Resistance of wheat genotypes to root-lesion nematode (*Pratylenchus thornei*) can be used to predict final nematode population densities, crop greenness and grain yield in the field

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ABSTRACT

The root-lesion nematode *Pratylenchus thornei* is a major pathogen of wheat (*Triticum aestivum*) in many regions globally.. Resistance of wheat genotypes to *P. thornei* can be determined from final nematode population densities in glasshouse experiments, but combining results across multiple experiments presents challenges. Here we use a factor analytic method for multi-experiment analysis of final population densities of *P. thornei* for 1096 unique wheat genotypes in 22 glasshouse experiments. The resistance to *P. thornei* of the genotypes was effectively represented by a two factor model with rotation of the axes to a principal components solution. Principal axes 1 and 2 (PA1 and PA2) respectively accounted for 79% and 11 % of the genetic variance over all experiments. Final population densities of *P. thornei* as empirical best linear unbiased predictors (PA(1+2)-eBLUPs)) from the combined glasshouse experiments were highly predictive (*P*<0.001) of final nematode population densities in the soil profile, of crop canopy greenness (NDVI) and of grain yield of wheat genotypes in *P. thornei* infested fields in the Australian subtropical grain region. Nine categories of resistance ratings for wheat genotypes from resistant to very susceptible were based on subdivision of the range of PA(1+2)-eBLUPs for use in growers' sowing guides. Nine genotypes were nominated as references for future resistance experiments. Most (62%) Australian wheat genotypes were in the most susceptible three categories (S, S–VS and VS). However, resistant germplasm characterized in this study could be used in plant breeding to considerably improve the overall resistance of Australian wheat crops

Abbreviations

A list of abbreviations is given in Table 1.

Additional keywords: root-lesion nematodes, wheat genotype resistance, MET analysis, nematode population densities predictions, wheat yield prediction

INTRODUCTION

The root-lesion nematode *Pratylenchus thornei* is a major pathogen of wheat (*Triticum aestivum*) in many regions of the world (Smiley and Nicol, 2009), particularly subtropical and warm temperate zones such as the subtropical or northern grain region of eastern Australia (Webb et al., 1997; Thompson et al., 2008). This region, which lies between Lat. 20ºS in Queensland and Lat. 32ºS in New South Wales, is characterized by rain-fed agriculture dependent on dryland farming practices with a range of broad-acre crop species grown throughout the year. Major cool-season crops termed 'winter' crops are wheat, barley (*Hordeum vulgare*) and chickpea (*Cicer arietinum*), while major warm-season crops termed 'summer' crops are sorghum (*Sorghum bicolor*) and mungbean (*Vigna radiata*) with a number of other cereal, pulse and oilseed crop species grown to lesser extents. Deep cracking clay soils (vertisols) are favoured for cropping in this region because of their high water-holding capacities to store fallow rainfall to supplement rainfall during the next crop phase (Webb et al., 1997).

Pratylenchus thornei is polyphagic being hosted by many cereal and pulse crop species including wheat and chickpea, which in other respects are valuable rotational crops for each other. Some wheat genotypes can lose up to 65% yield (Thompson et al., 1999) and some chickpea genotypes up to 25% yield (Reen et al., 2014) from high population densities of *P. thornei* in the soil profile at sowing. It has been estimated that *P. thornei* costs 4.3% of the total wheat production/year in the eastern Australian subtropical grain region with this loss valued at AU$38 M (Murray and Brennan, 2009). Other hosts of *P. thornei* among crop species grown in this region include winter crops barley, triticale (×*Triticosecale*), durum (*Triticum turgidum* ssp. *durum*), and faba bean (*Vicia faba*), and summer crops mung bean, black gram (*Vigna mungo*) and soybean (*Glycine max*) (Owen et al., 2012, 2014).

Management of *P. thornei* for wheat production depends on crop sequences that include moderately resistant crop species like sorghum (Thompson et al., 2008, 2012a; Owen et al., 2014), which is the major summer crop species in the subtropical grain region of Australia. However, sorghum cannot be grown profitably across the entire region. Fixed rotations are difficult to implement due to variable rainfall patterns in this region, and flexible crop sequencing (termed opportunity cropping) is often practiced. *Pratylenchus thornei* survives well in the clay soils of the region and, following growth of a susceptible wheat cultivar, ~3 years of fallow and/or resistant rotational crops are needed to reduce high nematode population densities to below the threshold for damage (Owen et al., 2014; Whish et al., 2017) which is ~2,000 nematodes/kg soil for intolerant wheat cultivars (Thompson et al., 2008). Protection of the major at-risk crops through breeding resistant and tolerant genotypes is essential for the long-term management of *P. thornei* in this region.

Tolerance and resistance to nematodes are treated as separately measured characteristics in nematology. Tolerance is defined as the capacity of plant genotypes to grow and yield with little loss in the presence of high initial nematode population densities, and resistance is defined as the capacity of plant genotypes to limit nematode reproduction in the roots (Trudgill, 1991; Roberts, 2002). Although tolerance and resistance can be measured independently they are not necessarily independent characteristics. Roberts (2002) indicated that a resistant plant genotype may not only have low nematode population densities in its roots, but also as a consequence of the low population density can have maximum plant growth at least equal to a tolerant genotype. In field experiments, *P. thornei* was shown to decrease the uptake by wheat plants of soil nutrients (Thompson et al., 2012a) and water (Whish et al., 2014) under both drier and wetter seasonal conditions than the long-term average. Previously, Wallace (1987) suggested genetic factors that confer plants with abilities to withstand stresses, like water and nutrient deficiencies, would function in a nonspecific way to confer tolerance to nematode attack. On the other hand, genetic factors for resistance to nematodes are specific, and in fact certain wheat genotypes resistant to *P. thornei* are susceptible to *Pratylenchus neglectus* (Farsi, 1995; Thompson, 2008). Similarly, other wheat genotypes resistant to cereal cyst nematode (*Heterodera avenae*) are susceptible to *P. thornei* (Nombela and Romero, 1999, 2001; Thompson, 2008).

Resistance to nematodes is measured by the increase in nematode population densities during plant growth. Resistance of crop genotypes to root-lesion nematodes can be assessed in the field or glasshouse, with the more resistant genotypes resulting in lower final population densities (P_f) of nematodes than the more susceptible genotypes. The advantage of glasshouse methods is that the initial population density (P_i) of a single nematode species can be made constant for all genotypes to be tested in an experiment, whereas under field conditions the initial population density of the site for the target nematode species has to be determined from soil sampling (De Waele and Elsen, 2002). Spatial variability of nematode population densities in a field can be a confounding factor that may require the P_i of every plot in a field experiment to be determined (Fanning et al. 2018), thereby considerably increasing the resources needed. Furthermore, better environmental control is possible under glasshouse conditions resulting in a greater proportion of experiments successfully completed with less variability between experiments. Another issue for assessing crop resistance to *P. thornei* in field experiments on vertisols is that the nematodes can be distributed down the soil profile to ~90 cm depth with various vertical distribution patterns (Owen et al., 2014; Thompson et al., 1999), further complicating the determination of nematode population densities in the field.

Glasshouse-based methods have been used to characterize crop genotypes in replicated experiments for resistance to *P. thornei*, including advanced lines in wheat breeding programs (Thompson et al., 1999) and cultivars for growers’ sowing guides (Lush, 2017; Matthews et al., 2017). These methods have also been used as a single plant test for selecting resistant genotypes within segregating populations for breeding programs. These glasshouse methods were calibrated during initial development with field results by comparing final *P. thornei* population densities associated with four selected wheat genotypes grown in both the glasshouse and field (Thompson et al., 2015a, 2015b). Over time, the glasshouse methods have been modified to provide conditions conducive for both plant growth and nematode reproduction so that differences in the final population densities among genotypes are controlled by genetic difference rather than environmental factors.

Resistance of a wheat genotype in the glasshouse method is assessed after 16 weeks of plant growth by the final nematode population density in the roots and soil, because *P. thornei* can migrate between the roots and soil. Reference or check genotypes that cover a range of resistance/susceptibility are included in each experiment for comparison with new genotypes to be tested and to gauge nematode reproduction in an experiment. This method allows ranking of genotypes on their resistance in any single experiment, but presents difficulties in comparing results across multiple unbalanced experiments in which many of the genotypes under consideration differ from experiment to experiment. This lack of balance arises from the on-going need to characterize the resistance of a changing suite of advanced plant breeding lines prior to their potential release to growers. To combine results across experiments we previously used the average reproduction factor, RF = final population density/initial population density. The range of average RF was then divided into nine arithmetically equal categories to produce resistance ratings of cultivars for sowing guides. Nine categories are used in Australian sowing guides ranging from resistant (R) to very susceptible (VS) (Lush, 2017), known as an ‘alpha’ rating scale to distinguish it from previous methods of assigning numbers 1 to 9 to these ordinal categories. Despite standardized experimental conditions, nematode reproduction rates can vary among experiments. This results in higher average RF values and susceptibility ratings of genotypes present in experiments with higher final population densities, but absent from experiments with lower final population densities, and vice versa. Clearly, a more rigorous statistical approach is required in order to compare the resistance to *P. thornei* of large numbers of wheat genotypes assessed across multiple glasshouse experiments.

In a previous study with chickpea, a factor analytic (FA) approach was used for a combined analysis of 10 glasshouse experiments that assessed resistance to *P. thornei* of 531 genotypes of chickpea, related wild species (*C. reticulatum*, *C. echinospermum* and *C. bijugum*) and interspecific hybrids (Thompson et al., 2011). This FA approach was based on methods developed for multi-environment trial (MET) analysis of crop yields in regional field trials (Smith et al., 2001). In the context of glasshouse studies, experiments are dealt with similarly to environments in MET analyses. Genotype by experiment (G×E) interaction effects are modelled by a FA regression model in a mixed model framework. This is in order to accommodate heterogeneity of genetic variance across experiments and heterogeneity of covariance and hence correlation, between experiments, while adjusting for spatial trends. These data sets from multiple glasshouse experiments on genotypes conducted over a period of years are typically unbalanced with respect to the occurrence of genotypes among experiments, and can involve large numbers of both genotypes and experiments. This is similar to the large numbers of genotypes and environments usually encountered in MET data (Cullis et al., 2010). The dimensionality of the data defined by the number of experiments can be reduced by FA models to a number of underlying ‘factors’. Best linear unbiased predictors (BLUPs) (Robinson, 1991; Piepho, 1998) of nematode population density for the genotypes are obtained from the variance parameter estimates. This FA approach has been shown to provide improved prediction of genotype performance relative to traditional variance component models and is also superior to conducting separate analysis of individual experiments (Kelly et al., 2007).

In this paper we apply FA methods for a combined analysis of 22 replicated glasshouse experiments conducted from 1996 to 2015 that were designed to characterize the resistance to *P. thornei* of a large number of genetically fixed genotypes of wheat. We further show that this approach to combining glasshouse resistance experiments provides a single strong predictor of relative final population densities of *P. thornei*, crop growth and grain yield associated with specific wheat genotypes grown in *P. thornei* infested fields. This provides a validated new method for ranking cereal genotypes on resistance to *P. thornei* for wheat improvement purposes and for growers' sowing guides.

MATERIALS AND METHODS

Glasshouse experiments The data analyzed are from a series of experiments that we have conducted annually to characterise resistance to *P. thornei* of advanced wheat lines for plant breeding programs and wheat cultivars for growers sowing guides. Data from a total of 22 glasshouse experiments on resistance to *P. thornei* of 1096 unique wheat genotypes were used for the combined analysis. Genotypes of other crops were present in some of these experiments, namely durum, barley and triticale. Canary grass (*Phalaris canariensis*, cv. Moroccan) as a resistant crop control and an unplanted soil control were also included in some experiments. The number of genotypes, experimental designs and any differences in experimental procedures for the experiments in each year are given in Table 2.

Glasshouse experimental methods In each experiment, single plants of each genotype were grown for 16 weeks in three replicate pots of soil, a black Vertosol (Isbell, 1996) of the Irving Series (Thompson and Beckman, 1959) containing 78% clay from Wellcamp (Lat. 27.55^{o}S, Long. 151.87^{o}E; Elevation ~500 m, near Toowoomba, Australia). In experiments from 1996 to 2012, the soil was pasteurized at 70ºC for 30 minutes to kill nematodes (Thompson, 1990a) and fungal pathogens like *Fusarium pseudograminearum* (Thompson, 1990b) that might damage the plants and thereby limit *P. thornei* reproduction. In later experiments (2013 to 2015) the temperature of pasteurization was increased to 85ºC to ensure control of *Pythium* spp. originating from oospores (PennState Extension, 2017). Each pot of soil was inoculated at sowing with a suspension of *P. thornei* at a rate of 10,000/kg soil (oven dry equivalent) extracted from open pot cultures on wheat (O'Reilly et al. 1993). The strain of *P. thornei* was originally isolated from Formartin, Queensland, Australia (Lat. 27.46ºS, Long. 151.43E; Elevation 364 m). In the experiments conducted from 1996 to 1997, methods for pot culture with top watering, as described by Thompson and Haak (1997), were used. In experiments conducted from 1999 to 2015, methods for pot culture with bottom watering, as described by Sheedy and Thompson (2009), were used. A summary of conditions for each experiment is given in Table 2. Experiments were laid out on the glasshouse benches as three randomized complete blocks which had row:column spatial arrangements (Williams 1986) except in the first two experiments.

Water supply to the pots was ceased at ~15 weeks after sowing so that the soil dried down to ~45% moisture content in preparation for sampling at 16 weeks after sowing. This moisture content expedited processing of this soil type for nematode extraction. The soil and roots from each pot were placed in a tray where they were cut and broken manually into pieces <1 cm, before thorough mixing. Soil moisture content was determined by drying a 150-g subsample at 105ºC in a forced draft oven for 48 hours. Nematodes were extracted from 150-g subsamples of soil in Whitehead trays (Whitehead and Hemming, 1965) for 48 hours at 22ºC and concentrated using a 20-µm aperture sieve into ~15 mL water. *Pratylenchus thornei* individuals were counted in a Peters 1-mL gridded slide (Chalex Corporation, Portland, Oregon, USA) under a compound microscope and population densities expressed as number/kg soil on an oven dry weight basis.

Field experiments Final population densities of *P. thornei* in the soil profile following the growth of wheat genotypes in field experiments and canopy greenness and grain yield were used to validate the glasshouse assessments of resistance/susceptibility of wheat genotypes. Two field experiments to assess advanced wheat breeding lines in comparison with existing cultivars were conducted in 2001 on a Black Vertosol of the Bongeen soil type (Harris et al., 1999) containing 60% clay, near Macalister, Australia (Lat. 27.03ºS, Long. 151.07ºE; Elevation 337 m). Experiment 1 had 23 late maturity wheat genotypes while Experiment 2 had 52 main maturity wheat genotypes, each with three replications. Both experiments were laid out in the field in three blocks as a row:column design (Williams 1986), with plots being 8 m long by seven drill rows on 25 cm spacing. The plots were fertilized with 55 kg N/ha as urea before sowing, and with 40 kg/ha Starter Z (Granulock Z, Incitec Pivot) supplying 4.4 kg N/ha, 8.7 kg P/ha, 1.6 kg S/ha, and 0.4 kg Zn/ha applied with the seed at sowing. Seeding rate was adjusted based on grain weight and germination percentage of each genotype to sow 100 viable seeds/m^2. The cropping history of the land immediately prior to the experiments was wheat cv. Hybrid Mercury, double cropped to black gram cv. Regur (*Vigna mungo*), then clean fallowed until the wheat experiments were sown 14 months later. During the course of the wheat growing season, symptoms of damage from root-lesion nematodes were noted on some of the *P. thornei*-intolerant cultivars in the experiments. Therefore, after grain was harvested by machine the three replicate plots of a subset of genotypes (11 in Experiment 1, and 19 in Experiment 2) were soil sampled to assess final population densities of root-lesion nematodes. Deep soil samples were taken with a vehicle-mounted hydraulic soil corer using push tubes of 45 mm diameter. Four positions were sampled per plot from the middle rows at approximately even intervals along the harvested length of 6 m of each plot. The four soil cores were subdivided and composited into one bulk in each of the following layers 0–15, 15–30, 30–45, 45–60, 60–90, 90–120 and 120–150 cm depth and placed in polythene bags. The soil was broken into pieces manually, mixed thoroughly, and a 100-g subsample was oven dried to determine soil water content, and another 150-g subsample was extracted in Whitehead trays to determine nematode population densities. *Pratylenchus thornei* was identified (Fortuner, 1977) and counted as described in Section 2.2.

A field experiment to assess Normalized Difference Vegetation Index (NDVI) as a measure of the tolerance of wheat genotypes to *P. thornei* conducted in 2013 (Robinson et al. 2019) was also used to validate the glasshouse resistance experiments. This experiment was located on a Black Vertosol of the Waco series (Beckmann and Thompson, 1960) with 70% clay, near Formartin. The land was managed in a 4-year rotation of sorghum, long fallow, bulk wheat, wheat experimental plots, then long fallow back to bulk sorghum as described previously (Thompson et al., 1999). The partially resistant wheat line QT8343 and the susceptible wheat cultivar Kennedy were grown in a 3-replicate strip design as the first wheat crop in the 4-year rotation to generate low and high *P. thornei* population densities respectively. All test wheat cultivars were sown into both low (2,570 *P. thornei* /kg soil at 0–90 cm from back-transformation of ln(x+1) mean following QT8343), and high (9,090 *P. thornei* /kg soil at 0–90 cm from back-transformation of ln(x+1) mean following cv. Kennedy) population densities in the following year (Robinson et al. 2019). Other field procedures were similar to those described for Macalister except the rate of urea applied before sowing supplied 100 kg N/ha to each crop.

After grain harvest in November, the soil was sampled by taking two cores/plot with a hydraulically driven push tube to 90 cm depth at one third intervals along the plot, and subdivided and composited in intervals of 0–30, 30–60 and 60–90 cm. Nematode population densities and soil water contents were determined as described above for the Macalister experiments in Section 2.3.1.

Statistical analysis of glasshouse experiments A consideration for the estimation of parameters in a multi-experiment model is the concurrence of genotypes, that is, the number of genotypes in common between pairs of experiments (Table 3). Most pairs of glasshouse experiments had suitable numbers of concurrent genotypes, except for the experiment 2009N, which had only two genotypes in common with eight other experiments (Table 3). The data on final *P. thornei* population densities were transformed by natural logarithms to ensure homogeneity of variance over the range of fitted values. The multi-experiment analysis modelled ln(*P. thornei*/kg soil+1) in a linear mixed model framework, following the approach of Smith et al. (2001). A fixed term was included for experiment effects, and a random term was included for replicate effects for all experiments. A FA variance structure was fitted to the genotype x experiment effects, allowing for a different genetic variance for each experiment, and heterogeneous covariance (and hence correlation) between each pair of experiments. Spatial location of the pots in the two-dimensional arrangement on the glasshouse benches was fitted through a spatial correlation process across rows and columns (where significant for experiments from 2002 to 2015) following the approach of Gilmour et al. (1997). Random terms for row and column effects were included through the spatial modelling process, where significant. A ‘crop type’ factor was included in the analysis as a fixed effect to account for wheat, durum, barley, triticale, canary grass and unplanted control.

The FA model was extended by including higher order terms in the model, until at least 90% of the genetic variance over all experiments was explained. The effective number of dimensions of the FA model was then tested with the Akaike information criterion as used by Beeck et al. (2010) and by assessing the percentage of variance accounted for by successively added factors. The estimated FA loadings were rotated to a principal components solution

(Cullis et al., 2010) such that the first component axis accounted for the maximum amount of genetic covariance in the data and the second accounted for the next greatest amount, and so on for subsequent axes, and all the axes were orthogonal. A genetic correlation matrix between pairs of experiments was produced. The output from the FA analysis gave predictions of genotype performance in each experiment as regression empirical best linear unbiased predictors (R-eBLUPs) (Cullis et al., 2010). For selected genotypes, the R-eBLUPs were plotted against loadings for PA1 of the individual experiments to produce a latent regression plot for which the slope is the PA1score of that genotype (Smith et al. 2015). The overall resistance or susceptibility of genotypes was compared using a single value for each genotype as PA(1+2)-eBLUPs where PA denotes principal axes from the principal components solution. The PA(1+2)-eBLUP for each wheat genotype was calculated as the respective PA1 score multiplied by the average of the 22 rotated loadings for PA1 plus the respective PA2 score multiplied by the average of the 22 rotated loadings for PA2. These values were rescaled by addition of the estimate for the overall mean for wheat in units of ln(*P. thornei*/kg soil+1) and then back-transformed by exponentiation where required.

These statistical analyses were performed using ASReml-R (Butler et al., 2009) in the R software environment (R Core Team, 2016). Variance parameters were estimated using residual maximum likelihood (REML) estimation (Patterson and Thompson, 1971).

Prediction of field final population densities of *P. thornei* from *P. thornei* resistance The population densities of *P. thornei* in the field after harvest of the two experiments at Macalister and the experiment at Formartin were subject to analysis of variance by depth interval after transformation by ln(x+1). Significant differences were obtained among cultivars to 45 cm depth at Macalister and to 90 cm depth at Formartin. Non-linear regression analysis was conducted between the mean population densities of *P. thornei* in the soil profile (0–45 cm depth at Macalister and 0−90 cm at Formartin) as response variables and PA(1+2)-eBLUPs of ln(*P. thornei*/kg soil+1) from the combined glasshouse experiments as the explanatory variable using Genstat® for Windows™ (VSN International, 2012).

Prediction of NDVI and grain yield of wheat cultivars in field experiments from *P. thornei* resistance

The relationships between the grain yield of the cultivars in the three field experiments and the PA(1+2)-eBLUPs of ln(*P. thornei*+1) from combined glasshouse experiments were examined graphically and appropriate non-linear regression equations fitted in Genstat® for Windows™ (VSN International, 2012). Similarly the relationships between the area under the disease progress curve (AUDPC) of seven readings of Normalized Difference Vegetation Index (NDVI) taken to measure vegetation greenness at intervals from 64 to 126 days after sowing of the genotypes in the Formartin experiment (Robinson et al., 2019) were determined.

Rating of resistance of wheat genotypes The single range of log transformed PA(1+2)-eBLUPs for the 1096 wheat genotypes from MET analysis of the combined experiments was divided into nine equal sub-ranges. Genotypes within these nine categories were assigned alpha ratings as used for diseases in Australian wheat variety guides for growers (Lush, 2017; Matthews et al., 2017) as follows: resistant (R), resistant to moderately resistant (R–MR), moderately resistant (MR), moderately resistant to moderately susceptible (MR–MS), moderately susceptible (MS), moderately susceptible to susceptible (MS–S), susceptible (S), susceptible to very susceptible (S–VS), and very susceptible (VS).

RESULTS

Combined glasshouse experiments A graphical display of the between environments genetic correlation matrix between all pairs of 22 experiments from the MET analysis of *P. thornei* population densities of wheat genotypes is shown in Fig. 1. The data from the experiments were well correlated having 75% of all correlation coefficients between pairs of experiments greater than 0.70 and with a median value of 0.80. This shows strong agreement in relative nematode population densities for individual genotypes between experiments.

Table 4 shows predicted values from the FA model for experiment mean population density of *P. thornei*, genetic variance and error variance, as well as principal components loadings and percentage genetic variance accounted for by PA1 and PA2 in individual experiments. An FA model of order 2 (designated FA-2) was retained as the final model, explaining 90% of the genetic variance over all experiments (79% by PA1 and 11% by PA2) (Table 4). The Akaike information criterion (value for FA-2=0 compared with FA-1=10 and FA-3=9) supported the decision to select the FA-2 model. Every experiment had at least 67% of genetic variance accounted for by this FA-2 model, and every experiment had greater than 55% genetic variance accounted for by PA1 alone, except for the 2006 experiment with 42% (Table 4). Loadings along PA1 were positive for all experiments, ranging from 0.169 to 0.709 (Table 4). Loadings along PA2 ranged from -0.358 to 0.389, with experiments having larger negative loadings being 2010N, 2009C, 2010C, 2008 and 2002, while experiments having larger positive loadings were 2012N, 2005, 1997, 2014, 2015, 2006 and 2009N. There was no noticeable difference between these two groups of experiments in relation to the chronology of the experiments or variation of the method used (Table 2), or the mean final *P. thornei* population densities of the experiments (Table 4).

Latent regression plots of R-eBLUPS of population densities of *P. thornei* for PA1 against experiment loadings for the 22 experiments are shown for some selected reference genotypes in Fig. 2. Genotypes with a positive slope or high PA1 score produced higher nematode densities in most experiments, while genotypes with a negative slope or low PA1 score produced lower nematode densities in most experiments. The deviation of R-eBLUPs from the line was an indication of additional variation for resistance of particular genotypes across the experiments measured in the dimension of PA2, that is, the PA2 score.

For genotypes that occurred in four or more experiments, scores for PA1 and PA2 and PA(1+2)-eBLUPs with probabilities of exceeding values of these for two reference genotypes are given in Accessory Table 1, while these results for a subset of 50 genotypes mentioned in this paper and/or present in the field experiments is given in Table 5.

Relationship between field final population densities of *P. thornei* and resistance In the Macalister field experiments, there were significant relationships for final *P. thornei* population densities at soil profile depths of 0–15 cm, 15–30 cm and 30–45 cm, but not at depths below 45 cm whereas in the Formartin experiment there were significant relationships at all depths of 0–30 cm, 30–60 cm and 60–90 cm (not shown). There were highly significant ($P<0.001$) linear relationships between the field population densities of *P. thornei* in the deep soil profile (0-45 cm at Macalister and 0-90 cm at Formartin) after growth of wheat genotypes in the three field experiments and the glasshouse derived PA(1+2)-eBLUPs of those genotypes (Fig. 3).

Relationship between crop greenness at high and low population densities of *Pratylenchus thornei* and resistance There were highly significant negative exponential relationships between AUDPC of NDVI measurements at both high and low *P. thornei* population densities in the field experiment at Formartin and glasshouse derived PA(1+2)-eBLUPs of *P. thornei* population densities. (Fig. 4).

Relationship between grain yield of wheat cultivars on *P. thornei* infested sites and resistance Grain yield of the wheat cultivars in the two field experiments at Macalister showed a significant negative sigmoidal relationships with glasshouse derived measures of resistance of the same wheat cultivars expressed as PA(1+2)-eBLUPs of ln(population density of *P. thornei*/kg soil) from combined glasshouse experiments (Fig. 5). There were highly significant negative exponential relationships between grain yields at both high and low *P. thornei* population densities in the field experiment at Formartin and glasshouse derived PA(1+2)-eBLUPs of *P. thornei* population densities (Fig. 6a and b). Also, there was a highly significant exponential relationship between grain yield loss (calculated as the percentage difference in yields between low and high *P. thornei* population densities) in the field experiment at Formartin and glasshouse derived PA(1+2)-eBLUPs of *P. thornei* population densities (Fig. 6c).

Resistance ratings of wheat genotypes The PA(1+2)-eBLUPS of the 1096 wheat genotypes (Accessory Table 1 and Table 5) ranged from a minimum for CPI133872 (present in 13 experiments with a back-transformed mean final population density of 7,171 *P. thornei*/kg soil) to a maximum for cv. Darwin (present in four experiments with a back-transformed mean final population density of 104,192 *P. thornei*/kg soil) (Table 5). The distribution of the 1096 wheat genotypes in this study in relation to the nine categories of resistance ratings based on sub-ranges of PA(1+2)-eBLUPs is given in Fig. 7.

Most of the wheat genotypes (62%) tested in these experiments were in the most susceptible three rating categories (S, S–VS, and VS) to *P. thornei*. In contrast, only 2% of the wheat genotypes were in the most resistant three rating categories (R, MR–R and MR). These most resistant genotypes were mainly germplasm sources of resistance, such as the synthetic hexaploid wheat CPI133872 (Thompson, 2008; Zwart et al., 2004) or GS50a (a resistant selection from wheat cultivar Gatcher) (Thompson et al., 1999), and lines derived from back-crossing these into susceptible wheat cultivars, for example QT8343 and QT9048 (Table 5). Two commercial cultivars, Impose CL Plus and Wyalkatchem, both adapted to the Mediterranean (western) grain region of Australia, were rated as MR. The category MR–MS included ten named cultivars (Table 5) of which Gauntlet, Wallup, Sunmate, Suntime, Suntop and Ventura are adapted to the subtropical (northern) grain region of eastern Australia, while

Bolac, Kiora, Amarok, and Corack are adapted to the more temperate (southern) grain region of Australia. At the other end of the resistance spectrum were the very susceptible (VS) wheat genotypes (Table 5) which included Petrie (a northern region cultivar) and Brennan (a northern region forage wheat), and the southern region cultivars Darwin, Wedgetail, Annuello and Forrest. The western region wheat cv. Yandanooka, previously proposed as a VS reference cultivar (Sheedy et al., 2015), was categorized as S–VS in this study.

DISCUSSION

This is the first large scale MET analysis of multiple glasshouse experiments to determine the resistance to *P. thornei* of an extensive range of wheat genotypes in which the output has been used to predict relative final nematode populations and grain yield of wheat genotypes in independent field experiments. We ranked more than one thousand wheat genotypes for resistance to *P. thornei* by combining results from 22 experiments conducted during the period 1996 to 2015. This was achieved using a FA approach with rotation of axes to a principal components solution. A strong effect of wheat genotype on the final population density of *P. thornei* in all experiments was exhibited in PA1, which can be considered a stable resistance axis accounting for 79% of the genetic variance. Further, PA2 which accounted for an additional 11% of genetic variance, can be considered a measure of additional genetic variability for resistance across different experiments. One possible cause of the greater variabilityfor resistance of some wheat genotypes could be incomplete genetic fixation of the genotype, whereas other genotypes might have been fixed through single plant selection and a greater number of inbred generations. Another possible reason is unidentified environmental variation among the experiments resulting in some GxE effects.

The overall predicted value for the final population densities of *P. thornei* based on PA(1+2)-eBLUPs from the FA-2 model can be considered the best single index for the resistance level of genotypes included in this investigation. A quantitative measure as used in this study rather than a qualitative approach to characterising the resistance to *P. thornei* is required in view of the knowledge that resistance to this nematode species is inherited quantitatively under the control of multiple genes having additive gene action (Zwart et al., 2004; Thompson and Seymour, 2011; Thompson et al., 2012b).

The PA(1+2)-eBLUP values for genotypes were shown to be a valuable parameter in predicting relative field population densities of *P. thornei* developed under different wheat genotypes. These results validate the glasshouse methods for assessing resistance of wheat genotypes to *P. thornei* and provide confidence in the application of this information to field situations. Foremost among these applications are as ordinal alpha ratings for growers' sowing guides, but they could also be valuable variables in crop growth models incorporating nematode population dynamics as influenced by wheat cultivar choice.

Previously, genetic correlation ($r > 0.66$) was found for data on final population densities of *P. thornei* between a single glasshouse experiment evaluating 47 genotypes of chickpea and six field experiments (five from the subtropical grain region and one from the warm temperate grain region of Victoria) sampled to either 15 or 30 cm soil depth evaluating a total of 85 chickpea genotypes in the one MET analysis (Rodda et al. 2016). Recently, high genetic correlation ($r>0.9$) was found between environments for population densities of *P. thornei* in the top soil (0–10 cm or 0−15 cm) after harvest of 68 cereal genotypes in six field experiments in the temperate region of southern Australia, except where the fungal pathogen *Rhizoctonia solani* was damaging (Fanning et al. 2018). In the present study with wheat, we have preferred to analyse our glasshouse data in a MET analysis separately from any field data and then to use the output of the MET analysis to predict relative *P. thornei* population densities in the independent field experiments. This approach has validated our glasshouse methods for assessing *P. thornei* resistance of wheat genotypes and demonstrated their value for predicting relative final *P. thornei* population densities developed in the field when various wheat cultivars are grown. In addition, the glasshouse method provides surety of results each year compared with field testing where some experiments can be lost through environmental extremes such as drought, flood and hail, or pests such as feral animals or fungal diseases. In contrast, only one glasshouse experiment, namely that conducted in 2004, was deemed unsuitable for combined analysis because of aberrant results caused by manually processing the soil for nematode extraction when it was too wet.

In the deep clay soils of the subtropical grain region of Australia, *P. thornei* can occur in the soil profile to 90 cm depth. Our results showed that the genotype PA(1+2)-eBLUPs from the combined glasshouse experiments were predictive of the genotype final population densities to depths of 45 cm at Macalister and to 90 cm at Formartin. This shows the influence of growing different wheat genotypes on *P. thornei* population densities throughout the soil profile, and that the combined analysis of the glasshouse experiments as described provides measures that can be used to rank genotypes on how they affect nematode population densities throughout the whole soil profile.

To produce resistance ratings of cultivars for wheat sowing guides, the subdivision of the range of PA(1+2)-eBLUPs into nine equal classes converted to nine alpha ratings as required is a useful simplification, but for other purposes the numeric values of PA(1+2)-eBLUPS are preferable. Each year there is a requirement to assess prospective new cultivars for resistance to *P. thornei* and our established data base is an asset for this purpose. Adding new experimental data to the existing data base for MET analysis will allow new wheat genotypes to be assessed reliably for resistance within the framework of covariance across experiments through concurrence of other genotypes including the reference set. We are applying a similar approach to analysis of glasshouse resistance experiments for *P. neglectus* of wheat genotypes for growers sowing guides (Lush, 2017; Matthews et al. 2017), and the methods used here could be useful in other crops and with other nematode species.

The fact that the wheat genotypes in this study are representative of Australian cultivars and plant breeders' advanced breeding lines and that most were found to be susceptible to very susceptible to *P. thornei* indicates the need for concerted efforts to improve resistance levels. Excellent levels of resistance have been identified in several unadapted germplasm sources which are now being hybridized into adapted wheat backgrounds for plant breeders use to produce more resistant cultivars for growers (Sheedy et al., 2017).

From analysis of six experiments comparing methods for testing for resistance to *P. thornei* in which 23 bread wheat genotypes were evaluated, Sheedy et al. (2015) selected seven for use as provisional reference cultivars for future experiments. The more comprehensive analyses reported here with 1096 genotypes and 22 experiments have permitted an improved selection of reference cultivars. One genotype has been selected to represent the resistance level in each of nine ordered categories ranging from resistant to very susceptible based on equal subdivision of the range of values for PA(1+2)-eBLUPs in units of ln(*P. thornei*/kg soil). These new reference genotypes for the nine resistance categories are: (R) CPI133872, (R–MR) GS50a, (MR) QT8447, (MR–MS) Suntop, (MS) Hartog, (MS–S) Gregory, (S) Cunningham, (S–VS) Strzelecki and (VS) Petrie. These reference genotypes have been selected based on their overall levels of resistance within each category and on a low standard error of the PA(1+2)-eBLUP. Of hose reference genotypes suggested by Sheedy et al. (2015), CPI133872 has been retained to represent the R category and GS50a has been retained to represent the R−MR category of resistance. Other genotypes have been nominated for categories in which no reference genotype was nominated by Sheedy et al. (2015), while others have been replaced by preferred reference genotypes.

Growers are primarily interested in producing grain and the capacity of wheat cultivars to do this under field environmental conditions in soil heavily infested with *P. thornei* in the subtropical grain region of eastern Australia is provided as tolerance ratings in sowing guides (e.g. Lush 2017). Resistance ratings are also provided in sowing guides and they are often regarded as a measure of the impact that a cultivar will have on the population densities of *P. thornei* residual in the soil to attack a subsequent crop. However, from this study it is apparent that the level of resistance/susceptibility of crop cultivars is a major determinant of their growth and grain yield on sites infested with *P. thornei* in this region. This effect of resistance on plant growth was illustrated diagrammatically by Roberts (2002) in which a resistant genotype produced not only fewer nematodes but also a larger plant than a tolerant genotype that allowed greater nematode reproduction. Clearly, because of the polycyclic nature of *P. thornei*, as the nematode numbers increase in the roots of susceptible wheat genotypes they cause more damage to the plant root systems, which results in poorer vegetative growth and grain yield than in wheat genotypes with greater levels of resistance. This better comprehension of the role that resistance plays in *P. thornei* population changes and grain yield of wheat cultivars in the subtropical grain region of Australia emphasizes the value of genetic resistance for growers, the importance of the trait as a target for wheat breeding, and the ongoing need to accurately characterize the resistance to *P. thornei* of all wheat cultivars to be released by plant breeding companies for growers' use.

In summary, combining data on final population densities of *P. thornei* for 1096 wheat genotypes in 22 glasshouse experiments by a MET analysis was an effective way to compare the resistance of wheat genotypes. A two factor model explained 90% of the genetic variance, with 79% of the genetic variance accounted for in PA1, regarded as a stable resistance axis, reflecting the high genetic correlation among experiments. PA2 explained an additional 11% of the genetic variance indicating the resistance levels of some genotypes could not be fully explained by PA1 alone. Genotype scores of PA(1+2)-eBLUPs in units of ln(*P. thornei*/kg soil +1) from these glasshouse results were highly predictive of relative final population densities of *P. thornei* to depth in the soil profile after growth of various wheat genotypes in three field experiments. There were also highly significant non-linear relationships between glasshouse-derived resistance levels and genotype performance in the field assessed by greenness of vegetative biomass and grain yield. Subdivision of the range of PA(1+2)-eBLUPs into nine sub-ranges is presented as an objective method for producing ordinal/alpha resistance ratings for growers' sowing guides. The majority of genotypes tested were in the top three susceptibility ratings, indicating the need for continued germplasm development to raise the level of resistance to *P. thornei* in wheat cultivars available to Australian growers.

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Table 1. List of abbreviations

Abbreviation	Meaning
AUDPC	area under the disease progress curve
BTM	back-transformed mean
FA	factor analysis
FA-k	factor analytic model of order k
G×E	genotype × experiment
ln	natural logarithm or $\log_e$ where *e* is Euler's number
NDVI	Normalized difference vegetation index
R-eBLUP	regression empirical best linear unbiased predictor
PA	principal axes from varimax rotation of FA axes
PAk	principal axis k
PA(1+2)-eBLUP	empirical best linear unbiased predictor based on PA1 and PA2
P_i	initial population density of nematodes
P_f	final population density of nematodes
RF	reproduction factor
MET	multi-environment trial

Table 2. Aspects of methods used for glasshouse experiments to assess wheat genotypes for resistance to *Pratylenchus thornei*

Experiment (year conducted)	Number of genotypes	Experimental design		Watering system[a]	Nutrient Application[b]	Under-bench control of soil temperature[c]	Inoculum (nematodes/kg soil)	Inoculum mode
		No. of Rows	No. of Columns					
1996	111	RB[d]	RB	top	solution	no	2500	in soil
1997	90	RB	RB	top	solution	no	2500	in soil
1999	125	RC[e]	RC	bottom	solution	yes	10000	suspension
2000	126	RC	RC	bottom	solution	yes	10000	suspension
2001	118	RC	RC	bottom	solution	yes	10000	suspension
2002	129	10	39	bottom	solution	yes	10000	suspension
2003	154	11	42	bottom	Osmocote[c]	yes	10000	suspension
2005	143	18	24	bottom	Osmocote	yes	10000	suspension
2006	139	18	24	bottom	Osmocote	yes	10000	suspension
2007	228	29	24	bottom	Osmocote	yes	10000	suspension
2008	27	9	9	bottom	Osmocote	yes	10000	suspension
2009C[f]	45	9	15	bottom	Osmocote	yes	10000	suspension
2009N[g]	117	13	27	bottom	Osmocote	yes	10000	suspension
2010C	156	36	13	bottom	Osmocote	yes	10000	suspension
2010N	156	36	13	bottom	Osmocote	yes	10000	suspension
2011C	110	11	30	bottom	Osmocote	yes	10000	suspension
2011N	156	39	12	bottom	Osmocote	yes	10000	suspension
2012C	110	33	10	bottom	Osmocote	yes	10000	suspension
2012N	143	39	11	bottom	Osmocote	yes	10000	suspension
2013	144	36	12	bottom	Osmocote	yes	10000	suspension
2014	110	33	10	bottom	Osmocote	yes	10000	suspension
2015	120	36	10	bottom	Osmocote	yes	10000	suspension

[a] Details of methods used with top-watered pots for 1996 to 1998 and with bottom-watered pots for 1999 to 2015 have been described by Thompson and Haak (1997) and by Sheedy and Thompson (2009) respectively. For top watering the soil was brought to 56% moisture content as required, while for bottom watering the soil was held at a constant 2 cm water tension. [b] Nutrient application: solution = nutrients added from solutions to provide (mg/kg soil) 200 NO_3–N, 25 P, 88 K, 36 S, 285 Ca and 5 Zn; and Osmocote = 1 g of Osmocote ® native gardens plus micronutrients (17–1.6–8.7 NPK) slow-release fertilizer pellets (Scotts Australia Pty Ltd., Baulkham Hills, Australia). [c] Soil temperature controlled at 22ºC.

All experiments had three replicates laid out as randomized complete blocks. [d] RB = randomized block design only; [e] RC = additional row column design, but exact positions not available for the combined analysis of experiments. [f] C = preponderance of released cultivars in the experiment; [g] N = preponderance of breeders' advanced lines in the experiment

Table 3. Concurrence of genotypes between experiments testing for resistance to *Pratylenchus thornei* in 22 glasshouse experiments conducted from 1996 to 2015. Total number of genotypes in each experiment is shown on the diagonal, and number of genotypes in common between pairs of experiments is shown in the off-diagonal cells.

Exp.																						
1996	111																					
1997	22	90																				
1999	33	24	125																			
2000	29	20	54	126																		
2001	27	21	45	63	118																	
2002	34	27	39	47	69	129																
2003	29	21	32	34	38	56	154															
2005	21	15	27	31	33	36	43	143														
2006	24	15	28	32	34	38	41	87	139													
2007	24	15	28	31	33	38	37	66	98	228												
2008	4	4	4	4	4	5	7	11	19	20	27											
2009C	17	12	20	21	25	30	30	27	29	33	9	45										
2009N	2	2	2	2	2	2	3	4	5	9	4	3	117									
2010C	30	15	31	36	40	59	41	44	50	53	14	40	7	156								
2010N	4	4	5	4	5	6	6	5	6	8	4	5	59	11	156							
2011C	15	6	16	17	21	31	22	25	31	37	11	28	9	96	20	110						
2011N	5	5	5	4	5	5	14	4	5	6	4	4	24	11	70	11	156					
2012C	6	5	6	6	7	23	12	8	6	9	7	11	15	79	31	75	24	110				
2012N	4	4	5	4	5	5	8	4	5	5	4	4	8	11	41	11	66	11	143			
2013	7	5	6	6	7	21	8	8	6	8	7	10	12	60	32	53	36	75	53	144		
2014	7	5	7	5	6	13	5	4	5	5	4	5	2	27	14	20	21	27	41	73	110	
2015	8	4	6	5	6	7	6	5	6	6	4	5	2	17	14	14	19	14	36	59	69	120
Exp.	1996	1997	1999	2000	2001	2002	2003	2005	2006	2007	2008	2009C	2009N	2010C	2010N	2011C	2011N	2012C	2012N	2013	2014	2015

Table 4. Parameters from combined analysis using a factor analytic structure of 22 experiments testing resistance to *Pratylenchus thornei* of wheat genotypes used for derivation of empirical best linear unbiased predictors of individual genotypes given in Table 5.

Experiment	Mean *P. thornei*/kg soil		Genetic variance	Error variance	Principal component loadings		% Genetic variance accounted for (VAF)		
	ln(x+1)	BTM[a]			PA1[b]	PA2	PA1	PA2	PA1+PA2
1996	10.663	42753	0.046	0.169	0.196	-0.044	83	4	88
1997	10.965	57804	0.105	0.270	0.277	0.169	73	27	100
1999	11.981	159764	0.303	0.357	0.542	-0.097	97	3	100
2000	11.063	63759	0.503	0.636	0.709	0.004	100	0	100
2001	12.092	178504	0.336	0.379	0.579	-0.039	100	0	100
2002	11.945	154095	0.180	0.266	0.394	-0.106	87	6	93
2003	10.597	39995	0.435	1.438	0.602	0.034	83	0	84
2005	11.528	101478	0.175	0.574	0.328	0.260	61	39	100
2006	11.564	105263	0.068	0.815	0.169	0.141	42	29	71
2007	12.510	271020	0.193	0.541	0.387	0.099	78	5	83
2008	11.226	75026	0.127	0.368	0.331	-0.132	86	14	100
2009C	12.103	180367	0.484	0.780	0.521	-0.232	56	11	67
2009N	12.313	222542	0.271	0.647	0.507	0.117	95	5	100
2010C	12.327	225763	0.407	0.777	0.597	-0.224	88	12	100
2010N	12.529	276301	0.606	0.381	0.691	-0.358	79	21	100
2011C	11.153	69746	0.335	0.618	0.514	-0.096	79	3	81
2011N	11.492	97959	0.520	0.308	0.613	-0.056	72	1	73
2012C	10.069	23590	0.441	1.019	0.571	0.108	74	3	76
2012N	9.315	11102	0.606	1.031	0.674	0.389	75	25	100
2013	11.372	86866	0.218	0.391	0.397	0.095	72	4	76
2014	10.952	57044	0.247	0.350	0.413	0.155	69	10	79
2015	9.723	16702	0.158	0.490	0.371	0.144	87	13	100
						Overall	79	11	90

[a] BTM = back-transformed mean by exponentiation; [b] PA = Principal axes after rotation to principal components solution

Table 5. Genotypic scores for PA1 and PA2 and predicted final population densities of *Pratylenchus thornei* for 60 selected wheat genotypes used in field experiments and present in four or more of 22 experiments comprising 1096 wheat genotypes in a combined analysis. Genotypes have been assigned resistance ratings based on subdivision of the PA(1+2)-eBLUP range of ln(*P*. thornei/kg soil) into nine arithmetically equal categories. BTM = back-transformed means by exponentiation. Probabilities of values greater than the reference genotypes GS50a and Yandanooka proposed by Sheedy et al. (2015) are given.. Derived resistance ratings are R: resistant, R−MR: resistant to moderately resistant, MR: moderately resistant, MR−MS moderately resistant to moderately susceptible, MS: moderately susceptible, MS−S: moderately susceptible to susceptible, S: susceptible, S-VS susceptible to very susceptible, VS very susceptible. Genotypes chosen to be resistance references in these nine categories for future experiments are highlighted in the Table.

Resist-ance		Principal axes scores		*P. thornei*/kg soil		Probability > reference cvs. GS50a	Yandanooka	No.	Alpha resistance rating based on PA(1+2)-eBLUP
Rank	Genotype	PA1	PA2	PA(1+2)-eBLUP	BTM	R–MR	S–VS	expts	
1	CPI133872	-3.783	0.917	8.88	7171	0	0	13	R
4	QT8343	-2.839	-2.363	9.28	10667	0.226	0	11	R-MR
5	QT9048	-2.694	-1.186	9.36	11625	0.425	0	9	R-MR
.	GS50a	-2.666	-0.040	9.39	11991	NA	0	22	R-MR
14	Impose CL Plus	-2.488	1.243	9.49	13279	0.694	0	4	MR
17	QT9050	-2.246	-0.232	9.59	14573	0.908	0	12	MR
20	QT8447	-2.086	0.577	9.67	15898	0.969	0	12	MR
24	Wyalkatchem	-1.937	0.657	9.75	17085	0.946	0	5	MR
28	Bolac	-1.790	0.356	9.81	18214	0.967	0	4	MR-MS
30	Kiora	-1.728	-0.748	9.82	18471	0.955	0	4	MR-MS
34	Gauntlet	-1.716	-0.355	9.84	18675	0.989	0	5	MR-MS
40	Sunmate	-1.594	-0.700	9.89	19672	0.974	0	4	MR-MS
41	Amarok	-1.597	-0.529	9.89	19711	0.988	0	5	MR-MS
51	Corack	-1.523	1.016	9.95	20868	0.996	0	4	MR-MS
62	Wallup	-1.368	0.329	10.01	22225	0.999	0	4	MR-MS
65	Suntime	-1.305	-0.389	10.03	22674	0.994	0	4	MR-MS
73	Suntop	-1.244	-0.979	10.05	23132	0.999	0	4	MR-MS
75	Ventura	-1.249	0.038	10.06	23411	1	0	9	MR-MS
79	Chara	-1.219	-0.059	10.07	23717	1	0	11	MS
107	Glover	-1.026	0.048	10.17	26029	1	0	5	MS
120	Hartog	-0.995	0.541	10.19	26608	1	0	14	MS
145	Sunzell	-0.845	-0.091	10.25	28282	1	0	5	MS
191	Leichhardt	-0.651	-0.267	10.34	30914	1	0	11	MS
287	Sunvale	-0.412	-0.517	10.45	34474	1	0	11	MS-S
310	Kidman	-0.385	0.000	10.47	35206	1	0	5	MS-S
329	Giles	-0.338	0.172	10.49	36061	1	0	11	MS-S
347	Gregory	-0.264	-0.532	10.52	36974	1	0	10	MS-S
374	Spitfire	-0.169	-1.272	10.55	38253	1	0.002	5	MS-S
378	Yenda	-0.189	-0.420	10.56	38368	1	0.004	4	MS-S
384	Wylie	-0.213	0.712	10.56	38560	1	0	9	MS-S

425	Bowerbird	-0.077	-0.443	10.61	40416	1	0.001	6	MS-S
437	Baxter	-0.029	-1.548	10.61	40700	1	0	12	MS-S
557	Sunco	0.142	-1.254	10.70	44311	1	0.003	11	S
10	Lang	0.214	-0.874	10.74	46119	1	0.005	11	S
654	Batavia	0.204	2.060	10.78	47905	1	0.003	21	S
659	Hume	0.260	0.687	10.78	48193	1	0.014	9	S
663	Sunguard	0.284	-0.020	10.78	48242	1	0.029	5	S
674	Sunvex	0.278	0.520	10.79	48484	1	0.054	5	S
688	Waagan	0.327	0.119	10.81	49315	1	0.049	6	S
691	Banks	0.375	-1.295	10.81	49414	1	0.016	11	S
715	Crusader	0.399	-0.151	10.84	50817	1	0.058	6	S
816	Cunningham	0.547	-0.050	10.91	54611	1	0.049	12	S
905	Janz	0.675	0.579	10.98	58512	1	0.100	13	S-VS
935	Babbler	0.781	-0.530	11.01	60535	1	0.186	4	S-VS
936	Stampede	0.772	0.139	11.02	60839	1	0.219	6	S-VS
60	Strzelecki	0.815	0.261	11.04	62254	1	0.185	10	S-VS
998	Kennedy	0.962	-0.872	11.09	65577	1	0.263	13	S-VS
1002	H91	0.956	-0.128	11.10	66104	1	0.313	4	S-VS
1004	Kukri	0.968	-0.423	11.10	66236	1	0.317	4	S-VS
1008	Gazelle	0.991	-0.712	11.11	66635	1	0.315	5	S-VS
1018	Gatcher	0.970	0.785	11.12	67507	1	0.314	18	S-VS
1054	Impala	1.162	-0.359	11.19	72619	1	0.481	5	S-VS
1059	Yandanooka	1.210	-1.222	11.20	73423	1	NA	9	S-VS
1070	Lincoln	1.243	1.158	11.25	77187	1	0.581	4	S-VS
1079	Forrest	1.380	0.176	11.30	81145	1	0.684	5	VS
1083	Annuello	1.445	-0.175	11.33	83199	1	0.699	4	VS
1084	Wedgetail	1.421	0.675	11.33	83365	1	0.722	5	VS
1091	Brennan	1.581	-0.050	11.40	88875	1	0.803	5	VS
095	Petrie	1.719	-0.356	11.46	94465	1	0.916	11	VS
1096	Darwin	1.893	0.714	11.55	104192	1	0.901	4	VS

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Fig. 1. Between experiments genetic correlation matrix from the factor analytic (order 2) model for resistance testing of *Pratylenchus thornei* in 22 glasshouse experiments from 1996 to 2015.

Fig. 2. Latent regression plots of predicted *Pratylenchus thornei* population density as R-eBLUPs against estimated loadings for principal axis one (PA1) in 22 glasshouse experiments showing a selection of wheat genotypes with lower, intermediate and higher nematode population densities and stabilities. Dark blue points indicate genotype present in the experiment associated with the loading, whereas light red points indicate an estimate where genotype was absent from the experiment associated with the loading.

Fig. 3. Predictive ability of glasshouse-derived PA(1+2)-eBLUPs of ln(*P. thornei*/kg soil) for field population densities of *P. thornei* in the soil profile of two experiments at Macalister and one at Formartin for various wheat genotypes. Bar marker is l.s.d. (*P*=0.05).

(a) For Macalister Experiment 1, soil profile to 45 cm depth

$FPD = 0.744 GHBLUP + 1.330, R^2 = 0.73, P < 0.001, n = 11$

(b) For Macalister Experiment 2, soil profile to 45 cm depth

$FPD = 0.76 GHBLUP + 1.330, R^2 = 0.65, P < 0.001, n = 19$

(c) For Formartin, soil profile to 90 cm depth

At low *P. thornei*: $FPD = 1.606 GHBLUP - 9.20, R^2 = 0.92, P < 0.001, n = 16$

At high *P. thornei*: $FPD = 1.335 GHBLUP - 5.78, R^2 = 0.89, P < 0.001, n = 16$

where *FPD* = Field population density ln(*P. thornei*/kg soil+1) and *GHBLUP* = Glasshouse (PA1+2)-eBLUP of ln(*P. thornei*/kg soil +1)

Fig. 4. Predictive ability of glasshouse-derived PA(1+2)-eBLUPs of ln(*P. thornei*/kg soil) for area under the disease progress curve (AUDPC) of seven measurements of crop greenness by Normalized Difference Vegetation Index (NDVI) at seven sensing times from 64 to 126 days after sowing of 28 wheat genotypes grown at two initial population densities of *Pratylenchus thornei* at Formartin. Bar marker is l.s.d. (*P*=0.05).

(a) NDVI measurements at high *P. thornei*

$AUDPC = 46.63 - 0.00000016 * 5.36^{(GHBLUP)}, R^2 = 0.62, P < 0.001, n = 28$

(b) NDVI measurements at low *P. thornei*:

$AUDPC = 43.7 - 0.000000000000286 * 16.3^{(GHBLUP)}, R^2 = 0.54, P < 0.001, n = 28$

where '*AUDPC*' area under the disease progress curve in NDVI units and '*GHBLUP*' is PA(1+2)-eBLUPs of ln(final population density of *P. thornei*/kg soil) from combined glasshouse experiments

Fig.5. Predictive ability of glasshouse-derived PA(1+2)-eBLUPs of ln(*P. thornei*/kg soil) for grain yield of wheat cultivars in a *Pratylenchus thornei*-infested field at Macalister for 23 late maturing wheat genotypes in Experiment 1 and 52 main maturity wheat genotypes in Experiment 2. Bar marker is l.s.d. (*P*=0.05).

(a) Grain yield in Experiment 1:

$GY = 0.931 + 1.519 / (1 + \exp(8.44 * (GHBLUP - 10.632), R^2 = 0.47, P = 0.002, n = 23$

(b) Grain yield in Experiment 2:

$$GY = 1.546 + 0.9589 / (1 + \exp(11.31 * (GHBLUP - 10.52),) R^2 = 0.50, P < 0.001, n = 52$$

where 'GY' is grain yield (t/ha) and 'GHBLUP' is PA(1+2)-eBLUPs of ln(final population density of *P. thornei*/kg soil) from combined glasshouse experiments.

Fig. 6. Predictive ability of glasshouse-derived PA(1+2)-eBLUPs of ln(*P. thornei*/kg soil) for grain yield of wheat cultivars in a *Pratylenchus thornei*-infested field at Formartin for 28 wheat genotypes grown with high and low initial population densities of *P. thornei.* Bar marker is l.s.d. (P=0.05).

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$$GY = 4.113 - 0.000000087 * 4.68^{(GHBLUP)}, R^2 = 0.58, P < 0.001, n = 28$$

(b) Grain yield at low *P. thornei*:

$$GY = 3.477 - 0.0000000000101 * 21.9^{(GHBLUP)}, R^2 = 0.45, P < 0.001, n = 28$$

(c) Grain yield loss

$$GYL = -17.1 + 0.000006 * 4.23^{(GHBLUP)}, R^2 = 0.56, P < 0.001, n = 28$$

Where '*GY*' is grain yield (t/ha), '*GYL*' is grain yield loss (%) and '*GHBLUP*' is PA(1+2)-eBLUPs of ln(final population density of *P. thornei*/kg soil) in combined glasshouse experiments. Grain yield loss (%) =100*(grain yield at low P_t - grain yield at high P_t)/grain yield at low P_t

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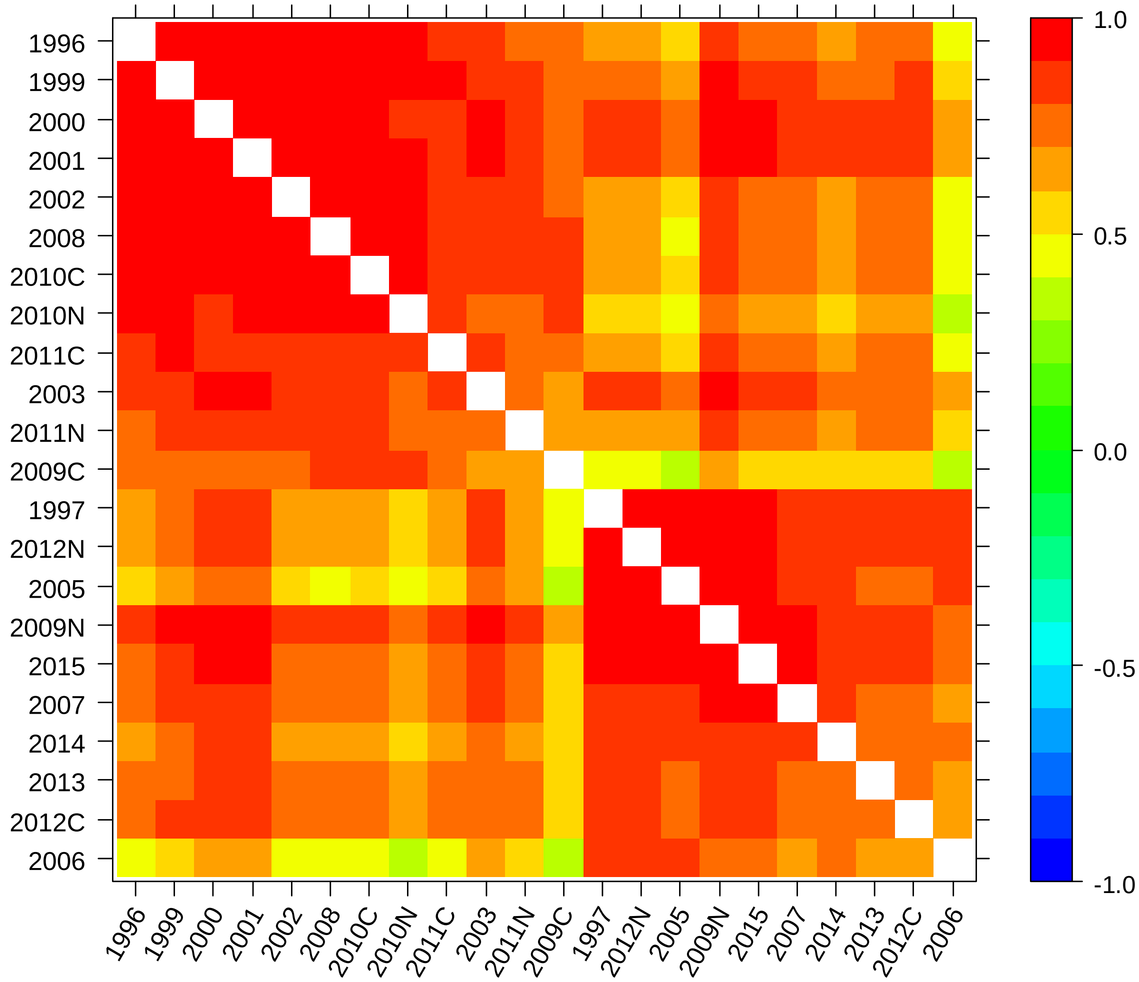

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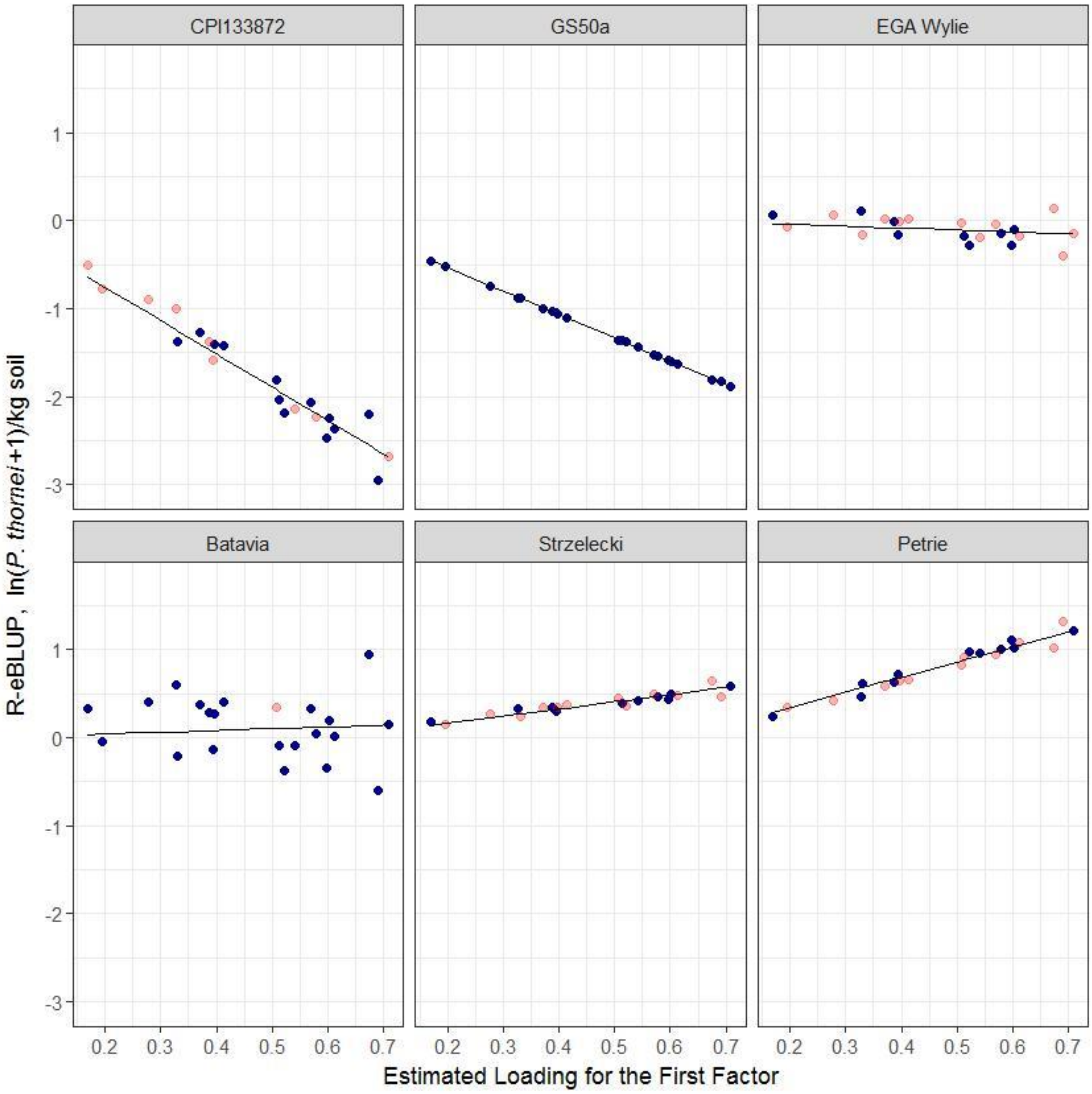

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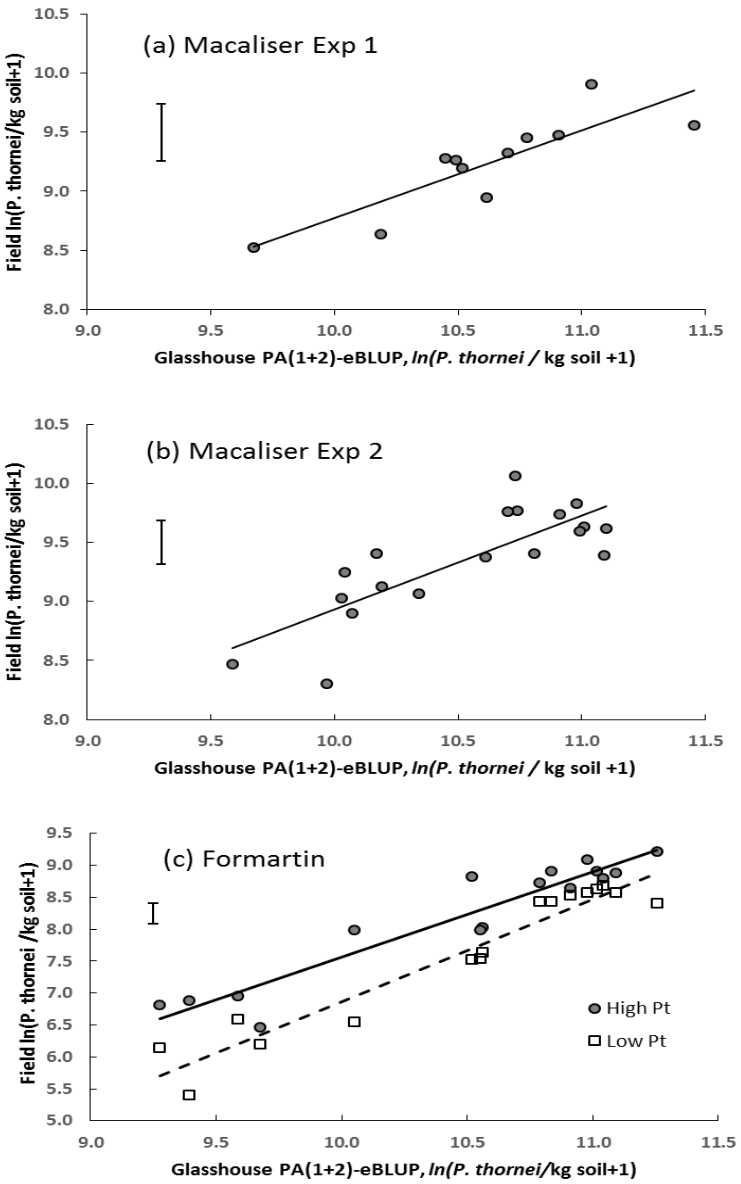

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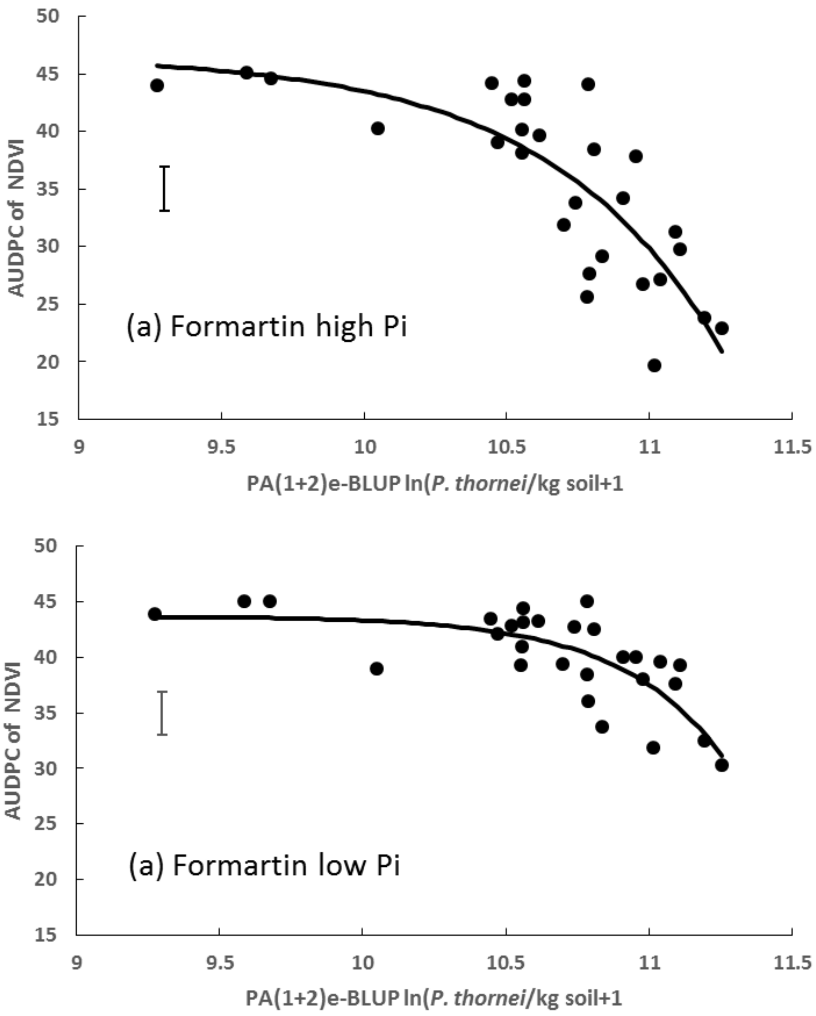

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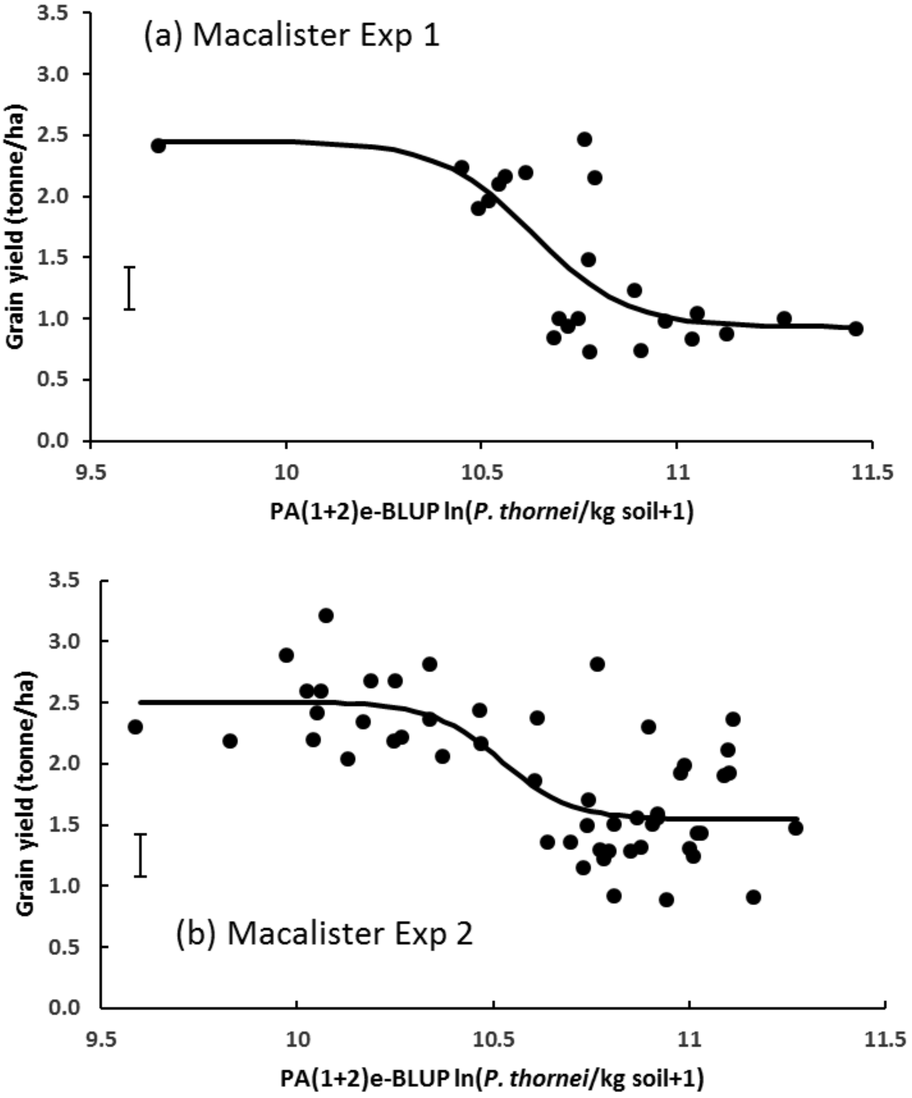

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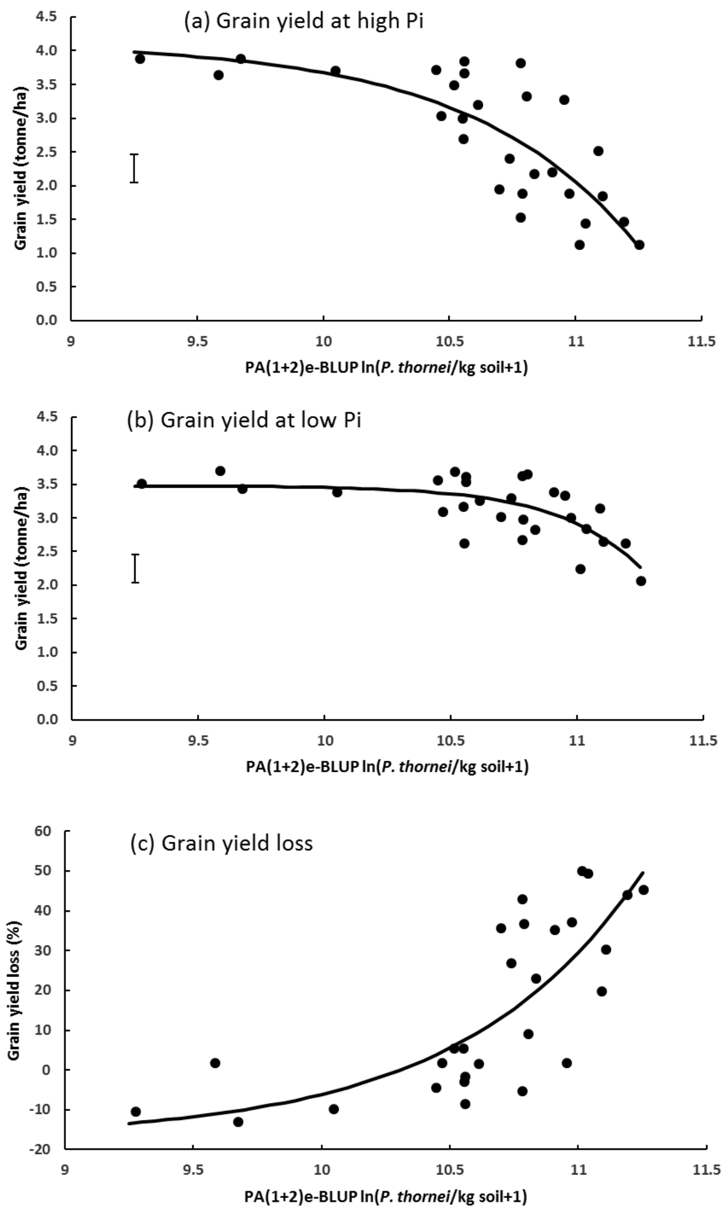
$$GY = 1.546 + 0.9589 / (1 + \exp(11.31 * (GHBLUP - 10.52),)R^2 = 0.50, P < 0.001, n = 52$$

where ‘GY’ is grain yield (t/ha) and ‘GHBLUP’ is PA(1+2)-eBLUPs of ln(final population density of *P. thornei*/kg soil) from combined glasshouse experiments.



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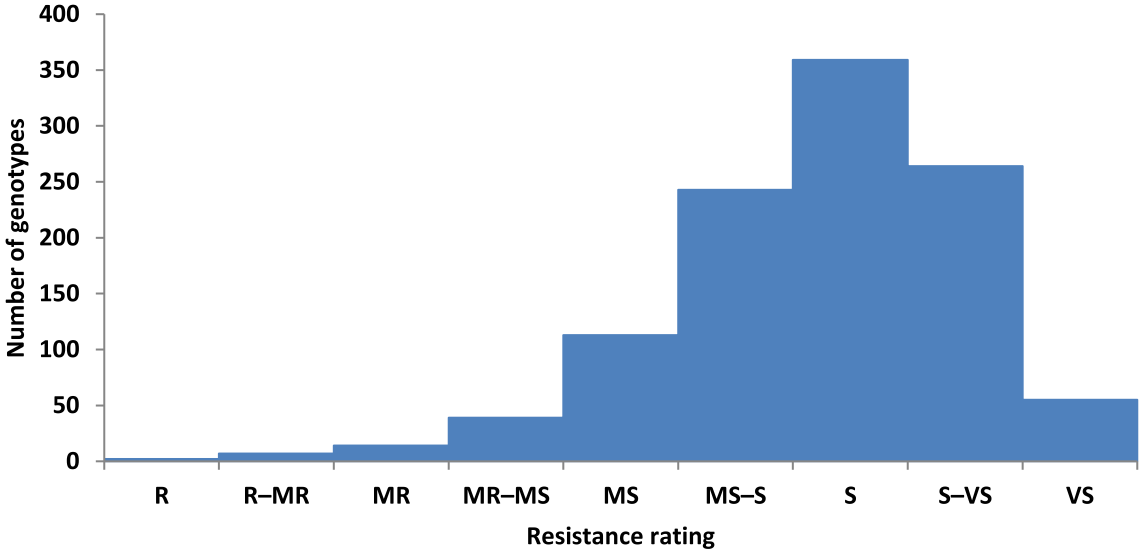
$$GYL = -17.1 + 0.000006 * 4.23^{(GHBLUP)}, R^2 = 0.56, P < 0.001, n = 28$$

Where '*GY*' is grain yield (t/ha), '*GYL*' is grain yield loss (%) and '*GHBLUP*' is PA(1+2)-eBLUPs of ln(final population density of *P. thornei*/kg soil) in combined glasshouse experiments. Grain yield loss (%) =100*(grain yield at low P_t - grain yield at high P_t)/grain yield at low P_t



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Resist- ance	Principal axes scores	*P. thornei*/kg soil	Probability > reference cvs.		No.	Alpha resistance rating based
			GS50a	Yandanooka		

Rank	Genotype	PA1	PA2	PA(1+2)-eBLUP	BTM	R–MR	S–VS	expts	on PA(1+2)-eBLUP
1	CPI133872	-3.783	0.917	8.88	7171	0	0	13	R
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5	QT9048	-2.694	-1.186	9.36	11625	0.425	0	9	R-MR
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14	Impose CL Plus	-2.488	1.243	9.49	13279	0.694	0	4	MR
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18	QT9616	-2.143	1.116	9.66	15599	0.929	0	5	MR
20	QT8447	-2.086	0.577	9.67	15898	0.969	0	12	MR
24	Wyalkatchem	-1.937	0.657	9.75	17085	0.946	0	5	MR
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51	Corack	-1.523	1.016	9.95	20868	0.996	0	4	MR-MS
57	QT8620	-1.443	0.211	9.97	21417	0.999	0	6	MR-MS
58	QT12903	-1.401	-0.429	9.98	21654	0.983	0	4	MR-MS
62	Wallup	-1.368	0.329	10.01	22225	0.999	0	4	MR-MS
65	Suntime	-1.305	-0.389	10.03	22674	0.994	0	4	MR-MS
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75	Ventura	-1.249	0.038	10.06	23411	1	0	9	MR-MS
78	EGA Burke	-1.259	1.019	10.07	23646	0.999	0	8	MS
79	Chara	-1.219	-0.059	10.07	23717	1	0	11	MS
81	Drysdale	-1.181	0.125	10.10	24221	0.999	0	6	MS
83	Mace	-1.183	0.562	10.10	24342	0.999	0	4	MS
105	QAL2000	-1.039	0.219	10.16	25925	1	0	6	MS
107	Glover	-1.026	0.048	10.17	26029	1	0	5	MS
120	Hartog	-0.995	0.541	10.19	26608	1	0	14	MS
126	Persia 20	-1.004	1.562	10.20	26875	0.999	0	5	MS
129	LPB10-0018	-0.914	-0.251	10.22	27309	0.999	0	4	MS
144	Rees	-0.856	0.266	10.25	28282	1	0	8	MS
145	Sunzell	-0.845	-0.091	10.25	28282	1	0	5	MS
157	Livingston	-0.782	-0.042	10.28	29143	1	0	4	MS
164	Wills	-0.752	0.122	10.30	29643	1	0	8	MS
172	Sunstate	-0.775	1.320	10.30	29851	1	0	9	MS
183	Merinda	-0.689	-0.324	10.32	30332	1	0	12	MS
184	QT12134	-0.654	-1.237	10.32	30423	0.999	0.002	4	MS
186	QT12302	-0.669	-0.501	10.33	30545	0.999	0.002	4	MS
191	Leichhardt	-0.651	-0.267	10.34	30914	1	0	11	MS
198	Pelsart	-0.665	0.660	10.35	31131	1	0	11	MS
197	Impress CL Plus	-0.637	-0.257	10.35	31131	1	0	4	MS
204	AUS4930	-0.650	0.907	10.36	31476	1	0	4	MS
228	Sunbrook	-0.543	-0.810	10.38	32272	1	0	6	MS-S

225	Jade	-0.561	-0.228	10.38	32272	1	0	5	MS-S
252	Diamondbird	-0.513	0.614	10.42	33422	1	0	5	MS-S
256	Mackellar	-0.480	-0.201	10.42	33556	1	0	4	MS-S
259	Condo	-0.477	-0.013	10.43	33690	1	0.002	4	MS-S
286	Pugsley	-0.452	0.604	10.45	34405	1	0.001	4	MS-S
287	Sunvale	-0.412	-0.517	10.45	34474	1	0	11	MS-S
300	Beaufort	-0.394	-0.207	10.46	34925	1	0.001	4	MS-S
301	Peake	-0.410	0.299	10.46	34925	1	0.001	4	MS-S
310	Kidman	-0.385	0.000	10.47	35206	1	0	5	MS-S
325	Eaglehawk	-0.329	-0.479	10.49	35881	1	0.003	5	MS-S
329	Giles	-0.338	0.172	10.49	36061	1	0	11	MS-S
332	QT13333	-0.348	0.959	10.50	36315	1	0	4	MS-S
347	Gregory	-0.264	-0.532	10.52	36974	1	0	10	MS-S
353	Sunbri	-0.267	0.061	10.53	37234	1	0.001	7	MS-S
371	Correll	-0.231	0.375	10.55	38062	1	0.004	4	MS-S
374	Spitfire	-0.169	-1.272	10.55	38253	1	0.002	5	MS-S
378	Yenda	-0.189	-0.420	10.56	38368	1	0.004	4	MS-S
384	Wylie	-0.213	0.712	10.56	38560	1	0	9	MS-S
393	Derrimut	-0.175	-0.242	10.56	38715	1	0.005	4	MS-S
416	Bounty	-0.133	0.291	10.59	39814	1	0.008	5	MS-S
425	Bowerbird	-0.077	-0.443	10.61	40416	1	0.001	6	MS-S
433	Ruby	-0.080	-0.172	10.61	40537	1	0.011	5	MS-S
435	Scout	-0.071	-0.266	10.61	40659	1	0.003	5	MS-S
437	Baxter	-0.029	-1.548	10.61	40700	1	0	12	MS-S
439	Young	-0.078	0.037	10.61	40700	1	0.007	4	MS-S
449	WW12885	-0.056	0.027	10.62	41109	1	0.012	4	MS-S
469	SUN577A	0.015	-1.485	10.64	41605	1	0.003	4	MS-S
491	Steel	0.006	0.086	10.65	42361	1	0.009	5	MS-S
489	Marombi	-0.001	0.323	10.65	42361	1	0.011	4	MS-S
495	Worrakatta	-0.004	0.469	10.66	42403	1	0.008	4	MS-S
503	Kord CL Plus	0.026	-0.133	10.66	42658	1	0.015	4	MS-S
505	Cook	0.046	-0.657	10.66	42701	1	0.002	10	MS-S
513	QT13164	0.020	0.405	10.67	42872	1	0.023	4	S
516	Dart	0.042	-0.154	10.67	42958	1	0.006	4	S
532	Whistler	0.052	0.143	10.68	43346	1	0.014	4	S
542	Bowie	0.068	0.387	10.69	43826	1	0.011	6	S
549	Axe	0.113	-0.702	10.69	44045	1	0.019	4	S
557	Sunco	0.142	-1.254	10.70	44311	1	0.003	11	S
555	Hatchet CL Plus	0.106	-0.127	10.70	44311	1	0.031	4	S
556	Sentinel	0.084	0.640	10.70	44311	1	0.020	4	S
559	Krichauff	0.114	-0.275	10.70	44355	1	0.009	6	S
564	Merlin	0.151	-1.147	10.71	44577	1	0.006	5	S
587	King Rock	0.160	-0.112	10.72	45432	1	0.019	4	S
593	Elmore CL Plus	0.156	0.319	10.73	45660	1	0.024	4	S
608	Braewood	0.197	-0.338	10.74	46073	1	0.020	5	S
610	Lang	0.214	-0.874	10.74	46119	1	0.005	11	S
614	Ovalo	0.204	-0.287	10.74	46257	1	0.045	4	S
622	QT7208	0.208	-0.018	10.75	46536	1	0.012	6	S

626	Catalina	0.204	0.340	10.75	46676	1	0.006	9	S
648	Emu Rock	0.259	0.091	10.77	47762	1	0.029	4	S
653	Virest	0.305	-1.284	10.78	47809	1	0.039	5	S
651	Guardian	0.285	-0.698	10.78	47809	1	0.041	4	S
654	Batavia	0.204	2.060	10.78	47905	1	0.003	21	S
659	Hume	0.260	0.687	10.78	48193	1	0.014	9	S
658	Barham	0.286	-0.161	10.78	48193	1	0.044	4	S
663	Sunguard	0.284	-0.020	10.78	48242	1	0.029	5	S
674	Sunvex	0.278	0.520	10.79	48484	1	0.054	5	S
679	Pardalote	0.253	1.549	10.79	48629	1	0.044	4	S
681	Hunter	0.282	0.700	10.79	48727	1	0.068	4	S
688	Waagan	0.327	0.119	10.81	49315	1	0.049	6	S
689	Wentworth	0.359	-0.857	10.81	49364	1	0.028	8	S
691	Banks	0.375	-1.295	10.81	49414	1	0.016	11	S
698	Jaeger	0.344	0.320	10.82	49910	1	0.110	4	S
705	Lancer	0.391	-0.655	10.83	50261	1	0.057	4	S
709	Sunlin	0.343	0.998	10.83	50361	1	0.032	8	S
711	Estoc	0.376	0.124	10.83	50462	1	0.080	4	S
714	Trojan	0.382	0.292	10.84	50766	1	0.062	4	S
715	Crusader	0.399	-0.151	10.84	50817	1	0.058	6	S
717	Hornet	0.393	0.111	10.84	50868	1	0.057	6	S
720	Justica CL Plus	0.385	0.453	10.84	50969	1	0.079	4	S
743	Tenfour	0.433	0.111	10.86	51843	1	0.102	4	S
772	Ellison	0.490	-0.210	10.88	52996	1	0.056	8	S
779	Potam	0.490	0.241	10.89	53369	1	0.048	7	S
787	Wylah	0.550	-1.246	10.89	53690	1	0.093	6	S
794	H45	0.527	-0.212	10.90	53959	1	0.082	5	S
806	Shield	0.505	0.845	10.90	54230	1	0.103	4	S
807	Carinya	0.522	0.363	10.90	54284	1	0.117	5	S
809	Mitch	0.536	0.001	10.90	54338	1	0.107	4	S
811	Preston	0.561	-0.745	10.90	54393	1	0.112	4	S
816	Cunningham	0.547	-0.050	10.91	54611	1	0.049	12	S
826	Harper	0.560	-0.251	10.91	54775	1	0.111	4	S
832	Clearfield Jnz	0.560	0.110	10.92	55049	1	0.122	4	S
850	Orion	0.578	-0.055	10.92	55380	1	0.095	5	S
853	Rosella	0.590	-0.281	10.93	55547	1	0.113	5	S
855	SQP Revenue	0.548	1.134	10.93	55602	1	0.098	5	S
862	Manning	0.631	-1.137	10.93	55881	1	0.098	4	S
873	Naparoo	0.623	0.003	10.94	56612	1	0.148	4	S
881	Espada	0.633	0.105	10.95	57010	1	0.153	4	S
899	QT12667	0.668	0.261	10.97	58046	1	0.214	4	S-VS
905	Janz	0.675	0.579	10.98	58512	1	0.100	13	S-VS
907	Cobalt	0.686	0.337	10.98	58629	1	0.167	5	S-VS
935	Babbler	0.781	-0.530	11.01	60535	1	0.186	4	S-VS
936	Stampede	0.772	0.139	11.02	60839	1	0.219	6	S-VS
949	Tennant	0.816	-0.522	11.03	61573	1	0.223	5	S-VS
955	Envoy	0.818	-0.075	11.04	62006	1	0.224	4	S-VS
960	Strzelecki	0.815	0.261	11.04	62254	1	0.185	10	S-VS

968	Sapphire	0.814	0.790	11.05	62692	1	0.261	6	S-VS
969	QALBis	0.841	-0.057	11.05	62754	1	0.246	6	S-VS
988	Mansfield	0.894	-0.368	11.07	64022	1	0.261	5	S-VS
998	Kennedy	0.962	-0.872	11.09	65577	1	0.263	13	S-VS
999	Rudd	0.932	0.437	11.10	65906	1	0.321	5	S-VS
1002	H91	0.956	-0.128	11.10	66104	1	0.313	4	S-VS
1004	Kukri	0.968	-0.423	11.10	66236	1	0.317	4	S-VS
1008	Gazelle	0.991	-0.712	11.11	66635	1	0.315	5	S-VS
1018	Gatcher	0.970	0.785	11.12	67507	1	0.314	18	S-VS
1021	Phantom	1.032	-0.461	11.13	68185	1	0.365	4	S-VS
1023	H46	1.035	-0.539	11.13	68254	1	0.364	6	S-VS
1026	Petrel	1.033	-0.170	11.14	68527	1	0.378	5	S-VS
1034	Sunsoft98	1.057	-0.002	11.15	69493	1	0.394	7	S-VS
1043	Excalibur	1.106	0.062	11.17	71181	1	0.440	7	S-VS
1045	QT12663	1.118	-0.311	11.17	71181	1	0.460	4	S-VS
1047	Dakota	1.115	0.087	11.18	71538	1	0.456	6	S-VS
1050	Gladius	1.124	0.174	11.18	71897	1	0.467	4	S-VS
1053	Currawong	1.150	-0.070	11.19	72547	1	0.4801	4	S-VS
1054	LR Impala	1.162	-0.359	11.19	72619	1	0.481	5	S-VS
1059	Yandanooka	1.210	-1.222	11.20	73423	1	NA	9	S-VS
1065	QAL1064	1.208	0.477	11.23	75131	1	0.536	4	S-VS
1070	Lincoln	1.243	1.158	11.25	77187	1	0.581	4	S-VS
1074	Opata85	1.336	0.052	11.28	79300	1	0.652	7	VS
1079	Forrest	1.380	0.176	11.30	81145	1	0.684	5	VS
1083	Annuello	1.445	-0.175	11.33	83199	1	0.699	4	VS
1084	Wedgetail	1.421	0.675	11.33	83365	1	0.722	5	VS
1091	Brennan	1.581	-0.050	11.40	88875	1	0.803	5	VS
1095	Petrie	1.719	-0.356	11.46	94465	1	0.916	11	VS
1096	Darwin	1.893	0.714	11.55	104192	1	0.901	4	VS