Euphytica (2012) 186:377–391
DOI 10.1007/s10681-011-0617-5

Diploid and tetraploid progenitors of wheat are valuable sources of resistance to the root lesion nematode *Pratylenchus thornei*

J. G. Sheedy · J. P. Thompson · A. Kelly

Received: 23 October 2011 / Accepted: 29 December 2011 / Published online: 9 February 2012

Abstract The root lesion nematode *Pratylenchus thornei* is widely distributed in Australian wheat (*Triticum aestivum*) producing regions and can reduce yield by more than 50%, costing the industry AU$50 M/year. Genetic resistance is the most effective form of management but no commercial cultivars are resistant (R) and the best parental lines are only moderately R. The wild relatives of wheat have evolved in *P. thornei*-infested soil for millennia and may have superior levels of resistance that can be transferred to commercial wheats. To evaluate this hypothesis, a collection of 251 accessions of wheat and related species was tested for resistance to *P. thornei* under controlled conditions in glasshouse pot experiments over two consecutive years. Diploid accessions were more R than tetraploid accessions which proved more R than hexaploid accessions. Of the diploid accessions, 11 (52%) *Aegilops speltoides* (**S**-[**B**]-genome), 10 (43%) *Triticum monococcum* ($\mathbf{A}^{\mathbf{m}}$-genome) and 5 (24%) *Triticum urartu* ($\mathbf{A}^{\mathbf{u}}$-genome) accessions were R. One tetraploid accession (*Triticum dicoccoides*) was R. This establishes for the first time that *P. thornei* resistance is located on the **A**-genome and confirms resistance on the **B**-genome. Since previous research has shown that the moderate levels of *P. thornei* resistance in hexaploid wheat are dose-dependent, additive and located on the **B** and **D**-genomes, it would seem efficient to target **A**-genome resistance for introduction to hexaploid lines through direct crossing, using durum wheat as a bridging species and/or through the development of amphiploids. This would allow resistances from each genome to be combined to generate a higher level of resistance than is currently available in hexaploid wheat.

Keywords *Aegilops speltoides* · *Triticum dicoccoides* · *Triticum monococcum* · *Triticum urartu* · *Pratylenchus thornei* · Root-lesion nematode · Wheat

Electronic supplementary material The online version of this article (doi:10.1007/s10681-011-0617-5) contains supplementary material, which is available to authorized users.

J. G. Sheedy (✉) · J. P. Thompson · A. Kelly
Department of Employment, Economic Development and Innovation, Agri-Science Queensland, Leslie Research Centre, PO Box 2282, Toowoomba, QLD 4350, Australia
e-mail: jason.sheedy@deedi.qld.gov.au

Introduction

Wheat (*Triticum aestivum*) is Australia's most important crop, covering an area of nearly 13 M ha, and producing on average 20–25 M t annually (Pink 2008) with a value of AU$4.7 billion (Murray and Brennan 2009). The root-lesion nematode *Pratylenchus thornei* is a migratory endoparasite that feeds and reproduces in the cortex of wheat roots and is found in all major Australian wheat-growing regions (Thompson et al. 2008; Hollaway et al. 2008; Vanstone et al. 2008). *P. thornei* can reduce yield by as much as 65% in

intolerant wheat cultivars (Thompson et al. 1999) and has been estimated to cost Australian wheat growers AU$50 M (wheat priced at AU$239/t) annually (Murray and Brennan 2009). Most of these losses occur in the northern grains region, where *P. thornei* is the dominant plant-parasitic nematode, being present in 67% of fields (Thompson et al. 2010).

A resistant (R) plant is one in which nematodes reproduce poorly and a tolerant plant is one that shows little injury, even under attack by large populations of nematodes (Rhode 1972). Incorporating partial resistance to *P. thornei* into wheat cultivars can increase yields by up to 17% compared to tolerant commercial cultivars (Thompson et al. 2001). Accordingly, genetic resistance is preferred over cultural, biological and chemical control methods. When resistance is coupled with tolerance, the crop will yield well while reducing nematode densities in the soil to non-damaging levels for subsequent crops, thereby allowing shorter and more flexible rotations (Roberts 2002). 'Putting the technology into the seed' through genetic resistance and tolerance requires no additional management costs to growers. Despite the development of partially R advanced breeding lines that have increased yield on a nematode infested site (Thompson et al. 1999, 2001), there remains a need to identify higher levels of resistance from genetically compatible species to facilitate the development of R parent lines and ultimately commercial cultivars.

Wheat is an allohexaploid comprising three genetically related genomes (**A**, **B** and **D**) that originated as a hybrid of emmer wheat (*Triticum turgidum* ssp. dicoccon, $\mathbf{BBA^uA^u}$) and *Aegilops tauschii* (**DD**) (Mukai et al. 1993). Emmer wheat is a hybrid of the diploid grasses *Aegilops speltoides* (**SS**, putative progenitor of the **B**-genome) and *Triticum urartu* ($\mathbf{A^uA^u}$) (Valkoun 2001). One of the richest sources of new genes for disease resistance for wheat improvement has been the progenitor and related species that have genomes homeologous to those of wheat, including the diploid species *A. tauschii*, *Triticum monococcum* ($\mathbf{A^mA^m}$), *T. urartu* and *A. speltoides* and the tetraploid species *Triticum tugidum* ($\mathbf{BBA^uA^u}$) and *Triticum timopheevii* ($\mathbf{GGA^uA^u}$) (Cox 1991).

Pratylenchus thornei is endemic to the region of the Middle East (Di Vito et al. 1994; Greco et al. 1988; Orion et al. 1979; Pourjam et al. 1999) where modern wheat and its progenitors have evolved (Feldman and Sears 1981). Much of the diversity among plant species is believed to reflect natural selection imposed by biotic stress, causing the evolution of a new resistance character that reduces pathogen attack (Rausher 2001). Therefore, it is conceivable that, through co-evolution, resistance to *P. thornei* might have developed in some of these species. For example, 39 of 244 accessions of *A. tauschii* originating from Iran and Azerbaijan were R to *P. thornei* (Thompson and Haak 1997) including three accessions that had previously been found to be highly R to cereal cyst nematode (CCN; *Heterodera avenae*) (Eastwood et al. 1991).

Until now, the resistance to *P. thornei* of diploid and tetraploid relatives of wheat carrying the **A, B** and related genomes has not been investigated. This paper establishes that *P. thornei* resistance is located on the **A**-genome, confirms resistance on the **B**-genome and identifies many accessions that could be valuable in developing wheat cultivars with resistance to *P. thornei*.

Materials and methods

Germplasm

Two glasshouse experiments were conducted to determine the resistance to *P. thornei* of 241 unique accessions of principally wild relatives of wheat compared to 10 reference treatments. The following species of wild relatives and number of accessions of each in this study were: 21 *A. speltoides*, 21 *T. urartu*, 23 *T. monococcum*, 2 *A. peregrina* ($\mathbf{S^pS^pU^pU^p}$; syn *A. variabilis*), 25 *T. timopheevii* ssp. *armeniacum*, 30 *T. carthlicum* (=*T. turgidium* ssp. *carthlicum*), 25 *T. dicoccoides* (=*T. turgidium* ssp. *dicoccoides*) and 1 *T. turanicum* (=*T.* turgidium ssp. *turanicum*, $\mathbf{BBA^uA^u}$). Up to 100 hexaploid wheats including 15 hard red winter wheat cultivars with disease resistance introgressed from *A. tauschii* at Kansas State University (KSU) (http://www.k-state.edu/wgrc/Germplasm/grmplsm.html), four lines derived from the French wheat cv. Lutin and an accession of *A. peregrina* (Rivoal et al. 2001) carrying two CCN-resistance genes designated *CreX* and *CreY* (Barloy et al. 2007), 18 selections from the Iraqi landrace AUS4930 (syn. Iraq 48) putatively R to CCN pathotype Ha13 (syn. *Heterodera australis*, Subbotin et al. 2002) and 43 doubled haploid lines derived from the moderately R bread wheat GS50a were also examined

in each experiment. The reference treatments comprised four susceptible Australian wheat cultivars (Batavia, Cunningham, Gatcher and Janz), three partially R wheat accessions (GS50a, QT8343 and QT9048), one partially R durum cultivar (Yallaroi), one partially R canarygrass cultivar (*Phalaris canariensis* cv. Moroccan) and one inoculated unplanted treatment to simulate fallow.

Glasshouse procedures

In both experiments, entries were replicated three times in a randomised block design with resistance determined by counting the final number of *P. thornei* in the roots and soil of each entry after 16 weeks of growth. Soil temperature was maintained at 22°C, the optimum temperature for *P. thornei* reproduction (Thompson et al. 1999), by under-bench heating. Air temperature was maintained between 20 and 25°C by the use of shade cloth (as required) and evaporative coolers. Plants were sprayed as required with 1 ml/l of Milcurb® (125 g/l dimethirimol) to control powdery mildew and with 20 ml/l of Yates Pyrethrum Insecticide® (16 g/l piperonyl butoxide, 4 g/l pyrethrins) or 1.5 g/l of Pirimor WG Aphicide® (500 g/kg pirimicarb) to control aphids.

Experiment 1 followed the procedure described by Thompson and Haak (1997). A polythene bag (100 μm thickness) was filled with 1 kg (oven-dry equivalent) of vertosolic soil of the Irving clay soil association (Thompson and Beckman 1959) pasteurised using aerated-steam at 70°C for 45 min (Thompson 1990). Pre-weighed soil and roots from open pot cultures supplying 2,500 *P. thornei*/kg was added to each bag of soil and mixed thoroughly by shaking. Nutrient solutions providing nitrogen (200 mg/kg), phosphorus (25 mg/kg), zinc (5 mg/kg), potassium (88 mg/kg) and sulphur (36 mg/kg) were then added and mixed thoroughly. The plastic bags and their contents were placed into 15 cm-diameter plastic pots and moved onto benches in the glasshouse. Three seeds per pot were laid on the soil surface and pressed 2 cm into the soil, covered and watered to a gravimetric content of 0.56 g/g (equivalent of pF2). After emergence, extra plants were removed to leave one plant per pot. Pots were watered as required to return the soil to 0.56 g/g moisture content.

Experiment 2 followed the procedure described by Sheedy and Thompson (2009). Plants in 70 mm-square (150 mm high) plastic pots containing 330 g (oven-dry equivalent) of soil fertilized with 1 g of Osmocote® Native Gardens plus micronutrients (17–1.6–8.7 NPK) slow-release fertilizer, (Scotts Australia Pty Ltd., Baulkham Hills, NSW, Australia) were grown on benches fitted with a bottom-watering system regulated by a float valve set to a water tension of 2 cm. Three seeds of each entry were placed on a base layer of soil (80% of total weight) and inoculated with 3,300 *P. thornei* (equivalent to 10,000/kg oven-dry soil) suspended in 15 ml of water pipetted around the seeds. The remaining soil was placed over the seeds as a cap. Extra plants were removed after emergence to leave one plant per pot.

In both experiments, plant growth stage (Zadoks et al. 1974), tiller number and height were recorded at 16 weeks after sowing. Then, the plant and soil were removed from the pot and a vertical section (Experiment 1) or a horizontal section (Experiment 2) removing 50% of the soil and roots was collected and stored at 3°C. Plants were re-potted with fresh pasteurised soil, staked and returned to the glasshouse, watered and grown on for seed.

Nematode extraction and enumeration

The sample of soil and roots was thoroughly mixed and the roots cut into $\approx$1 cm lengths. A 100 g subsample of the processed soil and roots was dried at 105°C for 48 h to determine gravimetric moisture content. A 150 g subsample was extracted at 22°C for 48 h using the Whitehead tray method (Whitehead and Hemming 1965) and nematodes were collected on a 20 μm sieve. Samples were stored in 30 ml vials at 3°C. Nematodes extracted from soil and roots were counted using a 1 ml Hawksley slide under a compound microscope (40×).

Statistical analysis

An analysis across years was conducted for ln (*P. thornei*/kg soil + 1) counts, where the ln transformation was applied to address variance heterogeneity. The data were analysed in a linear mixed model framework, with genotype by year effects fitted as random terms with an unstructured form for the genetic co-variance matrix across years. Replicate effects were fitted as random, and a separate residual

variance was fitted for each experiment. Estimates of variance parameters were obtained using residual maximum likelihood (REML) (Patterson and Thompson 1977) and best linear unbiased predictions (BLUPs) (Robinson 1991; Piepho 1998) were obtained for nematode counts of genotypes. The program ASReml-R (Butler et al. 2009) was used to fit the linear model and form predictions. The heritability of each experiment was calculated using the approach of Cullis et al. (2006), and probabilities of genotype effects being more R than GS50a were calculated from the full matrix of standard errors of differences. Additionally, the significance of the ploidy and species structure within the genotype set was tested as a fixed effect in the linear mixed model providing best linear unbiased estimates (BLUEs).

Average reproduction factor (RF) for each accession was calculated by dividing back-transformed final by initial *P. thornei* numbers in soil and roots for each experiment and then used to classify accessions according to the Australian national disease rating and management guide for nematode resistance (http://www.nvtonline.com.au/) into one of nine categories ranging from R to very susceptible (VS).

Results

Twenty-nine accessions, including 11 (52%) *A. speltoides*, 10 (43%) *T. monococcum*, 5 (24%) *T. urartu*, 1 (4%) *T. dicoccoides* and 2 (2%) *T. aestivum* were found to be R with a RF $\leq$ 1. A further 59 accessions, 10 *A. speltoides*, 11 *T. monococcum*, 13 *T. urartu*, 2 *A. peregrina*, 8 *T. dicoccoides*, 7 *T. timopheevii* and 8 *T. aestivum* were moderately R (Table 1). The probabilities calculated from the pair-wise comparison of each genotype with GS50a identified 18 accessions and the inoculated unplanted treatment in Experiment 1, and nine accessions and the inoculated unplanted treatment in Experiment 2, that produced significantly lower final *P. thornei* populations than GS50a. The nine accessions more R than GS50a in both years include three *T. urartu* ($\mathbf{A^u}$-genome; AUS26935, AUS26978, AUS26979), two *T. monococcum* ($\mathbf{A^m}$-genome; AUS27037, AUS27049), three *A. speltoides* (**S**-genome; AUS26952, AUS26983, AUS26984) and one *T. dicoccoides* ($\mathbf{BA^u}$-genomes; AUS27025). All of the *A. tauschii* derived germplasm from Kansas State University was susceptible, as were Lutin and the *A. peregrina* derived lines.

The strong genetic correlation between years (0.90) indicates that ranked performance for resistance to *P. thornei* was relatively stable across the two experiments. While Experiment 2 had a greater genetic variance, it also had a higher level of residual variance, resulting in an overall lower heritability than Experiment 1. Hence Experiment 1 gave slightly better discrimination between genotypes (Table 2).

Analysing accessions by ploidy level (Table 3) showed that the diploid accessions were significantly more R than the tetraploid accessions, which were significantly more R than the hexaploid accessions. The proportion of R accessions (RF $<$ 1) decreased from 41 to 1 or 2% as ploidy increased from diploid to tetraploid or hexaploid, respectively. The trend of susceptibility increasing as the level of ploidy increased remained evident when a less stringent level of selection (RF $<$ 4) was applied with 92% of diploid accessions, but only 21 and 13% of tetraploid and hexaploid accessions, being moderately R or better.

A total of 115 accessions in the species *A. speltoides*, *T. urartu*, *T. monococcum*, *T. dicoccoides* and *T. timopheevii* had passport data identifying country of origin. These had been collected from Armenia (3), Azerbaijan (2), Iran (2), Iraq (41), Israel (17), Italy (1), Lebanon (11), Syria (1) and Turkey (37). Overall, accessions from Lebanon had the lowest average RF, while accessions from Israel had the highest. Israel, Turkey and Lebanon had the lowest average RF for *A. speltoides*, *T. monococcum* and *T. urartu* accessions, respectively, with accessions from Italy, Iran and Turkey the highest. Armenia and Syria had the most R *T. timopheevii* and *T. dicoccoides* accessions while Azerbaijan and Israel had the most susceptible.

Discussion

A high strategic priority for practical cereal improvement worldwide is to enrich the cultivated gene pools by incorporating favourable alleles, genes or gene complexes from wild relatives (Feuillet et al. 2007). The *P. thornei*-R diploid and tetraploid species identified in this study belong mostly to the primary gene pool of common wheat, and gene transfer could be achieved by direct hybridization with adapted durum and bread wheat cultivars, homologous recombination, backcrossing and selection

Table 1 Final *P. thornei* population and RF of 251 accessions of wheat and related species tested in two glasshouse experiments

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
AUS26952	*Aegilops*	*speltoides*	*speltoides*	6.63	0.00	7.55	0.00	0.25	R
Unplanted				6.86	0.00	7.53	0.00	0.28	
AUS27049	*Triticum*	*monococcum*	*aegilopoides*	6.94	0.00	7.58	0.00	0.30	R
AUS26978	*Triticum*	*urartu*		7.11	0.00	7.62	0.01	0.35	R
AUS26935	*Triticum*	*urartu*		6.95	0.00	7.98	0.02	0.35	R
AUS26983	*Aegilops*	*speltoides*	*speltoides*	7.11	0.00	7.88	0.02	0.38	R
AUS26950	*Aegilops*	*speltoides*	*speltoides*	–	–	8.33	0.17	0.41	R
AUS26979	*Triticum*	*urartu*		7.24	0.00	7.94	0.02	0.42	R
AUS27045	*Triticum*	*monococcum*	*aegilopoides*	7.42	0.01	8.19	0.06	0.51	R
AUS27037	*Triticum*	*monococcum*	*aegilopoides*	7.56	0.01	7.94	0.01	0.53	R
AUS26984	*Aegilops*	*speltoides*	*speltoides*	7.47	0.01	8.24	0.05	0.54	R
AUS27025	*Triticum*	*turgidum*	*dicoccoides*	7.46	0.01	8.30	0.05	0.55	R
Canary grass	*Phalaris*	*canariensis*	Moroccan	7.56	0.01	8.36	0.08	0.60	R
AUS26948	*Aegilops*	*speltoides*	*speltoides*	7.46	0.01	8.53	0.12	0.60	R
AUS27090	*Triticum*	*monococcum*	*aegilopoides*	7.63	0.02	8.33	0.06	0.62	R
AUS27040	*Triticum*	*monococcum*	*aegilopoides*	7.59	0.02	8.63	0.15	0.68	R
AUS26957	*Aegilops*	*speltoides*	*ligustica*	7.84	0.06	8.37	0.09	0.72	R
AUS26956	*Aegilops*	*speltoides*	*ligustica*	–	–	8.88	0.34	0.72	R
AUS27044	*Triticum*	*monococcum*	*aegilopoides*	7.73	0.03	8.83	0.26	0.80	R
AUS26934	*Triticum*	*urartu*		7.89	0.15	8.64	0.24	0.81	R
AUS26949	*Aegilops*	*speltoides*	*speltoides*	7.82	0.05	8.74	0.23	0.81	R
AUS27046	*Triticum*	*monococcum*	*aegilopoides*	7.96	0.09	8.65	0.16	0.86	R
AUS26970	*Aegilops*	*speltoides*	*ligustica*	–	–	9.06	0.43	0.86	R
AUS27036	*Triticum*	*monococcum*	*aegilopoides*	8.05	0.13	8.61	0.16	0.90	R
AUS26954	*Aegilops*	*speltoides*	*speltoides*	8.02	0.11	8.72	0.21	0.91	R
AUS26951	*Aegilops*	*speltoides*	*speltoides*	8.01	0.11	8.75	0.22	0.92	R
DH1040-7	*Triticum*	*aestivum*	*aestivum*	7.74	0.04	–	–	0.92	R
AUS27041	*Triticum*	*monococcum*	*aegilopoides*	8.10	0.14	8.62	0.15	0.93	R
DH1040-12	*Triticum*	*aestivum*	*aestivum*	7.79	0.05	–	–	0.96	R
AUS27050	*Triticum*	*monococcum*	*aegilopoides*	8.20	0.20	8.52	0.12	0.98	R
AUS26946	*Triticum*	*urartu*		8.12	0.16	8.76	0.22	0.99	R
AUS26941	*Triticum*	*urartu*		8.12	0.16	8.80	0.24	1.00	R-MR
AUS26937	*Triticum*	*urartu*		8.13	0.16	8.79	0.23	1.01	R-MR
AUS27048	*Triticum*	*monococcum*	*aegilopoides*	8.08	0.14	8.93	0.32	1.02	R-MR
AUS27096	*Triticum*	*monococcum*	*aegilopoides*	8.05	0.13	8.98	0.35	1.03	R-MR
AUS27033	*Triticum*	*urartu*		8.23	0.22	8.69	0.19	1.05	R-MR
AUS4930-14	*Triticum*	*aestivum*	*aestivum*	7.89	1.00	–	–	1.07	R-MR
DH1040-3	*Triticum*	*aestivum*	*aestivum*	7.92	0.09	–	–	1.10	R-MR
AUS27081	*Triticum*	*timopheevii*	*armeniacum*	7.94	0.09	–	–	1.12	R-MR
AUS26972	*Aegilops*	*speltoides*	*speltoides*	8.38	0.33	8.66	0.18	1.16	R-MR
AUS26932	*Triticum*	*urartu*		8.26	0.24	8.99	0.36	1.17	R-MR
AUS26973	*Aegilops*	*speltoides*	*speltoides*	8.14	0.17	9.19	0.49	1.17	R-MR

Table 1 continued

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
AUS26955	*Aegilops*	*speltoides*	*speltoides*	8.33	0.29	8.86	0.28	1.18	R-MR
AUS26947	*Triticum*	*urartu*		8.36	0.32	8.89	0.30	1.22	R-MR
AUS26982	*Aegilops*	*speltoides*	*ligustica*	8.38	0.33	8.99	0.36	1.28	R-MR
AUS26945	*Triticum*	*urartu*		8.53	0.45	9.02	0.38	1.42	R-MR
AUS27091	*Triticum*	*monococcum*	*aegilopoides*	8.50	0.42	9.12	0.44	1.44	R-MR
AUS27012	*Triticum*	*monococcum*	*monococcum*	8.46	0.40	9.19	0.49	1.44	R-MR
AUS27047	*Triticum*	*monococcum*	*aegilopoides*	8.62	0.53	9.03	0.38	1.53	R-MR
AUS27038	*Triticum*	*monococcum*	*aegilopoides*	8.71	0.60	8.83	0.26	1.55	R-MR
AUS90633SH	*Aegilops*	*peregrina*		8.45	0.38	9.41	0.65	1.55	R-MR
GS50a	*Triticum*	*aestivum*	*aestivum*	8.59	NA	9.20	NA	1.57	R-MR
AUS27092	*Triticum*	*monococcum*	*aegilopoides*	8.60	0.51	9.26	0.54	1.61	R-MR
QT9048	*Triticum*	*aestivum*	*aestivum*	8.69	0.58	9.30	0.57	1.73	R-MR
AUS27034	*Triticum*	*urartu*		8.79	0.66	9.35	0.60	1.89	R-MR
AUS26962	*Aegilops*	*speltoides*	*ligustica*	–	–	9.86	0.76	1.91	R-MR
AUS27039	*Triticum*	*monococcum*	*aegilopoides*	8.87	0.72	9.33	0.58	1.99	R-MR
QT8343	*Triticum*	*aestivum*	*aestivum*	8.98	0.80	9.19	0.49	2.07	R-MR
CPI133962	Triticum	aestivum	synthetic	8.88	0.73	9.52	0.71	2.12	R-MR
AUS26960	*Aegilops*	*speltoides*	*speltoides*	8.58	0.49	–	–	2.13	R-MR
AUS26936	*Triticum*	*urartu*		8.92	0.76	9.53	0.72	2.18	R-MR
AUS26977	*Triticum*	*urartu*		8.86	0.72	9.67	0.80	2.20	R-MR
DH1039-9	*Triticum*	*aestivum*	*aestivum*	8.62	0.52	–	–	2.21	R-MR
AUS90633LH	*Aegilops*	*peregrina*		8.79	0.67	9.80	0.86	2.22	R-MR
AUS27031	*Triticum*	*urartu*		8.94	0.77	9.73	0.83	2.37	MR
AUS27022	*Triticum*	*turgidum*	*dicoccoides*	9.08	0.85	9.45	0.67	2.40	MR
AUS26976	*Aegilops*	*speltoides*	*speltoides*	–	–	10.12	0.91	2.48	MR
DH1039-13	*Triticum*	*aestivum*	*aestivum*	8.75	0.63	–	–	2.53	MR
AUS27042	*Triticum*	*monococcum*	*aegilopoides*	9.04	0.83	9.77	0.85	2.56	MR
AUS27086	*Triticum*	*timopheevii*	*armeniacum*	9.16	0.87	9.55	0.73	2.60	MR
AUS27095	*Triticum*	*monococcum*	*aegilopoides*	9.13	0.88	9.74	0.83	2.69	MR
DH1039-5	*Triticum*	*aestivum*	*aestivum*	8.82	0.68	–	–	2.70	MR
AUS27102	*Triticum*	*timopheevii*	*armeniacum*	–	–	10.21	0.91	2.73	MR
AUS27085	*Triticum*	*timopheevii*	*armeniacum*	9.26	0.92	9.56	0.74	2.82	MR
DH1040-4	*Triticum*	*aestivum*	*aestivum*	8.86	0.71	–	–	2.83	MR
AUS26959	*Aegilops*	*speltoides*	*speltoides*	9.19	0.86	9.88	0.83	2.93	MR
AUS4930-07	*Triticum*	*aestivum*	*aestivum*	8.92	0.93	–	–	3.00	MR
Yallaroi	*Triticum*	*turgidum*	*durum*	9.23	0.91	9.92	0.90	3.05	MR
AUS26988	*Triticum*	*turgidum*	*dicoccoides*	9.31	0.94	9.74	0.83	3.06	MR
AUS26938	*Triticum*	*urartu*		9.33	0.94	9.75	0.82	3.12	MR
AUS27017	*Triticum*	*turgidum*	*dicoccoides*	9.29	0.93	9.91	0.90	3.17	MR
AUS26940	*Triticum*	*urartu*		9.26	0.92	10.05	0.94	3.25	MR
AUS27024	*Triticum*	*turgidum*	*dicoccoides*	9.19	0.90	10.16	0.96	3.25	MR
AUS27101	*Triticum*	*timopheevii*	*armeniacum*	9.42	0.96	9.69	0.80	3.27	MR

Table 1 continued

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
AUS26971	*Aegilops*	*speltoides*	*speltoides*	9.31	0.93	10.00	0.89	3.32	MR
AUS27029	*Triticum*	*turgidum*	*dicoccoides*	9.39	0.95	10.05	0.93	3.56	MR
AUS27098	*Triticum*	*timopheevii*	*armeniacum*	9.35	0.95	10.19	0.96	3.65	MR
AUS26943	*Triticum*	*urartu*		9.45	0.97	10.05	0.93	3.71	MR
AUS27008	*Triticum*	*turgidum*	*dicoccoides*	9.36	0.93	10.28	0.95	3.78	MR
AUS27078	*Triticum*	*timopheevii*	*armeniacum*	9.43	0.96	10.20	0.96	3.85	MR
AUS26974	*Aegilops*	*speltoides*	*ligustica*	–	–	10.57	0.82	3.91	MR
AUS27094	*Triticum*	*monococcum*	*aegilopoides*	–	–	10.57	0.82	3.91	MR
AUS27021	*Triticum*	*turgidum*	*dicoccoides*	9.51	0.97	10.11	0.94	3.93	MR
AUS27020	*Triticum*	*turgidum*	*dicoccoides*	9.57	0.98	10.08	0.94	4.06	MR-MS
AUS27006	*Triticum*	*turgidum*	*dicoccoides*	9.45	0.96	10.33	0.97	4.07	MR-MS
AUS27089	*Triticum*	*timopheevii*	*armeniacum*	9.43	0.96	10.38	0.98	4.11	MR-MS
AUS27082	*Triticum*	*timopheevii*	*armeniacum*	9.42	0.96	10.44	0.98	4.17	MR-MS
AUS27032	*Triticum*	*urartu*		9.59	0.98	10.19	0.96	4.26	MR-MS
AUS27073	*Triticum*	*timopheevii*	*armeniacum*	9.60	0.98	10.18	0.96	4.28	MR-MS
AUS26939	*Triticum*	*urartu*		9.52	0.98	10.39	0.98	4.36	MR-MS
AUS27100	*Triticum*	*timopheevii*	*armeniacum*	9.58	0.98	10.30	0.97	4.37	MR-MS
AUS15824	*Triticum*	*turgidum*	*carthlicum*	9.59	0.98	10.29	0.97	4.39	MR-MS
AUS4930-09	*Triticum*	*aestivum*	*aestivum*	9.34	1.00	–	–	4.53	MR-MS
AUS27051	*Triticum*	*monococcum*	*aegilopoides*	9.67	0.99	10.23	0.97	4.55	MR-MS
AUS27084	*Triticum*	*timopheevii*	*armeniacum*	9.66	0.99	10.25	0.97	4.56	MR-MS
DH1039-15	*Triticum*	*aestivum*	*aestivum*	9.39	0.95	–	–	4.80	MR-MS
AUS27079	*Triticum*	*timopheevii*	*armeniacum*	9.68	0.99	10.40	0.98	4.83	MR-MS
CPI133979	Triticum	aestivum	synthetic	9.75	0.99	10.27	0.97	4.88	MR-MS
AUS27023	*Triticum*	*turgidum*	*dicoccoides*	9.82	1.00	10.14	0.95	4.93	MR-MS
AUS26989	*Triticum*	*turgidum*	*dicoccoides*	9.60	0.98	10.60	0.99	4.97	MR-MS
CPI133959	Triticum	aestivum	synthetic	9.76	0.99	10.39	0.98	5.08	MR-MS
CPI133953	Triticum	aestivum	synthetic	9.82	1.00	10.29	0.97	5.16	MR-MS
AUS27043	*Triticum*	*monococcum*	*aegilopoides*	9.81	1.00	10.38	0.98	5.26	MR-MS
DH1040-15	*Triticum*	*aestivum*	*aestivum*	9.48	0.96	–	–	5.26	MR-MS
AUS4930-10	*Triticum*	*aestivum*	*aestivum*	9.50	1.00	–	–	5.32	MR-MS
AUS27074	*Triticum*	*timopheevii*	*armeniacum*	9.70	0.99	10.63	0.99	5.33	MR-MS
AUS27077	*Triticum*	*timopheevii*	*armeniacum*	9.86	1.00	10.35	0.98	5.38	MR-MS
DH1040-6	*Triticum*	*aestivum*	*aestivum*	9.54	0.97	–	–	5.55	MR-MS
AUS22413	*Triticum*	*aestivum*		9.87	1.00	10.45	0.99	5.61	MR-MS
DH1040-11	*Triticum*	*aestivum*	*aestivum*	9.55	0.97	–	–	5.64	MR-MS
AUS27028	*Triticum*	*turgidum*	*dicoccoides*	9.88	1.00	10.55	0.99	5.81	MR-MS
AUS27027	*Triticum*	*turgidum*	*dicoccoides*	9.88	1.00	10.59	0.99	5.89	MR-MS
AUS27026	*Triticum*	*turgidum*	*dicoccoides*	9.87	0.99	10.73	0.99	6.16	MR-MS
AUS27087	*Triticum*	*timopheevii*	*armeniacum*	9.94	1.00	10.61	0.99	6.17	MR-MS
AUS27083	*Triticum*	*timopheevii*	*armeniacum*	9.93	1.00	10.72	0.99	6.35	MS
AUS27013	*Triticum*	*turgidum*	*dicoccoides*	10.01	1.00	10.68	1.00	6.62	MS

Table 1 continued

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
AUS27104	*Triticum*	*timopheevii*	*armeniacum*	9.99	1.00	10.76	1.00	6.71	MS
AUS27099	*Triticum*	*timopheevii*	*armeniacum*	10.03	1.00	10.81	1.00	7.01	MS
AUS27009	*Triticum*	*turgidum*	*dicoccoides*	10.21	1.00	10.48	0.99	7.21	MS
AUS3828	*Triticum*	*turgidum*	*carthlicum*	10.08	1.00	10.90	1.00	7.47	MS
AUS26987	*Triticum*	*turgidum*	*dicoccoides*	10.14	1.00	10.80	1.00	7.51	MS
AUS5289	*Triticum*	*turgidum*	*carthlicum*	10.09	1.00	10.91	1.00	7.56	MS
AUS4930-08	*Triticum*	*aestivum*	*aestivum*	9.90	0.97	–	–	7.97	MS
AUS12208	*Triticum*	*turgidum*	*carthlicum*	10.22	1.00	10.96	1.00	8.36	MS
DH1040-8	*Triticum*	*aestivum*	*aestivum*	9.95	1.00	–	–	8.40	MS
AUS27010	*Triticum*	*turgidum*	*dicoccoides*	10.27	1.00	10.93	1.00	8.56	MS
AUS27072	*Triticum*	*timopheevii*	*armeniacum*	10.25	1.00	10.98	1.00	8.60	MS
KS85WGRC01	*Triticum*	*aestivum*	*aestivum*	10.25	1.00	11.02	1.00	8.68	MS
AUS27075	*Triticum*	*timopheevii*	*armeniacum*	10.20	1.00	11.10	1.00	8.71	MS
DH1039-10	*Triticum*	*aestivum*	*aestivum*	10.02	1.00	–	–	8.95	MS
AUS22499	*Triticum*	*turgidum*	*carthlicum*	10.37	1.00	11.07	1.00	9.63	MS-S
CPI133975	Triticum	aestivum	synthetic	10.48	1.00	11.01	1.00	10.13	MS-S
AUS12151	*Triticum*	*turgidum*	*carthlicum*	10.44	1.00	11.13	1.00	10.23	MS-S
AUS22439	*Triticum*	*turgidum*	*carthlicum*	10.50	1.00	11.00	1.00	10.26	MS-S
AUS27097	*Triticum*	*timopheevii*	*armeniacum*	10.27	1.00	11.42	1.00	10.28	MS-S
AUS26942	*Triticum*	*urartu*		10.46	1.00	11.12	1.00	10.32	MS-S
AUS27019	*Triticum*	*turgidum*	*dicoccoides*	10.49	1.00	11.26	1.00	11.06	MS-S
AUS5287	*Triticum*	*turgidum*	*carthlicum*	10.54	1.00	11.20	1.00	11.23	MS-S
AUS22356	*Triticum*	*turgidum*	*carthlicum*	10.60	1.00	11.15	1.00	11.53	MS-S
AUS1762	*Triticum*	*turgidum*	*carthlicum*	10.59	1.00	11.19	1.00	11.55	MS-S
AUS27076	*Triticum*	*timopheevii*	*armeniacum*	10.54	1.00	11.31	1.00	11.64	MS-S
AUS27018	*Triticum*	*turgidum*	*dicoccoides*	10.51	1.00	11.38	1.00	11.72	MS-S
AUS10741	*Triticum*	*turgidum*	*carthlicum*	10.53	1.00	11.36	1.00	11.74	MS-S
AUS4930-16	*Triticum*	*aestivum*	*aestivum*	10.29	1.00	–	–	11.83	MS-S
AUS27007	*Triticum*	*turgidum*	*dicoccoides*	10.67	1.00	11.18	1.00	12.24	MS-S
AUS3158	*Triticum*	*turgidum*	*carthlicum*	10.60	1.00	11.36	1.00	12.27	S
N2 addition	*Triticum*	*aestivum*	addition	10.73	1.00	11.06	1.00	12.30	S
AUS22500	*Triticum*	*aestivum*		10.71	1.00	11.15	1.00	12.47	S
AUS3837	*Triticum*	*turgidum*	*carthlicum*	10.58	1.00	11.46	1.00	12.58	S
AUS3849	*Triticum*	*turgidum*	*carthlicum*	10.69	1.00	11.24	1.00	12.60	S
AUS22358	*Triticum*	*turgidum*	*carthlicum*	10.55	1.00	11.51	1.00	12.66	S
AUS4930-05	*Triticum*	*aestivum*	*aestivum*	10.37	0.75	–	–	12.77	S
AUS27016	*Triticum*	*turgidum*	*dicoccoides*	10.71	1.00	11.35	1.00	13.24	S
AUS3839	*Triticum*	*turgidum*	*carthlicum*	10.76	1.00	11.29	1.00	13.44	S
AUS4930-13	*Triticum*	*aestivum*	*aestivum*	10.42	1.00	–	–	13.46	S
AUS4930-S1	*Triticum*	*aestivum*	*aestivum*	10.44	1.00	–	–	13.70	S
X8 addition	*Triticum*	*aestivum*	addition	10.67	1.00	11.54	1.00	13.76	S
AUS3831	*Triticum*	*turgidum*	*carthlicum*	10.75	1.00	11.42	1.00	13.93	S

Table 1 continued

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
AUS3840	*Triticum*	*turgidum*	*carthlicum*	10.75	1.00	11.49	1.00	14.24	S
AUS4930-S2	*Triticum*	*aestivum*	*aestivum*	10.51	1.00	–	–	14.67	S
KS93WGRC26	*Triticum*	*aestivum*	*aestivum*	10.75	1.00	11.60	1.00	14.81	S
AUS4930-11	*Triticum*	*aestivum*	*aestivum*	10.57	1.00	–	–	15.55	S
AUS27088	*Triticum*	*timopheevii*	*armeniacum*	10.92	1.00	11.44	1.00	15.70	S
X35 addition	*Triticum*	*aestivum*	addition	10.96	1.00	11.46	1.00	16.24	S-VS
AUS27103	*Triticum*	*timopheevii*	*armeniacum*	10.90	1.00	11.64	1.00	16.55	S-VS
DH1038-11	*Triticum*	*aestivum*	*aestivum*	10.63	1.00	–	–	16.55	S-VS
CPI119825	*Triticum*	*turgidum*	*carthlicum*	10.96	1.00	11.52	1.00	16.58	S-VS
DH1039-12	*Triticum*	*aestivum*	*aestivum*	10.65	1.00	–	–	16.91	S-VS
AUS17973	*Triticum*	*turgidum*	*carthlicum*	10.91	1.00	11.71	1.00	17.05	S-VS
AUS1304	*Triticum*	*turgidum*	*carthlicum*	10.97	1.00	11.61	1.00	17.12	S-VS
KS92WGRC21	*Triticum*	*aestivum*	*aestivum*	10.82	1.00	11.88	1.00	17.22	S-VS
AUS4930-02	*Triticum*	*aestivum*	*aestivum*	10.72	1.00	–	–	18.13	S-VS
AUS22289	*Triticum*	*turgidum*	*carthlicum*	10.93	1.00	11.88	1.00	18.39	S-VS
Gatcher	*Triticum*	*aestivum*	*aestivum*	11.07	1.00	11.67	1.00	18.68	S-VS
AUS22359	*Triticum*	*turgidum*	*carthlicum*	11.04	1.00	11.73	1.00	18.70	S-VS
AUS3809	*Triticum*	*turgidum*	*turanicum*	11.17	1.00	11.47	1.00	18.95	S-VS
DH1038-10	*Triticum*	*aestivum*	*aestivum*	10.82	1.00	–	–	19.92	S-VS
AUS4930-15	*Triticum*	*aestivum*	*aestivum*	10.82	1.00	–	–	20.10	S-VS
Lutin	*Triticum*	*aestivum*	*aestivum*	11.25	1.00	11.88	1.00	22.54	VS
AUS4930-01	*Triticum*	*aestivum*	*aestivum*	10.96	1.00	–	–	23.04	VS
AUS17644	*Triticum*	*turgidum*	*carthlicum*	11.18	1.00	12.12	1.00	23.44	VS
AUS11488	*Triticum*	*turgidum*	*carthlicum*	11.27	1.00	11.97	1.00	23.58	VS
LXL addition	*Triticum*	*aestivum*	addition	11.33	1.00	11.86	1.00	23.82	VS
DH1039-3	*Triticum*	*aestivum*	*aestivum*	11.01	1.00	–	–	24.09	VS
AUS3917	*Triticum*	*turgidum*	*carthlicum*	11.25	1.00	12.08	1.00	24.23	VS
Janz	*Triticum*	*aestivum*	*aestivum*	11.27	1.00	12.08	1.00	24.55	VS
KS90WGRC10	*Triticum*	*aestivum*	*aestivum*	11.30	1.00	12.07	1.00	24.84	VS
AUS3834	*Triticum*	*turgidum*	*carthlicum*	11.38	1.00	12.05	1.00	26.08	VS
CR2-49	*Triticum*	*aestivum*	*aestivum*	11.09	1.00	–	–	26.23	VS
AUS22452	Triticum	aestivum	synthetic	11.45	1.00	12.05	1.00	27.42	VS
AUS27015	*Triticum*	*turgidum*	*dicoccoides*	11.47	1.00	12.06	1.00	27.90	VS
KS89WGRC03	*Triticum*	*aestivum*	*aestivum*	11.45	1.00	12.13	1.00	28.13	VS
AUS4930-04	*Triticum*	*aestivum*	*aestivum*	11.17	1.00	–	–	28.39	VS
KS92WGRC16	*Triticum*	*aestivum*	*aestivum*	11.54	1.00	12.04	1.00	29.00	VS
DH1039-11	*Triticum*	*aestivum*	*aestivum*	11.22	1.00	–	–	29.86	VS
DH1038-5	*Triticum*	*aestivum*	*aestivum*	11.28	1.00	–	–	31.60	VS
KS91WGRC13	*Triticum*	*aestivum*	*aestivum*	11.59	1.00	12.21	1.00	31.61	VS
AUS27014	*Triticum*	*turgidum*	*dicoccoides*	11.62	1.00	12.14	1.00	31.64	VS
AUS3999	*Triticum*	*turgidum*	*carthlicum*	11.53	1.00	12.35	1.00	31.90	VS
KS89WGRC05	*Triticum*	*aestivum*	*aestivum*	11.58	1.00	12.39	1.00	33.39	VS

Table 1 continued

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
DH1039-14	*Triticum*	*aestivum*	*aestivum*	11.36	1.00	–	–	34.28	VS
Genaro	*Triticum*	*aestivum*	*aestivum*	11.37	1.00	–	–	34.77	VS
AUS4930-12	*Triticum*	*aestivum*	*aestivum*	11.38	0.08	–	–	35.04	VS
Cunningham	*Triticum*	*aestivum*	*aestivum*	11.76	1.00	12.22	1.00	35.83	VS
Seri	*Triticum*	*aestivum*	*aestivum*	11.41	1.00	–	–	36.13	VS
Batavia	*Triticum*	*aestivum*	*aestivum*	11.76	1.00	12.31	1.00	36.81	VS
KS89WGRC07	*Triticum*	*aestivum*	*aestivum*	11.74	1.00	12.42	1.00	37.57	VS
AUS4930-03	*Triticum*	*aestivum*	*aestivum*	11.46	1.00	–	–	37.91	VS
DH1039-4	*Triticum*	*aestivum*	*aestivum*	11.46	1.00	–	–	38.03	VS
AUS4930-06	*Triticum*	*aestivum*	*aestivum*	11.47	1.00	–	–	38.18	VS
KS89WGRC04	*Triticum*	*aestivum*	*aestivum*	11.73	1.00	12.52	1.00	38.66	VS
KS91WGRC12	*Triticum*	*aestivum*	*aestivum*	11.77	1.00	12.46	1.00	38.83	VS
AUS11478	*Triticum*	*turgidum*	*carthlicum*	11.76	1.00	12.52	1.00	39.27	VS
DH1040-5	*Triticum*	*aestivum*	*aestivum*	11.52	1.00	–	–	40.36	VS
DH1039-17	*Triticum*	*aestivum*	*aestivum*	11.53	1.00	–	–	40.59	VS
DH1038-14	*Triticum*	*aestivum*	*aestivum*	11.53	1.00	–	–	40.68	VS
KS89WGRC06	*Triticum*	*aestivum*	*aestivum*	11.77	1.00	12.61	1.00	40.91	VS
KS92WGRC22	*Triticum*	*aestivum*	*aestivum*	11.85	1.00	12.54	1.00	42.05	VS
DH1038-13	*Triticum*	*aestivum*	*aestivum*	11.57	1.00	–	–	42.33	VS
DH1040-1	*Triticum*	*aestivum*	*aestivum*	11.59	1.00	–	–	43.41	VS
DH1040-2	*Triticum*	*aestivum*	*aestivum*	11.59	1.00	–	–	43.41	VS
11IBWSN50	*Triticum*	*aestivum*	*aestivum*	11.65	1.00	–	–	45.85	VS
DH1038-12	*Triticum*	*aestivum*	*aestivum*	11.65	1.00	–	–	45.85	VS
KS86WGRC02	*Triticum*	*aestivum*	*aestivum*	11.96	1.00	12.60	1.00	46.09	VS
DH1039-8	*Triticum*	*aestivum*	*aestivum*	11.66	1.00	–	–	46.14	VS
AUS11447	*Triticum*	*turgidum*	*carthlicum*	11.96	1.00	12.67	1.00	47.17	VS
KS91WGRC11	*Triticum*	*aestivum*	*aestivum*	11.96	1.00	12.67	1.00	47.27	VS
DH1038-2	*Triticum*	*aestivum*	*aestivum*	11.69	1.00	–	–	47.85	VS
DH1038-1	*Triticum*	*aestivum*	*aestivum*	11.70	1.00	–	–	48.18	VS
DH1038-4	*Triticum*	*aestivum*	*aestivum*	11.70	1.00	–	–	48.35	VS
DH1038-3	*Triticum*	*aestivum*	*aestivum*	11.71	1.00	–	–	48.69	VS
DH1038-9	*Triticum*	*aestivum*	*aestivum*	11.76	1.00	–	–	51.43	VS
DH1039-2	*Triticum*	*aestivum*	*aestivum*	11.77	1.00	–	–	51.95	VS
DH1039-6	*Triticum*	*aestivum*	*aestivum*	11.78	1.00	–	–	52.05	VS
DH1039-1	*Triticum*	*aestivum*	*aestivum*	11.80	1.00	–	–	53.50	VS
DH1040-16	*Triticum*	*aestivum*	*aestivum*	11.81	1.00	–	–	53.70	VS
DH1040-9	*Triticum*	*aestivum*	*aestivum*	11.82	1.00	–	–	54.38	VS
DH1040-14	*Triticum*	*aestivum*	*aestivum*	11.88	1.00	–	–	58.01	VS
DH1038-7	*Triticum*	*aestivum*	*aestivum*	11.92	1.00	–	–	60.32	VS
DH1038-6	*Triticum*	*aestivum*	*aestivum*	11.96	1.00	–	–	62.26	VS

Table 1 continued

Accession	Genus	Species	Subspecies	*P. thornei*/kg soil and roots				Mean RF[b]	Status[c]
				Experiment 1		Experiment 2			
				ln(x + 1)	Prob[a]	ln(x + 1)	Prob[a]		
DH1040-10	*Triticum*	*aestivum*	*aestivum*	12.00	1.00	–	–	65.17	VS

Values are BLUPs of ln(x + 1) transformed data from a linear mixed model

R resistant, *MR* moderately resistant, *MS* moderately susceptible, *S* susceptible, *VS* very susceptible

[a] Probabilities calculated from the pair-wise comparison of each genotype with the moderately *P. thornei*-R reference cultivar GS50a (*T. aestivum*). Probabilities <0.05 indicate accessions that were significantly more R than GS50a

[b] Mean RF (final population per kg soil ÷ initial inoculum rate per kg soil)

[c] Cultivar status for *P. thornei* resistance classified according to the Australian national disease rating and management guide for nematode resistance (http://www.nvtonline.com.au/)

Table 2 Variance components and heritability estimated from the linear mixed model for two experiments

Component of analysis	Experiment	
	1	2
Genetic variance	1.95	2.27
Replicate variance	0.02	0.06
Error variance	0.44	1.05
Heritability (h^2)	0.94	0.91

(Friebe et al. 1996). Several authors report that crosses between *A. speltoides* (Bijral et al. 1997; Valkoun 2001), *T. urartu* (Johnson and Dhaliwal 1976; Valkoun 2001), or *T. monococcum* (Johnson and Dhaliwal 1976; Ma and Hughes 1993) and common or durum wheats produced viable F_1s that were completely male sterile and partially female sterile. F_1s produced using a durum parent generally recovered full fertility after the first backcross (Valkoun 2001), whereas F_1s derived from common wheat have generally required several additional backcrosses before the progeny were self-fertile (Bijral et al. 1997; Schmolke et al. 2011; Qiu et al. 2005). The **A** and **B**-genome chromosomes of *T. dicoccoides* show high homology with those of durum and bread wheats (Valkoun 2001) and readily hybridize. Suppression of the resistance gene(s) or dilution of its products may result in a reduction of expressed disease resistance when transferred from a species of a lower level of ploidy to one of a higher level (Cox 1991; Gill et al. 1986; Kerber and Green 1980; Potgieter et al. 1991). However, many genes conferring resistance to diseases and pests have been transferred using direct hybridization (Cox 1991, 1998; Friebe et al. 1996), including CCN resistance from *T. monococcum* to durum and bread wheat cultivars (Singh et al. 2010).

Previous studies on moderately *P. thornei* R hexaploid wheats from the West Asia and North

Table 3 Diploid accessions were more R to *P. thornei* than tetraploid and hexaploid accessions

Ploidy and number of accessions	*n*	*P. thornei*/kg soil and roots				% accessions	
		ln(x + 1)[a]	SE		BTM[b]	RF[c] < 1	RF < 4
Unplanted treatment	1	7.03	0.99	a	1,128		
Diploid	65	8.56	0.15	b	5,203	41	92
Tetraploid	85	10.52	0.14	c	37,001	1	21
Hexaploid	100	11.14	0.13	d	69,022	2	13

Values are BLUEs of ln(x + 1) transformed data from a linear mixed model

[a] Means with similar letters do not differ significantly ($P = 0.05$)

[b] Back-transformed mean

[c] Mean RF (final population per kg soil ÷ initial inoculum rate per kg soil)

Africa (WANA) region have used single marker regression and QTL analysis to identify resistance loci on chromosomes **2B**, **3B**, **6D** and **7A** (Schmidt et al. 2005), **1B**, **2B** and **6D** (Toktay et al. 2006) and a susceptibility locus on **1B** (Schmidt et al. 2005). Similar studies on synthetic hexaploid derived populations have identified *P. thornei* resistance loci on chromosomes **6DS** and **6DL** (Zwart et al. 2005), **1B** and **3B** (Toktay et al. 2006) and **2BS**, **6DS** and **6DL** (Zwart et al. 2006, 2010). It is not surprising that virtually all the resistance loci have been identified on the **B** and **D**-genomes, considering all of the *A. speltoides* accessions examined in this study were at least moderately R to *P. thornei*, as were 16% of A. tauschii accessions screened by Thompson and Haak (1997). However, prior to this study there was only limited evidence for *P. thornei* resistance on the **A**-genome of wheat. The *P. neglectus* resistance gene *Rlnn1* has been mapped to chromosome **7A** (Williams et al. 2002), but the only *P. thornei* resistance locus identified on the **A**-genome (also **7A**) was detected only in single marker regression (Schmidt et al. 2005). The results of this study clearly establish that resistance to *P. thornei* exists on the **A**-genomes of both *T. urartu* and *T. monococcum*.

Since amphiploids are usually highly fertile and true-breeding (Cox 1998) they could be an alternative or concurrent method of exploiting these novel resistances. Synthetic hexaploids have been used widely by breeding programs (Feuillet et al. 2007) to introduce disease resistance into wheat cultivars (Ogbonnaya et al. 2008), and could be used to combine the *P. thornei* resistances of *T. dicoccoides* and *A. tauschii*. Although *A. speltoides* carries genes that support homoeologous chromosome pairing (Schneider et al. 2008), certain accessions, particularly from subspecies *aucheri* and *ligustica*, may also introduce gametocidal genes to wide cross progeny thereby reducing female fertility by 50% or more (Marais and Pretorius 1996). However, amphiploids between *A. speltoides* and *T. monococcum* have been successfully used to transfer disease resistance to hexaploid wheat (Kerber and Dyck 1990), suggesting that substitution of *T. monococcum* with *T. urartu* may also be effective. If successfully developed, the synthetic tetraploids could be hybridized with *P. thornei* R accessions of *A. tauschii* to produce synthetic hexaploids with *P. thornei* resistance on each of their genomes.

Previous experience in amphiploid production has shown that when partially *P. thornei*-R durums and *A. tauschii* accessions were combined in synthetic hexaploids, the resultant level of *P. thornei* resistance was not diluted and was equal to that of the parents and better than synthetic hexaploids derived from only one R parent (Thompson 2008). This was likely due to *P. thornei* resistance being polygenic and additive (Zwart et al. 2004; Thompson and Seymour 2011). As a result, a proportionate number of additive resistance genes may be required in hexaploids to limit *P. thornei* multiplication to levels observed in species of lower ploidy (Thompson 2008).

Although our research identifies *P. thornei* R accessions, the number of genes controlling the resistance remains unknown. Since 92% of the diploid accessions evaluated in this study were R or moderately so to *P. thornei*, it could be concluded that resistance is controlled by a few dominant genes of large effect. This would be comparable to the *Cre* genes that individually confer complete or partial resistance to pathotypes of CCN. Conversely, several studies have shown that combinations of two to five minor resistance genes can considerably reduce disease incidence or even result in near-immune reactions in wheat cultivars (Miedaner et al. 2006; Singh et al. 2011). Chromosome addition lines allow the study of the genetic effects of individual alien chromosomes in the background of hexaploid wheat and fortunately one such population has been developed for the *P. thornei* R *A. speltoides* accession AUS26955 (synonyms: TA2780, TAM9212-2) (Friebe et al. 2000). A preliminary study of the disomic chromosome addition lines indicated that *P. thornei* resistance in *A. speltoides* could be controlled by up to five genes of varying strength (Sheedy et al. 2008a). Interestingly the strongest *P. thornei* resistances, slightly weaker but statistically equal to *A. speltoides*, were observed in the DA6S and DA5S addition lines (Sheedy et al. 2008a). Neither of the corresponding **B**-genome chromosomes has been identified in QTL analysis of *P. thornei* resistance in landrace bread wheats and synthetic hexaploid wheats. The addition lines DA2S, DA3S and DA4S had an intermediate level of resistance, more susceptible than *A. speltoides* but more R than Chinese Spring (Sheedy et al. 2008a), with chromosome **2B** and/or **3B** commonly identified in QTL analysis of hexaploid wheat (Schmidt et al. 2005; Toktay et al. 2006; Zwart et al. 2006, 2010). Chromosome **1B** has been reported to have both susceptibility (Schmidt et al. 2005) and resistance

(Toktay et al. 2006) loci but the DA1S addition line was more susceptible than Chinese Spring (Sheedy et al. 2008a). Given there may be up to five genes controlling the *P. thornei* resistance in *A. speltoides* (Sheedy et al. 2008a) and that many studies of hexaploid wheat have concluded that *P. thornei* resistance is polygenic with additive gene action (Schmidt et al. 2005; Thompson and Seymour 2011; Toktay et al. 2006; Zwart et al. 2004, 2005, 2006, 2010), it seems reasonable to expect that *P. thornei* resistance in the diploid relatives of wheat may also be polygenic. Further evaluation of this set of addition lines and an associated set of disomic chromosome substitution lines (Friebe et al. 2000) would greatly aid our understanding of the chromosome locations and strengths of the various resistance genes.

If a proportionate number of additive resistance genes are required in hexaploids to produce *P. thornei* resistance levels similar to R diploids and the resistance of *A. speltoides* (and possibly *T. urartu* and *T. monococcum*) is controlled by up to five resistance genes, does this mean we would need to recover up to ten genes in tetraploids and 15 genes in hexaploids? Since it appears that the genes have varying effects, recovery of the genes with the largest effects from each of the **A**, **B** and **D**-genomes would likely confer levels of *P. thornei* resistance in hexaploids similar to the levels in the diploid species. *A. speltoides* appears to have two genes of large effect (Sheedy et al. 2008a) as does *A. tauschii* (Zwart et al. 2006, 2010) and if *T. urartu* or *T. monococcum* were similar there may only be a need to recover six genes to maintain the diploid level of resistance in a hexaploid background. That would be a similar position to some current breeding efforts that aim to recover up to six genes to transfer partial *P. thornei* resistance from landraces to adapted cultivars (Thompson and Seymour 2011).

Evaluation of wheat and durum landraces and *A. tauschii* accessions originating from the WANA region where *P. thornei* is widely distributed has proven successful in identifying R or moderately R accessions (Sheedy and Thompson 2009; Thompson and Haak 1997; Thompson et al. 2009). Many of the R wild relatives identified in this research, particularly *A. speltoides*, *T. monococcum*, *T. urartu* and *T. dicoccoides*, originated from the countries occupying the Levantine coast of the eastern Mediterranean where *P. thornei* is endemic (Di Vito et al. 1994; Greco et al. 1988; Orion et al. 1979). This supports the notion that germplasm collections selected from areas where a disease is endemic are more likely to contain R accessions.

The *A. peregrina* selections (AUS90633SH, AUS90633LH) classified as moderately R to *P. thornei* in this study are also CCN-R, but we found all of the CCN-R lines developed from *A. peregrina* (Barloy et al. 2007) were susceptible to *P. thornei* like their cultivated *T. aestivum* parent 'Lutin'. Evaluation of germplasm with the CCN resistance genes *Cre2* (Nombela and Romero 1999), *Cre3* (Thompson 2008), *Cre7* (Nombela and Romero 2001) and *CreR* (Sheedy et al. 2008b) also showed that they did not confer resistance to *P. thornei*. Similarly, the KSU germplasm with resistances to Hessian fly (*Mayetiola destructor*), greenbug (*Schizaphis graminum*), leaf rust (*Puccinia triticina*), powdery mildew (*Blumeria graminis* f.sp. *tritici*), soilborne mosaic virus and/or wheat spindle streak mosaic virus introgresssed from *A. tauschii* did not confer resistance to *P. thornei*. These results reinforce the need for targeted selection of R germplasm because serendipitous selection for *P. thornei* resistance is unlikely to be successful even if the germplasm is R to other nematodes, insects or diseases.

The wild relatives of common wheat appear to be very valuable sources of resistance to *P. thornei*, providing the opportunity to introduce one or more resistance genes into each of the three wheat genomes. Particular emphasis should be given to the novel **A**-genome resistances that so far have not been detected in hexaploid breeding lines. Direct hybridization with durum and bread wheat and the production of amphiploids seem the most efficient methods of utilizing the *P. thornei* R accessions identified here.

Acknowledgments The authors thank Dr. Jon Raupp (Kansas State University Wheat Genetics and Genomic Resource Center) for supplying wheat cultivars and a selection of related species representing the **A** and **B**-genomes used in this study, Prof. John Irwin (University of Queensland) for helpful advice, Mr. Andrew Skerman for technical assistance, and Mr. Michael McKay and Mr. Greg Grimes (Australian Winter Cereals Collection) for importing the seed.

References

Barloy D, Lemoine J, Abelard P, Tanguy AM, Rivoal R, Jahier J (2007) Marker-assisted pyramiding of two cereal cyst nematode resistance genes from *Aegilops variabilis* in wheat. Mol Breed 20:31–40

Bijral JS, Singh K, Sharma TR (1997) Morpho-cytogenetics of *Triticum aestivum* L. x *Aegilops speltoides* Tausch. hybrids. Wheat Inf Serv 84:51–52

Butler DG, Cullis BR, Gilmour AR, Gogel BJ (2009) ASReml-R reference manual version 3. Department of Primary Industries and Fisheries, Brisbane

Cox TS (1991) The contribution of introduced germplasm to the development of U.S. wheat cultivars. Use of Plant Introductions in Cultivar Development, Part 1, Crop Science Society of America Special Publication No. 17, USA

Cox TS (1998) Deepening the wheat gene pool. J Crop Prod 1:1–25

Cullis BR, Smith AB, Coombes N (2006) On the design of early generation variety trials with correlated data. J Agric Biol Environ Stat 11:381–393

Di Vito M, Greco N, Oreste G, Saxena MC, Singh KB, Kusmenoglu I (1994) Plant parasitic nematodes of legumes in Turkey. Nematol Mediter 22:245–251

Eastwood RF, Lagudah ES, Appels R, Hannah M, Kollmorgen JF (1991) *Triticum tauschii*: a novel source of resistance to cereal cyst nematode (*Heterodera avenae*). Aust J Agric Res 42:69–77

Feldman M, Sears ER (1981) The wild gene resources of wheat. Sci Am 244:102–112

Feuillet C, Langridge P, Waugh R (2007) Cereal breeding takes a walk on the wild side. Trends Genet 24:24–32

Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS (1996) Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status. Euphytica 91:59–87

Friebe B, Qi LL, Nasuda S, Zhang P, Tuleen NA, Gill BS (2000) Development of a complete set of *Triticum aestivum–Aegilops speltoides* chromosome addition lines. Theor Appl Genet 101:51–58

Gill BS, Multani DS, Dhaliwal HS (1986) Transfer of Isoproturon resistance from *Triticum monococcum* to *T. durum*. Crop Improv 13:200–203

Greco N, Di Vito M, Saxena MC, Reddy MV (1988) Investigation on the root lesion nematode *Pratylenchus thornei*, in Syria. Nematol Mediter 16:101–105

Hollaway GJ, Vanstone VA, Nobbs J, Smith JG, Brown JS (2008) Pathogenic nematodes of cereal crops in south–west Victoria, Australia. Australas Plant Pathol 37:505–510

Johnson BL, Dhaliwal HS (1976) Reproductive isolation of *Triticum boeoticum* and *Triticum urartu* and the origin of the tetraploid wheats. Am J Bot 63:1088–1094

Kerber ER, Dyck PL (1990) Transfer to hexaploid wheat of linked genes for adult plant leaf rust and seedling stem rust resistance from an amphiploid of *Aegilops speltoides* X *Triticum monococcum*. Genome 33:530–537

Kerber ER, Green GJ (1980) Suppression of stem rust resistance in the hexaploid wheat cv. Canthatch by chromosome 7DL. Can J Bot 58:1347–1350

Ma H, Hughes GR (1993) Resistance to *Septoria nodorum* blotch in several *Triticum* species. Euphytica 70:151–157

Marais GF, Pretorius ZA (1996) Gametocidal effects and resistance to wheat leaf rust and stem rust in derivatives of a *Triticum turgidum* ssp. *durum*/*Aegilops speltoides* hybrid. Euphytica 88:117–124

Miedaner T, Wilde F, Steiner B, Buerstmayr H, Korzun V, Ebmeyer E (2006) Stacking quantitative trait loci (QTL) for Fusarium head blight resistance from non-adapted sources in an European elite spring wheat background and assessing their effects on deoxynivalenol (DON) content and disease severity. Theor Appl Genet 112:562–569

Mukai Y, Nakahara Y, Yamamoto M (1993) Simultaneous discrimination of the three genomes in hexaploid wheat by multicolour fluorescence in situ hybridization using total genomic and highly repeated DNA probes. Genome 36: 489–494

Murray GM, Brennan JP (2009) Estimating disease losses to the Australian wheat industry. Australas Plant Pathol 38:558–570

Nombela G, Romero MD (1999) Host response to *Pratylenchus thornei* of a wheat line carrying the *Cre2* gene for resistance to *Heterodera avenae*. Nematology 1:381–388

Nombela G, Romero MD (2001) Field response to *Pratylenchus thornei* of a wheat line with the *CreAet* gene for resistance to *Heterodera avenae*. Eur J Plant Pathol 107:749–755

Ogbonnaya FC, Imtiaz M, Bariana HS, McLean M, Shankar MM, Hollaway GJ, Trethowan RM, Lagudah ES, van Ginkel M (2008) Mining synthetic hexaploids for multiple disease resistance to improve bread wheat. Aust J Agric Res 59:421–431

Orion D, Krikun J, Sullami M (1979) The distribution, pathogenicity and ecology of *Pratylenchus thornei* in the northern Negev. Phytoparasitica 7:3–9

Patterson HD, Thompson R (1977) Recovery of inter-block information when block sizes are unequal. Biometrika 58:545–554

Piepho HP (1998) Empirical best linear unbiased prediction in cultivar trials using factor-analytic variance-covariance structures. Theor Appl Genet 97:195–201

Pink B (2008) Year Book Australia 2008, No. 90. Australian Bureau of Statistics, Canberra. http://www.abs.gov.au/AUSSTATS/abs@.nsf/DetailsPage/1301.02008?OpenDocument

Potgieter GF, Marais GF, DuToit F (1991) The transfer of resistance to the Russian wheat aphid from *Triticum monococcum* L. to common wheat. Plant Breed 106:284–292

Pourjam E, Kheiri A, Geraert E, Alizadeh A (1999) Variations in Iranian populations of *Pratylenchus neglectus* and *P. thornei* (Nematoda: Pratylenchidae). Iran J Plant Pathol 35:23–27

Qiu YC, Zhou RH, Kong XY, Zhang SS, Jin JZ (2005) Microsatellite mapping of a *Triticum urartu* Tum. derived powdery mildew resistance gene transferred to common wheat (*Triticum aestivum* L.). Theor Appl Genet 111:1524–1531

Rausher MD (2001) Co-evolution and plant resistance to natural enemies. Nature 411:857–864

Rhode RA (1972) Expression of resistance in plants to nematodes. Annu Rev Phytopathol 10:233–252

Rivoal R, Bekal S, Valette S, Gauthier J-P, Bel Hadj Fradj M, Mokabli A, Jahier J, Nicol J, Yahyouhi A (2001) Variation in reproductive capacity and virulence on different genotypes and resistance genes of *Triticeae*, in the cereal cyst nematode species complex. Nematology 3:581–592

Roberts PA (2002) Concepts and consequences of resistance. In: Starr JL, Cook R, Bridge J (eds) Plant resistance to parasitic nematodes. CABI Publishing, Wallingford, pp 23–41

Robinson GK (1991) That BLUP is a good thing: the estimation of random effects. Stat Sci 6:15–51

Schmidt AL, McIntyre CL, Thompson JP, Seymour NP, Liu CJ (2005) Quantitative trait loci for root lesion nematode (*Pratylenchus thornei*) resistance in Middle-Eastern landraces and their potential for introgression into Australian bread wheat. Aust J Agric Res 56:1059–1068

Schmolke M, Mihler V, Hartl L, Zeller FJ, Hsam SLK (2011) A new powdery mildew resistance allele at the *Pm4* wheat locus transferred from einkorn (*Triticum monococcum*). Mol Breed (Online). doi:10.1007/s11032-011-9561-2

Schneider A, Molnar I, Molnar-Lang M (2008) Utilisation of *Aegilops* (goatgrass) species to widen the genetic diversity of cultivated wheat. Euphytica 163:1–19

Sheedy JG, Thompson JP (2009) Resistance to the root-lesion nematode *Pratylenchus thornei* of Iranian landrace wheat. Australas Plant Pathol 38:478–489

Sheedy JG, Raupp WJ, Thompson AL, Smiley RW (2008a) Resistance to root lesion nematodes of Chinese Spring x *Aegilops speltoides* addition lines, 2007. Plant Dis Man Rep (Online). Report 2:N038. The American Phytopathological Society, St. Paul, MN. doi:10.1094/PDMR02

Sheedy JG, Smiley RW, Easley SA, Thompson AL (2008b) Resistance of Pacific Northwest spring wheat and barley cultivars to root lesion nematode (*Pratylenchus thornei*), 2007. Plant Dis Man Rep (Online). Report 2:N007. The American Phytopathological Society, St. Paul, MN. doi:10.1094/PDMR02

Singh K, Chhuneja P, Singh I, Sharma SK, Garg T, Garg M, Keller B, Dhaliwal HS (2010) Molecular mapping of cereal cyst nematode resistance in *Triticum monococcum* L. and its transfer to the genetic background of cultivated wheat. Euphytica 176:213–222

Singh RP, Huerta-Espino J, Bhavani S, Herra-Foessel SA, Singh D, Singh PK, Velu G, Mason RE, Jin Y, Njau P, Crossa J (2011) Race non-specific resistance to rust diseases in CIMMYT spring wheats. Euphytica 179:175–186

Subbotin SA, Sturhan D, Rumpenhorst HJ, Moens M (2002) Description of the Australian cereal cyst nematode *Heterodera australis* sp. n. (Tylenchida: Heteroderidae). Russ J Nematol 10:139–148

Thompson JP (1990) Treatments to eliminate root-lesion nematode (*Pratylenchus thornei* Sher and Allen) from a vertisol. Nematologica 36:123–127

Thompson JP (2008) Resistance to root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) in synthetic hexaploid wheats and their durum and *Aegilops tauschii* parents. Aust J Agric Res 59:432–446

Thompson CH, Beckman GG (1959) Soils and land use in the Toowoomba area, Darling Downs, Queensland. Soils and land use series No. 28. CSIRO Melbourne

Thompson JP, Haak MI (1997) Resistance to root-lesion nematode (*Pratylenchus thornei*) in *Aegilops tauschii* Coss., the D-genome donor to wheat. Aust J Agric Res 48:553–559

Thompson JP, Seymour NP (2011) Inheritance of resistance to root-lesion nematode (*Pratylenchus thornei*) in wheat landraces and cultivars from the West Asia and North Africa (WANA) region. Crop Pasture Sci 62:82–93

Thompson JP, Brennan PS, Clewett TG, Sheedy JG, Seymour NP (1999) Progress in breeding wheat for tolerance and resistance to root-lesion nematode (*Pratylenchus thornei*). Australas Plant Pathol 28:45–52

Thompson JP, Sheedy JG, Seymour NP, Clewett TG, Mason LR, Sheppard JA, Banks PM (2001) Advances in breeding wheat for tolerance and resistance to *Pratylenchus thornei* and *P. neglectus* for the northern region. In Proceedings of the 10th assembly of the wheat breeding society of Australia. 16–21 September 2001, Mildura, Australia. pp 123–127

Thompson JP, Owen KJ, Stirling GR, Bell MJ (2008) Root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*): a review of recent progress in managing a significant pest of grain crops in northern Australia. Australas Plant Pathol 37:235–242

Thompson JP, O'Reilly MM, Clewett TG (2009) Resistance to the root-lesion nematode *Pratylenchus thornei* in wheat landraces and cultivars from the West Asia and North Africa (WANA) region. Crop Pasture Sci 60:1209–1217

Thompson JP, Clewett TG, Sheedy JG, Reen RA, O'Reilly MM, Bell KL (2010) Occurrence of root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) and stunt nematode (*Merlinius brevidens*) in the northern grain region of Australia. Australas Plant Pathol 39:254–264

Toktay H, McIntyre CL, Nicol JM, Ozkan H, Elekcioglu HI (2006) Identification of common root-lesion nematode (*Pratylenchus thornei* Sher et Allen) loci in wheat. Genome 49:1319–1323

Valkoun JJ (2001) Wheat pre-breeding using wild progenitors. Euphytica 119:17–23

Vanstone VA, Hollaway GJ, Stirling GR (2008) Managing nematode pests in the southern and western regions of the Australian cereal industry: continuing progress in a challenging environment. Australas Plant Pathol 37:220–234

Whitehead AG, Hemming JR (1965) A comparison of some quantitative methods of extracting small vermiform nematodes from soil. Ann Appl Biol 55:25–38

Williams KJ, Taylor SP, Bogacki P, Pallotta M, Bariana HS, Wallwork H (2002) Mapping of the root lesion nematode (*Pratylenchus neglectus*) resistance gene Rlnn1 in wheat. Theor Appl Genet 104:874–879

Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Res 14:415–421

Zwart RS, Thompson JP, Godwin ID (2004) Genetic analysis of resistance to root-lesion nematode (*Pratylenchus thornei*) in wheat. Plant Breed 123:209–212

Zwart RS, Thompson JP, Godwin ID (2005) Identification of quantitative trait loci for resistance to two species of root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) in wheat. Aust J Agric Res 56:345–352

Zwart RS, Thompson JP, Sheedy JG, Nelson JC (2006) Mapping quantitative trait loci for resistance to *Pratylenchus thornei* from synthetic hexaploid wheat in the International Triticeae Mapping Initiative (ITMI) population. Aust J Agric Res 57:525–530

Zwart RS, Thompson JP, Milgate AW, Bansal UK, Williamson PM, Raman H, Bariana HS (2010) QTL mapping of multiple foliar disease and root-lesion nematode resistances in wheat. Mol Breed 26:107–124