Detection of Dual *Heterodera avenae* Resistance plus Tolerance Traits in Spring Wheat

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Accepted for publication: March 23, 2016.

Abstract

Smiley, R. W., and Marshall, J. M. 2016. Detection of dual *Heterodera avenae* resistance plus tolerance traits in spring wheat. Plant Disease 100: xxx-xxx.

The cereal cyst nematode *Heterodera avenae* reduces wheat yield in the Pacific Northwest. Resistance and tolerance traits among spring wheat cultivars were poorly defined. Screening trials were conducted with 39 cultivars over a 2-yr period in irrigated commercial fields that were infested by *H. avenae*. Comparisons were made between drill strips treated or untreated with aldicarb at the time of planting. Root sampling at the time of plant anthesis indicated that cultivars differed greatly in susceptibility to *H. avenae*, with numbers of newly produced white *H. avenae* females ranging from <5 to 70/plant. Aldicarb reduced mean numbers of white females as much as 99% on the most susceptible cultivar (Glee) and increased mean grain yield as much as 77% for the least tolerant cultivar (Cataldo). Density of *H. avenae* eggs in untreated soil following harvest was significantly lower than the density in aldicarb-treated plots. Agronomically acceptable traits of resistance plus tolerance were identified in one cultivar of hard red spring wheat (WB-Rockland) and two cultivars of hard white spring wheat (Klasic and LCS Star) but in none of the soft white spring wheat cultivars. This is the first report of spring wheat cultivars expressing the dual traits of resistance plus tolerance to *H. avenae*.

The cereal cyst nematode *Heterodera avenae* Woll., 1924 infests soils of localized regions of the Pacific Northwest (PNW) (Smiley 2009). This nematode reduces grain yield of wheat and barley under both rainfed and irrigated conditions (Marshall and Smiley 2016; Smiley 2009; Smiley et al. 1994, 2005, 2011a, 2012, 2013). Rotation of cereal crop hosts of *H. avenae* with one year of a non-host broadleaf crop species or summer fallow are not effective in controlling losses caused by this nematode in the PNW (Marshall and Smiley 2016; Smiley et al. 1994). Extended intervals between susceptible cereal crops are seldom profitable in areas of the PNW where cereals and non-hosts such as potato or a pulse crop are produced in 2-year rotations. No chemical or biological nematicides are currently available to manage *H. avenae* (Smiley et al. 2012). Adequate management of cereal cyst nematodes in short rotations requires the production of cultivars that express both resistance and tolerance (Cook and Evans 1987). The objective of this research was to evaluate PNW spring wheat cultivars in an attempt to identify the dual resistance plus tolerance trait to *H. avenae*.

Resistance suppresses or prevents reproduction of the nematode, thereby reducing the density of inoculum available for invading roots of the next-planted cereal crop. Resistance is usually characterized by counting newly-formed gravid white females on roots either under controlled conditions in the greenhouse or from samples collected from cultivar screening trials in the field (Marshall and Smiley 2016; Smiley et al. 2011b, 2013). Resistance can also be estimated from numbers of eggs in soil following the harvest of cultivars grown in the field, with appropriate consideration of a 'background' of residual eggs from earlier susceptible crops, which are supplemented by newly-produced eggs from the most recent crop (Marshall and Smiley 2016; Smiley et al. 2013).

Tolerant cultivars are characterized as having an ability to withstand or recover from nematode invasion and to yield well in comparison with non-invaded plants. Tolerance is characterized in the field by comparing yields of individual cultivars grown in close proximity in an infested soil that is either left untreated or is treated with a nematicide such as aldicarb (Marshall and Smiley 2016; Smiley et al. 2013).

Roots of both resistant and susceptible cultivars are initially invaded by 2nd-stage juveniles of *H. avenae*, which may result in an intolerant reaction prior to the expression of resistance (O'Brien and Fisher 1977; Ogbonnaya et al. 2001; Oka et al. 1997). The intolerant reaction is characterized by a closely-grouped proliferation of adventitious roots at locations where female nematodes have established a feeding syncytium, resulting in a bushy or knotted appearance to the root. Invaded roots often fail to continue growing deeply into the soil. Some resistant cultivars are unable to produce competitive grain yields when compared to susceptible cultivars that are grown without nematode pressure (Wilson et al. 1983). Growers are often reluctant to plant resistant cultivars that produce lower yields than for susceptible cultivars in non-infested soils (Rivoal and Cook 1993). Cultivars exhibiting both resistance and tolerance are therefore required for optimal yield performance and for reducing the risk to subsequent plantings of intolerant cultivars or crops (Andersen 1961; Brown 1987; Fisher 1982; Smiley and Nicol 2009). An initial screening of 19 PNW wheat cultivars for resistance plus tolerance identified several cultivars with resistance to *H. avenae* but none that had acceptable levels of both traits (Smiley et al. 2013). There do not appear to be any commercial North American wheat cultivars for which the registration includes a report of resistance plus tolerance to *H. avenae* (USDA-ARS-GRIN 2015).

We evaluated 39 spring wheat cultivars in three market classes (soft white, hard white and hard red) over a 2-year period on infested commercial fields to examine our hypothesis that North American wheat cultivars with acceptable dual traits of resistance and tolerance could be identified.

Materials and Methods

Experiments during 2013 and 2014 were performed in fields infested by *H. avenae* on a farm near St. Anthony, ID. The spring wheat experiments reported here were conducted in the same fields and by using the same experimental methods described for three spring barley experiments (Marshall and Smiley 2016). Detailed experimental procedures were described in Marshall and Smiley (2016).

Briefly, the experiments were performed during 2013 in an irrigated field managed as a 2-year rotation of potato and a spring cereal. Experiments were repeated during 2014 in a different field under the same rotational management. Two experiments were performed each year. One experiment included 13 cultivars of soft white spring and the other experiment included 19 hard red and seven cultivars of hard white spring wheat. All cultivars were selected because they were being tested for other agronomic and disease traits at other locations (Marshall et al. 2015).

Experiments consisted of four replicates of each wheat entry planted into a split-plot design, with each plot consisting of two drill rows in a 0.9 x 9 m area. Cultivars were main plots (4 rows) and nematicide treatments were sub-plots, with two adjacent rows at one side of each drill strip being treated with nematicide (nematicide subplot) and the other two rows being untreated (control subplot). Each drill strip consisted of four replicates planted end-to-end, with the cultivar being changed at 9 m intervals. The nematicide treatment consisted of aldicarb (Temik 15G, Bayer CropScience, Research Triangle Park, NC) applied into the seed row at the rate of 4.2 kg of aldicarb/ha.

The seed drill, seed treatment, planting rate, fertilizer application, weed control, harvest procedures, and pre-plant and post-harvest soil sampling were described previously (Marshall and Smiley 2016). Methods of primary importance to data presented in this report are briefly described below.

Plants were dug after plant anthesis to examine roots for incidence and severity of the root knotting symptom (Fig. 1). Incidence was calculated as the percentage of plants exhibiting at least one knotted root. The severity scale (Smiley et al. 2013) was as follows: 1 = no evidence of knotting, 2 = 1 to 3 knots/root system, 3 = 3 to 5 knots, 4 = >5 knots and <20% reduction in root mass (estimated visually), and 5 = >5 knots and >20% reduction in root mass.

Resistance was measured by counting the number of *H. avenae* swollen white females on roots. The procedure was described by Marshall and Smiley (2016). Cultivars were rated as very resistant (VR; ≤1 swollen female/plant), resistant (R; 1.1 to 3), moderately resistant (3.1 to 6), moderately susceptible (6.1 to 12), susceptible 12.1 to 25), or very susceptible (>25).

Grain was harvested from all 2-row plots. Tolerance ratings were assigned to cultivars according to the scale used previously by Smiley et al. (2013) and Marshall and Smiley (2016): very tolerant (VT; ≤5% yield increase with nematicide), tolerant (T; 5.1 to 10%), moderately tolerant (MT; 10.1 to 15%), moderately intolerant (MI; 15.1 to 30%), intolerant (I; 30.1 to 50%), or very intolerant (VI; >50.1%).

The primary objective of this research was to identify cultivars that may have failed to meet criteria for full resistance or full tolerance but exhibited an acceptable balance among the moderate resistance and moderate tolerance traits. Data grouped over two years were used to establish a ranking of cultivars that exhibited at least a moderate level of resistance (≤6% swollen female/plant) plus at least a moderate level of tolerance (≤15% yield increase with nematicide).

In order to more fully interpret results of the resistance ratings based upon numbers of swollen white females developing on roots, we also determined the density of *H. avenae* eggs in soil after grain harvest. Eggs were counted after being manually released from cysts extracted from soil samples. The sampling and counting procedures were described in Marshall and Smiley (2016). Selected cultivars were sampled in both untreated and in nematicide-treated plots in each experiment during 2013. During 2014, soils were sampled from three replicate plots of all cultivars in the control treatment and from three replicates of two cultivars in the nematicide treatment; soft white cultivars Alpowa and UI Stone, and hard red cultivars Glee and Jefferson.

Statistical analyses. For clarity, data for the hard red plus hard white wheat experiment was divided into two groups to report results specific to each of the three market classes of spring wheat; soft white, hard red and hard white. Grain yield and disease data averaged over two years was analyzed using 3-way analysis of variance (ANOVA) for individual wheat classes, with year as the main plot, cultivar as the subplot, nematicide treatment as the sub-subplot, and replicates as blocks. Analyses were performed on nematode density data normalized by using the ln(x+1) transformation. Logarithmic means were back transformed into real numbers for presentation in the tables. Means of ordinate data for root knotting severity were analyzed by the Kruskal-Wallis Test. When the Pearson's chi-squared (χ^2) value for the experiment was significant at $\alpha < 0.05$, the treatments were examined pair wise to determine which treatments differed significantly. For the soft white and hard red wheat classes, selected cultivars were sampled from both control and nematicide-treated plots each year and those cultivars were analyzed separately to examine effects of year, cultivar and nematicide treatments. Data for those cultivars were analyzed using year as the main plot factor, cultivar as the subplot factor, and nematicide as the sub-subplot factor. ANOVA was performed using CoStat Statistical Software (Co-Stat v. 6.400, CoHort Software, Monterey, CA). When treatment means were significant at $\alpha < 0.05$, means were separated using the Tukey's Honestly Significant Difference (HSD) test. Because the main effect of year was highly significant in most analyses, the data for each of the three trials were also analyzed for individual years, using 2-way ANOVA with year as main plot, cultivar as the sub-plot, and replicates as blocks. Data for each wheat market class are reported as the means and standard error of the means for trials performed during each year. Regression analysis was used to determine if the number of white females produced on cultivars within the control treatment (no nematicide application) of the soft white and hard red plus hard white wheat market classes was associated with the number of eggs/kg of soil detected in soil following harvest. Linear and quadratic associations were modeled using both raw and transformed data for all plots within market groups, and also by using means of replicates of cultivars within market groups.

Results

Pre-plant nematode density. The initial density of *H. avenae* in the trial area during 2013 was 22,176 eggs plus juveniles/kg of soil. During 2014 the initial density was 3,309/kg for the combined block of hard red and hard white wheat cultivars, and 11,880/kg for the block of soft white wheat cultivars.

Plant growth and development. Seed was planted into soils that had seed-zone temperatures of 8.9°C in 2013 (4.0-cm depth) and 6.7°C in 2014 (2.4-cm depth). Seedlings emerged more than 3 wk after planting, on about 10 May 2013 and 5 May 2014. Anthesis was initiated on or about 1 July 2013 and 12 July 2014. Growth of some cultivars was visually taller and denser in aldicarb-treated plots than in non-treated plots but no measurements were made.

Disease incidence and severity. Root knotting was present on 98% to 100% of the plants in each trial during each year. This occurred in the nematicide-treated plots as well as in the non-treated control (data not shown). Severity of the root-knotting symptom in the control treatment of each wheat class differed significantly ($P < 0.0001$) for the main effect of year. Mean severity ratings during 2013 and 2014, respectively, were 4.3 (range of 3.7 to 4.5) and 5.0 (range of 4.8 to 5.0) for 19 hard red cultivars and the seven hard white cultivars ($HSD_{0.05}$ = 0.1; data not shown), and 4.3 (range of 4.0 to 4.5) and 4.9 (range of 4.3 to 5.0) for 13 soft white cultivars. Severity ratings did not differ among cultivars for each of the three wheat classes ($P > 0.05$) during either year, and the year × cultivar interaction was also not significant for any of the three wheat classes.

For the two cultivars in which roots were also evaluated in the nematicide treatment for the soft white and hard red wheat classes, the effects of year and nematicide treatment were each significant ($P < 0.0001$) and the effect of cultivar was not significant ($P > 0.25$). The mean severity of the root-knotting symptom in each experiment was greater during 2014 (4.9) than during 2013 (3.7; data not shown), and was greater in the control plots than in the nematicide treated plots; 4.6 and 3.9 ($HSD_{0.05} = 0.2$) for the hard red cultivars, and 4.6 and 4.0 ($HSD_{0.05} = 0.4$) for the soft white cultivars.

Disease resistance. Numbers of newly produced *H. avenae* swollen white females were significantly influenced ($P < 0.05$) by the main effect of year and cultivar for each market class. The year × cultivar interaction was not significant ($P < 0.05$) for any of the three wheat classes. Numbers of white females were greater during 2013 than during 2014 (Tables 1-3). For the two cultivars in which white females were quantified in the nematicide treatment for the hard red and soft white wheat classes, the main treatment effect for nematicide was significant ($P < 0.0001$) for both classes. For Glee, the most susceptible cultivar examined in these comparisons of treated and untreated plots, the application of nematicide reduced the number of white females by 99%, from 38.9 to 0.5 per plant. The effect of year was not significant ($P > 0.05$). The main treatment effect for cultivar was not significant ($P > 0.30$) for any wheat class, however the year × cultivar interaction was significant ($P = 0.02$) for the soft white wheat. In each case, the numbers of white females were much higher on roots in the control plots than in the nematicide-treated plots. The mean numbers of white females in the control and nematicide treatments, respectively, were 18.8 and 1.4 ($HSD_{0.05} = 7.6$) for the hard red wheats, and 18.3 and 3.7 ($HSD_{0.05} = 5.2$) for the soft white wheats.

Numbers of swollen white females extracted and counted during 2014 were too low to provide reliable distinctions among cultivars. WB-Rockland was the only hard red cultivar rated as resistant during both years (Table 1), and WB-Rockland plus 10 additional cultivars were rated as resistant during 2014. LCS Star was the only hard white cultivar rated as resistant during both years (Table 2), and it plus three additional cultivars were rated as resistant during 2014. No cultivars of soft white were rated as moderately resistant, resistant or very resistant to *H. avenae* during 2013 (Table 1). During 2014, nine of the 13 soft white cultivars rated at moderately resistant, resistant or very resistant.

Disease tolerance. Grain yields averaged across entries were significantly greater during 2014 than during 2013 for all three wheat classes. Treatment effects for cultivar ($P < 0.05$) and nematicide ($P < 0.0001$) also each differed significantly for each wheat class. Mean grain yields were higher in nematicide-treated plots compared to the controls; 5,164 vs. 2,967 kg/ha ($HSD_{0.05} = 711$) for hard red cultivars, and 5,517 vs. 3,351 kg/ha ($HSD_{0.05} = 5197$) for hard white cultivars, and 5,653 vs. 4,903 kg/ha ($HSD_{0.05} = 115$) for soft white cultivars. None of the treatment interactions were statistically significant at $P = 0.05$ for the three wheat classes. Grain yields for each cultivar and year are presented in Tables 1-3. Grain yields differed significantly ($P < 0.0001$) between nematicide treatments for all three classes, with yields being increased by 17%, 14% and 15% for hard red, hard white and soft white cultivars, respectively.

The percentage increase in grain yield due to application of nematicide differed significantly among cultivars only for the soft white cultivars during 2013 (Tables 1-3).

Dual resistance and tolerance to *H. avenae*. Cultivars with acceptable dual traits of resistance plus tolerance were identified by grouping data over two years (Table 4). The hard red cultivar WB-Rockland and the hard white cultivar Klasic met these dual-trait criteria, and yields of both cultivars were statistically equivalent to the highest yielding cultivar in that experiment. The hard white cultivar LCS Star was ranked as resistant but did not quite meet the dual criteria only because it had a mean tolerance rating of 15.5, which did not meet the strict pre-determined minimum limit of 15.0 to achieve the moderately tolerant rating. Nevertheless, LCS Star was considered to have agronomically acceptable levels of both resistance and tolerance. The hard red cultivar WB9576 and the soft white cultivar Alpowa were ranked as tolerant but they were moderately susceptible. The soft white cultivar Cataldo was ranked as moderately resistant but was intolerant. No soft white cultivar met the dual criteria.

Post-harvest density of eggs. Residual numbers of eggs from cysts were determined for selected cultivars in both aldicarb-treated and control plots during 2013. Cultivars examined in the hard wheat experiment during 2013 included Glee, Jefferson, LCS Star, Klasic, SY Basalt, WB-Rockland and Westbred 936. The nematicide application reduced ($P < 0.0001$) the mean post-harvest number of eggs by 59%, from 38,039 to 15,023 eggs/kg (data not shown). The range of percentage reduction in egg density due to nematicide application was from 24% to 82% for the least (WB-Rockland) and most (SY Basalt) susceptible cultivars, respectively. The main effect for cultivar was significant, with WB Rockland leaving fewer eggs in soil than Glee, Jefferson, SY Basalt and Westbred 936 (Table 5). Cultivars evaluated in the soft white wheat experiment included Alpowa, Cataldo, IDO 851, UI Stone and WB6430. The nematicide treatment significantly ($P < 0.0001$) reduced the mean post-harvest egg density by 82%, from 76,138 to 13,798 eggs/kg of soil in the control and nematicide treatments, respectively (data not shown). The range of percentage reduction in egg density due to nematicide application was from 71% to 92% for the least (Cataldo) and most (IDO 851) susceptible cultivars, respectively. The main effect for cultivar was also significant, with the number of eggs in control plots being less following Alpowa and Cataldo than following IDO 851 (Table 5).

Since the nematicide clearly reduced the density of *H. avenae* eggs in soil, with many or most of the remaining eggs in nematicide treatments representing eggs from cysts developed during earlier years, it was determined that sampling emphasis during 2014 should be focused on differences among cultivars in the control treatment. All cultivars in the control plots and two cultivars in the nematicide-treated plots were sampled during 2014. The cultivars sampled in the nematicide treatment were the same as those for which the root disease symptoms and numbers of swollen white females had been examined during 2013. For the two cultivars sampled in control and nematicide treatments during both years, the main effects of year and nematicide were significant ($P < 0.05$) for both experiments. The main effect for cultivar was significant ($P = 0.05$) for the soft wheats but was not significant ($P = 0.08$) for the hard wheat experiment. When all cultivars in the control treatment were examined during 2014, the cultivar effect was significant in both experiments; $P < 0.03$ for soft wheats and $P < 0.0001$ for hard wheats. The range of low to high *H. avenae* density for the soft wheat cultivars during 2014 was from 455 eggs/kg of soil for IDO 852 to 9,665 eggs/kg for UI Stone (Table 5). The range for the hard wheat cultivars was from 411 eggs/kg for WB-Rockland to 9,313 eggs/kg for Choteau (Table 5).

Regression analyses indicated the presence of significant associations between numbers of white females developed on roots and eggs extracted from cysts after harvest for both market groups of spring wheat during each year. The strongest models for entries of soft white spring wheat occurred with polynomial regressions of data averaged over three replicates for individual cultivars (Fig. 2). This relationship also occurred for hard wheats during 2013 (Fig. 2) but the strongest model during 2014 occurred with a linear regression of transformed data of all plots; $P = 0.0005$, $R^2 = 0.1599$, $n = 72$). For the latter group of hard wheats during 2014, the polynomial regression using means of raw data for each cultivar, as was used for other groups, was weaker than for the transformed data but is presented for uniformity of presentation in Fig. 2. Numbers of eggs increased with increasing numbers of white females for soft wheat cultivars each year. This also occurred up to a density of about 40 cysts/plant for the group of hard wheats during 2013, whereupon the egg count diminished when the density of white females exceeded 60 per plant. There was no clear association between white females and eggs in the hard wheats during 2014.

Discussion

Fisher (1982) demonstrated that wheat cultivars were generally more profitable in *H. avenae*-infested fields when the cultivars were resistant and tolerant rather than susceptible and intolerant to this cereal cyst nematode. Of the 39 cultivars examined, we detected dual traits of resistance plus tolerance in one cultivar of hard red wheat (WB-Rockland) and one cultivar of hard white wheat (Klasic). One additional cultivar of hard white wheat (LCS Star) also very nearly met our pre-established criteria for this dual-trait ranking and was considered agronomically acceptable for this purpose. We were unsuccessful in identifying these dual traits in soft white spring wheat cultivars.

These experiments contributed to an understanding of relative resistances and tolerances of North American spring wheat cultivars to *H. avenae*. We ranked nine of 39 wheat entries (23%) as tolerant (2 entries) or moderately tolerant (7 entries) and no entries as very tolerant. In a study with barley at the same location and during the same years (Marshall and Smiley 2016) we ranked 69% of 45 barley entries as very tolerant (11 entries), tolerant (11 entries) or moderately tolerant (9 entries). These data confirm previous reports that spring wheat yields are more negatively affected than spring barley yields in fields infested by *H. avenae* in Sweden (Andersson 1982) and Australia (Fisher 1982).

Earlier comparative studies of spring wheat cultivars in field trials or in greenhouse trials with *H. avenae*-infested soils collected from Idaho, Oregon and Washington have shown that the cultivars were equally resistant or tolerant to the *H. avenae* populations in each state (Smiley et al. 2011a, 2013). The resistance and tolerance traits identified for wheat cultivars in these trials in Idaho are therefore anticipated to be applicable to *H. avenae*-infested fields elsewhere in the PNW.

The origins of resistance traits detected in some cultivars examined in our trials are unknown. It appears that none of the accessions are designated as having resistance to *H. avenae* (USDA-ARS-GRIN 2015). We previously reported that WB-Rockland was resistant but intolerant of *H. avenae* in Idaho and Washington and that the source of the resistance trait was unknown (Smiley et al. 2013). In the current experiments WB-Rockland was determined to be both resistant and moderately tolerant. International exchanges of wheat germplasm are likely to have introgressed resistance genes into cultivars such as WB-Rockland, Klasic and LCS Star, and those previously undetected traits are being unveiled by tests such as those reported here. Additional studies are required to identify genes responsible for these traits, and to expand their distribution within PNW wheat cultivars expected to be adapted to areas where fields are infested by *H. avenae*.

We determined here and in our simultaneous studies of spring barley (Marshall and Smiley 2016) that wheat cultivars exhibiting resistance to *H. avenae* exhibited an incidence of root knotting similar to that found on susceptible cultivars. Second-stage juveniles penetrate epidermal cells behind the root cap (Price et al. 1983; Price and Hague 1981) and move intracellularly to the growth zone (Baldwin and Mundo-Ocampo 1991). These phases of disease development occur equally in resistant and susceptible cultivars (Andersen 1961; Cui et al. 2012; O'Brien and Fisher 1974, 1977; Ogbonnaya et al. 2001; Oka et al. 1997). The developing females reprogram root cells to induce the formation of specialized feeding cells (Hewezi et al. 2012) but cells of the developing syncytium then deteriorate in resistant cultivars, causing death or suppressed reproductive capacity of the female in resistant cultivars (Andres et al. 2001; Oka et al. 1997; Seah et al. 2000). Numbers of nematodes within roots and numbers of sites of root-knotting continue to increase as susceptible plants become older, and numbers of nematodes decrease but sites of root-knotting remain the same as resistant plants become older (O'Brien and Fisher 1977). Resistant cultivars therefore reduce the density of *H. avenae* in soil but may still be intolerant and have reduced grain yield if those cultivars exhibit a high level of sensitivity to root injury before the resistance mechanism becomes activated.

In our field studies the disease incidence (root-knotting symptom) did not differ significantly in resistant and susceptible cultivars sampled at the time of plant anthesis. However, the disease incidence was slightly, but significantly, less in aldicarb-treated compared to control plots. The application of aldicarb greatly reduced the development of swollen white females on susceptible cultivars and reduced the post-harvest density of *H. avenae* eggs by up to 82%. Resistant cultivars also reduced the number of swollen white females and the density of *H. avenae* eggs per kg of soil.

An initial density of more than 3,000 *H. avenae* eggs plus juveniles/kg of soil is generally capable of reducing yields of wheat, barley, oats and rye (Andersson 1982). During 2013 the post-harvest densities of *H. avenae* in plots of resistant wheat and in the aldicarb treatment were never reduced to a level that would be too low to affect the productivity of a subsequently-planted intolerant cultivar of wheat or barley because the dry soil contained a mixture of eggs from recently-developed cysts as well as from cysts produced on previous crops of wheat or barley. Forty to 90% of *H. avenae* eggs hatch from cysts during a single season (Andersen 1961; Andersen and Andersen 1970). Hatching from individual cysts is therefore spread over many years, causing two-year rotations of cereals with non-host crops to be inadequate for reducing the residual risk to a subsequent cereal crop. We demonstrated that this would occur even when a susceptible crop would follow a resistant cultivar or a soil that had been treated with a nematicide such as aldicarb. These observations have been consistent in our studies of wheat and barley resistance and tolerance to *H. avenae* (Marshall and Smiley 2016; Smiley et al. 2011a, 2013).

During 2014, with the exception of two hard red wheat cultivars (Volt and WB936), we detected very few white females on roots after heading but a high incidence and severity of the root-knotting symptom on seedlings. We had not encountered this apparent anomaly during seven previous years in which we conducted field trials on *H. avenae*-infested fields in three PNW states, including four years of testing on fields of the Idaho farm where the current research was conducted. We did, however, have a similar experience on three adjacent barley trials at that location during the same year (Marshall and Smiley 2016). The initial density of *H. avenae* eggs plus juveniles on the field where our 2014 trials were established was considered acceptable for assaying wheat (>3,000 *H. avenae* eggs plus juveniles/kg of soil; Andersson 1982). During 2014, the most susceptible cultivar in the soft wheat and hard wheat trial produced 12 and 51 white females/plant, respectively, with initial *H. avenae* densities of 11,880 and 3,309/kg of soil for the soft wheat and hard wheat experiments, respectively. It appeared that the initial density during 2014 was sufficient to attain a valid differentiation among cultivars.

While it remains unclear as to why so few new cysts developed in most cultivars during 2014, we believe the anomaly may have been associated with soil temperature. We planted our trials when the temperature at the depth of planting was 6.7°C during 2014. Seedlings emerged three weeks after planting. *Heterodera avenae* juveniles in the Bashkir region of central Russia emerged from cysts at temperatures of 5°C and above (Tikhanova 1971). During a single season of testing in the PNW, second-stage juveniles began emerging from cysts when average weekly air temperatures stabilized between 2°C and 5°C (Smiley et al. 2005). We assumed that juveniles began to emerge from cysts at the approximate time we planted our trials during 2014 (Kerry and Jenkinson 1976; Tikhonova et al. 1975). However, Anderson (1961) demonstrated that the specific chronological timing of the primary hatch can vary greatly over seasons.

Li et al. (2012) reported that 16°C was the optimum temperature for penetration of roots by *H. avenae*, and 18°C to 22°C was the optimum range of temperatures for juveniles to go through molts as they develop into gravid females. In this study, and in accordance with our previous experience (Smiley et al. 2005), we assumed that the density of juveniles in soil continued to increase sharply as the soil warmed during the three weeks between planting and seedling emergence. We also assumed that juveniles would be capable of invading roots for at least three weeks after they emerged from cysts, as was reported by Davies and Fisher (1976). In our study, during 2014, fewer *H. avenae* eggs than had been anticipated were detected in soil following the harvests of even the most susceptible wheat cultivars. This also occurred in each of three adjacent spring barley trials (Marshall and Smiley 2016). It is possible that the low numbers of swollen white females occurred because the primary hatching period occurred later than anticipated during 2014, which may have led to too few growing degree days for molting and egg production between the date of root invasion and crop maturation. However, it is also plausible that this observation could have been affected by marginal levels of initial inoculum, a temperature sub-optimal for development of gravid females, a difference of soil sampling methods during 2013 and 2014, or an undetected anomaly associated with the procedures used for extraction of cysts and counting of eggs released from cysts. A discussion of these potential explanations was provided by Marshall and Smiley (2016). In short, none of these potential reasons appears to plausibly explain the phenomenon we experienced during 2014.

Comparisons of numbers of white females developed on each cultivar and the number of eggs extracted from cysts after harvest showed that the two methods for assessing resistance to *H. avenae* were significantly correlated for soft white and hard red spring wheat cultivars during 2013, but only for soft white cultivars during 2014. The peak density of eggs recovered from the soils used to produce hard wheat cultivars occurred when about 40 white females had been produced on each plant. When the count of white females was elevated above 60 per plant, there was an apparent decrease in numbers of eggs/cyst, indicating the possibility of competition among white females for limited plant nutrients when the number of females exceeds a certain density. This relationship has been described previously (Andersen 1961). The lack of association between white females and eggs for the hard wheats during 2014 indicates the probability of an error either in counting white females or in recovering cysts from soil. A loss of white females could have occurred either when digging or washing roots. Alternatively, if the sampling occurred when white females were transitioning into brown cysts in the hard wheats, an error could have occurred in distinguishing some of the newly formed cysts from those remaining in soil after previous wheat crops.

In conclusion, we found that three spring wheat cultivars (Klasic, WB-Rockland and LCS Star) expressed acceptable levels of both tolerance and resistance to *H. avenae* in the USA. We also identified additional cultivars that were either resistant or tolerant to *H. avenae*. We conclude that the spring wheat cultivars identified in these experiments can be used to improve production efficiency on fields that are heavily infested by *H. avenae*. This finding indicates that it should be possible to identify even more cultivars with the resistance plus tolerance traits during evaluations of greater numbers and a greater diversity of wheat genotypes. Lastly, we found that the two methods used to evaluate resistance in these experiments were mostly well correlated although, for an unknown reason, that was not true for the hard wheats during 2014.

Acknowledgments

We appreciated land and crop management assistance provided by Dale Daw (St. Anthony, ID) and technical assistance by Chad Jackson, Tod Shelman, Suzette Arcibal, Linda Beck, Martha Carrillo, and Ester Serna (University of Idaho, Aberdeen) and by Jennifer Gourlie, Karl Rhinhart, Paul Thorgersen, Alysha Hitzman, and Nick Webster (Oregon State University, Pendleton). We also appreciated funding from the Idaho Wheat Commission, Oregon Wheat Commission, Washington Wheat Commission, Idaho Agricultural Experiment Station, Oregon Agricultural Experiment Station, and USDA-ARS Root Disease and Biological Control Unit (at Pullman, WA). Discounted nematode testing fees were provided by Western Laboratories (Parma, ID).

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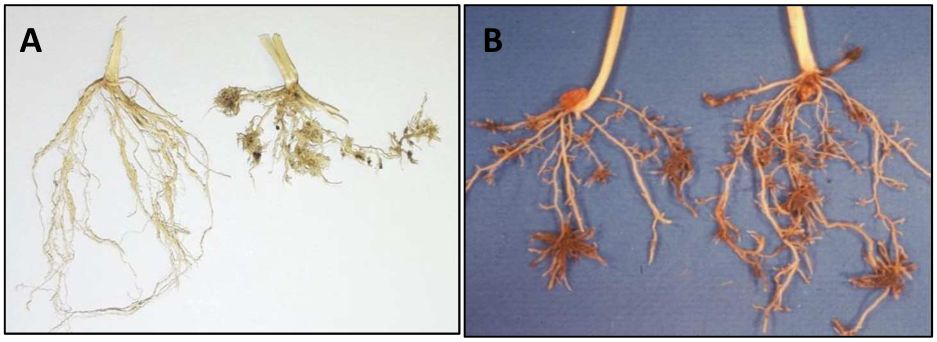

Fig. 1. Spring wheat with shallow, knotted roots caused by *Heterodera avenae*; (**A**) plant with very low intensity of nematode invasion (**left**) compared to a heavily-invaded plant (**right**), and (**B**) a close-up view of the classic proliferation of adventitious roots near feeding sites where cysts will develop.

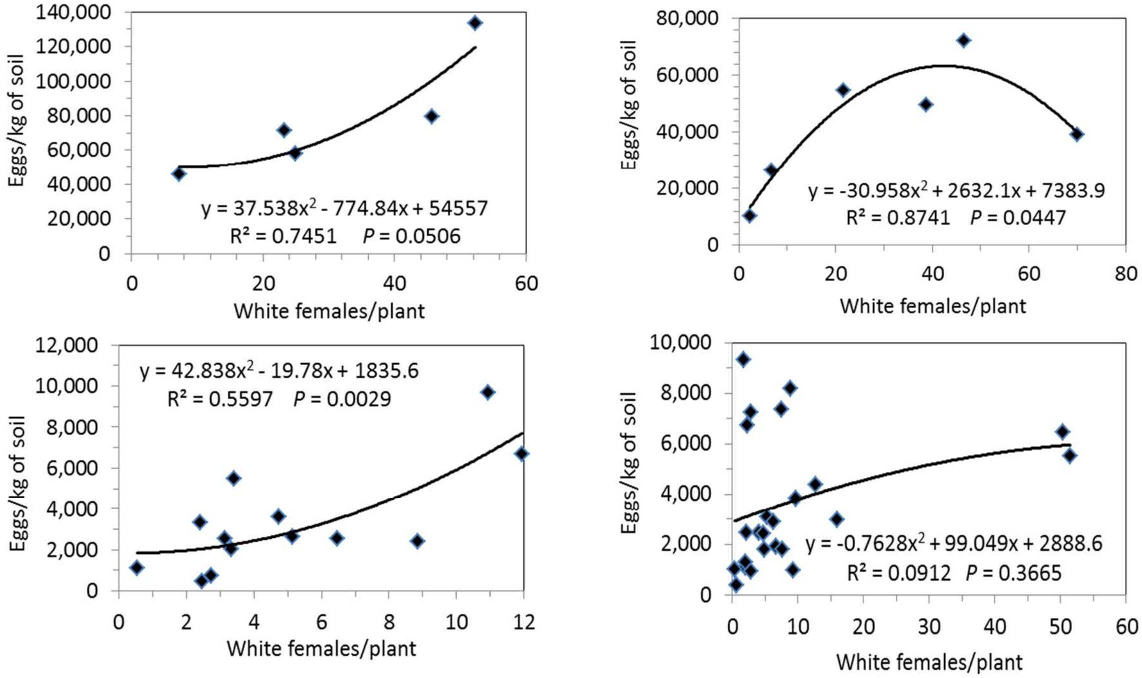

Fig. 2. Associations between number of white females produced on individual cultivars of spring wheat and the density of eggs extracted from cysts in the soils upon which those cultivars were produced during 2013; soft white spring wheat (**left column**) and hard red plus hard white spring wheat (**right column**) during 2013 (**top row**) and 2014 (**bottom row**).

Table 1. Evaluation of 19 hard red spring wheat cultivars for resistance and tolerance to *Heterodera avenae* in two fields near St. Anthony, ID during 2013 and 2014.

Cultivar	White females/ plant [u]	Resis- tance [v]	Grain yield (kg/ha) Control	Treated [w]	% increase [x]	Toler- ance [y]
2013						
WB-Rockland	2.3±0.5 g[z]	R	3,118±570 a	3,545±328 ab	20.2±12.7 a	MI
WB9576	10.9±5.5 e-g	MS	2,929±321 a	3,197±325 ab	10.2±6.7 a	MT
UI Platinum	11.0±7.8 e-g	MS	2,610±375 a	3,366±500 ab	28.6±3.0 a	MI
WB9229	11.6±5.8 e-g	MS	2,337±482 a	3,197±390 ab	41.3±16.2 a	I
Kelse	18.4±17.4 c-g	S	3,279±662 a	3,709±577ab	19.7±15.9 a	MI
Jefferson	21.7±10.6 b-g	S	2,735±78 a	4,442±460 a	61.7±13.3 a	VI
Choteau	22.3±8.2 b-g	S	2,498±310 a	3,143±243 ab	29.9±12.1 a	MI
IDO862T	22.9±12.4 b-g	S	2,377±315 a	2,709±266 ab	18.7±18.3 a	MI
IDO1202S	23.9±2.0 b-g	S	2,891±558 a	3,869±438 ab	42.6±15.8 a	I
Cabernet	27.4±1.8 b-f	VS	2,082±224 a	2,836±324 ab	39.1±15.1 a	I
LCS Iron	30.9±7.5 b-f	VS	3,035±415 a	4,061±247 ab	38.5±12.3 a	I
UI Winchester	36.3±15.3 b-e	VS	2,450±204 a	2,860±150 ab	18.6±9.3 a	MI
Glee	38.9±9.9 b-d	VS	3,230±609 a	3,907±356 ab	27.3±12.8 a	MI
Alzada	40.7±7.9 b-d	VS	2,616±622 a	2,743±579 ab	10.3±9.4 a	MT
Bullseye	44.4±5.8 a-c	VS	2,433±144 a	2,984±156 ab	25.0±13.3 a	MI
IDO862E	45.5±22.3 a-c	VS	2,012±344 a	2,517±381 b	31.9±19.8 a	I
SY Basalt	46.7±23.9 ab	VS	2,950±457 a	4,100±634 ab	39.4±10.6 a	I
Westbred 936	70.1±29.8 a	VS	1,855±51 a	3,028±298 ab	62.7±14.4 a	VI
Mean	26.7	VS	2,610	3,323	26.3	MI
$P > F$	0.0254		0.3920	0.0112	0.2191	
$HSD_{0.05}$	-		ns	1,040	ns	
2014						
WB-Rockland	0.7±0.1 c	VR	4,910±169 a	5,104±116 cd	8.7±5.7 a	T
LCS Iron	1.3±0.6 c	R	5,133±221 a	5,824±137 a-c	13.8±2.4 a	MT
Choteau	1.4±0.6 c	R	4,847±270 a	4,982±257 d	6.7±7.9 a	T

Alzada	2.1±1.2 c	R	4,817±236 a	5,135±156 cd	14.6±5.3 a	MT
UI Winchester	2.2±0.5 c	R	4,574±334 a	4,993±334 d	20.9±11.6 a	MI
IDO862E	2.3±1.1 c	R	4,880±358 a	5,292±420 b-d	18.0±8.4 a	MI
SY Basalt	2.8±2.1 c	R	5,379±427 a	5,512±235 b-d	8.1±10.3 a	T
Cabernet	2.9±1.0 c	R	5,024±370 a	5,093±255 cd	4.4±6.6 a	VT
Jefferson	5.3±2.2 bc	MR	5,103±378 a	5,465±344 b-d	15.7±3.4 a	MI
Bullseye	4.1±1.8 bc	MR	5,285±172 a	5,494±191 b-d	8.3±4.8 a	T
WB9576	4.7±1.3 bc	MR	5,458±347 a	5,449±216 b-d	1.3±8.0 a	VT
UI Platinum	6.7±3.1 bc	MS	5,309±333 a	5,629±240 a-c	12.9±4.5 a	MT
IDO862T	7.5±4.0 bc	MS	5,253±347 a	5,563±276 a-d	13.4±4.8 a	MT
Kelse	7.6±3.9 bc	MS	5,343±334 a	5,730±227 a-c	16.8±8.0 a	MI
Glee	8.9±2.5 bc	MS	5,202±305 a	5,359±301 b-d	6.5±2.6 a	T
WB9229	9.3±8.2 bc	MS	5,524±328 a	5,836±331 ab	11.9±0.7 a	MT
IDO1202S	12.7±6.5 b	S	5,886±336 a	6,232±240 a	12.6±4.7 a	MT
Volt	50.3±22.9 a	VS	5,137±337 a	5,671±181 a	23.4±2.8 a	MI
Westbred 936	51.4±34.7 a	VS	4,717±270 a	5,153±124 cd	21.0±7.3 a	MI
Mean	9.7	MS	4,880	5,448	12.5	MT
P > F	0.0279		0.0604	0.0353	0.3014	
$HSD_{0.05}$	-		ns	680	ns	

[u] Number of *H. avenae* white females produced/plant for the control (no-nematicide) treatment only; sampling was performed at about the time of anthesis.

[v] Phenotypic resistance reaction: very resistant (VR; ≤1 swollen female/plant), resistant (R; 1.1 to 3), moderately resistant (MR; 3.1 to 6), moderately susceptible (MS; 6.1 to 12), susceptible (S; 12.1 to 25), or very susceptible (VS; >25).

[w] Nematicide treatment included application of aldicarb (4.2 kg of aldicarb/ha) in the seed row at the time of planting.

[x] Percentage increase in grain yield due to application of nematicide.

[y] Phenotypic tolerance reaction: very tolerant (VT; <5% yield response to nematicide), tolerant (T; 5 to 10%), moderately tolerant (MT; 10 to 15%), moderately intolerant (MI; 15 to 30%), intolerant (I; 30 to 50%), or very intolerant (VI; >50%).

[z] Means followed by the same letter within a column did not differ significantly at α = 0.05 as determined by Tukey's Honestly Significant Difference (HSD) test.

Table 2. Evaluation of seven hard white spring wheat cultivars for resistance and tolerance to *Heterodera avenae* in two fields near St. Anthony, ID during 2013 and 2014.

			Grain yield (kg/ha)			
Cultivar	White females/ plant [u]	Resis- tance [v]	Control	Treated [w]	% increase [x]	Toler- ance [y]
2013						
LCS Star	4.2±3.1 a[z]	MR	3,723±547 a	4,200±679 a	12.4±5.5 b	MT
Klasic	6.9±2.6 a	MS	2,866±418 a	3,369±286 a	23.1±15.0 a	MI
Dayn	14.6±14.0 a	S	4,011±680 a	4,727±429 a	25.0±15.0 a	MI
WB-Idamax	26.1±12.8 a	VS	2,581±309 a	3,584±250 a	34.3±10.0 a	I
Snow Crest	35.9±16.4 a	VS	2,709±417 a	3,483±278 a	29.2±4.3 a	MI
Blanca Grande	36.7±6.0 a	VS	2,988±489 a	3,360±395 a	15.1±5.8 a	MI
WB-Paloma	42.7±16.8 a	VS	2,316±243 a	3,197±223 a	41.0±11.9 a	I
Mean	23.9	S	3,028	3,674	25.7	MI
P > F	0.1295		0.1991	0.1694	0.5510	
$HSD_{0.05}$	-		ns	ns	ns	
2014						
Dayn	0.5±0.3 b	VR	6,299±280 a	6,397±206 a	3.7±4.9 a	VT
LCS Star	0.9±0.3 b	VR	4,837±447 b	5,610±185 a	18.6±10.0 a	MI
Klasic	2.0±0.4 b	R	5,366±303 b	5,516±241 ab	6.8±6.6 a	T
Blanca Grande	4.9±3.7 ab	MR	5,273±237 b	5,419±277 ab	5.7±3.6 a	T
WB-Idamax	6.3±3.1 ab	MS	5,435±209 b	5,692±160 ab	10.5±7.1 a	MT
WB-Paloma	9.7±3.8 a	MS	5,539±218 b	5,801±115 ab	10.6±6.2 a	MT
Snow Crest	16.0±6.7 a	S	5,486±350 b	5,938±267 ab	18.2±1.4 a	MI
Mean	5.8	MR	5,267	5,768	10.6	MT
P > F	0.0326		0.0491	0.0815	0.3521	
$HSD_{0.05}$	-		749	ns	ns	

[u-z] Footnotes are the same as for Table 1.

Table 3. Evaluation of 13 soft white spring wheat cultivars for resistance and tolerance to *Heterodera avenae* in two fields near St. Anthony, ID during 2013 and 2014; means and standard error of the mean for three replicates of white female counts and four replicates of grain yield.

Cultivar	White females/ plant [u]	Resis-tance [v]	Grain yield (kg/ha) Control	Treated [w]	% increase [x]	Toler-ance [y]
2013						
Cataldo	7.3±3.5 a	MS	3,322±686 a	5,729±1,073 a	77.1±17.4 a	VI
IDO 852	18.8±7.6 a	S	4,124±364 a	5,240±538 a	26.7±3.5 bc	MI
UI Stone	23.2±14.9 a	S	4,221±333 a	5,128±364 a	22.8±8.7 bc	MI
Alpowa	24.9±1.2 a	S	4,418±255 a	4,631±224 a	5.2±8.2 c	T
Babe	28.6±5.7 a	VS	4,134±408 a	5,211±454 a	27.0±5.6 bc	MI
UI Petit	34.7±12.4 a	VS	4,125±488 a	5,107±459 a	26.0±10.9 bc	MI
WB6121	36.3±10.0 a	VS	4,110±580 a	4,642±488 a	14.6±5.0 bc	MT
Penawawa	40.0±6.9 a	VS	3,900±473 a	4,672±374 a	22.3±13.3 bc	MI
IDO 854	43.5±16.2 a	VS	3,619±740 a	4,833±264 a	42.3±22.6 b	I
Alturas	43.6±26.4 a	VS	4,280±612 a	5,083±326 a	23.8±12.9 bc	MI
Seahawk	44.4±7.2 a	VS	4,289±524 a	5,165±319 a	24.4±12.0 bc	MI
WB6430	45.8±18.3 a	VS	5,004±526 a	5,793±103 a	19.1±11.4 bc	MI
IDO 851	52.6±23.9 a	VS	4,174±483 a	5,066±509 a	21.9±3.3 bc	MI
Mean	34.1	VS	4,132	5,099	23.4	MI
P > F	0.5227		0.5806	0.6992	0.0251	
$HSD_{0.05}$	ns		ns	ns	30.5	
2014						
IDO 851	0.5±0.1 a	VR	5,581±297 a	6,363±404 a	14.1±4.2 a	MT
IDO 854	2.4±0.7 a	R	5,905±465 a	6,382±379 a	8.6±3.1 a	T
IDO 852	2.5±1.0 a	R	5,958±468 a	6,475±492 a	8.9±3.1 a	T
Babe	2.7±0.6 a	R	5,235±267 a	5,923±203 a	13.8±5.4 a	MT
Cataldo	3.1±2.3 a	MR	6,133±150 a	6,214±346 a	1.1±3.5 a	VT
Penawawa	3.3±1.2 a	MR	5,610±580 a	6,205±453 a	11.6±4.0 a	MT
UI Petit	4.7±2.5 a	MR	6,063±491 a	6,505±247 a	9.3±4.7 a	T
WB6121	4.7±3.5 a	MR	5,596±210 a	6,083±340 a	8.5±2.5 a	T

Alpowa	5.1±2.4 a	MR	5,190±226 a	5,639±197 a	8.9±3.4 a	T
Alturas	6.5±3.6 a	MS	5,543±132 a	6,008±168 a	8.4±2.4 a	T
Seahawk	9.9±3.0 a	MS	5,373±254 a	5,903±251 a	10.0±4.7 a	T
UI Stone	10.9±4.2 a	MS	5,630±265 a	6,451±326 a	14.7±3.2 a	MT
WB6430	11.9±2.9 a	MS	5,949±195 a	6,531±205 a	9.9±2.8 a	T
Mean	5.2	MR	5,674	6,206	9.4	T
P > F	0.1467		0.3972	0.5763	0.7341	
$HSD_{0.05}$	ns		ns	ns	ns	

[u-z] Footnotes are the same as for Table 1.

Table 4. Summary of cultivar tolerance and resistance traits for data grouped over two years.

Spring wheat market class and cultivar	White females/ plant [v]	Resistance rating [w]	Yield increase [x] (%)	Tolerance rating [y]	MR + MT [z]
Hard red					
WB-Rockland	1.5	R	14.5	MT	X
Jefferson	7.7	MS	38.7	I	
WB9576	7.8	MS	5.8	T	
UI Platinum	8.9	MS	20.7	MI	
WB9229	10.4	MS	26.6	MI	
Choteau	11.9	MS	18.3	MI	
Glee	12.4	S	16.9	MI	
Kelse	13.0	S	18.3	MI	
IDO862T	15.2	S	16.1	MI	
Cabernet	15.2	S	21.7	MI	
LCS Iron	16.1	S	24.1	MI	
IDO1202S	18.3	S	27.6	MI	
UI Winchester	19.3	S	19.7	MI	
Alzada	21.4	S	12.5	MT	
IDO862E	23.9	S	25.0	MI	
Bullseye	24.2	S	16.6	MI	
SY Basalt	24.7	S	23.8	MI	
Volt	31.2	VS	35.4	I	
Westbred 936	60.8	VS	41.9	I	
Hard white					
LCS Star	2.6	R	15.5	MI	
Klasic	4.4	MR	15.0	MT	X
Dayn	7.5	MS	14.3	MT	
WB-Idamax	16.2	S	22.4	MI	
Blanca Grande	20.8	S	10.4	MT	
Snow Crest	26.0	VS	23.7	MI	
WB-Paloma	26.2	VS	25.8	MI	
Soft white					
Cataldo	5.2	MR	39.1	I	
Alpowa	8.9	MS	7.1	T	
IDO 852	10.6	MS	17.8	MI	
UI Stone	11.1	MS	18.7	MI	
Babe	15.7	S	20.4	MI	
UI Petit	19.7	S	17.7	MI	
WB6121	20.5	S	11.6	MT	
Penawawa	21.7	S	17.0	MI	
IDO 854	23.0	S	27.9	MI	
Alturas	25.0	S	16.1	MI	
Seahawk	26.6	VS	17.2	MI	

IDO 851	26.6	VS	18.0	MI
WB6430	28.9	VS	14.5	MT

[v] Number of *H. avenae* white females produced/plant for the control (no-nematicide) treatment.
[w] Cultivars were rated as very resistant (VR; ≤1 swollen female/plant), resistant (R; 1.1 to 3), moderately resistant (MR; 3.1 to 6), moderately susceptible (MS; 6.1 to 12), susceptible (S; 12.1 to 25), or very susceptible (VS; >25).
[x] Percentage increase in grain yield due to application of nematicide.
[y] Tolerance ratings were very tolerant (VT; <5% yield response to nematicide), tolerant (T; 5 to 10%), moderately tolerant (MT; 10 to 15%), moderately intolerant (MI; 15 to 30%), intolerant (I; 30 to 50%), or very intolerant (VI; >50%).
[z] Cultivars that met the dual criteria of being at least moderately resistant (≤6% swollen females/plant) plus moderately tolerant (≤15% yield increase with nematicide).

Table 5. Density of eggs released from *Heterodera avenae* cysts extracted from soils following the grain harvest of spring wheat cultivars (13 soft white, 19 hard red, and 7 hard white) in two fields near St. Anthony, ID during 2013 and 2014; means and standard error of the mean for three replicates.

Soft white cultivars	Eggs/kg of soil [x] 2013	Eggs/kg of soil [x] 2014	Hard red and hard white cultivars [y]	Eggs/kg of soil 2013	Eggs/kg of soil 2014
IDO 852		455±240 b[z]	WB-Rockland	10,384±1,608 c	411±52 c
Babe		763±103 ab	LCS Iron		719±53 bc
IDO 851	133,584±6,709 a	1,129±222 ab	SY Basalt	72,218±13,099 a	953±431 bc
Penawawa		2,240±446 ab	WB9229		983±332 bc
Seahawk		2,390±561 ab	Dayn (W)		1,027±610 bc
Cataldo	45,672±10,759 b	2,523±706 ab	Alzada		1,085±375 bc
Alturas		2,537±726 ab	Klasic (W)	26,532±4,235 a-c	1,276±621 bc
Alpowa	57,904±14,605 b	2,655±131 ab	LCS Star (W)	15,620±3,588 bc	1,452±1,009 bc
IDO 854		3,344±1,286 ab	Blanca Grande (W)		1,804±466 a-c
UI Petit		3,583±2,599 ab	Kelse		1,804±954 a-c
WB6121		5,485±3,329 ab	UI Platinum		1,936±268 a-c
WB6430	78,669±20,364 ab	6,703±3,215 ab	WB9576		2,4240±159 a-c
UI Stone	71,192±11,979 ab	9,665±4,017 a	Bullseye		2,449±371 a-c
			UI Winchester		2,464±233 a-c
			WB-Idamax (W)		2,919±852 a-c
			Snow Crest (W)		2,992±753 a-c
			Jefferson	54,736±20,676 ab	3,095±2,062 a-c
			WB-Paloma (W)		3,828±1,836 a-c
			IDO1202S		4,385±997 a-c
			Westbred 936	39,204±15,376 ab	5,529±816 ab
			Volt		6,468±3,537 ab
			IDO862E		6,732±1,962 ab
			Cabernet		7,260±3,845 ab
			IDO862T		7,363±2,411 ab
			Glee	49,779±2,259 ab	8,169±3,590 ab
			Choteau		9,313±1,188 a

Mean	77,604	3,327	38,385	3,417
P > F	0.0008	0.0397	0.0011	<0.0001

[x] Number of *H. avenae* eggs/kg of soil for the control (no-nematicide) treatment only; extraction of cysts was performed from soil that was dry following harvest.

[y] All cultivars are hard red spring except those designated by a ‘(W)’, which are hard white spring wheat cultivars.

[z] Means followed by the same letter within a column did not differ significantly at $\alpha = 0.05$ as determined by Tukey’s Honestly Significant Difference (HSD) test.