

Crop Mineral Nutrient and Yield Responses to Aphids or *Barley Yellow Dwarf Virus* in Spring Wheat and Oat

Walter E. Riedell,* Shannon L. Osborne, and Abdullah A. Jaradat

ABSTRACT

Root system biomass reductions caused by aphid feeding or aphid-transmitted viral disease may affect root system function in spring wheat (*Triticum aestivum* L.) or oat (*Avena sativa* L.). A 2-yr field experiment was conducted to determine how leaf mineral nutrients (N, P, K, Ca, Mg, Zn, Fe, Mn, and Cu), chlorophyll (chl), and agronomic traits (leaf area index [LAI], leaf area plant⁻¹, midday differential canopy temperature deviation from control [dT], yield, and yield components) responded to crop stress imposed by aphid feeding (greenbugs [GB], *Schizaphis graminum* Rondani; Russian wheat aphids [RWA], *Diuraphis noxia* Mordvilko; bird cherry-oat aphids [BCOA], *Rhopalosiphum padi* L.) or by an aphid-vectored virus (*barley yellow dwarf virus*, *Luteovirus*, PAV strain [BYDV]). Leaf chl, N, Ca, and Mg concentrations (measured at the boot development stage) were about 25% less in BYDV-infected than control treatments. Grain yield deviation from control (dY) was most negative for BYDV treatment (−2164.5 kg ha⁻¹) and least negative for GB treatment (−745.5 kg ha⁻¹), with RWA (−900.6 kg ha⁻¹) and BCOA (−789 kg ha⁻¹) treatments having intermediate effects. Mineral nutrients (N, K, Mg, and Mn) and chl were significantly correlated (Canonical $r = 0.94$, $p < 0.0001$) with agronomic traits (LAI, dT, leaf area, and grain yield), and explained 62.1% of the variation in agronomic traits. Thus, leaf concentrations of certain chemical constituents of cereal plants are highly correlative to agronomic traits important in cereal plant responses to stress caused by aphid-feeding damage or aphid-vectored disease.

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Abbreviations: BCOA, bird cherry-oat aphids; BYDV, *barley yellow dwarf virus*; chl, chlorophyll; dT, midday differential canopy temperature deviation from control; dY, grain yield deviation from control; GB, greenbug; LAI, leaf area index; RWA, Russian wheat aphids; TKWT, thousand kernel weight.

CEREAL CROP PRODUCTIVITY in the U.S. Great Plains is often reduced by aphid infestations (*Rhopalosiphum padi* L., bird cherry-oat aphids [BCOA]; *Schizaphis graminum* Rondani, greenbug [GB]; and *Diuraphis noxia* Mordvilko, Russian wheat aphids [RWA]; Kieckhefer et al., 1995) and aphid-vectored virus infection (*barley yellow dwarf virus*, BYDV; Hoffman and Kolb, 1997). Assimilate removal from the shoot vascular tissue during aphid feeding causes stress in cereal crops (Riedell, 1989; Al-Mousawi et al., 1983). In addition, GB and RWA inject salivary substances during feeding, which causes leaf chlorosis and necrosis in and around the feeding site (Burd, 2002; Dorschner et al., 1987; Miles, 1999). Greenbug feeding damage is characterized by chlorotic and necrotic lesions in and around feeding sites on older leaves (Dorschner et al., 1987). Russian wheat aphids feed on younger leaves, causing symptoms that include longitudinal chlorotic streaking and leaf rolling, resulting in convolute leaf morphology (Webster et al., 1987). Bird cherry-oat aphids cause no dramatic leaf damage symptoms (Kieckhefer et al.,

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1995), suggesting that this aphid species does not inject toxic salivary substances during feeding. Yield losses of 35 to 60% have been reported for small grains damaged by each of these three cereal aphid species.

Barley yellow dwarf virus is a phloem-restricted *Luteovirus* obligately vectored by several species of aphids (Kolb et al., 1991). Plants infected with BYDV appear stunted and chlorotic when compared with uninfected plants (Hoffman and Kolb, 1997). Other symptoms of BYDV infection include red leaf discoloration, leaf chlorosis and necrosis, reduced tiller number, delayed heading, and yield losses up to 70% (Cook and Veseth, 1991). In general terms, BYDV infection can be considered to cause chronic injury in cereal plants because, once infected, plants will not recover from the infection. In contrast, under most conditions, cereal aphid infestation causes acute injury from which the plant can recover if the aphids are removed (Riedell et al., 2003).

Burton (1986) demonstrated that significant winter wheat (*Triticum aestivum* L.) root system biomass reductions occur when GB feeding causes substantial damage to plant shoots. Feeding by GB, RWA, or BCOA that resulted in shoot growth reductions in spring wheat also caused reductions in total root length (Riedell and Kieckhefer, 1995). Cereal plants treated with BYDV had about a 40% decrease in total root length compared with control plants (Riedell et al., 2003). The effects of BYDV infection on roots are more rapid and severe than on the shoots (Kolb et al., 1991). BYDV-infected plants had less root length and smaller root-to-shoot ratios than uninfected plants (Hoffman and Kolb, 1997). It is not known how root system function is affected by changes in root system length or biomass caused by aphid feeding or BYDV infection damage.

Because root systems provide shoot organs with essential mineral nutrients, potential reductions in root system function of aphid- or BYDV-infected plants may play an important role in grain yield reductions (Riedell et al., 2003). We hypothesized that a field study of cereal aphid and aphid-borne disease effects on cereal crop mineral nutrition would provide information on how root function and shoot mineral concentrations are affected when plants are damaged by these stress-causing biological organisms. The objectives of this 2-yr field study were to determine how plant stress caused by three different aphid species or an aphid-vectored viral disease affected leaf mineral nutrients, chlorophyll (chl), and agronomic traits (leaf area, canopy temperature, yield, and yield components) in wheat and oat (*Avena sativa* L.).

MATERIALS AND METHODS

Field Experiment Design and Treatments

Experiments were conducted at the Eastern South Dakota Soil and Water Research Farm near Brookings, SD (44° 19' N lat., 96° 44' W long., and 500 m altitude). The Barnes clay loam soils (fine-loamy, mixed, superactive, frigid calcic Hapludolls)

on the farm are characteristic of those found in eastern South Dakota and western Minnesota and are similar to those found in the northern Corn Belt (Pikul et al., 2001). Soil tests (Gelderman et al., 1987) conducted in spring 1997 indicated 65 kg ha⁻¹ NO₃-N (top 61 cm), and extractable ion concentrations of 4 mg kg⁻¹ P (Olsen et al., 1954) and 120 mg kg⁻¹ K. In 1998 soil tests indicated 118 kg ha⁻¹ NO₃-N, and extractable ion concentrations of 9 mg kg⁻¹ P and 131 mg kg⁻¹ K.

A 4000 kg ha⁻¹ yield goal for both wheat and oat was used to design soil fertilizer application rates for the 2-yr field experiment. Fertilizer products containing elemental N (93 kg ha⁻¹ in 1997; 44 kg ha⁻¹ in 1998), elemental P (25 kg ha⁻¹ in 1997; 14 kg ha⁻¹ in 1998), and elemental K (48 kg ha⁻¹ in 1997; 27 kg ha⁻¹ in 1998) were applied with a drop spreader and incorporated with a field cultivator before planting. Oat ('Jerry') and spring wheat ('Sharp') were planted (104 kg ha⁻¹) with 15-cm row spacing to a depth of 5 cm using a JD 750 drill (John Deere Inc., Moline IL) on 25 Apr. 1997 and 14 Apr. 1998.

Aphids used in these experiments came from nymphs deposited on Parafilm (American National Can Co., Greenwich, CT) membranes by adults collected in the field during 1991. Colonies begun with these aphids were maintained on barley (*Hordeum vulgare* L.) plants in growth chambers at the USDA-ARS North Central Agricultural Research Laboratory in Brookings, SD (Kieckhefer et al., 1995).

Crop damage and yield loss caused by GB, RWA, BCOA, or BYDV treatments were evaluated in a completely randomized experimental arrangement with three replications. Wire mesh cages (1-m long × 1-m wide × 0.5-m tall) were placed in the field, one cage for each treatment and replication combination, when the spring-planted small grains plants reached the two-leaf stage (16 May 1997 and 4 May 1998). Plants were infested at the three- to four-leaf stage with BCOA, RWA, or GB (at a rate of about 30 aphids per plant; 29 May 1997 and 13 May 1998). Plants and aphid populations were allowed to grow (about 10 d in 1997 and 18 d in 1998) until the cumulative aphid population in each cage reached 300 aphid-days (Kieckhefer et al., 1995) per plant, after which aphids were removed with a systemic insecticide (acephate). For the BYDV treatment, plants were infested (29 May 1997 and 13 May 1998) at the three- to four-leaf stage with viruliferous (PAV strain) BCOA for a period of 72 h, after which plants were treated with insecticide (acephate). Control plants, which were also caged, received no aphid infestations or virus infections but were treated with insecticide. Cage tops were removed after insecticide treatments and left off until crop harvest.

Crop Measurements

Plants at the boot and early head emergence (Tottman et al., 1979) development stage, 18 June 1997 (about 10 d after aphids were removed) and 14 June 1998 (about 14 d after aphids were removed), were measured for leaf area index (LAI) and number of leaves and tillers plant⁻¹, leaf area plant⁻¹, as well as leaf chl and mineral nutrient concentrations. Crop canopy temperatures near solar noon on cloudless days (17 June 1997 and 13 June 1998) were measured with a infrared thermometer (Model 510B, Everest Interscience, Inc., Tucson AZ). Midday differential canopy temperature was calculated by

subtracting the ambient air temperature from the measured canopy temperature. Midday differential canopy temperature values for the control treatments were then set to zero, and deviations from zero (dT) for each crop–treatment–year combination were calculated.

Canopy LAI measurements were obtained from a LAI-2000 crop canopy analyzer (LI-COR, Inc., Lincoln NE) equipped with a fish-eye lens that was partially covered by a 90° cap. Measurements of LAI were taken between crop rows in the center of each cage in the early morning on cloudy days (18 June 1997 and 14 June 1998). After LAI measurements, plants contained in 30.4 cm of row were then removed from the center of each cage and evaluated for number of leaves and tillers plant⁻¹ and crop development stage. Leaf blades, separated at the ligule, were measured for leaf area (Delta T Devices, Cambridge, UK), placed into paper bags, and dried to constant weight at 60°C in a forced air oven. Leaf tissue, ground to pass a 40-mesh screen in a Wiley mill, was measured for chl concentration (mg g⁻¹ DW; Moran 1982) and mineral nutrient content. An inductively coupled plasma-atomic emission spectrometer (Ward Labs, Kearney NE) was used to measure P, K, S, Ca, Mg, Zn, Fe, Mn, and Cu in the ground leaf tissue samples. Ground tissue was also analyzed for N using the Kjeldahl method. The number of seeds m⁻², thousand kernel weight (TKWT), and total grain yield were measured at crop maturity by hand harvesting 1.2-m length of row cage⁻¹. Hand samples for yield were not taken from those regions in the cage that were sampled at boot and early head development stage.

Statistical Analysis

The data were analyzed with a combination of variance component and canonical correlation analysis procedures. Two data sets, each representing chl and nutrient concentrations (N, P, K, S, Ca, Mg, Zn, Fe, Mn, and Cu) or agronomic traits (grain yield, seeds plant⁻¹, TKWT, dT, LAI, leaves plant⁻¹, tillers plant⁻¹, and leaf area plant⁻¹), were subjected to statistical analysis either singly or in combination. These analyses were performed with the relevant modules in STATISTICA Release 7.1 (StatSoft, 2005) software package.

Variance components analysis was used to estimate covariation between years, crops, and treatments and their interactions with the dependent variables. Variance due to all sources of variation (crops, treatments, years, and their two- and three-way interactions) were estimated. Grain yield deviation from control (dY) was calculated for each crop–treatment combination by subtracting the grain yield of the control treatment for each crop from grain yield of each crop–treatment combination. Grain yield deviation was subjected to variance components analysis to quantify and test the significance of variance components due to years, crops, treatments, and their interaction. The nutrient concentration and agronomic data set variables were also subjected to canonical correlation analysis to quantify the relationship between the two sets of variables and their impact on crop reaction to treatments.

RESULTS AND DISCUSSION

Growing Season Environments

The 1997 small grain growing season was characterized by below-average air temperature in April and May, fol-

lowed by above-average temperature in June. In 1998 air temperatures were above normal in April and May and below normal in June. Rainfall totals in both 1997 and 1998 were below average the entire growing season, with substantial deficits in May, June, and July. Pan evaporation measurements for June and July were greater in 1997 than in 1998 (Table 1). These environmental data suggest that the small grain plants were subjected to greater drought-stress conditions during the 1997 growing season than the 1998 growing season, especially during the month of June (National Climatic Data Center, 1997, 1998).

Chlorophyll and Mineral Nutrient Responses to Aphids and Disease

Between 20 and 37% of the total variation of leaf chl, N, Ca, and Mg concentrations were explained by aphid infestation and BYDV infection treatment effects (Table 2). Compared with control treatments, BYDV infection consistently caused the greatest reduction in leaf concentrations of these dependent variables (Fig. 1). The loss of chl is considered to be a diagnostic features of BYDV infection (Hoffman and Kolb, 1997). Because chl concentration is closely related to N concentration in wheat (Filella et al., 1995), it was not unusual to see that BYDV infection also resulted in reductions in leaf N concentration (Fig. 1). Treatment with BYDV also reduced leaf Ca and Mg concentrations (Fig. 1). Interception by roots and mass flow in the soil solution are the primary mechanisms for supplying Ca (Barber, 1984) and Mg (Oliver and Barber, 1966) to plants. Thus, it would be expected that treatments that cause reduction in root length (e.g., BYDV infection; Riedell et al., 2003) would also reduce root exploration of the soil profile, which in turn could lead to reduced uptake of these elements.

Cereal aphid infestations cause acute injury from which the plant can recover if the aphids are removed (Riedell et al., 2003). It has been reported that shoot dry weights (Burton, 1986) and chl concentrations (Riedell and Kieckhefer, 1995) in wheat plants previously infested with GB will recover to levels seen in control plants within 10 to 14 d after aphid removal. In the present study, either 10 d (in

Table 1. Average monthly air temperature, total monthly rainfall, and total monthly pan evaporation for 1997 and 1998 growing seasons near Brookings, SD.

Month	Air temperature		Rainfall		Pan evaporation	
	—°C—		—mm—		—mm—	
	1997	1998	1997	1998	1997	1998
April	3.9 (–2.8) [†]	7.4 (+0.7)	54 (+1)	46 (–7)	NA [‡]	NA
May	10.5 (–2.7)	16.4 (+3.2)	34 (–40)	39 (–35)	174 (–22)	203 (+7)
June	20.0 (+1.4)	17.2 (–1.4)	61 (–49)	52 (–58)	236 (+11)	174 (–51)
July	21.3 (–0.2)	21.2 (–0.3)	68 (–16)	40 (–44)	217 (–10)	208 (–19)

[†]Values in parentheses represent departure from normal (30-yr average).

[‡]NA, not available; pan evaporation data were not recorded during April.

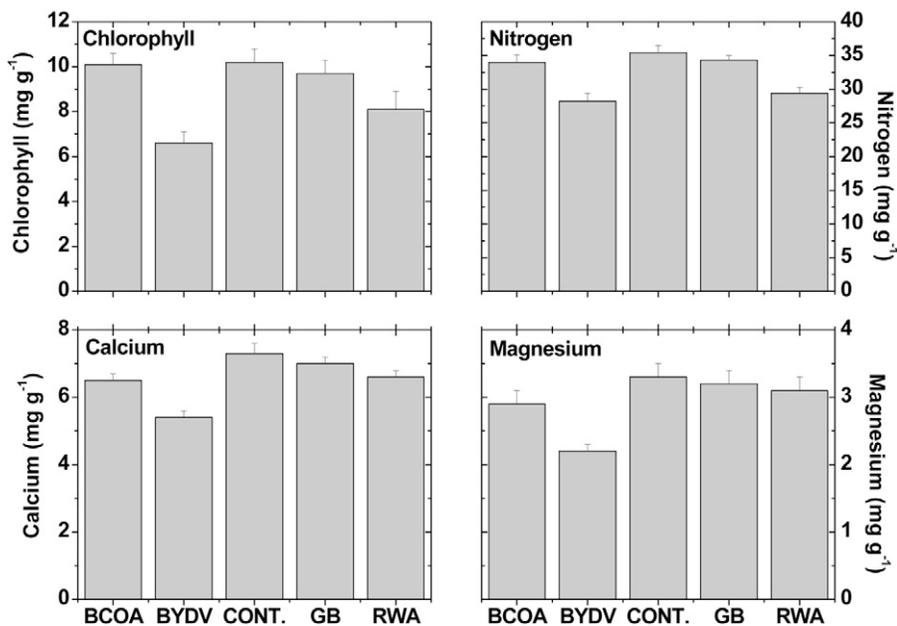


Figure 1. Treatment effects on leaf concentrations of chlorophyll, N, Ca, and Mg across years (1997 and 1998) and crops (wheat and oat). Error bars represent standard error of the mean. (BCOA, bird cherry-oat aphids; BYDV, *barley yellow dwarf virus*; Cont., control; GB, greenbug; RWA, Russian wheat aphids.)

1997) or 14 d (in 1998) elapsed from the time aphids were removed until the time when cereal plants were destructively sampled for chl and mineral nutrient concentrations. Thus, the observations that leaf chl, N, Ca, and Mg concentrations were not dramatically different in GB-treated cereal plants than in control plants (Fig. 1) were expected and tend to support and extend the findings of Riedell and Kieckhefer (1995). In contrast, RWA-treated cereal plants tended to have lower chl and N concentrations than control treatments (Fig. 1). Because RWA feeding damage is characterized by longitudinal chlorotic leaf streaking on younger leaves (Webster et al., 1987), the lower chl and N concentrations in RWA-treated plants suggest that these damage symptoms persisted longer than 10 to 14 d after the aphids were removed.

The observation that the chl and N concentrations of cereal plants infested with BCOA were very similar to control plants (Fig. 1) confirms that this aphid species does not cause dramatic feeding injury symptoms to leaves (Kieckhefer et al., 1995). In contrast, root systems of wheat damaged by BCOA took more than 20 d to reach root length levels seen in uninfested plants, while root systems damaged by GB recovered within 13 d (Riedell and Kieckhefer, 1995). Thus, the relatively lower leaf Ca and Mg concentrations in BCOA-infested cereal plants compared with the control could be the result of reduced root growth (which persisted longer than 10 to 14 d), which in turn may have reduced uptake of Ca and Mg.

Of the remaining nutrient minerals, all except Zn displayed highly variable response patterns to main factors and their interactions. Sizable portions of variation

in leaf Mg (42.4%) and Mn (55.1%) concentrations were due to year effects, while variations in leaf chl (23.1%), N (33.4%), P (47.3%), and Fe (51.6%) concentrations were due to year \times crop interactions (Table 2). These significant year \times crop interactions were likely due to genetic differences between oat and wheat, as well as a variable reaction of these two crops to annual differences in growing season characteristics (Cousens et al., 2003; Xu and Yu, 2006).

Three-way interaction between years, crops, and treatments were present for leaf P, K, S, and Cu concentrations. The three-way interaction explained between 11.9 to 17.2% of variation in leaf concentrations of these four elements (Table 2). The source of the three-way interaction for leaf K concentration appears to be a differential response across crops and years to BYDV infection. Leaf K concentration for BYDV-infected wheat was similar to control in 1998, while

about a 50% reduction due to BYDV was observed for oat (in 1997 and 1998) and for wheat in 1997 (data not shown).

Grain Yield Responses to Aphids and Disease

Average grain yield (3542 kg ha⁻¹) across years, crops, and treatments in this experiment was 11% lower than the planned yield goal (4000 kg ha⁻¹). This was likely due to a below-target wheat yield across both years of the experiment (Table 2). Grain yield in oat, which achieved the yield goal, was associated with significantly higher values for leaf area plant⁻¹ and chl concentration compared with wheat. Grain yield was significantly impacted by all main and interaction factors, except the year \times crop and the year \times crop \times treatment interactions (Table 2).

Yield-component agronomic traits (seeds m⁻¹ and TKWT) had significant crop \times treatment interactions (Table 2), suggesting that yield components of the two crops responded differently to the treatments across the 2 yr of the study. Oat produced similar numbers of seeds m⁻¹ in the BCOA, control, GB, and RWA treatments, while lower values for seeds m⁻¹ were recorded in the BYDV treatment (Fig. 2). In contrast, all treatments (BYDV, GB, BCOA, and RWA) reduced seeds m⁻¹ when compared with the control treatment in wheat (Fig. 2).

Thousand kernel weight values, which showed much greater uniformity across treatments than the seeds m⁻¹ values, differed in response to treatments between the two crops. Oat had very similar TKWT values in the BCOA, control, GB, and RWA treatments, while BYDV values were lower (Fig. 3). In wheat, TKWT for the control and GB treatments were similar while reductions were found

Table 2. Mean, mean separation among 19 traits measured on oat and wheat, percentage of total variance (V%), and level of significance (P) in the variance components analysis of agronomic and chemical traits accounted for by years, crops, treatments and their two- and three-way interactions. To improved the readability of this table, values for V% and P were not listed for P > 0.1.

Variable†	R ²	Mean		Year (1)		Crop (2)		Treatment (3)		1 × 2		1 × 3		2 × 3		1 × 2 × 3	
		Oat	Wheat	V%	P	V%	P	V%	P	V%	P	V%	P	V%	P	V%	P
Yield (kg ha ⁻¹)	0.81*	4030*	3055	11.6	0.05	28.7	0.01	32.4	0.024			5.8	0.030	7.4	0.020		
Seeds (m ⁻¹)	0.81	1985	1617	44.3	0.09			14.9	0.06	7.1	0.001	7.1	0.005	3.0	0.020		
TKWT (g)	0.88	31.4	34.6							5.5	0.02			12.3	0.020		
dT (°C)	0.77	0.5	1.0*	64.7	0.008							9.1	0.036				
LAI	0.93	2.4	2.2	92.0	0.001	1.7	0.08							1.5	0.060		
Leaves (plant ⁻¹)	0.24	8.4	9.9													26.8	0.048
Tillers (plant ⁻¹)	0.42	1.8	1.6													34.3	0.010
Leaf area (cm ² plant ⁻¹)	0.73	96.6*	68.5													27.5	0.001
Chl (mg g ⁻¹)	0.84	10.5*	7.4					20.5	0.048	23.1	0.008						
N(mg g ⁻¹)	0.63	31.9	32.6					34.0	0.017	33.4	0.025						
P(mg g ⁻¹)	0.77	1.7	2.1*							47.3	0.022					14.3	0.011
K(mg g ⁻¹)	0.64	23.7	22.6													17.2	0.026
S(mg g ⁻¹)	0.63	1.8	2.4*													16.0	0.020
Ca(mg g ⁻¹)	0.61	6.2	6.9					36.7	0.05								
Mg(mg g ⁻¹)	0.77	2.8	3.2	42.4	0.011	10.6	0.05	23.1	0.03			5.2	0.08				
Zn (mg kg ⁻¹)	0.51	20.1	26.3*														
Fe (mg kg ⁻¹)	0.67	114.8	425.5*							51.6	0.002						
Mn (mg kg ⁻¹)	0.81	54.0	84.9*	55.1	0.025					2.0	0.044	3.1	0.06				
Cu (mg kg ⁻¹)	0.64	6.7	8.6*													11.9	0.059

*Crop mean differs significantly (p < 0.05) from the respective mean of the other crop.

†Seeds are expressed as seeds m⁻¹ of row; TKWT, thousand kernel weight; dT; LAI, leaf area index; Chl (chlorophyll) and nutrient concentration data are presented on a tissue dry weight basis.

‡All R₂ values were significant (p < 0.05).

for the BYDV, RWA, and possibly BCOA treatments (Fig. 3). The effects of cereal aphid infestations or BYDV infection on seeds m⁻¹ and TKWT are similar to those previously reported for wheat and oat (Kieckhefer and Kantack, 1988; Quiroz et al., 1991; Riedell et al., 1999).

When treatment effects on grain yield are viewed as a grain yield deviation from control (dY; calculated by subtracting the grain yield of the control treatment for each crop from grain yield of each crop-treatment combination), 65.1% of total variance in this dependent variable was accounted for by crops (6.4%), treatments (33.5%), crop × treatment interaction (12.9%), and year × treatment interaction (12.3%). Averaged over years, crops, and treatments, dY was -1150 kg ha⁻¹. Comparable dY values were observed for 1997 (-1123 kg ha⁻¹) and 1998 (-1177 kg ha⁻¹). Average dY values for oat and wheat were -927 and -1373 kg ha⁻¹, respectively. Treatments varied widely in their effects on dY. BYDV treatment caused the most negative effect (-2164 kg ha⁻¹) on dY, while GB treatment (-745 kg ha⁻¹) caused the least negative effects. RWA (-900 kg ha⁻¹) and BCOA (-789 kg ha⁻¹) treatments caused intermediate effects on dY.

A significant crop × treatment interaction for dY, which accounted for 12.9% of total variation in this dependent variable, suggests that grain yield in oat and wheat

reacted differently to treatments. Wheat had a much more negative dY in response to RWA than oat (Fig. 4). This differential dY response to RWA by wheat compared with oats, as well as the significant crop × treatment interactions (Table 2) for seeds m⁻¹ (Fig. 2) and TKWT (Fig. 3), supports earlier findings of Webster et al. (1987) and

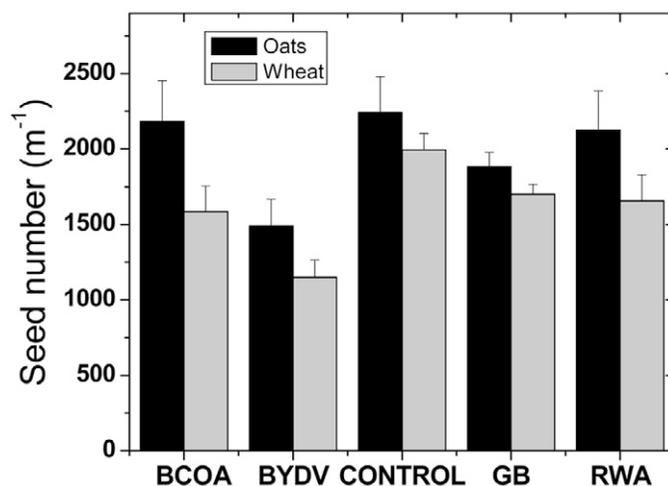


Figure 2. Plot of the crop × treatment interaction averaged over 2 yr for the seed m⁻¹ dependent variable. Error bars represent standard error of the mean. (BCOA, bird cherry-oat aphids; BYDV, barley yellow dwarf virus; Cont., control; GB, greenbug; RWA, Russian wheat aphids.)

Kindler and Springer (1989), who demonstrated that oat, but not wheat, is tolerant to RWA. By definition, if a plant is tolerant to a biological stress, the plant still will suffer damage by the stress-causing organism, but the detrimental effect of this damage on yield is reduced (Rausher, 2001). The lack of crop × treatment interactions for other agronomic and chemical traits (Table 2) confirms that oat is more tolerant to RWA than wheat.

The significant year × treatment interaction for dY, which accounted for 12.3% of total variation in this dependent variable, suggests that treatment effects were different across both years of the study. In a year with greater drought stress (1997), the BCOA treatment had a more negative dY,

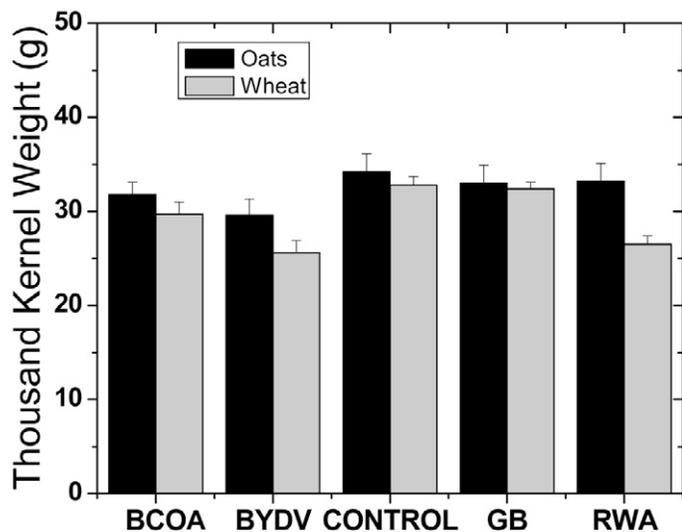


Figure 3. Plot of the crop × treatment interaction averaged over 2 yr for the thousand kernel weight dependent variable. Error bars represent standard error of the mean. (BCOA, bird cherry-oat aphids; BYDV, *barley yellow dwarf virus*; Cont., control; GB, greenbug; RWA, Russian wheat aphids.)

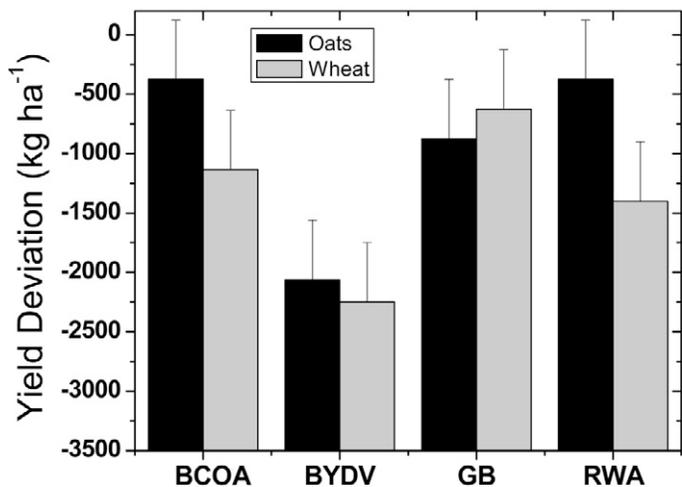


Figure 4. Grain yield deviation (kg ha⁻¹) from the control due to crop × treatment interaction averaged over 2 yr. Error bars represent standard error of the mean. (BCOA, bird cherry-oat aphids; BYDV, *barley yellow dwarf virus*; GB, greenbug; RWA, Russian wheat aphids.)

while the GB treatment had a less negative dY compared with a year (1998) with less drought stress (Fig. 5).

Canonical Correlation between Nutrients and Agronomic Characteristics

In addition to controlling the inflation of experimentwise (Type I) error rates, canonical correlation analysis allows examination of multiple causes and effects by considering all of the variables simultaneously (Thompson, 2000). A highly significant and positive canonical correlation ($R = 0.94$, $p < 0.0001$) was found between agronomic traits and nutrients (including chl) in this study (Fig. 6). The first canonical root extracted from agronomic trait data set accounted for 41.0% of total variation in these traits with high loadings of LAI, dT, leaf area plant⁻¹, and grain yield. The first canonical root extracted from the nutrient data set accounted for 27.0% of total variation and was dominated by chl, N, K, Mg, and Mn. Redundancies (i.e., how much variance of the original variables of one set of traits may be predicted from a canonical root of the other set) for the agronomic traits and nutrient data were 62.1 and 54.1%, respectively.

Crop-treatment combinations for both years were separated at the origin of both canonical roots, except for the wheat treated with BYDV (W-BYDV) which was negative on both canonical roots in 1998 (Fig. 6). Crop-treatment combinations displayed a larger variation (spread) during 1998 as compared to 1997. Growing season characteristics differed across these 2 yr, with 1998 characterized as having less drought stress and 1997 having more drought stress.

At a multivariate level, plants exhibited larger values of most variables in 1998 compared to 1997 (Fig. 6). Oat under the control treatment (O-Control in Fig. 6) clustered at the highest coordinates of both canonical roots in both years,

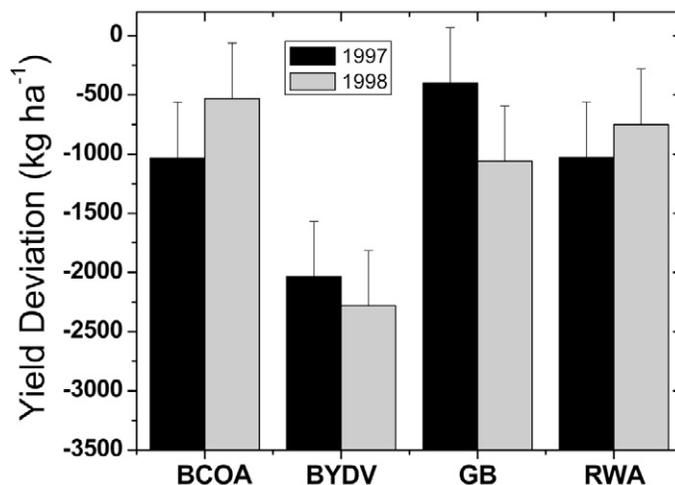


Figure 5. Grain yield deviation (kg ha⁻¹) from the control due to year × treatment interaction averaged over two crops. Error bars represent standard error of the mean. (BCOA, bird cherry-oat aphids; BYDV, *barley yellow dwarf virus*; GB, greenbug; RWA, Russian wheat aphids.)

while the wheat control treatment (W-Control) clustered in the middle coordinates. Crops also responded to treatments in variable patterns among years. For example, in a year with less drought stress (1998), both wheat and oat infected with BYDV (O-BYDV and W-BYDV) tended to cluster at the middle to lower coordinates (Fig. 6). In contrast, in a year with greater drought stress (1997), BYDV-infected wheat and oat were clustered in the middle coordinates. Wheat infested with RWA (W-RWA) clustered at the lowest coordinates of both canonical roots in both years, whereas oats infected with RWA (O-RWA) tended to cluster at the middle coordinates in 1997 and the highest coordinates in 1998 (Fig. 6). The differences in clustering may reflect the fact that oat is considered to be tolerant to RWA while wheat is considered to be susceptible (Webster et al., 1987; Kindler and Springer, 1989).

CONCLUSIONS

Year, crop, and treatment main factors, and their two- and three-way interactions, accounted for sizable portion of variation in 18 of the 19 traits under study as indicated by the adjusted R^2 values and the level of significance (p values) for these factors (Table 2). Agronomic traits were impacted more by two- and three-way interactions (12 of 18 significant p values), whereas nutrients were impacted almost equally by main factors (7 significant p values) and their interactions (9 significant p values).

There were relatively strong responses of dependent variables to year as well as to year \times crop, and year \times treatment interactions. Differences in weather conditions across the 2 yr of the study (greater drought stress in 1997 than 1998) likely were the cause of these effects and interactions. Cereal plants respond to drought stress with accelerated leaf senescence, reduced photosynthesis, and decreased vegetative carbohydrate reserves (Frederick and Bauer, 1999). Damage caused by cereal aphids or disease (leaf chlorosis, reduced shoot and root growth, and yield loss) to oat and wheat could have been obscured by these drought-stress responses, which, in turn, could have impacted dependent variable responses to year and the interactions of year \times crop and year \times treatment. In addition, significant crop \times treatment interactions for agronomic

variables (grain yield, seeds m^{-2} , and TKWT) likely were present because RWA tolerance is much greater in oat than in wheat.

Even with these potential interactive responses to drought stress and RWA tolerance, variance component and canonical correlation analyses identified leaf N, K, and Mg concentrations to be highly correlative to agronomic traits important in cereal plant responses to stress caused by aphid-feeding damage or aphid-vectored disease. Nitrogen is an important constituent of proteins and nucleic acids, K functions mainly in cellular osmoregulation and maintenance of electrochemical equilibria, and Mg is a constituent of organic molecules and is involved in enzyme catalytic function and as the central atom of the chlorophyll molecule (Marschner, 2002).

The soil likely contained an optimal supply of N and K because fertilizers containing these essential crop nutrients were applied to the experiment plots on the basis of soil tests and yield goals. While Mg-containing fertilizers were not applied, the cereal plants grown in this experiment had leaf Mg concentrations of about 3 $mg\ g^{-1}$ dry weight, well within the 1.5 to 3.5 $mg\ g^{-1}$ dry weight concentration required for optimal plant growth (Marschner, 2002). Additional data from future experiments is needed to determine if small grain producers should use soil testing

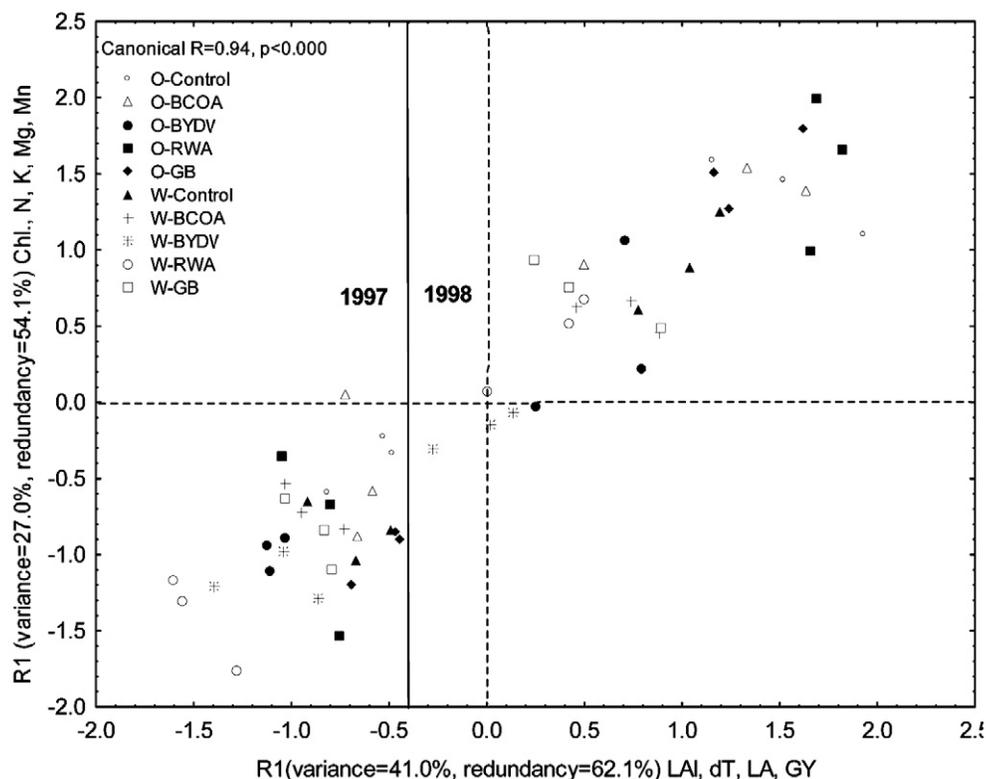


Figure 6. Scatter plot of 10 crop-treatment combinations over three replications and 2 yr (1997 and 1998) as a function of the first canonical root derived from agronomic traits (x axis) and chemical nutrients (y axis). The dotted lines mark the origin of each of the canonical roots. The solid vertical line delineates the boundary between the two growing seasons (1997 and 1998). (O, oat; W, wheat; BCOA, bird cherry-oat aphids; BYDV, *barley yellow dwarf virus*; GB, greenbug; RWA, Russian wheat aphids; LAI, leaf area index; dT, midday differential canopy temperature deviation from control; LA, leaf area; GY, grain yield.)

and yield goals to design fertilizer applications that guard against deficiencies in these three essential plant nutrients as a way to ameliorate the stress and yield loss caused by aphids or aphid-transmitted disease in cereal grains.

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References

- Al-Mousawi, A.H., P.E. Richardson, and R.L. Burton. 1983. Ultrastructural studies of greenbug (Hemiptera: Aphididae) feeding damage to susceptible and resistant wheat cultivars. *Ann. Entomol. Soc. Am.* 76:964–971.
- Barber, S.A. 1984. Soil nutrient bioavailability: A mechanistic approach. John Wiley & Sons, New York.
- Burd, J.D. 2002. Physiological modification of the host feeding site by cereal aphids (Homoptera: Aphididae). *J. Econ. Entomol.* 95:463–468.
- Burton, R.L. 1986. Effect of greenbug (Homoptera: Aphididae) damage on root and shoot biomass of wheat seedlings. *J. Econ. Entomol.* 79:633–636.
- Cook, R.J., and R.J. Veseth. 1991. Wheat health management. APS Press, St. Paul, MN.
- Cousens, R.D., A.G. Barnett, and G.C. Barry. 2003. Dynamics of competition between wheat and oat: I. Effects of changing the timing of phenological events. *Agron. J.* 95:1295–1304.
- Dorschner, K.W., J.D. Ryan, R.C. Johnson, and R.D. Eikenbary. 1987. Modification of host nitrogen levels by greenbug (Homoptera: Aphididae): Its role in resistance of winter wheat to aphids. *Environ. Entomol.* 16:1007–1011.
- Filella, I., L. Serrano, J. Serra, and J. Penuelas. 1995. Evaluating wheat nitrogen status with canopy reflectance indices and discriminant analysis. *Crop Sci.* 35:1400–1405.
- Frederick, J.R., and P.J. Bauer. 1999. Physiological and numerical components of wheat yield. p. 45–65. *In* E.H. Satorre and G.A. Slafer (ed.) *Wheat: Ecology and physiology of yield determination*. Food Products Press, New York.
- Gelderman, R., R. Neal, S. Swartos, and L. Anderson. 1987. Soil testing procedures in use at the South Dakota State Soil Testing Laboratory. Pamphlet 101. Plant Science Dep., South Dakota State Univ., Brookings.
- Hoffman, T.K., and F.L. Kolb. 1997. Effects of barley yellow dwarf virus on root and shoot growth of winter wheat seedling grown in aeroponic culture. *Plant Dis.* 81:497–500.
- Kieckhefer, R.W., and B.H. Kantack. 1988. Yield losses in winter grains caused by cereal aphids in South Dakota. *J. Econ. Entomol.* 81:317–321.
- Kieckhefer, R.W., J.L. Gellner, and W.E. Riedell. 1995. Evaluation of the aphid-day standard as a predictor of yield loss caused by cereal aphids. *Agron. J.* 87:785–788.
- Kindler, S.D., and T.L. Springer. 1989. Alternate hosts of Russian wheat aphid (Homoptera: Aphididae). *J. Econ. Entomol.* 82:1358–1362.
- Kolb, F.L., N.K. Cooper, A.D. Hewings, E.M. Bauske, and R.H. Teyker. 1991. Effects of barley yellow dwarf virus on root growth in spring oat. *Plant Dis.* 75:143–145.
- Marschner, H. 2002. Mineral nutrition of higher plants. 2nd ed. Academic Press, London, UK.
- Miles, P.W. 1999. Aphid saliva. *Biol. Rev.* 74:41–85.
- Moran, R. 1982. Formulae for determination of chlorophyllous pigments extracted with N,N-dimethylformamide. *Plant Physiol.* 69:1376–1381.
- National Climatic Data Center. 1997. Climatological data annual summary: South Dakota. Natl. Oceanic and Atmospheric Admin., Asheville, NC.
- National Climatic Data Center. 1998. Climatological data annual summary: South Dakota. Natl. Oceanic and Atmospheric Admin., Asheville, NC.
- Oliver, S., and S.A. Barber. 1966. An evaluation of the mechanisms governing the supply of Ca, Mg, K, and Na to soybean roots (*Glycine max*). *Soil Sci. Soc. Am. Proc.* 30:82–86.
- Olsen, S.R., C.V. Cole, F.S. Watanabe, and L.A. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. 939. U.S. Gov. Print. Office, Washington, DC.
- Pikul, J.L., Jr., L. Carpenter-Boggs, M. Vigil, T.E. Schumacher, M.J. Lindstrom, and W.E. Riedell. 2001. Crop yield and soil condition under ridge and chisel-plow tillage in the northern Corn Belt, USA. *Soil Tillage Res.* 60:21–33.
- Quiroz, C., R.M. Lister, J.E. Araya, and J.E. Foster. 1991. Effect of symptom variants derived from the NY-MAX isolate of barley yellow dwarf virus on the life cycle of the English grain aphid (Homoptera: Aphididae) and on yield components in wheat and oats. *J. Econ. Entomol.* 84:1920–1925.
- Rausher, M.D. 2001. Co-evolution and plant resistance to natural enemies. *Nature* 411:857–864.
- Riedell, W.E. 1989. Effects of Russian wheat aphid infestation on barley plant response to drought stress. *Physiol. Plant.* 77:587–592.
- Riedell, W.E., and R.W. Kieckhefer. 1995. Feeding damage effects of three aphid species on wheat root growth. *J. Plant Nutr.* 18:1881–1891.
- Riedell, W.E., R.W. Kieckhefer, S.D. Haley, M.A.C. Langham, and P.D. Evenson. 1999. Winter wheat responses to bird cherry-oat aphids and barley yellow dwarf virus infection. *Crop Sci.* 39:158–163.
- Riedell, W.E., R.W. Kieckhefer, M.A.C. Langham, and L.S. Hessler. 2003. Root and shoot responses to bird cherry oat aphids and barley yellow dwarf virus in spring wheat. *Crop Sci.* 43:1380–1386.
- StatSoft. 2005. STATISTICA (data analysis software systems) version 7.1. Available at www.statsoft.com (verified 9 May 2007). StatSoft, Tulsa, OK.
- Thompson, B. 2000. Canonical correlation analysis. p. 285–316. *In* L.G. Grimm and P.R. Yarnold (ed.) *Reading and understanding more multivariate statistics*. American Psychological Association, Washington, DC.
- Tottman, D.R., R.J. Makepeace, and H. Broad. 1979. An explanation of the decimal code for the growth of cereals, with illustrations. *Ann. Appl. Biol.* 93:221–234.
- Webster, J.A., K.J. Starks, and R.L. Burton. 1987. Plant resistance studies with *Diuraphis noxia* (Homoptera: Aphididae), a new United States wheat pest. *J. Econ. Entomol.* 80:944–949.
- Xu, Z.-Z., and Z.-W. Yu. 2006. Nitrogen metabolism in flag leaf and grain of wheat in response to irrigation regimes. *J. Plant Nutr. Soil Sci.* 169:118–126.