Resistance and Tolerance of Landrace Wheat in Fields Infested with Pratylenchus neglectus and P. thornei

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Resistance and tolerance of landrace wheat in fields infested with *Pratylenchus neglectus* and *P. thornei*

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Abstract
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Pratylenchus neglectus and *P. thornei* reduce wheat yields in the Pacific Northwest USA. Resistant landrace cultivars have been identified using controlled environments. Field resistance and tolerance characteristics were compared over three years and two locations for four spring wheat cultivars; the susceptible cultivars Alpowa and Louise, and the resistant landraces AUS28451 and Persia 20. Proportions and densities of *P. neglectus* and *P. thornei* differed across seasons and locations. Resistance was evaluated by comparing pre-plant and post-harvest densities of nematodes in soil. Tolerance was evaluated by comparing grain yield and grain quality in plots treated or untreated by the nematicide aldicarb. Alpowa was susceptible and intolerant, Louise was susceptible and moderately tolerant, AUS28451 was resistant and intolerant, and Persia 20 was moderately susceptible and moderately intolerant. The species dominance shifted from *P. neglectus* to *P. thornei* in one field over a period of three years in apparent response to cultivars and crops planted. Estimates of economic loss caused by *Pratylenchus* spp. ranged from $8 to $20/ha. Economic benefits appear to be achievable by developing a spring wheat genotype with tolerance plus resistance, such as with a cross between AUS28451 and Louise.

Root-lesion nematodes, *Pratylenchus neglectus* (Rensch) Filipjev Schuurmanns & Stekhoven and *P. thornei* Sher & Allen), occur as individual or mixed populations in a majority of the rainfed fields in low-precipitation regions of the Pacific Northwest (PNW) states of Idaho, Montana, Oregon and Washington (8,9,25,30). These root-lesion nematode species often occur as mixtures in infested fields and both species substantially reduce grain yields for spring and winter wheat (*Triticum aestivum* L.) (20,23,27,28). It was estimated that these *Pratylenchus* spp. reduce the farm-gate revenue for wheat by at least $51 million annually from the 1.7 million hectares planted annually in the states of Idaho, Oregon and Washington (20).

Practices recommended for managing the impacts of *Pratylenchus* spp. are currently limited (21,24). These practices include rotations to crop species that are not typically produced in the region, or planting tolerant cultivars that may not produce the highest grain yields in fields with low nematode densities. Currently there are no resistant varieties or chemical or biological nematicides available to manage these root parasites. Development of cultivars with genetic resistance will be important to reduce *Pratylenchus* spp. densities in soil, thereby reducing the economic risk associated with planting intolerant cultivars or crops into infested fields.

Wheat cultivars that greatly suppress reproduction of nematodes are classed as resistant and those that allow high rates of reproduction are susceptible (3). Wheat cultivars resistant to *P.*

neglectus are not necessarily resistant to *P. thornei*, and vice versa (14,15,16,17,18,33). Wheat cultivars with an ability to withstand or recover from nematode invasion and to yield well in comparison with non-invaded plants are classed as tolerant and sensitive plants are considered as intolerant (3). Tolerance is usually estimated in the field by comparing the yield of a wheat cultivar in a naturally-infested soil that is either left untreated or is treated with the nematicide aldicarb (5,11,20,31,34,35,36). Genotypes with comparable yields in both treatments are tolerant and genotypes with yields that are considerably higher in treated than in untreated soil are intolerant.

Wheat cultivars with both resistance and tolerance are required for optimal performance in existing plantings as well as for reducing the risk to subsequent plantings of intolerant cultivars or crops (26). Most commercial wheat cultivars tested in the PNW are susceptible and intolerant to both *P. neglectus* and *P. thornei* (14,16,17,18,20,33). Several imported landrace wheat cultivars were resistant to both *P. neglectus* and *P. thornei* under controlled conditions (14,15,16,17,18,33) but have not been examined for tolerance or resistance in the field.

The objectives of this research were to compare resistance and tolerance of two resistant and two susceptible wheat cultivars over a period of three years at two locations having mixtures of *P. neglectus and P. thornei*. Comparison of yields in plots treated or not treated with nematicide was used as an estimate of tolerance. Post-harvest densities of *Pratylenchus* spp. in soil of control plots (not treated with nematicide) was used as an estimate of resistance.

Materials and Methods

Experimental sites. Trials were performed near Mission and Pendleton, OR in a Mediterranean, semi-arid climate having cool, moist winters and warm, dry summers. Each field was selected based on previous knowledge that it was infested by *P. neglectus, P. thornei*, or a mixture of these species.

Trials during 2011, 2012, and 2013 were located on different sites within a single field managed by the Confederated Tribes of the Umatilla Indian Reservation (CTUIR), located 10 km southeast of Pendleton in Umatilla County, at 450 m elevation and coordinates 45°37.853′ N, 118°41.130′ W; here after these trials are referred to as Mission. The experimental sites within the Mission location were located within 200 m of one another. This location receives 330 mm mean annual precipitation, nearly all of which occurs from late autumn (November) through spring (May). The soil is a Hermiston silt loam, a deep (>200 cm), coarse-silty, mixed, mesic Cumulic Haploxeroll (42). The field was maintained without tillage (no-till) and was planted to winter wheat cultivars 'Madsen' and 'Rod' (1:1 blend) during 2008, was left as unplanted chemical fallow during 2009, and was planted to no-till canola cv. 'DeKalb RR 536' during 2010. The trial during 2011 followed the canola crop of 2010, and was planted on Apr 5 and harvested on Aug 18. The 2012 trial followed a crop of spring wheat cv. 'Louise' and was planted on May 9 and harvested on Aug 22. The 2013 trial also followed a crop of Louise and was planted on Mar 18 and harvested on Aug 8.

Trials identical to those at Mission were conducted during the same years near Pendleton. Trials were performed at the Oregon State University Columbia Basin Agricultural Research Center 14 km northeast of Pendleton, in Umatilla County, at 457 m elevation and coordinates of 45°43.158′ N, 119°37.656′ W. Annual precipitation averages 442 mm and the soil is a variable depth (90 to 150 cm) Walla Walla silt loam; a coarse-silty, mixed, superactive, mesic Typic Haploxeroll. The trial during 2011 was on a field managed as a 3-year no-till rotation of winter wheat, spring wheat, and chemical fallow. This trial was planted on Apr 5 following the harvest of winter wheat cv. 'ORCF 102' during July 2010. The trial during 2012 was in a no-till field planted annually to wheat; spring wheat Louise preceded this experiment during 2012. The trial was planted on May 9 and harvested on Aug 22. During 2013 another field in the 3-year no-till rotation of winter wheat, spring wheat, and chemical fallow was used. This trial was planted on Mar 18 following the harvest of winter wheat ORCF 102 during July 2012.

Experimental design and treatments. Each trial consisted of six replicates of each cultivar entry planted as a split-plot design. Replicates were blocks placed successively across the experimental area. Cultivars were randomized within each replicate (main plot) and each plot was split (sub-plots) as an adjacent nematicide-treated or nontreated plot. Each treatment consisted of four drill rows in 1.8 × 9 m plots. Four spring wheat cultivars were evaluated. Cultivars included two that are susceptible and two that are resistant to *P. neglectus* and *P. thornei* under controlled environments.

Alpowa (PI566596) was the most-planted soft white spring wheat cultivar in the PNW from 1997 to 2006 (40) and was used as a control. It was derived from the pedigree Fielder/Potam 70//Walladay/3/Walladay/Potam70 (1). Alpowa was reported as being susceptible to *P. neglectus* and *P. thornei* (14,15,16,33) and as intolerant to *P. neglectus* and moderately tolerant to *P. thornei* (20).

Louise (PI634865) succeeded Alpowa as the leading soft white spring wheat cultivar in the PNW (41) and served as a second control. Louise was derived as a cross between cultivars 'Wakanz' and 'Wawawai' (10) and was reported as susceptible to *P. neglectus* and *P. thornei* (14,15,16,33) and moderately intolerant to both *P. neglectus* and *P. thornei* (20).

AUS28451 (PI621458; CIMMYT CWI57134) is a hard white spring landrace wheat line collected near Sharghi, East Azerbaijan. AUS28451 had been selected in Australia for resistance to *P. thornei* (19). In the PNW, AUS28451 was highly resistant to both *P. neglectus* and *P. thornei* (14,15,16) under controlled conditions but had not been evaluated for field resistance or tolerance to these root-lesion nematode species.

Persia 20 (AUS5202; CI 11283) is a hard white facultative landrace wheat line of Iranian origin selected for resistance to *P. neglectus* in Australia (39). In the PNW, Persia 20 was moderately resistant or resistant to both *P. neglectus* and *P. thornei* (14,15,16). However, conflicting reports in the USA and in Australia indicated that Persia 20 was susceptible to *P. thornei* (33,37). This line had not been evaluated for resistance or tolerance to root-lesion nematodes under field conditions in the PNW.

Seed was planted with or without application of the nematicide aldicarb (4.2 kg/ha, as Temik 15G, Bayer CropScience, Research Triangle Park, NC). Untreated controls and aldicarb treatments were in adjacent drill rows (sub-plots) to provide side-by-side comparisons of cultivar performance in treated and untreated plots.

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. Aldicarb was metered from a second Gandy distributor on the drill and was placed into the seed row in alternate drill rows (sub-plots). Seed was dispensed through a cone seeder at a rate of 205 seed/m^2 and was placed into moist soil at 3 cm depth.

Seed during 2011 was treated with difenoconazole plus mefanoxam (0.18+0.04 g/kg, as Dividend Extreme, Syngenta Crop Protection, Greensboro, NC). Seed treatment during 2012 and

2013 included difenoconazole, mefanoxam, ipconazole and thiamethoxam (0.18+0.04+0.02+0.13 g/kg, as a proprietary custom blend from Pendleton Grain Growers, Pendleton, OR). Pre-plant weed control using glyphosate and post-harvest broadleaf weeds in each trial were managed using standard practices for the weed species of importance at each location.

Fertilizer was applied at the time of planting and was banded by the seed drill. For five of the six trials the fertilizer was applied at 123 kg N/ha formulated as a 1:1 blend of 16-20-0 and 46-0-0 (Pendleton Grain Growers, Pendleton, OR). During 2011, wet soil caused the fertilizer shanks to plug at Mission. Therefore the same fertilizer blend was broadcast onto the soil surface one week after planting, using a rate of 145 kg N/ha.

During 2012, stripe rust (*Puccinia striiformis*) in each experiment was prevented by two applications of propiconazole plus trifloxystrobin (12+12 g/ha, as Stratego, Bayer CropScience, Research Triangle Park, NC).

Wheat yield and quality assessment. Grain yields and test weights were calculated after harvesting entire plots using a Hege plot combine (Wintersteiger Inc., Salt Lake City, UT). The effect of *Pratylenchus* spp. on wheat quality was estimated by comparing test weights in control and nematicide treatments. Test weight estimates the plumpness of wheat kernels and its potential for efficient milling. Minimal test weights for U.S. No. 1–5 are 78.9, 76.4, 73.8, 71.2, and 67.3 kg/hl, respectively (4).

Nematode assessment and identification. Pre-plant density of plant-parasitic nematodes in each experimental area (800 m^2) was determined by collecting two composite soil samples from each experimental area at or before the time of planting. Each composite sample consisted of 25 soil cores of 2.5-cm diam × 30-cm depth.

Post-harvest nematode densities during 2011 were determined by collecting samples consisting of a composite of 20 soil cores (2.5-cm diameter × 30-cm depth) in each 17 m^2 plot. Due to dry soil conditions, sampling during 2012 and 2013 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 soil cores separated by two meters were collected to 30-cm depth in each plot. Soil from the two cores was composited into a single sample for each plot. The two sampling methods have provided highly correlated results (23). The mechanized sampling device is favored when soils are dry following harvest.

Initial and post-harvest soil samples were submitted to Western Laboratories (Parma, ID) for extraction and enumeration of nematodes. Dry samples were moistened and incubated at ambient laboratory air temperature for at least one week before nematodes were extracted. A modified Oosterbrink elutriator and centrifugal flotation extraction method was used (6). Vermiform nematodes and Heteroderid cysts were extracted and collected on separate sieves. Cysts were broken to release eggs plus juveniles and the suspension was combined with the suspension of vermiform nematodes. The composite suspension was then concentrated through multiple sequences of centrifugation and density flotation using a magnesium sulfate solution (6), as described by Smiley and Machado (23). The density of plant-parasitic nematodes was reported and nematodes were identified to the genus level.

Pratylenchus species present at each location were identified during previous research (25,27,28,43,44,45). Samples of nematode suspensions from Western Labs were also returned to our laboratory for identification of *Pratylenchus* spp. in randomly selected samples. Identification of species was made by examining features such as vulval position and tail shape (2,7) and by examining DNA of nematodes extracted directly from soil using species-specific endpoint PCR or real-time PCR (43,44,45). The PCR band patterns or the melting curve profiles were compared to that of DNA from pure nematode control cultures.

Resistance ratings were scaled on the basis of post-harvest *Pratylenchus* spp. densities averaged across years and locations, and compared to the mean density following the susceptible commercial cultivar Alpowa. Ratings were resistant (post-harvest *Pratylenchus* spp. densities < 25% of the susceptible control entry Alpowa), moderately resistant (26-50%), moderately susceptible (51-75%) and susceptible (≥ 76%). Tolerance ratings were scaled on the basis of mean improvement of grain yield between nematicide-treated and untreated plots when averaged across years and locations. Ratings were tolerant (< 5% mean increase in grain yield), moderately tolerant (6-10%), moderately intolerant (11-15%), and intolerant (≥16%).

Statistical analyses. Data grouped across locations during each year were analyzed as a split-split plot design to examine treatment effects of trial location, cultivar and nematicide, using trial as the main plot factor, cultivar as the subplot factor, nematicide as the sub-subplot factor, and replicates as blocks. Analyses were performed using CoStat Statistical Software version (Co-Stat v. 6.400, CoHort Software, Monterey, CA). Within individual experiments the means for grain yield, grain test weight, and nematode density were analyzed as a split-plot design, with cultivar as the main plot, nematicide treatment as the sub-plot, and replicates as blocks. Data were also analyzed individually for control and nematicide treatments at each location, using the randomized complete block design with cultivars as main effects and replicates as blocks. When treatment means were significant at $\alpha < 0.05$, means were separated using the Tukey's Honestly Significant Difference (HSD) test when numbers of replicates were equal for all treatments and the Least Significant Difference (LSD) test when replicates or treatments were unequal. 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. The percentage change in *Pratylenchus* spp. density over the life cycle of the wheat plant was calculated for cultivars in untreated control plots by using the formula:

$$\% \text{ change} = 100\,(Pf - Pi) / Pi,$$

where Pf was the non-transformed mean density/kg of soil for replicates of a specific cultivar after harvest, and Pi was the mean density for the experimental area prior to planting.

Economic analysis. Yield data averaged over years were evaluated to estimate the economic impact of yield suppression by *Pratylenchus* spp. Yield improvement from application of nematicide was multiplied by the average farm-gate value of wheat sales for the corresponding year. Wheat price was based upon the monthly average reported for the Portland, OR export market, available at http://www.ers.usda.gov/data-products/wheat-data.aspx. The potential economic impact of yield improvement from growing a resistant variety was calculated by comparing average grain yield for two locally-adapted cultivars, Alpowa and Louise, in soil treated or untreated with nematicide. Yields in treated plots were assumed to have comparable yields to what may have been produced by the same cultivars if nematode densities had been reduced to an extent which had no influence on potential grain yield.

RESULTS

Pre-plant density of *Pratylenchus* spp. Initial densities of *Pratylenchus* spp. at Mission and Pendleton were lower during 2011 than during 2012 or 2013. At Mission, there were 1,316 *Pratylenchus* spp./kg of soil during 2011. There was a much greater proportion of *P. neglectus* than *P. thornei* but specific proportions were not determined. During 2012, pre-plant density was 12,144 *Pratylenchus* spp./kg of soil (2:1 ratio of *P. thornei* to *P. neglectus*). During 2013 the pre-plant nematode density was 26,400 *Pratylenchus* spp./kg of soil (9:1 ratio of *P. thornei* to *P. neglectus*). The proportion of *Pratylenchus* spp. therefore changed within the single field at Mission during the course of this investigation. This trend could not be assessed at Pendleton, where different fields were used each year. Similar to results at Mission, population densities of *Pratylenchus* spp. at Pendleton were lower in 2011 than in 2012 and 2013. In 2011 there were 1,213 *P. thornei*/kg of soil during 2011. During 2012 the pre-plant samples contained 6,732 *Pratylenchus* spp./kg of soil. During 2013 there were 10,516 *Pratylenchus* spp./kg of soil (3.3:1 ratio of *P. thornei* to *P. neglectus*).

Post-harvest density of *Pratylenchus* spp.: The post-harvest density of *Pratylenchus* spp. was significantly ($\alpha < 0.01$) influenced each year by the main effects of cultivar and nematicide (Table 1). The effect of trial location was also significant during 2012 and 2013. All three main effects were significant when data were grouped over three years. Few interactions among main effects were significant at $\alpha < 0.05$ (data not presented) and none were considered as being biologically significant. The cultivar × location interaction was significant each of the three years and the interactions of nematicide × location and nematicide × cultivar interactions were significant during 2012, the year in which a late planting led to abnormally late growth and low yields for the region.

Averaged across cultivars and trial locations, the application of nematicide reduced nematode densities by 68%, 65% and 50% during 2011, 2012 and 2013, respectively (Table 2). The reductions in densities were greater at Pendleton than at Mission during 2011 (83% vs. 59%) and 2013 (61% vs. 48%), and were greater at Mission than at Pendleton during 2012 (68% vs. 57%). Nematode population densities were significantly reduced by application of nematicide for Alpowa, Louise and Persia 20 each year at both location (Table 2). The nematode population densities following AUS28451 were generally reduced by nematicide at Pendleton but not at Mission. Relative to Alpowa, the post-harvest densities of *Pratylenchus* spp. in untreated control plots were significantly higher following Louise during two of six site years of observation, with each of those instances occurring at Pendleton during two years of 'normal' wheat productivity (Tables 2 and 3). In untreated control plots, the post-harvest densities of *Pratylenchus* spp. were significantly lower following Persia 20 than Alpowa in three of six site years of observation, with each of those instances occurring at Mission. The post-harvest densities following AUS28451 were significantly lower than following Alpowa during each of the five site years in which that comparison could be made.

The lowest post-harvest densities of *Pratylenchus* spp. were always detected in plots of the resistant landrace wheat line AUS28451. The final densities of *Pratylenchus* spp. in control plots following Persia 20 were always higher than that following AUS28451. Highest densities of *Pratylenchus* spp. occurred in control plots planted to one of the locally-adapted cultivars, Alpowa or Louise. In the control treatment, the final nematode densities were as much as 12-times higher following Alpowa compared to following AUS28451, which occurred during 2012 at Mission (Table 2). When all six experiments were grouped, final *Pratylenchus* spp. densities were reduced for all cultivars when nematicide was applied (Table 4). However, density in control plots was always least following AUS28451, which was the only entry with significantly fewer *Pratylenchus* spp. than Alpowa and Louise.

Alpowa, Louise and Persia 20 were each rated as susceptible to these *Pratylenchus* spp. (Table 4). Reductions in nematode densities in response to nematicide application ranged from

37% to 86% for the commercial cultivars during the course of the experiment (Table 2). AUS28451 was rated resistant (Table 4). Post-harvest densities of *Pratylenchus* spp. for AUS28451 in untreated controls were always lower than for other cultivars and reductions due to nematicide application were significant in only two of the five observations, both of which occurred at Pendleton where *P. thornei* was the dominant species (Table 2). Compared to Alpowa, AUS28451 significantly reduced *Pratylenchus* spp. densities in control plots in each of the five observations available. Persia 20 was rated as moderately susceptible (Table 4). Compared to Alpowa, Persia 20 significantly reduced the nematode densities in all three trials at Mission but not in the three trials at Pendleton (Table 2), possibly due to the greater prevalence of *P. neglectus* in the species mixture at Mission than at Pendleton.

Each year, the percentage change in *Pratylenchus* spp. densities over the growing season was neutral to positive for Alpowa and Louise and were negative for AUS28451 and Persia 20 (Fig. 1). The percentage change was always significantly different between AUS28451 and the commercial control cultivars, and between AUS28451 and Persia 20. These findings support the designations of AUS28451 as resistant, Persia 20 as moderately susceptible, and Alpowa and Louise as susceptible to species of *Pratylenchus* present at these sites.

Other nematode genera and species detected: Several plant-parasitic nematode genera and species other than *Pratylenchus* spp. were detected during these studies. Low numbers of stunt nematodes, *Tylenchorynchus* spp., were detected at each site during 2011 (292 and 324 *Tylenchorhynchus* spp./kg of soil at Mission and Pendleton, respectively) but not during pre-plant samplings in 2012 or 2013. Very small numbers of stunt nematodes (<40/kg of soil) were detected in 3 of the 48 plots at the Pendleton site during post-harvest sampling in 2013. Previous experience at nearby sites (25,29) has shown that the stunt nematodes were likely to be *T. clarus*. During 2012 the pre-plant samples at Pendleton included 44 *Heterodera avenae*/kg of soil but this nematode was not detected in any other sampling. The stubby root nematode, *Trichodorus* spp., was detected at a low density (176 *Trichodorus* spp./kg of soil) during pre-plant but not post-harvest sampling at Mission during 2013; the species was not determined and was not detected in other samplings.

Plant growth and grain yield: Establishment of seedling stands was excellent for each of the six trials (data not presented). A later-than-usual planting date during one very wet spring (2012) caused AUS28451 to remain mostly vegetative and to produce too few heads to be harvested.

Main treatment effects for grain yield were significant ($\alpha < 0.0001$) each year for cultivar, nematicide, and trial location (Table 1). The cultivar × location interaction was significant for grain yield each year, and during 2012 the nematicide × location and the nematicide × cultivar interactions were also significant. When yield data were grouped over years, the main effects for cultivar and nematicide were highly significant.

When data were grouped across the four cultivars and two nematicide treatments, the mean grain yield was greater at Mission than at Pendleton each year; 4,328 vs. 3,411 kg/ha ($HSD_{0.05}$ = 381), 1,248 vs. 700 kg/ha ($HSD_{0.05}$ = 156), and 2,449 vs. 2,115 kg/ha ($HSD_{0.05}$ = 152) during 2011, 2012 and 2013, respectively (Table 3). Application of nematicide increased mean grain yield by 16%, 77%, and 19% during 2011, 2012 and 2013, respectively (Table 3). Yields were unusually low at both locations during 2012 and were therefore excluded from additional analysis. When grain yield data over both locations were grouped for 2011 and 2013 (Table 4), the main effects were significant ($\alpha < 0.01$) for location, cultivar and nematicide, and the interaction between location and cultivar was also significant. Application of nematicide increased mean grain yield by 18% (Table 4) and yields in the non-treated controls and in the nematicide-treated plots were statistically similar for Alpowa, Louise and AUS28451 (Table 4). Yield of Persia 20 was significantly lower than for Alpowa and Louise in each of the control and nematicide treatments. Alpowa and AUS28451 were categorized as intolerant, Persia 20 as moderately intolerant, Louise as moderately tolerant (Table 4).

Grain quality: Grain test weight differed significantly ($\alpha < 0.01$) each year in response to main effects of cultivar and nematicide (Table 1). When data for 2011 and 2013 were grouped, as explained above, mean test weights across locations were 3% greater in the nematicide-treated than in the untreated plots; 77.7 vs. 75.5 kg/hl, respectively ($LSD_{0.05} = 1.4$) (data not shown). Test weights were higher ($LSD_{0.05} = 2.1$) for Alpowa (79.5 kg/hl), Louise (78.0 kg/hl) and Persia 20 (77.0 kg/hl) than for AUS28451 (70.4 kg/hl). When test weights of the two locally-adapted cultivars were averaged together over two years (2011 and 2013) and two trial locations, the test weight was significantly greater ($HSD_{0.05} = 1.9$) in nematicide-treated than untreated plots; 79.8 vs. 77.7 kg/hl, respectively. These test weights fall within the limits of market grades U.S. No. 1 and No. 2, respectively. For both control and nematicide treatments, these cultivars each met the standard for U.S. No. 1 at both locations during 2011. However, during 2013 at Pendleton grain was graded as U.S. No. 2 in each treatment and, at Mission, graded as U.S. No. 2 in the nematicide-treated plots and as U.S. No. 4 in the control plots.

Profitability: When yields for Alpowa and Louise were averaged across two years (2011 and 2013) and two trial locations (Table 5), the yield improvement from nematicide application was greater for Alpowa (23%) than for Louise (9%). Grouped together, the mean yield for these locally-adapted cultivars was 16% (495 kg/ha) greater in nematicide-treated plots (3,645 kg/ha) than in control plots (3,140 kg/ha). Based upon a mean September wheat price of US$2.72/hl ($2.31/hl during 2011 and $3.13/hl during 2013), *Pratylenchus* spp. were estimated to have reduced the average profitability of wheat production in these fields by $13.90/ha; $19.69/ha for Alpowa and $7.88/ha for Louise. For a typical farm in the region, consisting of about 480 ha of wheat planted each year, the farm scale economic impact from nematodes would have equated to a loss ranging from $3,784 for Louise to $9,449 for Alpowa. The average loss for these two cultivars would have equated to a loss of $6,671 to the farm enterprise.

DISCUSSION

This research provides further evidence that *Pratylenchus* spp. reduce both wheat yield and grain quality in the PNW. Our estimates from this work indicated that the value of spring wheat production was reduced by $8 to $20/ha in infested fields, depending upon the cultivar planted and the level of infestation. For an average-size farm in the region, this level of crop damage would equate to a reduction in farm profitability of between $4,000 and $10,000 annually. These are conservative estimates because they did not include a likely reduction in wheat price associated with reduced wheat quality in control plots that were not treated with nematicide, and because application of aldicarb in a *Pratylenchus* spp.-infested field failed to improve yield of an intolerant wheat cultivar to a level equaling that of the same cultivar in a nearby field that had an undetectably low density of *P. thornei*, in comparison to a tolerant cultivar that produced comparable yields under those conditions (38). Since our research was conducted in fields infested with both *P. neglectus* and *P. thornei*, it was not possible to determine if the commercial cultivars differed in tolerance to one or both individual species. Smiley (20) reported that Louise was more tolerant of *P. neglectus* than of *P. thornei* and Alpowa was more tolerant of *P. thornei* than of *P. neglectus*. Those differences would have been obscured in many of the tests performed in this study at sites with mixtures of these species. During the course of these studies, Louise was more tolerant than Alpowa to the mixtures of *Pratylenchus* spp. encountered.

We also present the first evidence that a spring wheat genotype with resistance to both *P. neglectus* and *P. thornei* can substantially reduce the post-harvest density of mixtures of *Pratylenchus* spp. in infested fields. This was demonstrated in fields that had varying initial proportions of *P. neglectus* and *P. thornei* during the course of experiments conducted in different fields, different sites within fields, different locations, and over three growing seasons. Owen et al. (13) recently reported a nearly 70% lower biomass of a *P. thornei*-intolerant wheat cultivar that was planted after *P. thornei*-susceptible crops compared to more resistant crops in a field infested by *P. thornei*. Although the dual-species resistance trait exhibited by AUS28451 will undoubtedly become important to PNW agriculture, the yield penalty associated with genotypic intolerance to *Pratylenchus* spp. will limit the acceptance by growers of cultivars that express resistance but not tolerance. In the current investigation, AUS28451 was much less tolerant than Louise. It will be important to introgress resistance from a cultivar such as AUS28451 with the greater tolerance expressed by a cultivar such as Louise. A resistant plus tolerant cultivar would enable growers to attain acceptable yields while also reducing the density of nematodes that pose an increased risk to subsequent plantings of intolerant cultivars or crops. Fortunately, gross yields of AUS28451 were competitive with those of the commercial cultivars, indicating the possibility that high-yielding lines should be able to be identified that also are resistant to *P. neglectus* and *P. thornei*.

While AUS28451 carries *Pratylenchus*-resistance traits of value to the PNW field crops industries, this cultivar was recently determined to also possess several undesirable agronomic traits that would need to be selected against while incorporating *Pratylenchus* resistance into lines that could be advanced into commercial cultivars. In particular, Thompson (32) determined that AUS28451 carried traits for leaf and head pubescence and for tenacious glumes. These traits cannot be allowed to be advanced into a commercial cultivar. This same study (32) also identified the presence of the *Vrn-D1a* vernalization gene in AUS28451, providing evidence that our premise for the failure of this cultivar to produce normal numbers of heads during 2012 resulted from our late planting date, and therefore an insufficient period of vernalization for the 2012 planting. It was clear that AUS28451 produced heads in a normal manner during other years, and that plantings of this cultivar two weeks earlier during 2012 in plots adjacent to both of our trial locations produced a normal number of heads (Alison Thompson, unpublished data). Vernalization requirements will be advantageous when the *Pratylenchus*-resistance trait is incorporated into susceptible winter wheat cultivars in the PNW but will be less advantageous for crossing into spring wheat. Fortunately, Thompson (32) also identified other land-race wheat lines having dual-species resistance to *Pratylenchus*, plus acceptable agronomic traits that include resistance to races of *Puccinia striiformis* of current importance in the PNW.

AUS28451 was more resistant than Persia 20 to the mixture of *Pratylenchus* spp. encountered in this study. Although early assays of Persia 20 indicated that this cultivar conferred dual-species resistance (15,16,17), more recent assays under controlled conditions revealed that Persia 20 enabled reproduction more similar to that of Louise for *P. neglectus* and similar to that of Alpowa for *P. thornei* (32,33,37). In this study, reproduction of *Pratylenchus* spp. on Persia 20 was intermediate between that of AUS28451 and the commercial cultivars Alpowa and Louise. These results indicate that future emphasis in the PNW should be shifted from Persia 20 to a landrace having improved agronomic characteristics and resistances comparable to AUS28451 (32).

We detected a shift in proportions of *P. neglectus* and *P. thornei* over a period of three years in a field near Mission. While the experiments were placed on different sites within that field, the experiments each year were all located within 200 m of one another in a single corner of that field. Shifts over time have also been reported for other Oregon locations. For instance, assays of *Pratylenchus* spp. in a 12-year cropping systems experiment at another low-precipitations site (280 mm) in northcentral Oregon revealed that winter wheat selected for a dominance of *P. neglectus* and spring wheat selected for a dominance of *P. thornei* (24). Comparable findings of *Pratylenchus* spp. selections occurred in 83-year-old monoculture blocks of cultivated winter wheat and spring wheat and in 16-year-old non-tilled blocks of these crops at the Columbia Basin Agricultural Research Center at Pendleton (Smiley, unpublished). Furthermore, a corresponding difference in species prevalence was reported by wheat producers on two neighboring farms in eastern Idaho which produce only winter wheat or only spring wheat.

In this study, at Mission, *P. neglectus* was the dominant species during 2011. In this year the experiment followed multiple crops of winter wheat Madsen and Rod, followed by canola. Spring wheat Louise was planted in the field by the grower during 2011 and again in 2012. Therefore, subsequent experiments followed one year of Louise during 2012 and two years of Louise during 2013. Sheedy et al. (17,18) reported that in concurrent controlled-environment assays, some popular PNW winter wheat cultivars strongly favored reproduction of *P. neglectus* compared to *P. thornei*. For example, respective relative reproductive values (Pf/Pi = final/initial density) were 29 and 7 for ORCF 102, 24 and 7 for Rod, and 31 and 10 for Brundage 96. In contrast, other popular cultivars were less discriminating as hosts for *P. neglectus* and *P. thornei*. For example, respective Pf/Pi values were 10 and 10 for Stephens, and 13 and 18 for Madsen for *P. neglectus* and *P. thornei*, respectively. We also recently determined from greenhouse assays that Louise is a much better host of *P. thornei* than of *P. neglectus*, and that multiple cultivars of canola are much better hosts for *P. neglectus* than for *P. thornei* (Smiley, unpublished). It is likely that the shift in species dominance at Mission was due to influences of different wheat genotypes than to differences in plant growth habit; e.g., a 10-month winter wheat crop vs. a 4-month spring wheat crop, with associated differences in temperature and moisture cycles. Since different wheat cultivars vary in tolerance to these two *Pratylenchus* spp. (20), our recent observations of crop management effects on species dominance indicates an urgent need to incorporate identification of *Pratylenchus* spp. by commercial nematology laboratories that currently only report this group of nematodes at the genus level. Recent development of DNA-based tests can be used to alleviate the difficulties associated with distinguishing *P. neglectus* and *P. thornei* using only morphometric characteristics (43,44,45).

Aldicarb was used as a research tool in these experiments. This pesticide is not registered for commercial application by wheat producers in the USA. High expense, ecological concerns, and lack of registration preclude it from consideration as a potential solution to crop losses being caused by *Pratylenchus* spp. Nevertheless, aldicarb is a long-favored research tool for examining effects of plant-parasitic nematodes on wheat (5,11,20,27,28,31,36). Aldicarb is typically applied as a band below or with the seed at planting to suppress damage and reproduction of nematodes. This nematicide has a half-life up to five weeks, reduces the *Pratylenchus* population early in the plant growth period, and results in improved grain yields for genotypes that are intolerant to the nematode (20,27,28,31). Aldicarb is favored for this research use because it does not influence diseases caused by soilborne root-infecting fungi (11,12), does not stimulate wheat yield in the absence of plant-parasitic nematodes or insect pests (27), but occasionally has been shown to suppress wheat yields due to phytotoxicity or to a more severe expression of root diseases caused by soilborne fungi (22,27).

We clearly demonstrated that *Pratylenchus* spp. are causing economic losses to the PNW wheat industry, and that resistant cultivars can reduce the level of risk that would be encountered by subsequent plantings of intolerant crops. Specifically, we have shown that imported landrace wheat cultivars such as AUS28451 will play an important role in the development of commercial wheat cultivars that are both resistant and tolerant to *Pratylenchus* spp.

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Table 1. Significance of main treatment effects for data presented in Tables 2, 3 and 4[a].

Year and treatment effect	Post-harvest *Pratylenchus* spp./kg of soil		Grain Yield (kg/ha)		Grain Test weight (kg/hl)	
	df	P>F	df	P>F	df	P>F
Year 1 - 2011						
Trial	1	0.1051	1	<0.0001	1	<0.0001
Cultivar	3	0.0001	3	<0.0001	3	<0.0001
Nematicide	1	<0.0001	1	<0.0001	1	<0.0001
Year 2 - 2012						
Trial	1	<0.0001	1	<0.0001	1	0.7691
Cultivar	3	0.0058	2	<0.0001	2	<0.0001
Nematicide	1	<0.0001	1	<0.0001	1	<0.0001
Year 3 - 2013						
Trial	1	<0.0001	1	<0.0001	1	0.3284
Cultivar	3	<0.0001	3	<0.0001	3	0.0003
Nematicide	1	<0.0001	1	<0.0001	1	0.0031
Grouped over 3-Years						
Trial	1	<0.0001	1	0.1320	1	<0.0001
Cultivar	3	<0.0001	3	<0.0001	3	<0.0001
Nematicide	1	0.0031	1	<0.0001	1	<0.0001

[a] Experimental design was a split-split plot with trial locations as main plots, cultivars as subplots, nematicide treatments as sub-subplots, and replicates (n = 6) as blocks. Degrees of freedom for Year 2 differed between grain production parameters and nematode density data because one cultivar could not be harvested during 2012.

Table 2. Post-harvest density of *Pratylenchus* spp.[z] (nematodes/kg of soil) in naturally-infested fields following growth of four spring wheat cultivars treated or untreated by nematicide[y] during three years at Mission and Pendleton, OR.

Year and cultivar	Mission				Pendleton				2-location means			
	Control	Treated	% red.[x]	Rel. to Alpowa[w]	Control	Treated	% red.	Rel. to Alpowa	Control	Treated	% red.	Rel. to Alpowa
2011												
Alpowa	3,858 a[v]	1,034 ab	73%*	-	2,101 b	486	77%*	-	2,980 b	760	74%*	-
Louise	4,530 a	2,380 a	47%*	+17%	4,852 a	728	85%*	+131%*	4,691 a	1,554	67%*	+57%*
AUS28451	732 b	556 b	24%	-81%*	nt	nt	-	-	732 c	556	24%	-75%*
Persia 20	2,375 ab	711 b	70%*	-38%*	1,952 b	264	86%*	-7%	2,164 b	488	77%*	-27%
Mean	2,874	1,170	59%*		2,968	493	83%*		2,642	840	68%*	
P > F	0.0068	0.0170			0.0007	0.6738			<0.0001	0.1082		
2012												
Alpowa	35,514 a	14,062 a	60%*	-	6,789 a	4,700 a	44%*	-	21,151 a	9,381 a	56%*	-
Louise	32,737 a	6,432 ab	80%*	-8%	6,568 a	1,433 ab	78%*	-3%	19,652 a	3,933 ab	80%*	-7%
AUS28451	3,007 b	3,073 b	-2%	-92%*	1,193 b	530 b	56%*	-82%*	2,100 b	1,802 b	14%	-90%*
Persia 20	11,843 ab	3,376 b	71%*	-67%*	5,474 a	1,986 ab	64%*	-19%	8,559 a	2,681 b	69%*	-60%*
Mean	20,775	6,736	68%*		5,006	2,162	57%*		12,866	4,449	65%*	
P > F	0.0015	0.0507			0.0438	0.0204			0.0001	0.0008		
2013												
Alpowa	42,357 ab	20,360 b	52%*	-	6,352 ab	3,666 a	42%*	-	24,354 a	12,013 a	51%*	-
Louise	55,504 a	32,416 a	42%*	+31%	9,743 a	4,104 a	58%*	+53%*	32,624 a	18,260 a	44%*	+34%*
AUS28451	5,342 c	5,891 d	-10%	-87%*	1,696 c	223 b	87%*	-73%*	3,519 b	3,057 b	13%	-86%*
Persia 20	27,083 b	9,386 c	37%*	-36%*	4,907 b	866 ab	82%*	-23%	15,995 a	5,126 b	68%*	-34%*
Mean	32,572	17,013	48%*		5,675	2,215	61%*		19,123	9,614	50%*	
P > F	<0.0001	<0.0001			0.0308	0.0159			<0.0001	<0.0001		

[z] *Pratylenchus* spp. included mixtures of *P. neglectus* and *P. thornei* at Mission, and mostly *P. thornei* at Pendleton; numbers are back-transformed means from the ln (x+1) transformation used to analyze data for statistical analysis. nt = not tested.

[y] Nematicide treatment included application of aldicarb banded into the seed row at the time of planting.

[x] Percentage reduction of *Pratylenchus* spp. density in nematicide treatment compared to the untreated control. Differences that are significantly different ($\alpha < 0.05$) from the controls are designated by an asterisk (*).

[w] Nematode density in untreated control treatments, relative to that of the Alpowa control. Differences that are significantly different ($\alpha < 0.05$) from Alpowa are designated by an asterisk (*).
[v] Numbers followed by the same letter within a column are not significantly different at $\alpha < 0.05$ as determined by Tukey's Honestly Significant Difference (HSD) test, based upon analysis of ln(x+1) transformed data.

Table 3. Grain yield (kg/ha) of four spring wheat cultivars in fields naturally infested with *Pratylenchus* spp.[z] and treated or untreated by nematicide[y] during three years at Mission and Pendleton, OR.

Year and cultivar	Mission			Pendleton			2-location means		
	Control	Treated	Incr. (%)[x]	Control	Treated	Incr. (%)	Control	Treated	Incr. (%)
<u>Year 1 - 2011</u>									
Alpowa	4,217	5,337 a[w]	27*	3,344 b	4,192 a	25*	3,780 a	4,765 a	26*
Louise	4,263	4,831 a	13*	4,031 a	4,138 a	3	4,147 a	4,485 a	8
AUS28451	4,115	4,728 a	15*	nt	nt	-	4,115 a	4,729 a	15*
Persia 20	3,216	3,910 b	22*	2,325 c	2,437 b	5	2,770 b	3,174 b	15*
Mean	3,953	4,702	19*	3,233	3,589	11*	3,644	4,225	16*
$LSD_{0.05}$	ns	563		440	527		389	341	
P > F	0.1018	0.0007		<0.0001	<0.0001		<0.0001	<0.0001	
<u>Year 2 – 2012</u>[v]									
Alpowa	1,200 a	2,208 a	84*	647 a	1,162 a	80*	923 a	1,635 a	77*
Louise	1,078 a	1,690 b	57*	740 a	1,022 a	38*	909 a	1,356 b	49*
Persia 20	323 b	987 c	206*	200 b	428 b	114*	261 b	709 c	172*
Mean	867	1,628	88*	529	871	65*	698	1,233	77*
$HSD_{0.05}$	375	309		406	333		204	162	
P > F	<0.0001	<0.0001		0.0018	0.0001		<0.0001	<0.0001	
<u>Year 3 – 2013</u>									
Alpowa	2,498	3,054 a	22*	2,456 a	2,777 a	13*	2,477 a	2,916 a	18*
Louise	2,150	2,211 b	3	2,166 a	2,539 b	17*	2,158 ab	2,375 ab	10*
AUS28451	2,455	3,368 a	37*	1,537 b	1,992 c	30*	1,996 ab	2,680 a	34*
Persia 20	1,815	2,038 b	12*	1,598 b	1,846 c	16*	1,707 b	1,942 b	14*
Mean	2,229	2,668	20*	1,940	2,289	18*	2,084	2,478	19*
$HSD_{0.05}$	ns	458		229	174		402	409	
P > F	0.1769	<0.0001		<0.0001	<0.0001		0.0039	0.0002	

[z] *Pratylenchus* spp. included mixtures of *P. neglectus* and *P. thornei* at Mission, and mostly *P. thornei* at Pendleton.

[y] Nematicide treatment included application of aldicarb banded into the seed row at the time of planting.

[x] Percentage increase in yield due to applications of nematicide. Differences that are significantly different ($\alpha < 0.05$) from the controls are designated by an asterisk (*).

[w] Numbers followed by the same letter within a column are not significantly different at $\alpha < 0.05$ as determined by Tukey's Honestly Significant Difference (HSD) test; ns = not significant.

[v] AUS28451 was planted but not harvested during 2012 because it remained mostly vegetative, apparently due to a failure to vernalize in response to a later-than-normal planting date.

Table 4. Grain yield (kg/ha) and post-harvest density of *Pratylenchus* spp. (nematodes/kg of soil) for four sping wheat cultivars grouped over years at naturally-infested field sites treated or untreated by nematicide[z].

	Post-harvest *Pratylenchus* density[y]					Grain yield[x]			
Cultivar	Control	Treated	Reduction[w]	Rel. to Alpowa[v]	Rating[u]	Control	Treated	Incr.[t]	Rating
Alpowa	9,974 ab[s]	4,274 a	57%*	100%	S	3,128 a	3,840 a	23%*	IT
Louise	13,344 a	3,928 a	71%*	134%	S	3,152 a	3,430 a	9%	MT
AUS28451	1,982 c	1,071 b	40%*	20%*	R	2,702 ab	3,363 a	24%*	IT
Persia 20	6,403 b	1,648 b	74%*	64%	MS	2,239 b	2,558 b	14%*	MI
Mean	7,926	2,730	65%*	-		2,805	3,298	18%*	
P > F	<0.0001	0.0004				0.0076	0.0020		

[z] Nematicide treatment included application of aldicarb banded into the seed row at the time of planting.

[y] Post-harvest *Pratylenchus* spp. density include data for all site years because AUS28451 exerted similar influences on these nematodes even though it failed to produce heads during 2012. *Pratylenchus* spp. included mixtures of *P. neglectus* and *P. thornei*.

[x] Grain yield data include 2 trial locations and 2 years (4 site years); data for 2012 were eliminated due to abnormally low yields and the failure of one entry (AUS28451) to produce heads due to failure to fully vernalize.

Table 5. Economic value of production for two locally-adapted soft white spring wheat cultivars (Alpowa and Louise) produced in *Pratylenchus*-infested[z] fields at two locations (Mission and Pendleton, OR) during two years (2011 and 2013) in which production was typical for the region; comparisons are for cultivars produced in plots treated or untreated with nematicide[y].

	Alpowa			Louise		
Grain production and value	Nematicide	Control	Increase	Nematicide	Control	Increase
Yield (kg/ha; and %)	3,840	3,129	711 (22.7%)	3,430	3,153	277 (8.8%)
Test weight (kg/hl)	81.1	78.0	3.1 (4.0%)	78.6	77.4	1.2 (1.6%)
U.S. Wheat Market Grade[x]	No. 1	No. 2		No. 2	No.2	
Volume produced (hl/ha)	47.3	40.1	18.0%	43.6	40.7	7.1%
Value: ($/ha)[w]	$ 128.86	$ 109.17	$ 19.69	$ 118.74	$ 110.86	$ 7.88
Value: ($/average-size farm)[v]	$ 61,851	$ 52,402	$ 9,449	$ 56,997	$ 53,213	$ 3,784

[z] *Pratylenchus* species included mixtures of *P. neglectus* and *P. thornei* at Mission, and mostly *P. thornei* at Pendleton.

[y] Nematicide treatment included application of aldicarb into the seed row at the time of planting.

[x] Minimal test weights for the five U.S. Market Grades of soft white wheat are 78.9, 76.4, 73.8, 71.2, and 67.3 kilograms/hectoliter for U.S. No. 1–5 (4).

[w] Market prices for soft white wheat at Portland, OR during September averaged $2.31/hl and $3.13/hl during 2011 and 2013, respectively; available at http://www.ers.usda.gov/data-products/wheat-data.aspx.

[v] Average farm size in the region of this research is approximately 960 ha, about half of which is planted to wheat each year. A farm with 480 ha of soft white spring wheat was assumed for this calculation.

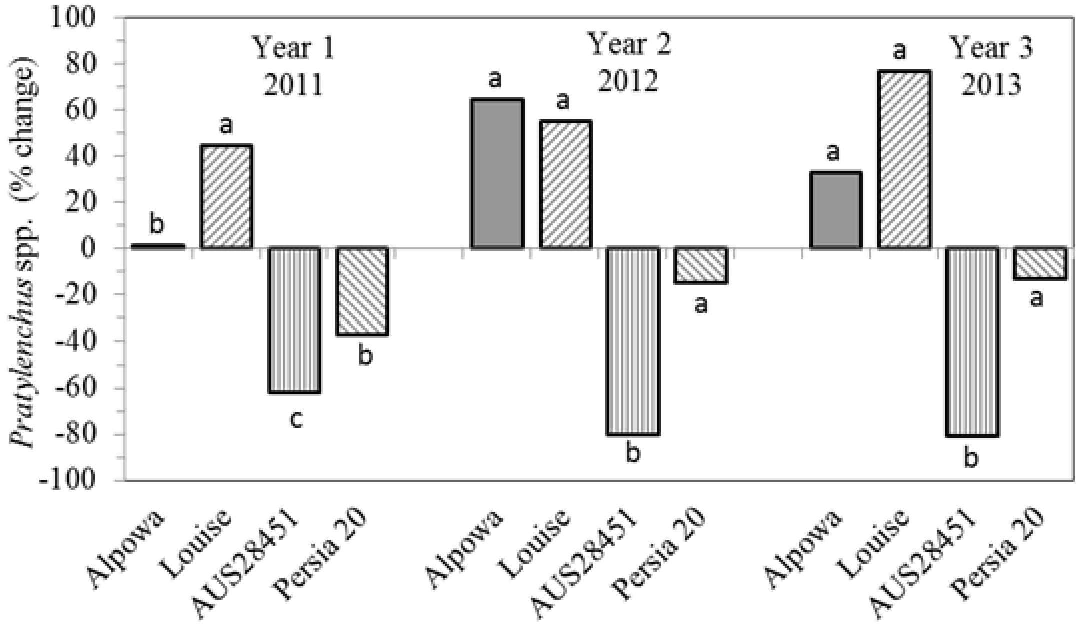

Figure 1. Percentage change in *Pratylenchus* spp. density during three seasons of growth by four spring wheat cultivars in naturally-infested fields; data for each year are grouped over two locations (Mission and Pendleton, OR); calculated using the formula: % change = 100 ($Pf - Pi$) / Pi, where Pf and Pi were the non-transformed final and initial *Pratylenchus* spp. densities/kg of soil, respectively. Bars labeled with the same letter do not differ at the $\alpha < 0.05$ level of significance.