets with no apparent symptoms of aphid injury such as chlorosis. The results from the current study support the evidence that substantial physiological impact on plants is possible even at relatively low aphid densities. Also, the conventional view of aphid injury acting primarily through reductions in chlorophyll content is not supported by our findings.

In conclusion, this study demonstrates that the wheat near-isogenic lines with different *D. noxia*-resistance mechanisms differentially affected nonchlorosis-eliciting *R. padi* and chlorosis-eliciting *D. noxia.* Reproductive capacity of *R. padi* seemed not to be affected by any of the *D. noxia*-resistant near-isogenic lines, except Tugela-*Dn2.* Although *R. padi* has a higher reproductive capacity than *D. noxia* on Tugela, Tugela-*Dn1* and Tugela-*Dn5* lines, reproductive capacity of both *R. padi* and *D. noxia* on Tugela-*Dn2* was similar. The finding indicates that Tugela-*Dn2* might be resistant to both *D. noxia* and *R. padi.* The photosynthetic pigment data suggest that aphid injury symptom development in wheat plants might be highly species specific. In contrast, glucose and photosynthetic measurement data suggest that nonchlorosis-eliciting *R. padi* and chlorosis-eliciting *D. noxia* feeding elicit similar primary physiological responses. Further, by examining two aphid species and different near-isogenic wheat lines, photosynthetic impairment does not seem to be a direct consequence of chlorophyll degradation or end-product inhibition.

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