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Inheritance of resistance to root-lesion nematode (*Pratylenchus thornei*) in wheat landraces and cultivars from the West Asia and North Africa (WANA) region

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Abstract. The root-lesion nematode *Pratylenchus thornei* causes substantial loss to bread wheat production in the northern grain region of Australia and other parts of the world. West Asia and North Africa (WANA) wheat accessions with partial resistance to *P. thornei* were analysed for mode of inheritance in a half-diallel crossing design of F_1 hybrids (10 parents) and F_2 populations (7 parents). General combining ability was more important than specific combining ability as indicated by components of variance ratios of 0.93 and 0.95 in diallel ANOVA of the F_1 and F_2 generations, respectively. General combining ability values of the 'resistant' parents were predictive of the mean nematode numbers of their progeny in crosses with the susceptible Australian cv. Janz at the F_1 ($R^2 = 0.86$, $P < 0.001$, 8 crosses), F_2 ($R^2 = 0.83$, $P < 0.001$, 9 populations) and F_∞ ($R^2 = 0.71$, $P < 0.05$, 5 doubled-haploid populations). The F_2 and F_∞ populations showed relatively continuous distributions. Heritability was 0.68 for F_2 populations in the half-diallel of resistant parents and 0.82–0.92 for 5 'resistant' parent/Janz doubled-haploid populations (narrow-sense heritability on a line mean basis). The results indicate polygenic inheritance of *P. thornei* resistance with a minimum of from 2 to 6 genes involved in individual F_∞ populations of 5 resistant parents crossed with Janz. Morocco 426 and Iraq 43 appear to be the best of the parents tested for breeding for resistance to *P. thornei.* None of the *P. thornei*-resistant WANA accessions was resistant to *Pratylenchus neglectus.*

Additional keywords: *Pratylenchus neglectus*, transgressive segregants.

Introduction

Wheat is cultivated worldwide with an annual production of ~780 M tonnes, which is third after maize and rice of all cereals. Because of wheat's higher protein content it is the most important source of vegetable protein for human nutrition. Spring wheat (*Triticum aestivum*) is the major cereal grown in winter in the subtropical, subhumid, northern grain region of Australia (Webb *et al*. 1997) with average annual production of 3.7 M tonnes from 2.24 M hectares (Murray and Brennan 2009). Hard white wheat of high protein content that is favoured for bread and ramen noodles is produced. Root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) are a significant problem for wheat production in the northern region (Thompson *et al*. 2008), other regions of Australia (Vanstone *et al*. 2008) and other countries (Nicol *et al*. 2003; Smiley and Nicol 2009). *P. thornei* occurs more frequently and at higher population densities than *P. neglectus* in the Australian northern grain region (Thompson *et al*. 2010). Present economic loss from *P. thornei* in the northern grain region has been estimated at AUD$38 M/year based on a 10-year average wheat price of AUD$239/tonne, whereas the potential economic loss without existing management of the problem would be AUD$104 M/year (Murray and Brennan 2009).

Root-lesion nematodes feed, reproduce and migrate in the root cortex of wheat resulting in lesions and debilitated root systems that are inefficient at extracting nutrients and water from the soil. Evidence of the belowground pathogenic activity of the nematodes can be seen as aboveground symptoms of chlorosis and wilting of leaves, and reduced tillering, biomass and grain yield. Key components of effective integrated management of *P. thornei* in the northern grain region are crop rotation and the use of tolerant and resistant crop cultivars (Thompson *et al*. 2008). Tolerant cultivars suffer little yield reduction even though their roots are invaded by nematodes, whereas resistant cultivars retard the rate of nematode multiplication in the roots (Roberts 2002). Resistant cultivars leave fewer nematodes in the soil to attack subsequent crops thereby contributing to productivity of the whole farming system, and growing cultivars that have greater resistance than current cultivars would also diminish chances for continued spread of *P. thornei* to uninfested fields in the northern grain region (Thompson *et al*. 2010). For polycyclic nematode species like *P. thornei*, resistance can also reduce yield loss in the current crop by delaying the build up of nematodes during the growing season and thereby reducing plant damage (Trudgill 1991; Thompson *et al*. 2000).

Although progress has been made with breeding some tolerant bread wheat cultivars for the northern grain region of Australia such as Baxter, EGA Gregory, EGA Wylie and Sunvale, most

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cultivars are susceptible allowing the nematodes to multiply to high populations (DPIF 2009; Thompson *et al*. 1999, 2008). One bread wheat source of partial resistance is GS50a, which was selected from within the Australian wheat cv. Gatcher, which itself is susceptible and intolerant (Thompson *et al*. 1999). To find other sources of resistance to *P. thornei*, research was conducted on accessions from the West Asia and North Africa (WANA) region (Thompson *et al*. 2009) in the Watkins Collection of wheat landraces (Miller *et al*. 2001) and the McIntosh Collection of cultivars (described by Thompson *et al*. 2009). Thirteen bread wheat accessions that produced nematode numbers similar to the partially resistant GS50a were identified. These new sources of resistance offer possibilities for breeding wheat cultivars that have a high level of durable resistance to *P. thornei*. One challenge is choosing which among these partially resistant wheat accessions would produce the best genetic gains when used as resistant parents in a breeding program.

This paper describes research on some of the more resistant of the WANA wheat accessions identified by Thompson *et al*. (2009) that aimed to (*i*) determine whether the resistances to *P. thornei* are genetically different from each other, (*ii*) determine whether combining resistance genes from more than one source will provide greater levels of resistance, (*iii*) determine the most efficient breeding strategies for genetic gain in resistance to *P. thornei*, and (*iv*) introduce the most resistant gene combinations into an adapted bread wheat background for use in wheat breeding programs. To achieve these ends, a half-diallel of crosses was made between 9 of the resistant WANA wheat accessions and GS50a. In a half-diallel mating design each parent is crossed once with every other parent without reciprocal crosses (Falconer and Mackay 1996). Reciprocal crossing is required only if cytoplasmic inheritance might influence the trait of interest, which is considered to be rare in plant breeding (Falconer and Mackay 1996). Resistance to *P. thornei* of progeny from this half-diallel was investigated at the F_1 and F_2 generations and diallel ANOVA and other analyses conducted to determine the relative values of these sources of resistance as parents in crosses. From these data, combining abilities of the parents (Griffing 1956) were determined. General combining ability (GCA) is the average performance (in this instance for *P. thornei* resistance) of a parent in hybrid combinations, whereas specific combining ability (SCA) refers to crosses where hybrid performance is relatively better or worse than expected from the sum of the GCA of the two parents (Sprague and Tatum 1942; Christie and Shattuck 1992). In addition, crosses between the 'resistant' parents and the susceptible Australian wheat cv. Janz were investigated for resistance to *P. thornei* at the F_1, F_2 and F_∞ (doubled-haploid, DH) generations. The 10 parental sources of resistance to *P. thornei* were also tested for resistance to *P. neglectus* in order to find accessions with resistance to both nematode species.

Materials and methods

Wheat accessions

Seven of the most *P. thornei*-resistant bread wheat accessions from the study described by Thompson *et al*. (2009) were selected for this investigation, namely, 5 from the Watkins Collection [Iraq 43 (AUS 4926), Morocco 426 (AUS 13124), Persia 11 (AUS 5197), Persia 28 (AUS 5216) and Persia 62 (AUS 5221)], and 2 from the McIntosh Collection [El Neilain (ISR 455.3) from Sudan and C-70-3 (ISR 484.14) from Iran]. Two other WANA wheats were included that were not among the most resistant in the study of Thompson *et al*. (2009). These were Persia 92 (AUS 5258), which showed excellent tolerance to *P. thornei* in field tests conducted as described by Thompson *et al*. (1999), and Iraq 48 (AUS 4930), which had previously been found to be resistant to cereal cyst nematode (CCN, *Heterodera avenae*) (the late F. Green, pers. comm. 1995) and to *P. thornei* (Nicol 1996). Also included were GS50a (the partially resistant selection from Gatcher), and Janz a widely adapted Australian cultivar susceptible to *P. thornei*.

Half-diallel and progeny generations

A half-diallel mating design of pair-wise crosses between the 10 'resistant' accessions was made in the crossing plots at the Leslie Research Centre, Toowoomba, Australia (27.55°S, 151.95°E), in 1997. Out of the 45 crosses in the half-diallel, seed was not available for 2, namely C-70-3/GS50a and El Neilain/Iraq 48. In addition, crosses were made between Janz and the 10 'resistant' parents. The F_1 seed from the half-diallel of 'resistant' parents and the F_1 seed from the crosses of the 'resistant' parents with Janz were used in Expts 1 and 2, respectively, as described below. F_2 seed that was harvested from Expts 1 and 2 was used in Expts 3 and 4, respectively. DH lines from F_1 seed of crosses of selected 'resistant' accessions with Janz were produced by Dr N. Howes at the South Australian Research and Development Institute using procedures similar to that described by Thomas *et al*. (1997) with colchicine treatment for chromosome doubling (N. Howes, pers. comm. 1999). Plants from this DH seed were tested for resistance to *P. thornei* in Expt 5. *P. thornei*-'resistant' parents used in the half-diallel were tested for resistance to *P. neglectus* in Expt 6.

Experiment 1. Resistance to P. thornei *of F_1 hybrids from a half-diallel design of crosses of 10 'resistant' wheat accessions*

An experiment was designed to test the resistance to *P. thornei* of F_1 plants from all crosses except those involving Janz, i.e. 43 F_1 hybrids, as well as the 10 parental lines, using methods similar to those described by Thompson and Haak (1997) and Thompson *et al*. (2009). Nine other treatments included in the experiment as reference standards were an unplanted control, canaryseed (*Phalaris canariensis* cv. Morocco), the partially resistant durum wheat cv. Yallaroi, the susceptible bread wheat cvv. Cunningham, Janz, Gatcher and Batavia, and the partially resistant fixed lines QT9048 and QT8343 derived from previous crossing of GS50a with cvv. Janz and Cunningham.

Single plants were grown in pots (15 cm diameter × 15 cm high) containing 1 kg vertosolic soil of the Irving Series (Thompson and Beckmann 1959) previously pasteurised by aerated steam at 70°C for 30 min. The soil for each pot was fertilised with nutrients in solution to provide 200 mg NO_3-N, 25 mg P, 88 mg K, 36 mg S, 285 mg Ca and 5 mg Zn/kg soil and inoculated with 2500 *P. thornei*/kg soil, which had been raised as pure cultures on wheat. All treatments were replicated 6 times and the pots were laid out in a randomised complete block design in a glasshouse at the Leslie Research Centre, Toowoomba. The

plants were grown from June to October on benches with under-bench heating to maintain the soil temperature at 22°C. Soil moisture content was initially brought to pF 2 (0.56 g g^{-1} gravimetric) and readjusted as required during plant growth. At 16 weeks after sowing, the intact plant was removed from the pot and one vertical half of the soil and roots was excised and stored in a sealed plastic bag in a cold room at 3°C pending nematode enumeration. Fresh soil was added to the pot and the plant was grown on for seed harvest. The excised soil containing roots was manually broken into pieces <5 mm. Nematodes were extracted from 150-g subsamples by the Whitehead tray method (Whitehead and Hemming 1965) during 48 h at 22°C, and counted in a Hawksley slide under a compound microscope.

Nematode populations were expressed as number/kg oven-dry soil equivalent. These data were transformed by $\ln(x+c)$ (Proctor and Marks 1974) with the c-value optimised using a Chi-square test in Genstat (Payne *et al*. 2008) to minimise residuals (Berry 1987) in an ANOVA. Values for missing crosses were estimated by the method of Eckhardt (1952). DIALLEL analysis and simulation software (Burow and Coors 1994) was used to analyse the transformed data by Griffing's (1956) Method 4 (no parents or reciprocals) with Model 1 (fixed effects), to determine variances and effects of GCA and SCA of the resistant parents in terms of nematode numbers. The components of variance ratio (Baker 1978; Navabi *et al*. 2004) was calculated as:

$$2\sigma^2_{GCA}/(2\sigma^2_{GCA} + \sigma^2_{SCA}) \quad (1)$$

where σ^2_{GCA} = GCA mean square and σ^2_{SCA} = SCA mean square from the half-diallel ANOVA. Baker (1978) stated that the closer the resultant value is to unity the greater the predictability of hybrid performance based on GCA alone.

Experiment 2. Resistance to P. thornei *of F_1 hybrids from crosses between 10 'resistant' wheat accessions and the susceptible Australian wheat cv. Janz*

The 10 F_1 hybrids from Janz crossed with the respective 'resistant' parents as well as the parents themselves and reference standards (as for Expt 1) were tested for *P. thornei* resistance in 6 replications. Single plants were grown in 330 g (oven-dry equivalent) of pasteurised soil in 70-mm^2 pots (150 mm high) designed for bottom watering and inoculated with 3300 *P. thornei* per pot. Plants were grown with nutrients as for Expt 1. Soil temperature was maintained at 22°C by under-bench heating and water tension at 2 cm by capillary matting and a float valve. At 16 weeks after sowing, the soil (including roots) from the bottom one-third of each pot was excised and processed for nematode enumeration as described in Expt 1. Soil was replaced in the pots and the plants were grown on for seed collection. Nematodes were extracted and counted as described for Expt 1.

Experiment 3. Resistance to P. thornei *of F_2 populations from a half-diallel design of crosses of 7 'resistant' wheat accessions*

From the analysis of F_1 data, parents were ranked in order of GCA effects. Crosses involving the 6 parents with greatest GCA effects for resistance, namely, Iraq 43, Morocco 426, Persia 11, Persia 62, GS50a and C-70-3, as well as Iraq 48 (because of its previous use as a resistant parent in breeding programs (Nicol 1996; P. S. Brennan, pers. comm. 1997), were selected for an F_2 experiment. One-hundred F_2 seeds of each of the selected crosses (17 seeds from each of 5 replicate F_1 plants in Expt 1 and 15 from the 6th replicate) along with 6 replicates of parents and reference standards were tested for resistance to *P. thornei* using methods similar to those for Expt 2. Diallel analysis (Burow and Coors 1994) was conducted as described for Expt 1 using data for individual F_2 (first 87 plants in each cross; because of plant death, data were available for 87–97 plants in individual crosses) without blocking. A second diallel analysis was conducted using all plant data for each cross entered as 6 mean values based on the source of the F_2 seed from the 6 F_1 plants; these results were similar to those obtained from analysis based on the 87 individuals and will not be presented here.

Numbers of *P. thornei* produced in the roots of individual F_2 progeny of each cross were examined graphically and statistically [using $\ln(x+500)$ transformations] in relation to their parents to learn whether transgressive segregation towards greater resistance and/or greater susceptibility occurred within the F_2 population. Estimates of residual error variance for each cross were available from replicated reference standards; however, these were excluded from the estimates of genetic variance for each population. The variance-covariance matrix of the predicted (transformed) numbers of *P. thornei* for parents and F_2 progeny from a random effects analysis was used to assess transgressive segregation. An individual F_2 was deemed to be a resistant (or a susceptible) transgressive segregant if it had a transformed count with a probability of at least 0.95 of being lower (or higher) than the resistant (or susceptible) parent.

Experiment 4. Resistance to P. thornei *of F_2 from crosses between each 'resistant' wheat and the susceptible Australian wheat cv. Janz*

One-hundred and ten F_2 seeds from each of the 10 families from the 10 'resistant' wheat accessions crossed with Janz, along with 6 replicates of parents and reference standards, were tested for *P. thornei* resistance by methods as described for Expt 2.

Experiment 5. Resistance to P. thornei *of DH populations from crosses between 5 'resistant' wheat accessions and Janz*

The DH seed produced from F_1 plants of crosses between the susceptible wheat Janz and each of 5 of the 'resistant' wheats, namely, Iraq 43, Morocco 426, GS50a, Persia 11 and El Neilain [which had been selected for this purpose as the most resistant bread wheats in the first experiment on WANA wheats described by Thompson *et al.* (2010)], were assessed for resistance to *P. thornei.* From each population, 126 DH lines were tested in 6 replications along with parents and reference standards as listed in Expt 1. The pots were laid out in spatial designs on glasshouse benches and all other procedures were as described under Expt 2 above.

Initial ANOVA was conducted on data for number of *P. thornei* by treating DH lines in each population, parents and standards as fixed effects. Subsequently, transformed numbers of *P. thornei* for the DH lines were analysed as random effects in order to estimate variance components using ASReml (Gilmour *et al*. 2002). Variance components were used to estimate

narrow-sense heritability from the ANOVA of each DH population on a line-mean basis using the following formula (Fehr 1987):

$$h^2 = \sigma^2_g/(\sigma^2_g + \sigma^2_e/r) \quad (2)$$

$$\sigma^2_g = (\sigma^2_{dhl} - \sigma^2_e) \quad (3)$$

where h^2 = heritability estimate, σ^2_g = genetic variance, σ^2_{dhl} = variance of the DH lines, σ^2_e = error variance, and r = number of replicates.

Since DH are genetically fixed homozygotes at F_∞ there is no dominance effect and therefore h^2 is an estimate of narrow-sense heritability (additive effects).

The minimum number of genes controlling resistance to *P. thornei* in each DH population was calculated using Wright's (1968) method as modified by Cockerham (1983) for the level of inbreeding and as applied by Singh *et al*. (1995) to F_6 populations and by Herrera-Foessel *et al*. (2008) to F_5 populations. The modified formula applicable to DH is $n = (GR)^2/4\sigma^2_g$ in which n = minimum number of effective genes, GR = genotypic range, and σ^2_g = genetic variance of the DH lines (Herrera-Foessel *et al*. 2008; S. A. Herrera-Foessel, pers. comm. 2010). GR was determined by multiplying the phenotypic range of the DH mean values by the heritability (h^2).

Experiment 6. Resistance to P. neglectus *of* P. thornei*-'resistant' parents*

All of the parents used in the half-diallel for resistance to *P. thornei* were assessed for resistance to *P. neglectus.* In addition to the reference standards listed in Expt 1, the following accessions were included in the experiment: Persia 20 (AUS 5205) and Virest (AUS 11984) both considered to be resistant to *P. neglectus* (Das *et al*. 2004), Abacus a resistant triticale (Farsi *et al*. 1995), and various South Australian wheat cultivars with different reactions to *P. neglectus*, namely, partially resistant Krichauff, Excalibur and Worrakata, and susceptible Machete and Spear (Vanstone *et al*. 1998). The experiment was conducted as described for Expt 2 but inoculated with 3300 *P. neglectus*/pot of 330 g soil instead of with *P. thornei*.

Results

Experiments 1 and 3. Resistance to P. thornei *of F_1 hybrids and F_2 populations from a half-diallel of crosses of 'resistant' parents*

Diallel ANOVA for a number of *P. thornei* in F_1 hybrids (Expt 1) and F_2 populations (Expt 3) showed highly significant variation for both GCA and SCA (Table 1). Baker's (1978) ratio of components of variance was 0.93 and 0.95 for the F_1 and F_2 analyses, respectively, indicating the greater relative importance of GCA over SCA.

Values of GCA effects for parents based on both F_1 and F_2 analyses are given in Table 2, together with the nematode counts for the parents and reference standards. The number of *P. thornei* after growth of the parents and standards (Table 2) ranged from 280 530 and 285 290/kg soil for the susceptible Australian cv. Batavia down to 1390 and 770/kg soil for the resistant crop canaryseed in Expts 1 and 3, respectively. Among the parents, C-70-3 (3780/kg soil) and Iraq 43 (2940/kg soil) produced the lowest number of *P. thornei* in Expts 1 and 3, respectively, while Iraq 48 (64 140 and 47 890/kg soil) produced the greatest number of *P. thornei* in both experiments. The parents with the greatest GCA effects for resistance (largest negative values) were Iraq 43, Morocco 426 and Persia 11 (Table 2). The parents with the greatest GCA effects towards susceptibility (largest positive values) were Persia 92, Iraq 48, Persia 28 and El Neilain. The parents GS50a, C-70-3 and Persia 62 occupied a middle position in GCA effects.

Table 1. Diallel ANOVA for combining ability of resistance to *Pratylenchus thornei* in F_1 hybrids (Expt 1) and F_2 populations (Expt 2) from a half-diallel of crosses of 'resistant' parents

Analysis based on ln(*P. thornei*/kg soil + 2300) for F_1 hybrids and ln(*P. thornei*/kg soil + 500) for F_2 populations. *$P < 0.05$; ***$P < 0.001$; n.s., not significant

Source	F_1 hybrids		F_2 populations	
	d.f.	Mean squares	d.f.	Mean squares
Replicates	5	1.78 n.s.	–	–
Crosses	44	3.19***	20	26.22***
GCA[A]	9	10.06***	6	70.10***
SCA[B]	33	1.43*	14	7.42***
Error	220	0.36	1806	1.4

[A]GCA = general combining ability.
[B]SCA = specific combining ability.

In Fig. 1, the mean nematode counts (observed values) of the F_1 hybrids (Fig. 1*a*) and F_2 populations (Fig. 1*b*) are shown plotted against the expected values calculated from the GCA values of the respective parents and the grand mean. The difference between the observed and expected values (that is the vertical distance of the observed nematode count from the 1 : 1 diagonal) is the SCA of the particular cross together with the error associated with determining the nematode numbers. Figure 1 clearly shows the generally strong GCA effects on the nematode counts and names all crosses in which there was significant modification by SCA effects. These SCA effects were towards resistance in the F_1 hybrids Iraq 43/Iraq 48 and Persia 11/C-70-3 with nematode counts lower than expected from GCA effects alone (Fig. 1*a*), and towards susceptibility in Persia 92/El Neilain, Persia 92/C-70-3, Persia 11/Iraq 48, and Persia 28/Morocco 426 with nematode counts higher than expected from GCA alone (Fig. 1*a*). In the F_2 populations (Fig. 1*b*), significant SCA effects towards resistance were shown by GS50a/Iraq 48, Morocco 426/Iraq 48 and Persia 62/Persia 11 and towards susceptibility by Persia 62/Iraq 48, Persia 11/Iraq 48 and Morocco 426/Iraq 43. Out of the crosses that were tested as both F_1 and F_2 generations, only Persia 11/Iraq 48 showed consistently significant SCA effects (towards susceptibility).

There were highly significant relationships between the means of the 20 F_2 populations regressed against either the mid-parent value (Fig. 2*a*) or the sum of the GCA effects of the respective two parents based on diallel analysis of F_1 data (Fig. 2*b*). The slope of the regression equation of progeny means against mid-parent values provides an estimate of heritability h^2 (Falconer and Mackay 1996). Based on these F_2 populations, $h^2 = 0.68$ (Fig. 2*a*) for *P. thornei* resistance.

Transformed means of *P. thornei* numbers for F_1 hybrids and F_2 populations were compared with respective mid-parent values (data available as Accessory Publication on journal's website,

Table 2. Number of *Pratylenchus thornei*/kg soil after 16 weeks' growth of 'resistant' parents and reference standards with estimates of general combining ability (GCA) effects from a half-diallel of crosses at the F_1 (Expt 1) and F_2 (Expt 3) generations

Parents are ordered on GCA values from F_1 diallel analysis. Larger negative values of GCA effects indicate better combining ability for resistance. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Genotype	F_1 (Expt 1) *P. thornei*/kg soil		F_2 (Expt 3) *P. thornei*/kg soil		Expt 1 GCA (F_1)	Expt 3 GCA (F_2)
	ln(x + 2300)	Back-transformed	ln(x + 500)	Back-transformed		
			'Resistant' parents			
Iraq 43	9.13	6918	8.14	2943	–0.78***	–0.44***
Morocco 426	9.30	8649	8.72	5649	–0.55**	–0.45***
Persia 11	9.01	5885	9.08	8234	–0.24	–0.05
Persia 62	9.31	8717	10.70	43 989	–0.12	0.14
GS50a	9.30	8631	8.45	4166	–0.09	0.01
C-70-3	8.71	3775	9.08	8260	0.01	0.06
El Neilain	10.32	27 920	–	–	0.27	–
Persia 28	10.15	23 413	–	–	0.33*	–
Iraq 48	11.10	64 138	10.79	47 888	0.58**	0.74***
Persia 92	9.66	13 431	–	–	0.60**	–
			Reference standards			
Unplanted	7.92	451	7.19	823	–	–
Canaryseed	8.21	1385	7.14	765	–	–
QT9048	9.27	8317	8.66	5268	–	–
Yallaroi	9.57	12 047	9.22	9597	–	–
QT8343	9.67	13 506	8.50	4405	–	–
Janz	11.25	74 440	11.19	71 686	–	–
Gatcher	11.77	127 244	11.41	89 990	–	–
Cunningham	12.23	202 462	11.77	128 556	–	–
Batavia	12.55	280 528	12.56	285 286	–	–
F l.s.d. (P = 0.05)	0.65	–	0.95	–	–	–
CV (%)	5.8	–	8.7	–	–	–

supplementary table 1). In the F_1 generation, only the mean of Iraq43/Iraq 48, (which had the greatest SCA for resistance) was significantly less ($P < 0.001$) than the mid-parent value, whereas 9 other hybrids were significantly greater ($P < 0.001$ for Persia 92/Iraq 48, Persia 92/El Neilain, Persia 92/C-70-3; $P < 0.01$ for Persia 11/Iraq 48, Persia 28/Morocco 426; and $P < 0.05$ for Persia 62/C-70-3, Persia 28/C-70-3, Persia 92/GS50a, C-770-3/Iraq 48) than respective mid-parent values. Overall these results indicate very little heterosis for resistance to *P. thornei* among these 'resistant' parents. In the F_2 generation, the means of 2 crosses, Persia 62/Morocco 426 and Persia 62/Persia 11 were significantly less than the mid-parent values. Of these 2, Persia 63/Persia 11 had significant SCA effects for resistance in the F_2 diallel analysis.

All 20 F_2 populations from the half-diallel of crosses between the 7 'resistant' parents showed continuous distributions of nematode numbers. Examples of two extremes of populations are given in Fig. 3. The F_2 population of the hybrid Iraq 43/Morocco 426 (Fig. 3*a*) had a much lower mean number of nematodes than the hybrid Persia 62/Iraq 48 (Fig. 3*b*), although in both populations there were individuals with relatively lower and relatively higher nematode numbers.

Numbers of transgressive segregants for resistance and susceptibility (based on transformed data) in each of the crosses are given in Table 3. The highest number of transgressive segregants for resistance (Table 3) was produced by Persia 62/Iraq 48, the 2 least resistant parents. Persia 62 also produced transgressive segregants for resistance in other crosses with C-70-3, GS50a, Persia 11 and Morocco 426. Of the 2 parents with significant GCA effects for resistance, Morocco 426 produced moderately large numbers of transgressive segregants for resistance in several crosses (with Persia 62, GS50a and Iraq 48) whereas Iraq 43 did not. Most transgressive segregants for susceptibility were produced in the crosses Morocco 426/GS50a and Iraq 43/C-70-3. Transgressive segregation for resistance or susceptibility is measured against respective parental values within a cross whereas greatest genetic variation for resistance/susceptibility in these populations is among crosses. Transgressive segregants for resistance in one cross can be more susceptible than progeny in another cross that are not considered to be transgressive segregants for resistance.

Experiments 2 and 4. Resistance to P. thornei *of F_1 hybrids and F_2 populations from crosses between 'resistant' wheat accessions and the susceptible Australian wheat cv. Janz*

Number of *P. thornei* after growth of the wheat reference standards and parents ranged from 349 340 nematodes/kg soil for the susceptible Australian cv. Gatcher down to 28 010 for the resistant parent Morocco 426 in Expt 2 for F_1, and from 48 040 for Janz down to 4710 for Morocco 426 in Expt 4 for F_2 (full results available as Accessory Publication, supplementary table 2). The

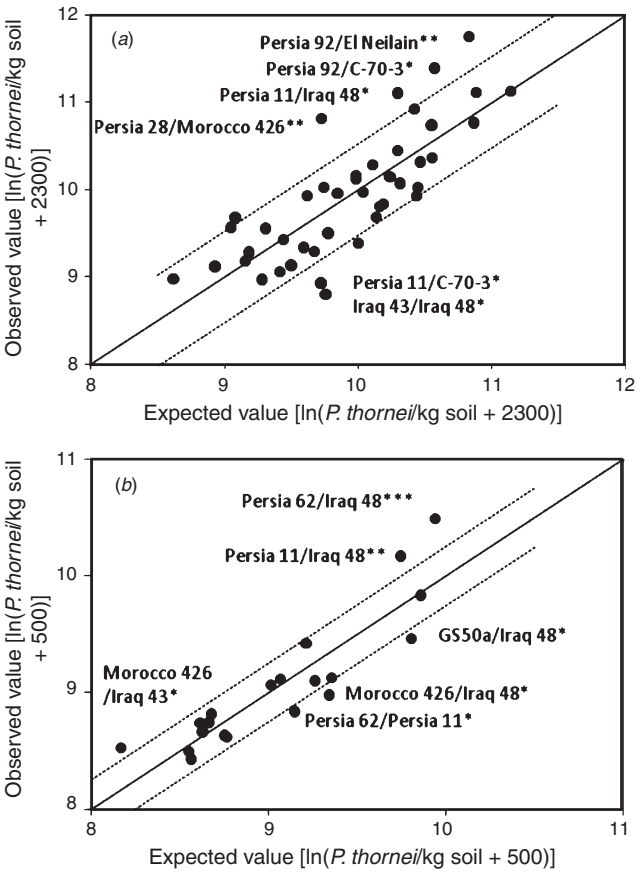

Fig. 1. Observed *versus* expected *Pratylenchus thornei* [ln(x+c) transformed means] for (*a*) 'resistant' × 'resistant' F_1 hybrids and (*b*) their F_2 populations from a half-diallel of crosses. Expected value is the grand mean plus the GCA of the respective 2 parents. The dotted lines show deviations of ±2 standard errors for observed cross means from the diagonal. The vertical distance of any point from the diagonal is the SCA together with the sampling error of the nematode numbers for the cross. SCA effect significantly different from zero at *$P<0.05$, **$P<0.01$ and ***$P<0.001$, respectively, from half-diallel ANOVA.

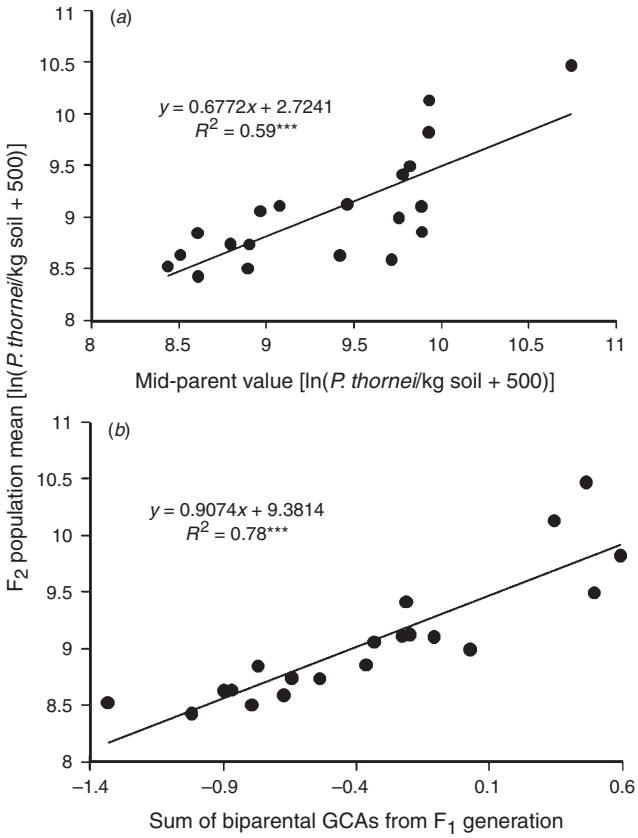

Fig. 2. Mean numbers of *Pratylenchus thornei* for 20 F_2 populations (Expt 3) regressed against (*a*) mid-parent values (Expt 3) and (*b*) sum of biparental GCA effects based on the F_1 generation (Expt 1).

F_1 mean was significantly lower than the mid-parent value for Iraq 48/Janz ($P<0.001$), El Neilain/Janz ($P<0.05$) and Iraq 43/Janz ($P<0.05$) and significantly higher for Persia 92/Janz ($P<0.01$). All plants of the F_1 hybrid Iraq 48/Janz grew as 'grass clumps' with phenological development arrested at growth stage 11 (Zadoks *et al*. 1974). It is probable that this genetic condition also affected root growth resulting in abnormally low nematode reproduction in Iraq 48/Janz F_1. Parameters to the F_2 populations are summarised in Table 4. The F_2 mean was significantly lower ($P<0.05$) than the mid-parent value for Morocco 426/Janz and Persia 62/Janz. The mean back-transformed values ranged from 5730 and 7295 *P. thornei*/kg soil for Morocco 426/Janz and Iraq 43/Janz, respectively, up to 51 354/kg soil for Persia 92/Janz. Morocco 426/Janz and Iraq 43/Janz also had lower median values than the mean indicating some skewing towards resistance.

Regression analyses were conducted to investigate whether GCA effects of the 'resistant' parents obtained from F_1 and F_2 diallel analyses were predictive of the mean number of *P. thornei* produced in crosses of these 'resistant' parents with the susceptible wheat cv. Janz at the F_1 and F_2 generations (Fig. 4). There were highly significant linear regression relationships (Fig. 4) between (*i*) F_1 means of crosses of 'resistant' parents with Janz against GCA of the 'resistant' parent from F_1 diallel analysis ($R^2=0.86$, d.f. = 7, $P<0.001$), (*ii*) F_2 means of crosses of 'resistant' parents with Janz against GCA of the 'resistant' parent from F_1 diallel analysis ($R^2=0.83$, d.f. = 8, $P<0.001$), and (*iii*) F_2 means of crosses with Janz against GCA of the resistant parent from F_2 diallel analysis ($R^2=0.90$, d.f. = 5, $P<0.001$).

The F_2 populations of the 'resistant' parent × Janz crosses showed relatively continuous distribution patterns (see Accessory Publication, supplementary fig. 1). Frequency histograms of transformed nematode counts (Accessory Publication, supplementary fig. 2) showed relatively normal distributions with skewing towards resistance in the case of Morocco 426/Janz and Iraq 43/Janz, crosses of the 2 wheats with greatest GCA effects for resistance and Janz.

Experiment 5. Resistance to P. thornei *of DH populations from crosses between 'resistant' parents and Janz*

Frequency distribution histograms of the DH populations (see Accessory Publication, supplementary fig. 3) showed relatively continuous distributions with skewing towards resistance in the case of Morocco 426/Janz and Iraq 43/Janz and a somewhat

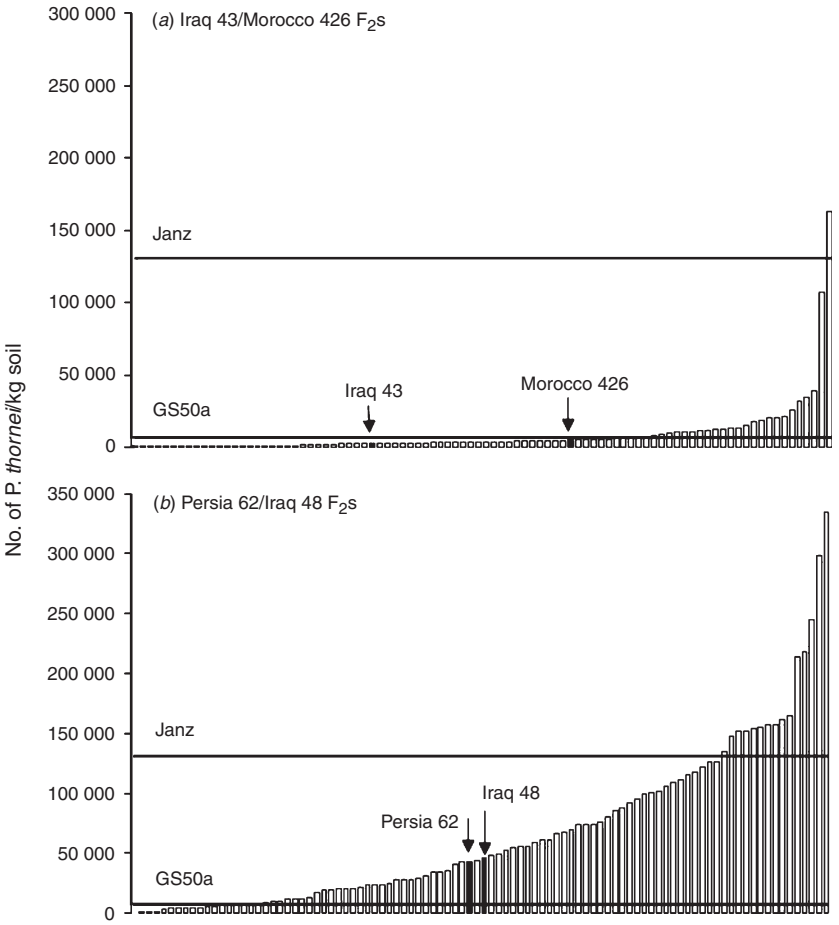

Fig. 3. Number of *Pratylenchus thornei*/kg soil after growth of F_2 populations from crosses of (*a*) Iraq 43 × Morocco 426 (parents with the largest GCA effects for resistance in F_1 hybrids) and (*b*) Persia 62 × Iraq 48 (parents with the largest GCA effects for susceptibility in F_1 hybrids), compared with the susceptible cv. Janz and the partially resistant GS50a shown as horizontal lines.

Table 3. Number of transgressive segregants for resistance (above the diagonal) and for susceptibility (below the diagonal) to *Pratylenchus thornei* in F_2 populations from crosses of 'resistant' × 'resistant' wheat accessions (Expt 3)

Transgressive segregants are individuals with 95% probability of falling below or exceeding the means of the more resistant or more susceptible parent based on ln(*P. thornei*/kg soil + 500) transformations

Parent	Iraq 43	Morocco 426	Persia 11	Persia 62	GS50a	C-70-3	Iraq 48
Iraq 43		0	0	0	0	0	0
Morocco 426	2		3	7	11	2	10
Persia 11	0	0		6	2	7	1
Persia 62	0	0	0		5	7	18
GS50a	0	8	3	1		–	3
C-70-3	7	0	1	0	–		1
Iraq 48	0	0	1	2	0	0	

bimodal distribution in the case of El Neilain/Janz. The mean number of *P. thornei* for the DH populations was lower for Morocco 426/Janz, Iraq 43/Janz and GS50a/Janz than for Persia 11/Janz and El Neilain/Janz (Table 5). There were no significant differences between means of the DH populations and mid-parent values (Table 5). The heritability (narrow-sense) on a line mean basis of *P. thornei* resistance ranged from 0.82 for the GS50a/Janz population to 0.91–0.92 for the 4 'resistant' parent/Janz populations (Table 5). Estimates of the minimum number of genes controlling resistance to *P. thornei* ranged from 1.7 in GS50a/Janz to 5.5 in Morocco 426/Janz (Table 5).

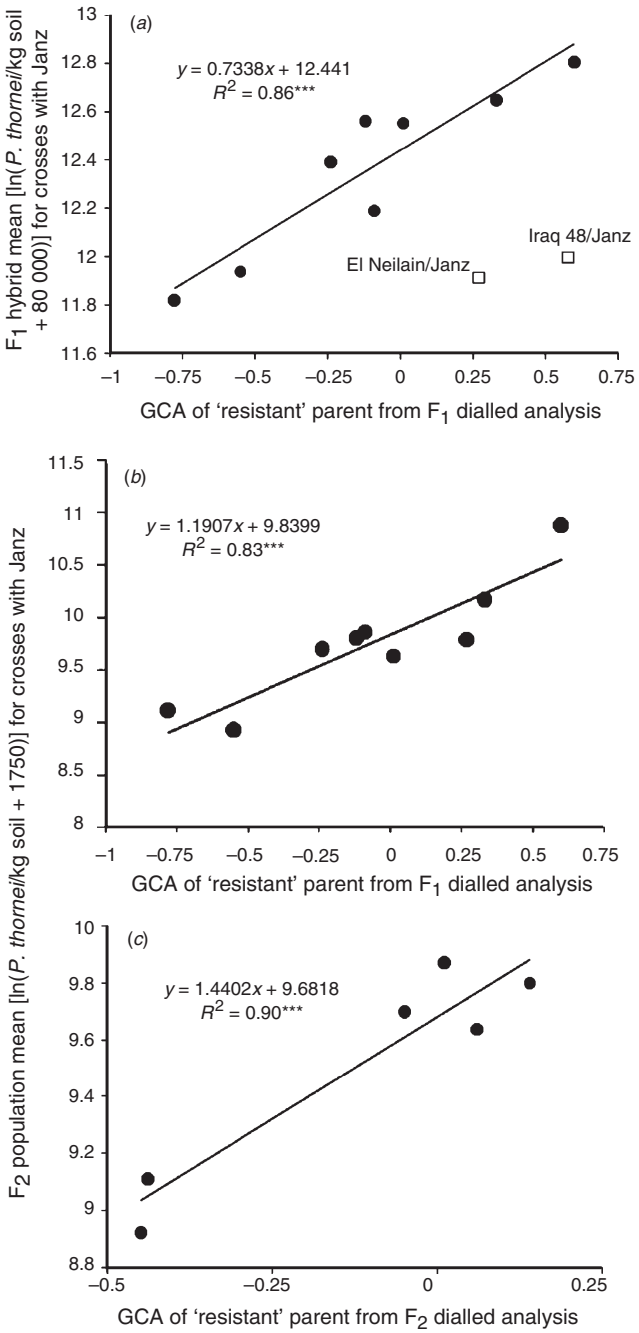

Fig. 4. Mean number of *Pratylenchus thornei*/kg soil [ln(x+c) transformations] after 16 weeks' growth in the glasshouse of crosses of 'resistant' parents × Janz (*a*) F_1 hybrid means (Expt 2) and (*b*) F_2 population means (Expt 4) regressed against GCA values from F_1 half-diallel analysis (Expt 1) and (*c*) F_2 population means (Expt 4) regressed against GCA values from F_2 half-diallel analysis (Expt 3). Two F_1 hybrids (Iraq 48/Janz, which grew as 'grass clumps', and El Neilain/Janz) were apparent outliers and were not included in the regression analysis in Fig. 4*a*. *** = coefficient of determination statistically significant at $P < 0.001$.

The mean number of *P. thornei* for the DH populations was significantly related to the GCA value of the resistant parents determined by half-diallel analysis of F_1 crosses in Expt 1 (Fig. 5).

Experiment 6. Resistance to P. neglectus *of WANA wheats resistant to* P. thornei

The *P. thornei*-resistant WANA wheats and GS50a produced high populations of *P. neglectus* comparable to Australian cultivars used as reference standards (Table 6). Persia 28 produced the lowest number of *P. neglectus* among this group of *P. thornei*-resistant WANA wheat accessions, but this was significantly higher than the resistance standards for *P. neglectus*, namely Persia 20 and Virest.

Discussion

The results of this investigation show that GCA is much more important than SCA in the inheritance of resistance to *P. thornei* among the best sources of resistance that had previously been identified in 2 collections of wheat from WANA countries (Thompson *et al*. 2009). Christie and Shattuck (1992) stated that a relatively large GCA/SCA variance ratio indicates the importance of additive gene effects, and a low ratio implies the presence of dominant and/or epistatic gene effects (Griffing 1956; Bhullar *et al*. 1979). Where SCA is small relative to GCA, performance of single-cross progeny can be predicted on the basis of the GCA of the parents. For inbred parents, the closer Baker's ratio of components of variance is to unity, the greater the predictability based on GCA (Baker 1978). Thus, the GCA effects for *P. thornei* resistance established at the F_1 generation of the half-diallel of 'resistant' parents were quite predictive of the average performance of their crosses at the F_2 generation, and of crosses of these 'resistant' parents with Janz at the F_1, F_2 and F_∞ (DH) generations. Comparison of mean values of hybrids with their mid-parent values provided little evidence that heterosis was important in reducing numbers of *P. thornei* and consequently in an inbreeding crop like wheat the resistance identified in early generations will be retained in successive generations. The presence of transgressive segregants for resistance in the F_2 progeny indicated that different resistance genes from the 2 parents are segregating in many of the crosses and contributing to the level of resistance obtained. In particular, Morocco 426 resulted in transgressive segregants for resistance in most crosses whereas Iraq 48 did not. There were 2 transgressive segregants for susceptibility in the cross Morocco 426/Iraq 43 indicating that some of the resistance genes in the 2 accession with the highest GCA values for resistance are different. Thus, it is likely that in several instances by using more than one source of resistance in polycrosses, progeny that are more resistant than the parents might be obtained. The lack of transgressive segregants for susceptibility in many of the crosses indicates that their parents are likely to have at least 1 resistance gene in common.

Analysis of DH populations indicated that a minimum of from 2 to 6 effective resistance genes were involved in different crosses of 5 'resistant' parents with Janz, which is consistent with other research showing the polygenic nature of resistance to *P. thornei* in synthetic hexaploid wheat (Zwart *et al*. 2004, 2005; Thompson 2008). The parents Morocco 426 and Iraq 43 that had the largest GCA effects for resistance in both F_1 and F_2

Table 4. Parameters of F_2 populations from 9 crosses of 'resistant' parents × Janz for ln(*Pratylenchus thornei*/kg soil + 1750)

Parameter of F_2 population	'Resistant' parent in cross with Janz								
	Morocco 426	Iraq 43	C-70-3	Persia 11	Persia 62	GS50a	El Neilain	Persia 28	Persia 92
Number	103	107	108	108	107	107	107	108	109
Minimum	7.47	7.56	7.66	7.70	7.59	7.64	7.84	7.47	8.60
Maximum	11.92	12.00	12.05	11.97	12.73	12.14	12.43	12.45	13.5
Median	8.73	8.80	9.65	9.65	9.82	9.98	9.76	10.40	10.88
Mean	8.92*	9.11	9.64	9.70	9.80*	9.87	9.80	10.17	10.88
Mean (BT)[A]	5730	7295	13 617	14 568	16 284	17 591	16 284	24 358	51 354
MPV[B]	9.79	9.81	9.91	10.16	10.71	9.83	10.16	10.39	10.39
Variance	0.90	1.14	1.31	0.82	1.04	0.98	1.24	1.41	1.02

[A]BT = back-transformed mean from ln(*P. thornei*/kg soil + 1750).
[B]MPV = mid-parent value; * = mean significantly different from MPV at $P < 0.05$.

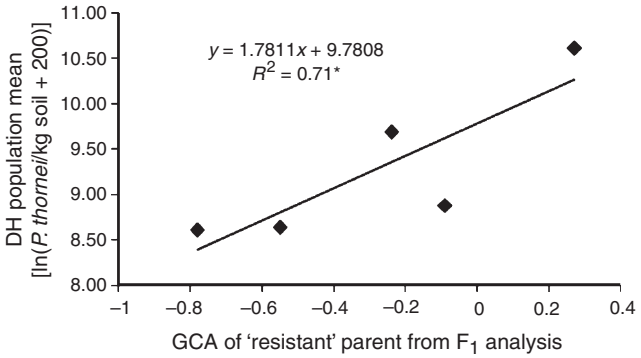

Fig. 5. Number of *Pratylenchus thornei*/kg soil after 16 weeks' growth of doubled-haploid populations (126 individuals) from crosses between 5 'resistant' parents and the susceptible Australian cv. Janz (Expt 5), regressed against GCA values of the 'resistant parents' determined from half-diallel analysis of F_1 hybrids (Expt 1). * = coefficient of determination statistically significant at $P < 0.05$.

diallel analyses consistently produced the most resistant progeny, both in crosses with other 'resistant' parents and in crosses with Janz. Morocco 426 and Iraq 43 crosses with Janz had respectively a minimum of 6 and 4 genes segregating for resistance. Morocco 426 and Iraq 43 would be the best parents to use in wheat breeding programs and some of their resistant DH derivatives identified in this study offer a fixed source of resistance in a background that is already half of the widely adapted Australian cv. Janz. However, none of these sources of resistance to *P. thornei* are resistant to *P. neglectus* and additional crossing with a source of resistance to *P. neglectus* would be necessary if dual resistance was required. In this regard synthetic hexaploid wheat accessions with dual resistance (Thompson 2008) offer initial advantages in a crossing program but may result in more linkage drag than landraces.

The polygenic, quantitative nature of resistance to *P. thornei* in wheat and lack of races of the nematode species, contrasts with resistance to CCN where single major genes for resistance have been used in wheat breeding programs and pathotypes of the nematode species exist (Smiley and Nicol 2009). Sources of resistance to *P. thornei* such as Morocco 426 and Iraq 43 already have resistance genes combined (pyramided) and the task will be to retain these when crossing with susceptible Australian cultivars and selecting progeny for resistance. This study has found relatively high heritabilities for *P. thornei* resistance with the genetic material and the screening methods used here. Because of the additive mode of inheritance, heterozygous plants show an intermediate level of resistance between homozygous resistant and homozygous susceptible plants. Therefore, BC_1 plants can be selected by the quantitative test for nematode resistance as used

Table 5. Parameters of doubled-haploid (DH) populations from 5 crosses of 'resistant' parents × Janz for ln(*Pratylenchus thornei*/kg soil + c[A])

Parameter	Resistant parent of DH with Janz				
	Morocco 426	Iraq 43	GS50a	Persia 11	El Neilain
Mean of DH	8.64 (5431)	8.61 (5292)	8.88 (6708)	9.71 (16 216)	10.62 (40 364)
Mid-parent value[B]	8.56	8.72	8.98	9.89	10.35
l.s.d. (P = 0.05)	1.01	0.94	1.04	0.77	1.13
Minimum	6.70	7.09	7.17	7.98	8.72
Maximum	12.02	11.37	10.66	12.07	12.35
Range (Ra)	5.32	4.28	3.48	4.09	3.63
Genetic variance[C] (σ^2_g)	1.515	1.130	0.645	0.821	0.914
Error variance (σ^2_e)	0.802	0.685	0.848	0.463	0.572
Heritability[D] (h^2)	0.92	0.91	0.82	0.91	0.91
Minimum no. of effective genes[E] (n)	5.5	3.4	1.7	3.2	2.4

[A]c = 200 for first 3 crosses and 500 for last 2; back-transformed means (*P. thornei*/kg soil) in parentheses.
[B]No significant difference between mid-parent value and mean of DH populations.
[C]Genetic variance (σ^2_g) = ($\sigma^2_{dhl} - \sigma^2_e$)/$r$ where σ^2_{dhl} = phenotypic variance of the DH lines, σ^2_e = error variance and r = no. of replicates.
[D]Heritability (h^2) = $\sigma^2_g/(\sigma^2_g - \sigma^2_e/r)$ on a line mean basis for fixed lines in an experimental design (Fehr 1987).
[E]Minimum number of effective genes (n) = Ra* $h^2/4*\sigma^2_g$ (Herrera-Foessel *et al.* 2008; S. A. Herrera-Foessel, pers. comm. 2010).

Table 6. Number of *Pratylenchus neglectus*/kg soil after 16 weeks' growth in the glasshouse of *P. thornei*-'resistant' WANA wheats compared with reference standards and other Australian wheat cultivars

Genotype	*P. neglectus*/kg soil	
	ln(x + 1150)	Back-transformed
WANA wheats and GS50a		
Persia 28	11.58	106 093
Persia 92	12.12	182 741
C-70-3	12.72	333 372
Iraq 43	12.75	343 562
Persia 11	12.80	362 551
Persia 62	12.95	417 984
Iraq 48	13.24	561 199
El Neilain	13.32	608 275
GS50a	13.40	662 047
Morocco 426	13.40	659 396
Reference standards and other Australian cultivars		
Unplanted	8.25	2684
Persia 20 (W)	9.95	19 883
Virest (W)	10.42	32 463
Abacus (T)	10.85	50 617
Spear (SW)	11.91	147 509
Suneca (NW)	11.95	154 386
Yallaroi (ND)	11.96	155 020
Canaryseed	11.97	156 440
Gatcher (NW)	12.49	263 800
Krichauff (SW)	12.59	292 309
Cunningham (NW)	12.66	313 765
Excalibur (SW)	12.67	316 955
QT9048 (NW)	12.80	361 979
Janz (NW)	12.93	410 117
Machete (SW)	12.94	417 037
Worrakatta (SW)	12.96	422 897
Batavia (NW)	13.00	441 720
QT8343 (NW)	13.48	714 977
F l.s.d. (P = 0.05)	0.84	–
CV (%)	7.3	–

W = wheat, D = durum, T = triticale, NW = Australian wheat cultivar from northern region, SW = Australian wheat cultivar from southern region.

here and this facilitates backcrossing resistance into adapted parents (J. P. Thompson and J. G. Sheedy, unpubl. data). Molecular markers may be useful in this regard with further development and validation. Significant quantitative trait loci (QTL) for resistance to *P. thornei* coming from Moroccco 426 were found on chromosomes 2B and 3B in the cross Morococo 426/Janz, and coming from Iraq 43 on chromosomes 2B, 3B and 6D in the cross Iraq 43/Janz by composite interval mapping (Schmidt *et al*. 2005). Composite interval mapping also revealed a susceptibility locus coming from Janz on chromosome 1B in the cross Iraq 43/Janz (Schmidt *et al*. 2005). While QTL for resistance to *P. thornei* had previously been reported on group 6 chromosomes (6B and 6D) in GS50a (Vicars *et al*. 1999) and on chromosomes 2BS, 6DS and 6DL in synthetic hexaploid wheat accessions (Zwart *et al*. 2005, 2006, 2009), 3B was a novel locus for resistance found in Morocco 426 and Iraq 43.

While several QTL for resistance to *P. thornei* have been discovered, in total they explain only a fraction of the variation for resistance in the populations studied and fewer QTL have been detected than the number of effective genes for resistance calculated in this study (Morocco 426/Janz, 2 QTL, minimum 6 genes), (Iraq 43/Janz, 4 QTL, minimum 4 genes), (GS50a/Janz, 2 QTL, minimum 2 genes). To obtain a reliable system for marker-assisted selection for resistance to *P. thornei*, further research is required to find more loci, develop more closely associated markers and validate them in breeding populations.

Hill (2010) recently indicated that in selection for quantitative genetic variation, methods based on summary statistics and predictions will continue to be more useful than selection at the individual gene level for some time yet. Similarly, Keane (2010) advocated selection for 'resistance' rather than for 'resistance genes' giving the example of successful selection for resistance to vascular-streak dieback (caused by the basidiomycete *Oncobasidium theobromae*) among a genetically diverse population of cocoa clones in New Guinea. Results from the International Maize and Wheat Improvement Centre, Mexico (CIMMYT) in using polygenically inherited resistance to leaf rust (Singh *et al*. 2004) provide an analogous model for utilising polygenic resistance to *P. thornei.* Singh *et al*. (2004) reported that deploying wheat cultivars with durable resistance to leaf rust based on additively inherited minor genes is necessary for long-term success. Their studies showed that at least 10–12 slow-rusting genes were involved in adult plant resistance of CIMMYT wheat germplasm and the combination of 2–3 or 4–5 of these minor genes in a single cultivar provided moderate and high levels of resistance, respectively. They also indicated their success has depended on a relevant phenotypic screen for resistance and the recombination of enough of these genes in single parental lines.

This study confirms the polygenic nature of resistance to *P. thornei* and shows the potential value of these WANA sources of resistance in contributing a diversity of resistance genes to Australian bread wheat cultivars. Such wheat cultivars with enhanced resistance would also be of value in other countries where *P. thornei* causes yield loss. The accessions identified with the best GCA effects for resistance can be used effectively to breed resistance into adapted Australian cultivars using current phenotypic screening methods.

Acknowledgements

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