Spring Barley Resistance and Tolerance to the Cereal Cyst Nematode *Heterodera avenae*

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Abstract

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Heterodera avenae is a cereal cyst nematode that reduces wheat yields in the Pacific Northwest USA. Barley is also susceptible but there were no previous reports of resistance or tolerance to *H. avenae* in the USA. Spring barley cultivars were assayed in *H. avenae*-infested fields over two years. Cultivars were planted in plots treated or not treated with aldicarb. Forty-five cultivars were evaluated for the market classes of 2- and 6-row feed barleys and 2- and 6-row malt barleys. One 2-row feed barley (Lenetah) was ranked as resistant and four were tolerant or very tolerant. One 2-row malt barley (Odyssey) was very resistant and 10 were tolerant or very tolerant. Two 6-row feed and two 6-row malt barleys were tolerant or very tolerant but none were resistant. Seven feed barleys were ranked as having a balance of at least moderate resistance plus moderate tolerance; Champion, Lenetah, Xena, Idagold II, Transit, Millenium and Goldeneye. This is the first report of resistance and tolerance of barley in *H. avenae*-infested fields in the Pacific Northwest. Barley productivity can be improved by planting resistant plus tolerant cultivars or by using highly resistant and highly tolerant cultivars as parents in barley improvement programs.

Barley (*Hordeum vulgare* L.) is harvested from about 300,000 hectares annually in the Pacific Northwest (PNW), with 22%, 5% and 1% harvested from the states of Idaho, Washington, and Oregon respectively (USDA-NASS, 2013). The cereal cyst nematode, *Heterodera avenae* Woll., reduces grain yield of wheat in localized regions of each of these states (Smiley, 2009; Smiley et al., 1994, 2005b, 2011a, 2012, 2013). An initial density of more than 3,000 *H. avenae* eggs plus juveniles is generally capable of reducing yields of wheat, barley, oats and rye (Andersson, 1982).

Rotation of cereal crop hosts of *H. avenae* with two years of non-host broadleaf crop species or fallow have long been recommended to reduce the density of this nematode on highly-infested fields (Andersson, 1982; Fisher and Hancock, 1991; Rivoal and Sarr, 1987; Smiley et al., 1994; Tikhonova et al., 1975). The three-year rotation for this purpose alone is seldom profitable in the PNW and is generally not an accepted practice in regions where 2-year rotations of a cereal crop and potato, or a cereal crop and a pulse crop are most profitable in fields where *H. avenae* is absent or at low density. No chemical or biological nematicides are currently available to manage *H. avenae* (Smiley et al., 2012).

Resistance is characterized by cultivars that greatly suppress or prevent reproduction of nematodes (Cook and Evans, 1987). Resistance to *H. avenae* in barley was first discovered in 1920 and was characterized in 1961 (Andersen, 1961). Resistance of barley to *H. avenae* has been a specific crop improvement objective in other countries for more than five decades (Andersen

1961; Andersen and Andersen, 1973; Cotten, 1967; Holgado et al., 2009; Nielsen, 1982; O'Brien and Fisher, 1974; Valocká et al., 1994; Williams, 1970). The best currently characterized sources of resistance to *H. avenae* in barley are the genes mapped to the *Ha2* locus on chromosome 2H (Kretschmer et al., 1997) and to the *Ha4* locus mapped on chromosome 5H (Barr et al., 1998). According to the gene nomenclature system of Moseman (1972), these gene loci should be designated as *Rha2* and *Rha4*, respectively. However, except for 12 non-commercial barley entries in an international screening array to identify pathotypes of *H. avenae*, which were evaluated under controlled-environment conditions (Smiley et al., 2011b), we are not aware of any contemporary barley cultivars or breeding lines having been evaluated for resistance to *H. avenae* in the USA. There are apparently no commercial barley cultivars in the USA for which the registration includes a report of resistance to *H. avenae* (USDA-ARS-GRIN, 2015).

Barley is generally more tolerant to invasion by *H. avenae* than are oats and wheat (Andersson, 1982; O'Brien and Fisher, 1977) but tolerance also has not been evaluated in North America. 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 (Cook and Evans, 1987; Fisher, 1982). Tolerance is usually estimated in the field by comparing the yield of a specific plant cultivar in a naturally-infested soil that is either left untreated or is treated with a nematicide such as aldicarb to reduce the impact of the existing nematode population (Brown, 1987; Meagher et al., 1978; Smiley, 2009; Taylor et al., 1999).

Roots of both resistant and tolerant cultivars are invaded by *H. avenae*, which may cause an intolerant reaction in some cultivars before the resistance trait becomes expressed in resistant cultivars (O'Brien and Fisher, 1977; Ogbonnaya et al. 2001; Oka et al., 1997). This contributes to the inability of some resistant cultivars to produce grain yields that are competitive with more susceptible cultivars to which they are being compared (Wilson et al., 1983). Growers are often reluctant to plant resistant cultivars that produce yields that are lower than some susceptible cultivars (Rivoal and Cook, 1993). Cultivars with both resistance and tolerance are therefore required for both optimal yield performance in existing plantings and for reducing the future risk to subsequent plantings of intolerant cultivars or crops (Andersen, 1961; Brown, 1987; Fisher, 1982). Because barley is generally more tolerant of *H. avenae* than are other cereals, it has been predicted that there is a greater potential in barley than in other cereal species to identify cultivars that are both resistant and tolerant of this nematode (Andersson, 1982; O'Brien and Fisher, 1977).

The objective of this research was to perform the first evaluation of barley cultivars for tolerance and resistance to *H. avenae* in the USA. We evaluated 45 spring barley cultivars in four market classes (2-row feed, 2-row malt, 6-row feed, and 6-row malt) over a 2-year period in naturally-infested fields to examine our hypotheses that North American barley cultivars differ in tolerance and resistance, and that cultivars with acceptable balances of both resistance and tolerance could be identified.

Materials and Methods

Location. Trials during 2013 and 2014 were performed on fields on a farm near St. Anthony in Fremont County of Idaho; latitude 43.922N, longitude -111.638W, and altitude of 1,521m. The climate is characterized as a semi-arid continental type with cold winters and warm, dry summers. The mean annual precipitation is 352mm and the soil is a St. Anthony gravelly sandy loam. Supplemental water was applied to each field by sprinkler irrigation. Fields were selected based upon a previous knowledge that they were infested by *H. avenae*. In each field, the spring barley trials were performed during the spring grain cycle of a 2-year rotation of potato and

a spring cereal. Soil was cultivated and seed was planted as soon as possible after the soil thawed and became friable after the winter freeze. Cultivation by deep disking (20-cm depth) was performed during the autumn following the potato crop and a light rotovating (10-cm depth) was performed to prepare a uniform surface prior to planting the spring barley. Pre-plant density of plant-parasitic nematode genera was determined at the time of planting, and the processing procedure for preplant and post-harvest soil samples is described later.

Experimental design. Three spring barley experiments were planted at St. Anthony, ID on 18 Apr 2013. Experiment #1 included 16 cultivars of 2-row feed barley. Experiment #2 included 19 cultivars of 2-row malting barley, and Experiment #3 included 10 cultivars of 6-row barley that included four feed and six malting barleys. Cultivars for each trial were those that were evaluated for agronomic traits, grain yield, grain quality, and foliar diseases at four other locations in southeast and south-central Idaho (Marshall et al., 2014).

The three experimental blocks were planted end-to-end without a border area between trials. Each trial consisted of four replicates of each barley entry planted into a split-plot design. Each plot consisted of two drill rows in a 0.9 × 9 m area. Cultivars were randomized within each replicate (main plot) and each cultivar was split (sub-plots) as an adjacent nematicide-treated and a control plot. The field had been previously determined to be infested rather uniformly with *H. avenae* and the pre-plant estimation of nematode density therefore consisted of a single composite soil sample from the total area encompassed by the three experiments. The composite sample consisted of 25 soil cores (2.5-cm diam.) collected to 30-cm depth.

The three experiments were repeated during 2014. Entries and experimental designs were identical except that the trials were separated by about 20-m from one another within a field in which the *H. avenae* density was found to be more aggregately distributed than in the field used during 2013. Pre-plant sampling for nematode density was therefore taken individually from each of the three experimental blocks. Planting was performed on 10 Apr 2014.

Experimental procedures. A locally-fabricated no-till drill was used to plant each trial. The drill was equipped with a cone-seeder, two Gandy distributors, and four series of row openers spaced at 36-cm. Fluted opening coulters were mounted on a front tool bar and were followed by a sweep-type deep-bander for dispensing fertilizer. A second toolbar was used to mount double-disk openers to dispense seed in line with the opening coulter and deep bander. One Gandy distributor was used to dispense fertilizer 5-cm below and 4-cm to each side of the seed row. Seed was dispensed through a cone-seeder and placed into moist soil at 4.0- and 2.5-cm depths during 2013 and 2014, respectively. Seed was planted at a density of 205 seed/m^2.

Seed was planted with or without application of the nematicide aldicarb (Temik 15G, Bayer CropScience, Research Triangle Park, NC) at the rate of 4.2 kg of aldicarb/ha. Aldicarb was metered from a Gandy distributor on the drill and was placed with the seed into two rows on one side of the seed drill. Untreated controls and aldicarb treatments (sub-plots) therefore each consisted of two rows to provide side-by-side comparisons of varietal performance in replicated treated and untreated plots.

Fertilizer was banded uniformly under all four seed rows at the time of planting, at a rate of 123 kg N/ha formulated as a 1:1 blend of 16-20-0 and 46-0-0. During 2013, seed was treated with difenoconazole plus mefenoxam at 120 and 30 mg ai/kg of seed, respectively (Dividend Extreme, Syngenta Crop Protection, Greensboro, NC). During 2014, the seed was treated with the fungicides difenoconazole, mefenoxam and ipconazole and the insecticide thiamethoxam at 180, 44, 15, and 129 mg ai/kg of seed, respectively (Dividend Extreme + Rancona 3.8FS + Cruiser 5FS, formulated as Cruiser Maxx Custom Blend, Pendleton Grain Growers, Pendleton, OR).

Weed control consisted of a pre-plant application of glyphosate and a post-emergence application of a mixture of pyrasulfotole, bromoxynil, fluroxypyr and florasulam; Huskie (Bayer CropScience, Research Triangle Park, NC) mixed with Starane Flex (Dow AgroSciences, Indianapolis, IN). During 2013, stripe rust was prevented by application of propiconazole plus trifloxystrobin (Stratego, Bayer CropScience) mixed with the herbicides.

The timing of plant sampling to determine resistance was based upon plant growth stages predicted using the on-line barley phenology model 'Barley R Miller MSU' (http://www.uspest.org/cgi-bin/ddmodel.pl). The model is based upon accumulation of growing degree days (GGD) expressed using 0°C as the base temperature at which no heat accumulation or plant growth is calculated. We used data from a site located close to our experiment; 'Saint Anthony 1 WNW AM ID'. Calculations are initiated when the seed is planted and the predicted date of coleoptile emergence occurs at 144 GGD after barley seed begins to imbibe water. The Miller phenological model for barley predicts that anthesis will occur at the time 967 GDD have accumulated after the date of planting, and is when females swollen with eggs are most visible.

The development of a closely related species, *H. filipjevi*, is best fitted to a base temperature of 8°C (Hajihassani et al., 2010). Yuan et al (2014) determined that the invasion and development dynamics of *H. avenae* and *H. filipjevi* are almost the same. Growing degree day calculations for development of these nematodes begins when roots become invaded, which can occur as soon as roots begin to appear (Kerry and Jenkinson, 1976). Root establishment can be approximated to the time of coleoptile emergence. Juveniles in the soil matrix retain their ability to invade roots for many weeks (Davies and Fisher, 1976). White females of *H. filipjevi* start to become visible at about 209 GDD (8°C base) and eggs become embryonated in fully swollen white females at about 358 GDD (Hajihassani et al., 2010). The timing of sampling for *H. avenae* therefore differs somewhat from the barley phenological model parameters stated above.

For this study, we collected roots of 10 plants from each of three replicates of each treatment when more than 500 GDD had accumulated after seedling emergence, which occurred 20 days after fully embryonated eggs were predicted and 15 days after anthesis; 13 June 2013 and 23 July 2014. Roots were used to examine the incidence and severity of the classical root knotting symptoms in which adventitious roots proliferate at points on the root axis where the nematode established a specialized feeding cell. Roots were dug to a depth of about 15 cm from three locations within each of the plots examined. Roots were washed and were rated visually for incidence and severity. Incidence was calculated as the percentage of plants exhibiting at least one knotted root. The severity scale was as follows: 1 = no evidence of damage, 2 = 1 to 3 knots/root system, 3 = 3 to 5 knots, 4 = >5 knots and <20% reduction in plant height or root mass, and 5 = >5 knots and >20% reduction in plant height or root mass.

Resistance was measured by counting the number of *H. avenae* swollen white females on roots of five plants per plot by manually rubbing roots to dislodge the white females from washed roots. The swollen females were collected on a 60-mesh sieve and were washed onto filter papers and counted with the aid of a dissecting microscope. 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 yield and test weight were calculated by harvesting 2-row plots of all four replicates using a Wintersteiger plot combine (Wintersteiger Inc., Salt Lake City, UT) on 20 Aug 2013 and 9 Sep 2014. Tolerance ratings were assigned to cultivars according to the scale used previously by Smiley et al. (2013): 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%).

A primary objective of this research was to identify cultivars that failed to meet criteria for full resistance or tolerance but exhibited an acceptable balance among those 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). A second measure of resistance was performed by determining nematode density in soil samples collected after grain harvest. Samples during 2013 were taken using manually-operated soil probes and consisted of 20 soil cores (2.5-cm diam. × 30-cm depth) composited from each plot. Cores were taken directly below rows of stubble from three replicates of each treatment sampled. For the 2-row feed barleys, five cultivars were sampled in both untreated and in nematicide-treated plots. Six cultivars were examined for the 2-row malt barley and the 6-row barleys. Two cultivars from the nematicide-treated plots were selected to represent those for which we had found a high number of white females on roots in untreated plots, for two that had a low number, and for two cultivars of special interest to local growers. During 2014, post-harvest sampling for nematode density was from three replicates of all cultivars in the control treatment and two cultivars in the nematicide treatment. Due to dry soil conditions, post-harvest sampling during 2014 consisted of cores being collected using a tractor-mounted Giddings GSTRS Hydraulic Soil Sampler (Giddings Machine Company, Windsor, CO) with a 5-cm-diameter, 150-cm-long slotted soil tube. Two cores separated by 2 m were collected to 30-cm depth in each plot. Soil from the two cores was composited into a single sample for each plot.

Nematode density and identification. All pre-plant and post-harvest soil samples were submitted to Western Laboratories (Parma, ID) for extraction and enumeration of nematodes. The lab uses a modified Oosterbrink elutriator extraction method described in greater detail by Smiley et al. (2011a). Briefly, vermiform and encysted life stages were extracted and collected on separate sieves. Cysts were broken mechanically to extract eggs and larvae and the suspension was added to the suspension of vermiform life stages present in the soil. The suspension was then concentrated through multiple sequences of centrifugation and density flotation using a magnesium sulfate solution. Western Laboratories reported numbers of plant-parasitic nematodes that were identified to the genus level. These methods were used to calculate the density of *H. avenae* eggs plus juveniles/kg of soil in each sample.

Heterodera spp. extracted from fields where the trials were established during the two years were identified as *H. avenae* during previous research (Smiley et al., 2011b; Yan and Smiley, 2010; Yan et al., 2013). Key morphological features for cysts examined under a compound light microscope included color, underbridge in the vulval cone, semi-fenestrae shape, and development of bullae. The PCR products of DNA extracted from cysts were digested with six restriction endonucleases (*Taq*I, *Hinf*I, *Pst*I, *Hae*III, *Rsa*I, and *Alu*I) and the species of *Heterodera* was determined by comparing the restriction pattern with those of nine pure *Heterodera* control species (*H. avenae*, *H. filipjevi*, *H. latipons*, and *H. schachtii*) in agarose gels by electrophoresis.

Statistical analyses. Grain yield and test weight over two years were analyzed using 3-way analysis of variance (ANOVA) for individual experiments, with year as the main plot, cultivar as the subplot, nematicide treatment as the sub-subplot, and replicates as blocks. ANOVA was performed using CoStat Statistical Software (Co-Stat v. 6.400, CoHort Software, Monterey, CA). Percentage yield increase for each pair of control and nematicide treatments for individual

cultivars within each experiment were analyzed using 2-way ANOVA, with year as main plot, cultivar as the sub-plot, and replicates as blocks. Disease incidence and number of white females/plant and eggs/kg of soil after harvest only in the control (non-nematicide treatment) plots were also analyzed by 2-way ANOVA. When treatment means were significant at $\alpha < 0.05$, means were separated using the Tukey's Honestly Significant Difference (HSD) test. 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. Six 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 six cultivars were analyzed using year as the main plot factor, cultivar as the subplot factor, and nematicide as the sub-subplot factor. Because the main effect of year is highly significant in most analyses, the data for each of the three trials were also analyzed for individual years. Data are reported as the means and standard error of the means for trials performed during each year.

Results

Pre-plant nematode density. *Heterodera avenae* was the only *Heterodera* species detected. The initial density of *H. avenae* across the 3-trial block during 2013 was 22,176 eggs plus juveniles/kg of soil. During 2014 the mean densities for the three experimental blocks were 3,516, 27,000 and 4,980/kg for 2-row feed, 2-row malt and 6-row barleys, respectively.

Plant growth and development. Soil temperature at the depth of seed placement was 8.9°C in 2013 and 6.7°C in 2014. The estimated dates of seedling emergence (0°C base for growing-degree days) were 20 May 2013 and 10 May 2014, which were 22 and 20 days after planting, respectively. Accumulation of heat units during early spring (until 1 June) was greater during 2014 than during 2013. After 1 June the GGD accumulation was more rapid during 2013 than during 2014. Initiation of anthesis was estimated to have occurred on 25 June 2013 and 1 July 2014.

Incidence and severity of root-knot symptom. Barley roots were sampled to determine incidence and severity of the root-knotting symptom and to count numbers of swollen white *H. avenae* females on 13 July 2013; 59 days or 619 growing-degree days (8°C base) after seedling emergence and 18 days after anthesis. During 2014 the root sampling was performed on 23 July 2014; 79 days or 633 growing-degree days (8°C base) after seedling emergence and 23 days after anthesis. Disease incidence was near 100% for all plants in these experiments. The root-knotting symptom occurred on 98%-100% of the plants of all cultivars in each experiment during both years, and in the nematicide-treated plots as well as in the control treatment (data not presented).

Severity of the root-knotting symptom in the control treatment of each experiment differed significantly ($P < 0.0001$) for the main effect of year but did not differ significantly among cultivars ($P = 0.38$), and the year × cultivar interaction was also not significant. For the two cultivars in which roots were also evaluated in the nematicide treatment, the effects of year and nematicide treatment were each significant ($P < 0.0001$) and the effect of cultivar was not significant ($P = 0.23$). The mean severity of the root-knotting symptom in each experiment was greater during 2014 than during 2013 (Tables 1-3), and was greater in the control plots than in the nematicide treated plots (data not shown). The control and nematicide treatments had respective mean severity ratings of 4.5 and 3.8 ($HSD_{0.05} = 0.4$) for the two 2-row feed barleys, 4.6 and 4.3

($HSD_{0.05}$ = 0.2) for the two 2-row malt barleys, and 4.5 and 2.9 ($HSD_{0.05}$ = 0.5) for the two 6-row barleys.

White females on roots. Numbers of newly produced *H. avenae* swollen white females were significantly ($P < 0.01$) influenced by the effect of year in each experiment and by the main effect of cultivar in only the 2-row malting barley experiment. The year × cultivar interaction was significant for the malting barley experiment. Numbers of white females were greater during 2013 than during 2014 for the 2-row malting barleys (Table 2). For the two cultivars in which white females were quantified in the nematicide treatment, the main treatment effect for nematicide was the only significant treatment effect for the 2-row feed barley experiment ($P < 0.0001$). In that experiment, none of the interactions were significant. In the 2-row malt barley experiment, the treatment effects for year and nematicide were significant ($P < 0.001$), as was the year × nematicide interaction ($P < 0.01$). Likewise, the effects of year and nematicide were each significant ($P < 0.05$) for the 6-row barley experiment. 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 9.4 and 1.2 ($HSD_{0.05}$ = 4.1) for the two 2-row feed barleys, 24.8 and 1.4 ($HSD_{0.05}$ = 17.4) for the two 2-row malt barleys, and 16.3 and 1.9 ($HSD_{0.05}$ = 3.4) for the two 6-row barleys.

Numbers of swollen white females extracted and counted during 2014 were too low to provide reliable distinctions among cultivars. During 2013, Lenetah was the only 2-row feed barley cultivar to be rated as moderately resistant to *H. avenae*, and no cultivars were rated as resistant or very resistant (Table 1). Odyssey was the only 2-row malt barley to be rated as resistant during 2013 (Table 2). Numbers of white females in the 6-row barley experiment were low each year and there was no consensus of resistance and susceptibility ratings between years (Table 3). For instance, the five 6-row barley cultivars that were rated as resistant or moderately resistant during 2013 were each rated as moderately susceptible or susceptible during 2014. In contrast, the two cultivars that were rated as moderately resistant during 2014 were rated as moderately susceptible during 2013.

Post-harvest density of *H. avenae* eggs from cysts. Soil samples during 2013 were evaluated for five cultivars in the 2-row feed barley experiment; Baronesse, Champion, Lenetah, Spaulding and Tetonia. There was a significant effect of nematicide treatment ($P < 0.0001$) on mean egg density, with 141,265 and 64,519 eggs/kg of soil in the control and nematicide treatments, respectively, which equated to a 54% reduction in *H. avenae* density in aldicarb-treated versus control plots (data not shown). The main effect for cultivar was not significant. A similar relationship occurred for the six cultivars examined in the 2-row malting barley experiment (167,002 vs. 76,894 eggs/kg; 54% reduction) and in the 6-row barley experiment (58,212 vs. 12,600 eggs/kg; 78% reduction). Cultivars examined in the 2-row malting experiment included ABI Voyager, Conrad, LCS1820, Merit 57, Metcalf and Odyssey. Cultivars of 6-row barleys tested included Celebration, Goldeneye, Legacy, Millenium, Morex and Steptoe.

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. The main effect of year was highly significant ($P < 0.0001$) for all three experiments. The main effect for nematicide was also

significant ($P < 0.01$) and the effect of cultivar was not significant in each experiment. None of the interactions were significant. When all cultivars in the control treatment were examined during 2014, the cultivar effect was not significant for any of the three experiments. The range of low to high *H. avenae* density for the 2-row feed barleys was from 56 eggs/kg of soil for Xena to 209 eggs/kg for 08ID1549 ($P = 0.78$). The range for the 2-row malt barleys was from 100 eggs/kg for Pinnacle to 412 eggs/kg for Merem ($P = 0.27$), and the range for the 6-row barleys was from 750 eggs/kg for Tradition to 627 eggs/kg for 01Ab9663 ($P = 0.13$).

Grain yield and test weight. Mean grain yield for all entries in each experiment were significantly greater during 2013 than during 2014 for the 2-row feed and 2-row malting barleys ($P < 0.0001$) and for the 6-row barleys ($P = 0.0567$). Treatment effects for cultivar and nematicide each differed significantly ($P < 0.01$) within each experiment. Mean grain yields were higher in nematicide-treated plots compared to the controls; 4,873 vs. 4,496 kg/ha ($HSD_{0.05} = 148$) for 2-row feed barleys, 4,784 vs. 4,366 kg/ha ($HSD_{0.05} = 185$) for 2-row malt barleys, and 4,847 vs. 4,434 kg/ha ($HSD_{0.05} = 246$) for 6-row barleys. The year × nematicide, cultivar × nematicide, and year × cultivar × nematicide interactions were not statistically significant for any of the three experiments. However, the year × cultivar interaction was significant ($P < 0.01$) for the 2-row malt and 6-row barleys, and for the 2-row feed barleys ($P = 0.0567$). Grain yields for individual cultivars and for individual years in the three experiments are presented in Tables 1-3. Grain yields for cultivars differ significantly ($P < 0.05$) within each nematicide treatment of the 2-row feed barley and the 2-row malt barley experiments during both years. For the 6-row barleys, grain yield did not differ among cultivars in the control treatment during either year, and differed significantly in the nematicide treatment only during 2014.

The percentage increase in grain yield due to application of nematicide did not differ significantly in the 2-row feed barley experiment (Table 1). For the 2-row malt barleys, the increase in grain yield was significant for the main effect of cultivar during 2014 but not during 2013 (Table 2). For the 6-row barleys the main effects of year and cultivar were each significant. The year × cultivar interaction was significant ($P < 0.01$) for all three experiments.

Grain test weight differed significantly ($P < 0.0001$) between years for each of the three experiments. Respective mean test weights in the controls during 2013 and 2014 were 657 and 616 g/l ($HSD_{0.05} = 6$) for 2-row feed barleys, 635 and 584 g/l ($HSD_{0.05} = 6$) for 2-row malt barleys, 592 and 556 g/l ($HSD_{0.05} = 8$) for 6-row barleys (data not presented). The main effect of cultivar also differed significantly ($P < 0.05$) for test weights in each experiment. Test weight data are not presented in the tables. The main effect of nematicide treatment differed significantly ($P = 0.03$) for the 2-row malt barley experiment but did not differ significantly for the other two experiments.

Balanced resistance and tolerance to *H. avenae*. When data in our trials were grouped over two years, the percentage increase in grain yield due to application of nematicide differed significantly among years only for the 6-row barley experiments. The main effect of cultivar was significant for the 2-row malt barley and the 6-row barley experiments. The influence of year on numbers of white females produced on roots was significant for all three experiments, as was the main effect of cultivar for the 2-row malt barley experiment. Recognizing the limits of the variability encountered, we used data grouped over two years to develop recommendations for managing barley fields that are infested by *H. avenae* (Table 4). This table identifies cultivars that could provide an acceptable balance of both resistance and tolerance, of resistance alone, of tolerance alone, or none of these traits.

Over the 2-year testing period, seven feed-type cultivars were ranked as having a balance of being at least moderately resistant and moderately tolerant (Table 4). These cultivars included

the 2-row barleys Champion, Lenetah, Xena, Idagold II and Transit, and the 6-row barleys Millenium and Goldeneye. No malting-type cultivar met these criteria. The 2-row malt barley Odyssey was the only cultivar that exhibited resistance but not tolerance; it ranked as very resistant with a mean of <1 swollen female/plant over the 2-year test period. This cultivar was not considered both resistant and tolerant because the tolerance rating of 15.5 did not strictly meet our maximum value of 15.0 to achieve that rating. Four cultivars also limited reproduction of *H. avenae* and were ranked as moderately resistant, including the food barley CDC Fibar, feed barley Steptoe, and the malt barleys Legacy and Tradition, with means of 4.4, 5.3, 3.8 and 5.6 swollen females/plant, respectively. Eighteen barley cultivars (five 2-row feed types, ten 2-row malt types, one 6-row feed type, and two 6-row malt types) were ranked as being tolerant or very tolerant, but not resistant or moderately resistant. Overall, 69% of the barley cultivars in these trials (31 of 45 entries) were at least moderately tolerant to *H. avenae* (Table 4).

Discussion

Small grain cultivars that are both resistant and tolerant to *H. avenae* are typically more profitable than cultivars that are susceptible and intolerant when planted into fields that are highly infested with this cereal cyst nematode (Fisher, 1982). O'Brien and Fisher (1977) predicted that a combination of resistance and tolerance was more likely to be achieved in barley cultivars than in wheat or oats because barley is generally more tolerant of *H. avenae* than the other two crop species. We report the first-known screening trials to quantify both resistance and tolerance of barley to *H. avenae* in the USA.

We detected a balance of agronomically acceptable resistance plus tolerance in seven feed barleys (five 2-row and two 6-row types) but not in any malting barleys. However, one malting type (Odyssey) nearly met this dual-trait criterion, in that it was very resistant and nearly moderately tolerant. While neither the resistant cultivars nor the tolerant cultivars were always the highest-yielding cultivars in each trial, the long-term goals of producing a cultivar with these dual traits will be to simultaneously 1) minimize the potential yield suppression caused by the nematode in the current crop and 2) reduce the post-harvest density of eggs to reduce the economic risk for the next host crop that will be planted in that field. Six of the seven cultivars with balanced levels of resistance and tolerance (Xena, Champion, Goldeneye, Idagold II, Millenium and Lenetah) produced grain yields in control plots that did not differ significantly from the highest yielding cultivar in the experiment during either year. However, when compared to the highest-yielding cultivars in the 2-row feed barley trial, the cultivar Transit was categorized as resistant and tolerant but produced low yields each year. Transit, Julie, CDC Fibar, and CDC McGwire are hulless high ß-glucan cultivars developed for human food, not as a feed barley which are hulled. Likewise, each of the four cultivars that were rated as susceptible but moderately resistant (CDC Fibar, Legacy, Steptoe and Tradition) were not consistently among the highest-yielding cultivars within each of their experiments. Of the 18 cultivars that were rated as very tolerant or tolerant but not resistant, there were seven cultivars that yielded among the top-ranked within their experiments both years, including the 2-row feed-types Baronesse, RWA 1758, Tetonia and Vespa, the 2-row malt-types 2AB04-X001084-27 and 2Ab07-X031098-31, and the 6-row feed-type Herald. Cultivars such as Copeland and 01AB9663 were among the highest yielding entries in their trials during 2013 but did not produce competitive yields during 2014, and the converse occurred for cultivars such as Merit 57, Overture and Pinnacle.

We previously determined that wheat cultivars responded equally to *H. avenae* populations in Idaho, Oregon and Washington (Smiley et al., 2011b, 2013). It is therefore anticipated that the resistance and tolerance traits identified for barley cultivars in these trials will also be applicable in *H. avenae*-infested fields elsewhere in the PNW.

Where resistance is the primary trait of interest to reduce the density of *H. avenae* in highly-infested fields, we found that emphasis could be placed upon the seven dual-trait cultivars or upon the very resistant, resistant and moderately resistant 2-row food barley CDC Fibar, the 2-row malt barley Odyssey, the 6-row feed barley Steptoe, and the 6-row malt barleys Legacy and Tradition. Where tolerance is considered the primary trait of importance to achieve the maximum potential yield of feed barley or to achieve the highest malting quality, results of our study showed that emphasis could be placed either upon the dual-trait cultivars or upon production of five tolerant but not resistant 2-row feed barleys, one 2-row feed barley, ten 6-row feed barleys, and two 6-row malt barleys.

The origins of resistance traits detected in some cultivars examined in our trials are unknown. It appears that no North America accessions listed in the barley database of USDA-ARS-GRIN (2015) are designated as having resistance to *H. avenae*. Rivoal and Cook (1993) reviewed reports of unidentified sources of resistance to *H. avenae* being identified in locally-selected barleys in several countries. They also stated that "Undoubtedly, resistance genes have been dispersed … by the extensive collection and interchange of germplasm by plant breeders." It is likely that international exchanges of barley germplasm have led to the introgression of resistance genes into cultivars of current importance in the USA, and that these cultivars have not been assayed for resistance to *H. avenae*. The cultivars we report as resistant to *H. avenae* under field conditions should be verified as resistant using controlled-environment assays. Likewise, cultivars that are validated as resistant in subsequent investigations should be assayed using molecular markers (Barr et al., 1998; Chełkowski et al., 2003; Dayteg et al., 2008; Karakousis et al., 2003c; Kretschmer et al., 1997; Seah et al., 1998) to identify the presence of one or more specific resistance genes, or to provide provisional evidence for the occurrence of one or more new sources of resistance.

We ranked 69% of the 45 barley entries as being very tolerant, tolerant or moderately tolerant; 11, 11, and 9 entries, respectively. Results of our research contribute to the understanding of differences in tolerance that occur among North American spring barley cultivars but the origins of the tolerance traits we detected are unknown. Differences in tolerance to *H. avenae* are known to occur among cultivars of all small grain cereals, and it is generally accepted that there is an increasing order of yield damage caused by *H. avenae* on rye and winter barley, spring barley, winter wheat, spring wheat, winter oats and spring oats (Andersson, 1982; Fisher, 1982). As such, a comparatively higher level of tolerance among spring barley than spring wheat or spring oat cultivars has been reported for many years. Attempts to characterize the mechanism(s) of tolerance have generally been associated with the timing of root development in these cereals. For instance, Kerry and Hague (1974) found that juveniles that invade seminal roots tend to mature into males and those that invade coronal roots tend to mature as females. In their study, in the United Kingdom, the nodal roots of spring barley contained few *H. avenae* and nodal roots of winter wheat and winter oats were heavily invaded. The difference was attributed to development of nodal roots in spring barley during June and July when few second-stage juveniles were present in soil, compared to the development of nodal roots for the winter-sown cereals during April at a time when juveniles were most numerous in soil. Price and Hague (1981) determined that newly formed roots of oats in controlled-environment studies became more heavily invaded by *H. avenae*

compared to barley, wheat or rye, suggesting differences in a trait such as attraction, penetration or establishment of juveniles in the oat roots, or the emigration of juveniles from roots. Most studies have failed to identify any influence of leachates from various plant species on the stimulation of hatching of juveniles from cysts (Zheng et al., 1997). Other studies have shown that barley plants produce higher volumes and numbers of roots compared to other cereals (O'Brien and Fisher, 1978; Price and Hague, 1983; Stanton and Fisher, 1988), which leads to a dilution effect of a given density of *H. avenae* in soil relative to the root mass available for penetration and establishment.

Although some barley cultivars were resistant to *H. avenae* it was also clear that the incidence of root knotting on these resistant cultivars was similar to that for susceptible cultivars. This was attributed to the fact that second-stage juveniles penetrate epidermal cells behind the root cap (Price and Hague, 1981; Price et al., 1983) and move intracellularly to the growth zone (Baldwin and Mundo-Ocampo, 1991). The juveniles of both *H. avenae* and *H. filipjevi* successfully penetrate roots in equal numbers for resistant as well as susceptible cultivars (Andersen, 1961; Cui et al., 2012; O'Brien and Fisher, 1977; Ogbonnaya et al. 2001; Oka et al., 1997). After a succession of molts the females reprogram root cells to induce the formation of specialized feeding cells (Hewezi et al., 2012). Cells of the syncytium develop but then deteriorate in resistant cultivars, causing death or suppressed reproductive capacity of the female associated with the deteriorated syncytium (Andres et al., 2001; Oka et al., 1997; Seah et al., 2000). Resistance is expressed by a reduced ability of the nematode to produce viable eggs. Therefore, resistant cultivars may reduce the density of *H. avenae* in soil, but may still be sensitive to earlier root injury that leads to a reduction of plant growth and grain production. O'Brien and Fisher (1977) reported that similar numbers of larvae invaded seedling roots of both susceptible and resistant wheat cultivars but then the number of nematodes within roots and the number of sites of root-knotting continued to increase as susceptible plants became older, and the number of nematodes decreased but the sites of root-knotting remained the same as resistant plants became older. In our field studies we were not able to detect differences in the amount of the root-knotting symptom in resistant and susceptible cultivars sampled at the time of plant anthesis. However, we did measure minor but significant reductions in the root-knotting symptom in aldicarb-treated compared to control plots. In contrast, the application of aldicarb greatly reduced the development of swollen white females on susceptible cultivars, and reduced the mean post-harvest densities of *H. avenae* eggs by 54% to 78%. Resistant cultivars also reduced the number of swollen white females when measured at the time of plant anthesis, and the post-harvest density of *H. avenae* eggs per kg of soil. Post-harvest densities of *H. avenae* in plots of resistant barley 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. A background density of the nematode was present because only a portion of *H. avenae* eggs hatch from cysts during a single season (Andersen, 1961). Forty to 90% of the eggs remaining within cysts typically hatch to produce the invasive juvenile stage each year (Andersen, 1961; Andersen and Andersen, 1970). Hatching from individual cysts is therefore spread over many years and in the soils where our trials were performed, a rotation away from cereals for only a single year is insufficient to adequately reduce the residual risk to subsequent cereal crops even when they follow a resistant cultivar or soil that was previously treated with a nematicide such as aldicarb. These observations on barley were very similar to our observations of root knotting, development of gravid white females, and post-harvest density of *H. avenae* eggs on spring wheat (Smiley et al., 2011a, 2013).

Aldicarb is a long-favored research tool for examining effects of *H. avenae* on spring cereals (Brown, 1987; Meagher et al., 1978). Granules of aldicarb are banded with or below the

seed at the time of planting (Smiley et al., 2005b, 2013; Taylor et al., 1999). Wu et al. (2007) recently reported that aldicarb was the best of four nematicides tested for reducing reproduction of *H. avenae* in wheat. This nematicide has a half-life up to five weeks and is taken up by roots to reduce the *Heterodera* population early in the plant growth period. Aldicarb does not suppress effects of fungal root pathogens (Kimpinski and Johnson, 1995; Kimpinski et al., 1987), typically results in improved grain yields for genotypes that are intolerant to the nematode and, in our experience, had no influence on growth or yield of spring wheat where densities of plant-parasitic nematodes were very low (Smiley et al., 2005a). In this study we found that aldicarb had a minimal but significant effect on the incidence and severity of the root knotting symptom, greatly reduced the development of gravid white females, greatly reduced the post-harvest density of *H. avenae* eggs in soil, and generally led to an increase of grain yield.

The initial density of *H. avenae* in the trial area was high during 2013 (22,176 eggs plus juveniles/kg of soil) and was variable for the three experiments during 2014; 3,516, 27,000 and 4,980 eggs plus juveniles/kg of soil in the 2-row feed, 2-row malt and 6-row feed plus malt barley experiments, respectively. Each of these initial densities was high enough that yield suppression could be expected to occur during 2014 (Andersson, 1982). Nearly all plants displayed the root-knotting symptom caused by *H. avenae* when roots were inspected at the time of anthesis during each year. This finding of root damage in all trials suggested that the nematode densities were sufficiently high in all trials to potentially suppress yields. Andersen (1960) reported that spring barley yields in Sweden were reduced by 16, 17, 21, 40 and 55% when the initial density of *H. avenae* was 1,000, 2,500, 5,000, 10,000 and 20,000 eggs plus juveniles/kg of soil. However, it is also recognized that the damage threshold is highly variable and differs among plant cultivars, geographical areas, timing of the hatching interval relative to the planting date, climate, and variations of seasonal weather, soil moisture, soil temperature and other edaphic factors (Andersen, 1961; Handa et al., 1985; Li et al., 2012; Rivoal and Cook, 1993; Yang et al., 2008).

During 2014 we observed a high incidence and severity of the root-knotting symptom but detected very few white females when roots were evaluated after heading and anthesis. This had not occurred during the previous seven years in which field trials on *H. avenae*-infested fields were conducted at multiple locations throughout the PNW, including on fields of the same Idaho farm during the previous four years; 2010 to 2013. The initial density of *H. avenae* eggs plus juveniles on the field where our 2014 trials were established was considered acceptable for assaying barley, as described above. The most susceptible cultivars in the 2-row feed, 2-row malt and 6-row barley trials produced means of 6, 10 and 21 cysts/plant during 2014, with initial densities of 3,516, 27,000 and 4,980 eggs plus juveniles/kg of soil, respectively. In an adjacent trial with spring wheat during 2014 the most susceptible cultivar produced means of 51 cysts/plant with an initial density of 3,309 eggs plus juveniles/kg of soil. Andersen (1961) reported that the number of cysts produced per barley plant was 12, 24, 26 and 33 cysts/plant at initial densities of 1,000, 2,500, 5,000 and 10,000 eggs plus juveniles/kg of soil. Using that guideline, we would have anticipated means of at least 20 swollen females on roots of the most susceptible cultivars during 2014.

Our trials during 2014 were planted when the soil temperature at the depth of planting was 6.7°C. Seedling emergence occurred about three weeks after planting. Tikhanova (1971) reported that *H. avenae* juveniles in the continental climate of the Bashkir region of central Russia emerged from cysts at temperatures of 5°C and above. Smiley et al. (2005b) reported that during a single late winter and spring season in eastern Oregon, where the climate is only slightly milder than where our barley trials were performed in eastern Idaho, that second-stage juveniles of *H. avenae* began emerging from cysts very rapidly when average weekly air temperatures stabilized between

2°C and 5°C, and that peak densities of juveniles in soil occurred in March and April before declining sharply during May and becoming almost non-detectable in June. However, the specific chronological timing of the primary hatch can vary greatly over seasons (Andersen, 1961).

Li et al. (2012) found16°C to be the optimum temperature for penetration of roots by *H. avenae*, and 18°C to 22°C to be the optimum temperature range for those juveniles to develop into gravid cysts. Although not evaluated, we assumed that juveniles had begun to move from cysts into the soil matrix at the approximate time we planted our trials (Kerry and Jenkinson, 1976; Tikhanova, 1971), that the density of juveniles in soils continued to increase sharply as the soil warmed during the three weeks between planting and seedling emergence (Smiley et al., 2005b), and that juveniles were capable of invading roots for at least three weeks after they emerged from cysts (Davies and Fisher, 1976).

In our study during 2014, it is possible that the low numbers of swollen white females occurred because the primary hatching period occurred later than anticipated, which may have led to too few growing degree days for molting and egg production between the date of root invasion and crop maturation. Accumulation of growing-degree days for nematode development (8°C) following seedling emergence was much slower during 2014 than during 2013, causing us to dig roots for evaluations nearly three weeks later on a chronological scale during 2014 than during 2013; samplings were, respectively, at 79 versus 59 days and 633 versus 619 growing-degree days after seedling emergence. It was unclear as to whether the soil temperature was more sub-optimal for penetration of roots during 2014 compared to 2013, which could have delayed or reduced invasion and led to development of low numbers of gravid females.

The low numbers of swollen white females counted during 2014 could have also been an artifact of the sampling time if the juveniles invaded roots at low soil temperatures and developed sooner than we anticipated, causing them to turn brown and to become indistinguishable from the residual density of cysts formed on previous cereal crops. In a similar continental climate of south-central Russia, Tikhonova (1971) reported that juveniles required 35 to 45 days from the time of root penetration to sexual maturity. Our samplings at 59 and 79 days after planting were based upon our understanding of the greater importance of heat units than of chronological time for the development of swollen white females. It is possible, therefore, that our sampling during 2014 was too late to detect the greatest number of white females. We believe, however, that this possibility was unlikely because we conducted exploratory samplings in these trials on June 12 and July 1, corresponding to 33 and 52 days or 211 and 343 growing-degree days after seedling emergence. On both preliminary sampling dates we were unable to detect more than a few swollen white females, leading us to perform our comprehensive sampling on July 23, corresponding approximately to the equivalent number of growing-degree days as used for our sampling during 2013.

During 2014, as compared to 2013, very few *H. avenae* eggs were detected in soil following the harvests of even the most susceptible barley cultivars. It is unknown as to whether this observation of uniformly low densities was a result of marginal levels of initial inoculum, a temperature sub-optimal for development of gravid females, a difference of soil sampling methods, an undetected anomaly associated with the procedures used for extraction of cysts and counting of eggs released from cysts, or some other reason. As discussed previously, the initial inoculum density is unlikely to have been responsible because the number of eggs plus juveniles at the time of planting was presumed to have been adequate for producing at least 20 cysts per plant on susceptible cultivars in each of the three barley trials. The low production of gravid females we counted in each trial during 2014 could have led to the low post-harvest densities of *H. avenae*. In

effect, it may have been possible for the low production of gravid females to result in a greater net loss of *H. avenae* inoculum due to few newly-produced eggs in the newly-formed cysts and the continued hatching and/or mortality of eggs plus juveniles from cysts produced two years earlier. There are large differences in number of eggs developed within individual cysts (Andersen, 1961). The mean fecundity reported by Anderson (1961) was 200 to 250 eggs/cyst, a range from near zero to 600 eggs/cyst, and with a trend for an increasing number of eggs/cyst when increasing numbers of cysts are produced. We used different soil sampling methods during the two years but that is unlikely to have led to the uniformly low *H. avenae* densities we detected. For sampling root-lesion nematodes, using the same equipment as for the current experiments, we reported similar results using twenty 2.5-cm diam. manually-collected cores/plot and two 5.1-cm diam. mechanically-collected cores/plot (Smiley and Machado, 2009). However, it is possible that the depth of sampling during 2014 was consistently closer to the target depth of 30 cm compared to the less-consistent depths that were possible when we sampled with hand probes during 2013. If true, the consistently deeper cores would have led to lower apparent densities of *H. avenae* because about 35% of cysts are found in the 5- to 10-cm depth interval and nearly 90% of cysts occur in the top 20 cm of non-cultivated soil (Li et al., 2014; Xiang et al., 2013). We feel that it would be very unlikely for soil sampling methods alone to be responsible for the much lower magnitude of apparent egg counts during 2014 compared to 2013. Similarly, the extraction of cysts and counting of the released eggs is unlikely to have differed so greatly as to be responsible for the differences we encountered from year to year. The commercial laboratory that enumerated the numbers of *H. avenae* eggs for our trials is a high-throughput lab that used the same processing procedures and skilled staff each year.

In conclusion, we provided the first evaluations of tolerance and resistance of barley cultivars to *H. avenae* in the USA. Acceptable balances of resistance plus tolerance were detected in seven feed barleys. One malting barley nearly met our criteria for this duality of traits. We also provided the first evidence of resistant but not tolerant cultivars in each of the four market classes of barley. Lastly, we also reported the occurrence of barley cultivars in each market class that are tolerant but not resistant to *H. avenae*. Results of these studies provide the first basis for selecting barley cultivars and classes to improve production efficiency where barley is a desired crop on fields that are heavily infested by the cereal cyst nematode *H. avenae*.

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Table 1. Evaluation of 16 2-row spring feed barley 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 each disease parameter and four replicates of grain parameters.

Cultivar	Root knot severity (1-5) [s]	White females /plant [t]	Eggs/kg of soil [u]	Grain yield (kg/ha) Control	Treated [v]	% increase [w]	Resis-tance [x]	Toler-ance [y]
2013								
08ID1549	4.0±0.0 a [z]	11.30±3.5 a		4,232±467 a-c	5,047±79 ab	23.5±13.0 a	MS	MI
08ID2661	4.1±0.1 a	22.1±15.5 a		4,706±557 ab	5,349±831 ab	12.1±4.6 a	S	MI
Baronesse	4.2±0.1 a	11.7±4.8 a	165,036±22,942 a	4,991±490 ab	5,748±576 a	15.4±4.2 a	MS	MI
CDC Fibar	4.0±0.1 a	7.9±1.5 a		3,730±318 bc	3,875±180 bc	5.0±4.5 a	MS	T
CDC McGwire	3.9±0.1 a	23.6±14.7 a		3,845±445 bc	3,872±366 a-c	12.1±4.0 a	S	MT
Champion	3.8±0.2 a	10.9±4.0 a	223,305±54,378 a	5,007±665 ab	5,375±607 ab	9.1±7.1 a	MS	T
Clearwater	3.9±0.1 a	15.1±4.9 a		3,691±216 bc	4,394±310 a-c	20.3±11.6 a	S	MI
Idagold II	4.1±0.1 a	6.5±2.1 a		4,326±427 a-c	4,399±445 a-c	2.1±7.0 a	MS	VT
Julie	4.2±0.1 a	12.3±1.4 a		4,646±239 ab	4,363±396 a-c	-6.4±5.4 a	S	VT
Lenetah	4.2±0.1 a	4.7±1.4 a	112,189±12,813 a	4,923±611 ab	5,101±695 ab	3.4±6.3 a	MR	VT
RWA 1758	4.3±0.1 a	9.5±4.6 a		5,303±834 a	5,471±446 a	8.7±11.6 a	MS	T
Spaulding	4.0±0.3 a	43.6±21.6 a	113,717±6,538 a	4,668±335 ab	5,329±397 ab	14.3±3.2 a	VS	MT
Tetonia	4.2±0.1 a	26.9±11.0 a	92,081±20,324 a	5,346±325 a	5,416±172 a	2.0±3.7 a	VS	VT
Transit	4.2±0.1 a	9.7±6.8 a		3,124±424 c	3,299±444 c	6.2±7.1 a	MS	T
Vespa	4.2±0.1 a	21.1±6.2 a		5,522±332 a	5,626±451 a	1.9±5.7 a	S	VT
Xena	4.2±0.1 a	7.6±3.2 a		5,527±368 a	5,546±403 a	0.3±4.6 a	MS	VT
Mean	4.1	15.3	117,721	4,600	4,912	8.1	S	T
P > F	0.5567	0.3021	0.4501	<0.0001	<0.0001	0.3033		
$HSD_{0.05}$	ns	ns	ns	1,409	845	ns		
2014								
08ID1549	4.1±0.2 a	2.6±0.4 a	309±188 a	4,025±284 c-e	4,428±324 c-f	8.7±4.1 a	R	T
08ID2661	5.0±0.0 a	1.3±0.5 a	191±110 a	4,346±270 b-d	4,882±240 b-f	12.6±3.0 a	R	MT
Baronesse	5.0±0.0 a	4.9±2.8 a	327±140 a	4,758±163 a-c	4,851±150 b-f	2.1±1.9 a	MR	VT
CDC Fibar	4.4±0.2 a	1.5±1.0 a	573±280 a	3,019±290 e	3,869±120 fg	31.5±14.2 a	R	I

CDC McGwire	5.0±0.0 a	1.5±0.6 a	264±78 a	4,138±487 b-e	4,401±333 d-f	11.6±13.4 a	R	MT
Champion	5.0±0.0 a	3.2±1.7 a	427±283 a	4,620±162 a-c	4,854±190 b-f	5.3±5.4 a	MR	T
Clearwater	5.0±0.0 a	1.3±0.6 a	491±177 a	3,226±317 de	3,968±235 e-g	25.9±12.2 a	R	MI
Idagold II	5.0±0.0 a	3.9±1.9 a	339±231 a	4,825±272 a-c	5,729±108 ab	19.1±4.2 a	MR	MI
Julie	5.0±0.0 a	0.3±0.2 a	267±165 a	4,048±148 c-e	4,426±158 c-f	9.4±4.6 a	VR	T
Lenetah	4.7±0.1 a	0.9±0.1 a	145±64 a	4,429±260 a-d	5,115±225 a-d	16.2±7.7 a	VR	MI
RWA 1758	5.0±0.0 a	6.3±3.1 a	345±48 a	4,880±99 a-c	4,912±122 b-e	0.7±2.7 a	MS	VT
Spaulding	4.3±0.3 a	1.7±0.8 a	200±92 a	4,978±253 a-c	5,451±185 a-c	9.9±3.2 a	R	T
Tetonia	4.1±0.4 a	3.1±1.2 a	185±27 a	5,001±219 a-c	5,335±140 a-d	7.2±3.4 a	MR	T
Transit	5.0±0.0 a	3.1±1.2 a	385±106 a	2,666±169 e	3,289±141 g	14.8±1.4 a	MR	MT
Vespa	4.9±0.1 a	0.6±0.2 a	373±146 a	5,650±155 a	5,869±99 ab	4.1±2.1 a	VR	VT
Xena	5.0±0.0 a	0.5±0.3 a	130±99 a	5,406±282 ab	5,965±350 a	10.4±6.8 a	VR	MT
Mean	4.8	2.3	309	4,391	4,834	11.9	R	MT
P > F	0.4488	0.0585	0.7817	<0.0001	<0.0001	0.2230		
$HSD_{0.05}$	ns	ns	ns	707	578	ns		

[s] Severity ratings for control (no-nematicide) treatment only, with a scale of 1 = no evidence of damage, 2 = 1 to 3 knots/root system, 3 = 3 to 5 knots, 4 = >5 knots and <20% reduction in plant height or root mass, and 5 = >5 knots and >20% reduction in plant height or root mass. More than 98% of all cultivars exhibited the root knotting symptom on at least one root; e.g., the incidence was 98-100%.

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

[u] 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.

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

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

[x] 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).

[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 $\alpha = 0.05$ as determined by Tukey's Honestly Significant Difference (HSD) test. Means of severity data for the root knot symptom were analyzed by the Kruskal-Wallis test and when the Pearson's χ^2 value for the experiment was significant at $\alpha < 0.05$, cultivars were examined pair-wise to determine which treatments differed significantly.

Table 2. Evaluation of 19 2-row malt barley 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 each disease parameter and four replicates of grain parameters.

Cultivar	Root knot severity (1-5) [s]	White females /plant [t]	Eggs/kg of soil [u]	Grain yield (kg/ha)			Resis-tance [x]	Toler-ance [y]
				Control	Treated [v]	% increase [w]		
2013								
2Ab04-X001084-27	4.1±0.1 a	45.5±12.8 a		4,834±250 ab	5,067±311 a	5.8±9.0 a	VS	T
2Ab07-X031098-31	4.0±0.1 a	31.0±16.6 ab		4,712±573 a-c	4,938±397 a	6.3±5.0 a	VS	T
2B05-0811 (B0811)	4.2±0.1 a	20.1±6.9 ab		4,172±612 a-f	3,784±539 b-d	-7.4±11.1 a	S	VT
ABI Voyager	4.3±0.0 a	92.7±43.2 a	210,432±22,374 a	3,507±651 ef	4,478±854 a-d	28.0±8.3 a	VS	MI
B1202	4.0±0.0 a	55.6±23.8 a		4,094±592 a-f	4,442±660 a-d	8.5±3.6 a	VS	T
Conrad	4.1±0.1 a	19.8±6.1 ab	139,642±15,425 a	3,961±756 b-f	4,527±939 a-c	13.5±9.6 a	S	MT
Copeland	4.2±0.1 a	37.6±9.8 a		5,058±514 a	5,140±569 a	1.7±5.6 a	VS	VT
Genie	4.2±0.0 a	66.7±5.0 a		4,283±515 a-e	4,893±480 a	15.0±3.5 a	VS	MT
Harrington	4.2±0.1 a	40.5±6.3 a		3,278±492 f	3,522±367 d	10.1±7.5 a	VS	MT
Hockett	4.4±0.0 a	51.7±14.5 a		4,263±432 a-f	4,718±426 ab	11.9±8.4 a	VS	MT
LCS1820	4.2±0.1 a	18.8±7.3 ab	231,212±32,425 a	3,723±619 c-f	3,829±630 b-d	2.9±0.5 a	S	VT
Meredith	4.2±0.0 a	25.3±5.1 a		3,964±742 b-f	4,619±561 a-c	25.0±17.6 a	VS	MI
Merem	4.1±0.1 a [z]	26.8±12.4 ab		4,631±426 a-c	4,657±365 ab	1.1±3.0 a	VS	VT
Merit	4.1±0.1 a	27.9±11.5 a		3,570±466 d-f	3,868±580 b-d	7.4±5.3 a	VS	T
Merit 57	4.1±0.1 a	67.9±37.3 a	163,622±5,278 a	3,388±881 ef	3,658±937 cd	8.0±4.3 a	VS	T
Metcalf	4.1±0.1 a	48.9±32.7 a	232,572±37,765 a	3,861±665 b-f	4,572±869 a-c	17.8±6.7 a	VS	MI
Odyssey	4.1±0.1 a	1.8±0.4 b	24,593±6,560 b	4,511±682 a-d	5,354±951 a	17.3±10.3 a	R	MI
Overture	4.2±0.0 a	33.4±3.8 a		4,237±969 a-f	4,404±536 a-d	4.5±3.9 a	VS	VT
Pinnacle	4.1±0.1 a	37.1±21.4 a		3,562±814 d-f	3,732±808 b-d	6.4±3.4 a	VS	T
Mean	4.2	39.5	167,012	4,085	4,432	9.7	VS	T
P > F	0.2930	0.0018	0.0004	0.0180	0.0058	0.2651		
$HSD_{0.05}$	ns	-	-	997	996	ns		
2014								
2Ab04-X001084-27	4.7±0.3 a	1.9±0.8 a	364±229 a	4,876±366 a-d	4,844±221 c	0.2±4.4 b	R	VT
2Ab07-X031098-31	4.9±0.1 a	3.1±1.0 a	282±118 a	4,816±125 a-d	5,060±99 a-c	5.1±1.3 b	MR	T

2B05-0811 (B0811)	4.7±0.3 a	6.7±1.9 a	709±481 a	4,884±291 a-d	5,370±275 a-c	10.3±3.6 b	MS	MT
ABI Voyager	5.0±0.0 a	2.1±1.4 a	182±66 a	4,594±343 a-d	4,998±291 bc	10.0±7.4 b	R	T
B1202	5.0±0.0 a	1.5±0.8 a	642±270 a	3,747±136 d	5,641±301 a-c	51.9±13.2 a	R	VI
Conrad	5.0±0.0 a	2.2±1.4 a	273±192 a	4,352±324 a-d	5,125±227 a-c	20.0±11.4 ab	R	MI
Copeland	4.9±0.1 a	10.1±8.8 a	364±271 a	4,438±250 a-d	4,724±203 c	7.2±6.2 b	MS	T
Genie	5.0±0.0 a	1.1±0.7 a	185±128 a	5,026±188 a-d	5,334±289 a-c	6.3±5.8 b	R	T
Harrington	4.7±0.1 a	2.6±1.2 a	736±129 a	4,176±61b-d	4,609±177 c	10.5±5.3 b	R	MT
Hockett	5.0±0.0 a	2.1±1.4 a	400±87 a	4,012±220 cd	4,840±176 c	21.2±4.9 ab	R	MI
LCS1820	4.5±0.1 a	0.8±0.3 a	91±66 a	4,850±285 a-d	5,534±453 a-c	14.8±10.0 b	VR	MT
Meredith	4.9±0.1 a	3.4±1.0 a	527±224 a	4,492±252 a-d	4,559±90 c	2.1±3.9 b	MR	VT
Merem	5.0±0.0 a	4.6±2.1 a	424±69 a	4,199±319 a-d	4,542±238 c	10.1±8.8 b	MR	MT
Merit	5.0±0.0 a	7.1±1.8 a	948±658 a	5,093±408 a-c	5,064±240 a-c	0.2±3.3 b	MS	VT
Merit 57	4.7±0.3 a	5.1±2.5 a	448±390 a	5,211±244 a-c	5,447±160 a-c	5.1±4.5 b	MR	T
Metcalf	5.0±0.0 a	1.7±1.0 a	284±88 a	4,143±198 b-d	4,790±257 c	15.8±4.5 b	R	MI
Odyssey	5.0±0.0 a	0.1±0.1 a	197±148 a	5,527±236 a	6,264±184 a	13.8±4.6 b	VR	MT
Overture	5.0±0.0 a	1.4±0.7 a	115±27 a	5,411±130 ab	6,134±248 ab	13.6±5.4 b	R	MT
Pinnacle	5.0±0.0 a	3.3±1.7 a	100±5 a	4,443±314 a-d	4,721±171 c	7.4±6.1 b	MR	T
Mean	4.9	3.2	382	4,647	5,137	11.9	MR	MT
P > F	0.2716	0.1036	0.2724	0.0001	<0.0001	0.0011		
$HSD_{0.05}$	ns	ns	ns	730	670	18.8		

[s] Severity ratings for control (no-nematicide) treatment only, with a scale of 1 = no evidence of damage, 2 = 1 to 3 knots/root system, 3 = 3 to 5 knots, 4 = >5 knots and <20% reduction in plant height or root mass, and 5 = >5 knots and >20% reduction in plant height or root mass. More than 98% of all cultivars exhibited the root knotting symptom on at least one root; e.g., the incidence was 98-100%.

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

[u] 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.

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

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

[x] 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).

[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 $\alpha = 0.05$ as determined by Tukey's Honestly Significant Difference (HSD) test. Means of severity data for the root knot symptom were analyzed by the Kruskal-Wallis test and when the Pearson's χ^2 value for the experiment was significant at $\alpha < 0.05$, cultivars were examined pair-wise to determine which treatments differed significantly.

Table 3. Evaluation of four 6-row feed barley and six 6-row malting (designated by a suffix 'M') 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 each disease parameter and four replicates of grain parameters.

Cultivar	Root knot severity (1-5) [s]	White females /plant [t]	Eggs/kg of soil [u]	Grain yield (kg/ha) Control	Treated [v]	% increase [w]	Resis-tance [x]	Toler-ance [y]
2013								
Goldeneye	4.2±0.0 a [z]	7.9±4.7 a	35,563±1,702 a	6,238±597 a	6,240±482 a	0.6±2.2 a	MS	VT/MS
Herald	4.0±0.0 a	5.3±3.4 a		5,827±516 a	5,887±213 a	2.9±7.6 a	MR	VT/MR
Millenium	4.2±0.0 a	2.2±0.5 a	81,816±8,814 a	6,065±376 a	6,026±214 a	-0.3±4.9 a	R	VT/R
Steptoe	4.2±0.3 a	2.9±1.4 a	58,233±1,717 a	4,855±297 a	5,728±741 a	17.8±11.6 a	R	MI/R
01AB9663 (M)	3.9±0.1 a	8.8±8.3 a		6,447±506 a	6,266±411 a	-2.4±3.0 a	MS	VT/MS
Celebration (M)	3.9±0.1 a	9.3±6.8 a	63,734±6,104 a	4,910±515 a	5,520±478 a	14.2±10.1 a	MS	MT/MS
Legacy (M)	3.9±0.2 a	2.5±0.5 a	49,997±13,571 a	5,558±496 a	6,080±91 a	11.8±9.4 a	R	MT/R
Morex (M)	4.2±0.1 a	13.1±6.8 a	59,929±2,005 a	5,280±257 a	5,293±342 a	0.0±1.6 a	S	VT/S
Quest (M)	3.8±0.3 a	8.2±1.6 a		5,413±535 a	5,190±383 a	-3.3±3.4 a	MS	VT/MS
Tradition (M)	3.9±0.2 a	5.7±2.3 a		5,032±396 a	5,310±345 a	6.7±7.4 a	MR	T/MR
Mean	4.0	6.6	58,212	5,563	5,754	4.8	MS	VT/MS
P > F	0.5429	0.7669	0.5214	0.1948	0.4484	0.4128		
$HSD_{0.05}$	ns	ns	ns	ns	ns	ns		
2014								
Goldeneye	4.7±0.3 a	5.9±2.1 a	591±87 a	3,397±253 a	4,312±443 a	27.0±9.8 a	MR	MI
Herald	5.0±0.0 a	17.4±0.8 a	457±236 a	3,844±471 a	4,067±319 ab	8.3±9.1 a	S	T
Millenium	4.7±0.3 a	10.1±5.1 a	221±53 a	4,139±338 a	4,326±192 a	5.5±4.0 a	MS	T
Steptoe	4.9±0.1 a	8.4±1.7 a	1,136±237 a	3,817±280 a	4,341±338 a	16.7±15.0 a	MS	MI
01AB9663 (M)	4.1±0.5 a	14.2±4.7 a	682±182 a	2,710±150 a	2,808±129 b	4.0±3.6 a	S	VT
Celebration (M)	4.9±0.1 a	7.9±1.5 a	361±32 a	2,747±314 a	3,933±230 ab	46.7±11.9 a	MS	I
Legacy (M)	4.7±0.3 a	7.3±3.5 a	621±218 a	2,941±210 a	4,138±268 ab	42.5±12.6 a	MS	I
Morex (M)	5.0±0.0 a	21.1±16.3 a	1,167±591 a	3,021±303 a	4,076±382 ab	35.2±2.8 a	S	I
Quest (M)	4.7±0.3 a	4.9±0.5 a	721±421 a	3,243±326 a	3,471±351 ab	9.3±13.0 a	MR	T
Tradition (M)	4.5±0.5 a	6.6±1.3 a	782±162 a	3,202±631 a	3,947±312 ab	35.0±24.7 a	MS	I

Mean	4.7	10.4	707	3,306	3,942	23.0	MS	MI
P > F	0.6880	0.3752	0.1326	0.0624	0.0345	0.1304		
$HSD_{0.05}$	ns	ns	ns	ns	878	ns		

[s] Severity ratings for control (no-nematicide) treatment only, with a scale of 1 = no evidence of damage, 2 = 1 to 3 knots/root system, 3 = 3 to 5 knots, 4 = >5 knots and <20% reduction in plant height or root mass, and 5 = >5 knots and >20% reduction in plant height or root mass. More than 98% of all cultivars exhibited the root knotting symptom on at least one root; e.g., the incidence was 98-100%.

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

[u] 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.

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

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

[x] 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).

[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%).

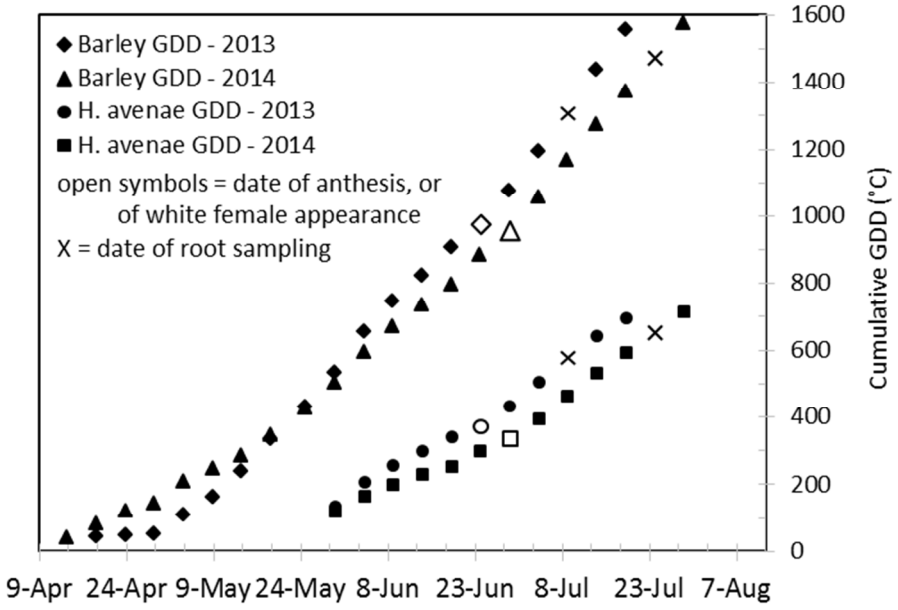
[z] Means followed by the same letter within a column did not differ significantly at $\alpha = 0.05$ as determined by Tukey's Honestly Significant Difference (HSD) test. Means of severity data for the root knot symptom were analyzed by the Kruskal-Wallis test and when the Pearson's χ^2 value for the experiment was significant at $\alpha < 0.05$, cultivars were examined pair-wise to determine which treatments differed significantly.

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

Cultivar	White females/ plant [v]	Resistance rating [w]	Yield increase [x] (%)	Tolerance rating [y]	MR + MT [z]
2-row feed barley					
Julie	6.2	MS	1.5	VT	
RWA 1758	6.3	MS	4.7	VT	
Tetonia	13.1	S	4.6	VT	
Vespa	10.1	MS	3.0	VT	
Baronesse	6.2	MS	8.7	T	
Champion	5.9	MR	7.2	T	X
Lenetah	2.6	R	9.8	T	X
Xena	3.4	MR	5.4	T	X
08ID2661	7.1	MS	12.4	MT	
CDC McGwire	8.6	MS	11.8	MT	
Idagold II	4.5	MR	10.6	MT	X
Spaulding	14.5	S	12.1	MT	
Transit	4.5	MR	10.5	MT	X
08ID1549	6.3	MS	16.1	MI	
CDC Fibar (hulless)	4.4	MR	18.2	MI	
Clearwater	7.3	MS	23.1	MI	
2-row malt barley					
2Ab04-X001084-27	21.5	S	3.0	VT	
2B05-0811 (B0811)	12.2	S	1.5	VT	
Copeland	19.4	S	4.4	VT	
Merit	15.3	S	3.8	VT	
Merem	11.8	MS	5.6	T	
2Ab07-X031098-31	11.4	MS	5.7	T	
LCS1820	7.9	MS	8.9	T	
Merit 57	26.4	VS	6.5	T	
Overture	17.1	S	9.1	T	
Pinnacle	19.1	S	6.9	T	
Genie	33.6	VS	10.7	MT	
Harrington	20.8	S	10.3	MT	
Meredith	13.8	S	13.6	MT	
ABI Voyager	38.6	VS	19.0	MI	
Conrad	9.8	MS	16.8	MI	
Hockett	24.1	S	16.6	MI	
Metcalf	16.5	S	16.8	MI	
Odyssey	0.9	VR	15.5	MI	
B1202	23.8	S	30.2	I	
6-row feed (F) *and 6-row malt* (M) *barley*					
01Ab9663 (M)	7.8	MS	0.8	VT	
Millenium (F)	5.0	MR	2.6	VT	X
Quest (M)	6.4	MS	3.0	VT	

Herald (F)	10.5	MS	5.6	T	
Goldeneye (F)	5.5	MR	13.8	MT	X
Legacy (M)	3.8	MR	27.2	MI	
Morex (M)	10.2	MS	17.6	MI	
Steptoe (F)	5.3	MR	17.2	MI	
Tradition (M)	5.6	MR	20.8	MI	
Celebration (M)	6.4	MS	30.5	I	

[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 were neither resistant nor tolerant but which met a balanced criteria of being at least both moderately resistant (≤6% swollen females/plant) and moderately tolerant (≤15% yield increase with nematicide).



E-Extra Figure 1. Cumulative growing-degree days during 2013 and 2014 for estimating the development of barley (0°C base) after the date of planting and for development of *Heterodera avenae* (8°C base) after the date of barley seedling emergence (20 May 2013 and 10 May 2014); including the estimated dates of appearance of the first-formed swollen white females, in relation to the time of root sampling to evaluate incidence and severity of the root-knotting symptom and to count numbers of swollen white females.

E-Extra Table 1. Table of significance (*P>F*) for three spring barley experiments[a] over two years, including the disease severity rating (scale of 1-5; n = 6) and number of *H. avenae* white females produced/plant in the control treatments only (n = 6), and the grain yield (kg/ha; n = 8) and test weight (g/l; n = 8) for both control and nematicide treatments; n = number of replicates included in the analysis.

Treatment and interaction	df	Severity rating	White females/ plant	Grain yield	Grain test weight
		2-row feed barley			
Year (Y)	1	<0.0001	<0.0001	0.0567	<0.0001
Cultivar (C)	15	0.3835	0.2811	<0.0001	<0.0001
Nematicide (N)	1			<0.0001	0.9360
Y × C	15	0.4848	0.0897	0.0567	<0.0001
Y × N	1			0.3850	0.3391
C × N	15			0.9740	0.9527
Y × C × N	15			0.9246	0.4546
CV (%)		9.7	39.5	12.8	3.8
		2-row malt barley			
Year (Y)	1	<0.0001	<0.0001	<0.0001	<0.0001
Cultivar (C)	18	0.2328	0.0005	0.0001	<0.0001
Nematicide (N)	1			<0.0001	0.0292
Y × C	18	0.2788	0.0232	0.0009	<0.0001
Y × N	1			0.4475	0.7533
C × N	18			0.9684	0.6528
Y × C × N	18			0.9887	0.4040
CV (%)		4.5	30.4	17.9	4.4
		6-row feed barley and 6-row malting barley			
Year (Y)	1	<0.0001	0.0079	<0.0001	<0.0001
Cultivar (C)	9	0.4344	0.7082	0.0146	0.0307
Nematicide (N)	1			0.0012	0.3136
Y × C	9	0.8536	0.4978	0.0081	0.0003
Y × N	1			0.0766	0.5124
C × N	9			0.6244	0.8165
Y × C × N	9			0.9844	0.7746
CV (%)		9.9	39.5	17.0	4.4

[a] Experimental design was a split-split plot for each of three trials, with year as main plot, cultivar as subplot, nematicide treatments as sub-subplot, and replicates as blocks.

E-Extra Table 2. Comparisons of control and nematicide treatments for two cultivars in three spring barley experiments[a] over two years, including the significance (*P*>*F*) the disease severity rating (scale of 1-5; n = 6), number of *H. avenae* white females produced/plant (n = 6), number of *H. avenae* eggs/kg of soil following harvest (n = 6), grain yield (kg/ha; n = 8) and test weight (g/l; n = 8); n = number of replicates included in the analysis.

Treatment and interaction	df	Severity rating	White females/ plant	Eggs/kg of soil	Grain yield	Grain test weight
2-row feed barley: Baronesse and Champion						
Year (Y)	1	<0.0001	0.1198	<0.0001	0.0002	0.0001
Cultivar (C)	1	0.2332	0.7985	0.8456	0.5091	0.7732
Nematicide (N)	1	<0.0001	0.0023	0.0025	0.2104	0.7793
Y × C	1	0.2332	0.3071	0.8854	0.7240	0.5264
Y × N	1	<0.0001	0.1217	0.4492	0.2677	0.8655
C × N	1	0.7195	0.8694	0.6353	0.4730	0.4536
Y × C × N	1	0.7195	0.6165	0.5454	0.5067	0.6425
CV (%)		6.7	61.3	8.4	10.0	3.1
2-row malt barley: Conrad and Metcalf						
Year (Y)	1	<0.0001	0.0001	<0.0001	0.0291	0.0075
Cultivar (C)	1	0.1525	0.3155	0.0631	0.8531	0.1501
Nematicide (N)	1	0.0050	0.0002	0.0086	0.2215	0.9914
Y × C	1	0.9211	0.5299	0.0931	0.1561	0.2520
Y × N	1	0.1084	0.0046	0.5551	0.4292	0.3543
C × N	1	0.1525	0.8253	0.3753	0.6307	0.8390
Y × C × N	1	0.9211	0.5765	0.0740	0.4386	0.4735
CV (%)		4.6	45.9	12.6	18.5	4.1
6-row feed barley: Goldeneye and Steptoe						
Year (Y)	1	0.0324	0.0292	<0.0001	0.0001	<0.0001
Cultivar (C)	1	0.5252	0.8287	0.1568	0.1164	0.0015
Nematicide (N)	1	<0.0001	0.0026	<0.0001	0.1451	0.5474
Y × C	1	0.2008	0.3935	0.9652	0.1538	0.0042
Y × N	1	0.8530	0.4563	0.2461	0.8922	0.9464
C × N	1	0.2988	0.4304	0.0716	0.8853	0.6034
Y × C × N	1	0.0985	0.2778	0.7063	0.1702	0.2321
CV (%)		15.5	50.2	5.0	18.7	3.3

[a] Experimental design was a split-split plot for each of three trials, with year as main plot, cultivar as subplot, nematicide treatments as sub-subplot, and replicates as blocks.